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Ecology and climates of early Middle Pleistocene interglacials in Britain

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Ecology and climates of early Middle Pleistocene interglacials in Britain

by

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At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Sub-Committee. Work submitted for this research degree at the Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment. This study was financed with the aid of a studentship from Plymouth University. Relevant scientific seminars and conferences were regularly attended at which work was often presented. Royal Holloway University of London was visited for consultation purposes and to obtain sedimentary samples.

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Abstract

This thesis refines and develops understanding of the ecological and climatic characteristics of early Middle Pleistocene (MIS 19-13, *c.* 780-430 ka) interglacial environments in Britain. This period is characterised by globally muted (i.e. low amplitude) glacial-interglacial cycles, which increased in amplitude *c.* 430 ka with the Mid-Brunhes Transition (MBT). However, the influence of these global climatic characteristics on climates and ecology at regional and local scales is yet to be fully understood. Local ecological processes, particularly disturbance processes, have also received limited attention in pre-Holocene interglacial settings, despite their likely importance for vegetation and habitat structure.

Chapters 4, 5 and 6 present in-depth multi-proxy palaeoenvironmental studies from three early Middle Pleistocene sites: West Runton, Pakefield and Brooksby. A combination of Coleoptera, pollen, coprophilous fungal spores, microcharcoal and sedimentology is used to reconstruct local ecological attributes for each site. Multivariate analyses of these datasets indicate the importance of disturbance processes (herbivore activity, wildfire, hydrogeomorphic processes) in driving and maintaining local vegetation structure and habitat heterogeneity. This is explored further (in Chapter 8), emphasising the apparent importance of site-specific factors, rather than those shared between sites, in determining the relative influence of each disturbance factor.

In Chapter 7, new approaches to the coleopteran Mutual Climatic Range (MCR) method are applied to a suite of coleopteran records from interglacial sites spanning the Middle and Late Pleistocene (*c.*712-126 ka, MIS 17-5e). Summer temperatures, winter temperatures and temperature seasonality are reconstructed, to test whether there is

evidence for MBT expression in Northwest European thermoclimates. No evidence for this is found, and it is suggested (in Chapter 8) that MBT expression in this region may instead be reflected in hydroclimatic variables (e.g. enhanced annual precipitation).

Finally, it is suggested that disturbance processes and potentially wetter climates were beneficial to contemporary Lower Palaeolithic populations in Northwest Europe.

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Chapter 1

Introduction

1.1. Introduction

This thesis refines and develops understanding of the ecological and climatic characteristics of early Middle Pleistocene (Marine Oxygen Isotope Stages 19-13, *c.* 780-430 ka) interglacial environments in Britain. At a global scale, this period is characterised by glacial-interglacial cycles dominated by 100 kyr periodicities, with a tendency towards muted (i.e. low amplitude) glacial-interglacial cycles, relative to the late Middle Pleistocene (*c.* 430-126 ka) (Jansen *et al.* 1986; EPICA 2004; Lisiecki & Raymo 2005; Lang and Wolff 2011; Pillans & Gibbard 2012; Berger *et al.* 2015). The transition from lower to higher amplitude glacial-interglacial cycles at *c.* 430 ka is known as the Mid-Brunhes Transition (or Event) (MBT), and is recognised in records of Antarctic surface temperatures, greenhouse gases (CO_2 and CH_4), global ice volumes and global sea levels (Jansen *et al.* 1986; EPICA 2004; Lisiecki & Raymo 2005; Jouzel *et al.* 2007; Loulergue *et al.* 2008; Lüthi *et al.* 2008; Tzedakis *et al.* 2009; Lang and Wolff 2011; Berger *et al.* 2015). However, the influence of these global climatic characteristics on climates and ecology at regional and local scales are yet to be fully understood in Britain and Northwest Europe (Candy *et al.* 2010; Lang and Wolff 2011; Candy & McClymont 2013; Berger *et al.* 2015). In this region, the terrestrial environments of the early Middle Pleistocene ('Cromerian Complex') have a long and distinguished history of research (e.g. Reid 1882; Blake 1890; West *et al.* 1960; Duigan 1963; Turner 1970; West 1980a, b; Zagwijn 1996a; Preece & Parfitt 2000, 2008, 2012;

Parfitt *et al.* 2005; Coope 2006, 2010a; Preece *et al.* 2009; Candy *et al.* 2010; Schreve & Candy 2010), including recognition of some of the earliest range expansions of *Homo* into Northern Europe (Parfitt *et al.* 2005; Hosfield *et al.* 2011; Ashton & Lewis 2012; Preece & Parfitt 2012). Nevertheless, there remains much to be learned, particularly in terms of intra-annual climatic characteristics (e.g. summer temperatures, winter temperatures, temperature seasonality), local ecological processes, (e.g. influence of herbivory, wildfire and hydrogeomorphic processes on vegetation), and landscape characteristics (e.g. habitat heterogeneity, landscape openness). These themes, summarised in the following section, form the basis of the present thesis, and are addressed using a combination of sub-fossil Coleoptera, pollen, coprophilous fungal spores, microcharcoal and sedimentology.

1.2. Research Themes

The investigations presented in this thesis comprise both exploratory and hypothesis-testing elements. Chapters 4, 5 and 6 present in-depth local palaeoenvironmental reconstructions for three early Middle Pleistocene sites (West Runton, Pakefield and Brooksby), and in Chapter 7 a test of whether the MBT is discernible in British thermoclimates is presented.

1.2.1. Local ecological processes and characteristics

Local ecological processes, particularly disturbance processes, have received limited attention in pre-Holocene interglacial settings (*cf.* Kuneš *et al.* 2013), despite their influence on local vegetation structure and diversity (Fischer *et al.* 2013). In chapters 4, 5 and 6 in-depth analyses of multi-proxy palaeoecological records (Coleoptera, pollen, coprophilous fungi, microcharcoal, sedimentology) from three chronologically-distinct early Middle Pleistocene sites (West Runton, Pakefield and Brooksby) are used to explore the relative importance of different disturbance processes (herbivory, wildfire, hydrogeomorphic processes), and their influence on vegetation assemblages and landscape openness. Rationale for site choice is provided in Chapter 2 (Section 2.5.)

1.2.2. Middle Pleistocene interglacial climates

The expression of the MBT in Northwest European terrestrial environments has yet to be determined (Candy *et al.* 2010). In Chapter 7, new approaches to the coleopteran Mutual Climatic Range (MCR) method (Milne 2016) are applied to test whether there is evidence for this transition in British (and, by extension, Northwest European) thermoclimates. Summer temperatures, winter temperatures and temperature seasonality are reconstructed for a suite of Middle and Late Pleistocene (MIS 17-5e) sites in Southern, Central and Eastern England, based on secondary coleopteran assemblage data. This represents a significant advancement on previous work, which was primarily based on summer temperature reconstructions (Candy *et al.* 2010).

Coleopteran MCR (Milne 2016) is also used to reconstruct temperatures at a site-specific scale in chapters 4, 5 and 6. This offers the opportunity to explore climatic variations within single records in detail, and provides climatic context for palaeoecological reconstructions.

1.2.3. Archaeological context

The early Middle Pleistocene in Britain is associated with evidence for some of the earliest evidence of *Homo* in Northern Europe (Parfitt *et al.* 2005; Preece & Parfitt 2012). This is not an archaeologically-focussed thesis, but brief comments are given on the potential implications of the palaeoecological and palaeoclimatic reconstructions for contemporary Lower Palaeolithic populations.

1.3. Thesis Aims and Objectives

The overarching aim of this thesis is to refine understanding of the ecological and climatological characteristics of early Middle Pleistocene interglacial environments in Britain. This is achieved through two primary avenues of study, relating to the above research themes (Section 1.2.).

Firstly, local ecological characteristics and dynamics are explored at three early Middle Pleistocene sites (West Runton, Pakefield, Brooksby), with the following research objectives:

- To produce new in-depth reconstructions of local ecological characteristics (vegetation, habitats, disturbance processes) for each site using a combination of sub-fossil Coleoptera, pollen, coprophilous fungal spores, microcharcoal and sedimentological properties.
- To use the aforementioned palaeoenvironmental proxies to infer vegetation and habitat structure, the local importance of disturbance processes (herbivory, fire, hydrogeomorphic processes), and the dynamics of these factors at each site.
- To contextualise these reconstructions within previous work at the same sites, and within broader discussions of disturbance dynamics in the past.

Secondly, coleopteran records are used to test whether there is an observable expression of the Mid-Brunhes Transition in British thermoclimatic conditions, with the following research objectives:

- To reconstruct average warmest month temperatures (TMax), average coldest month temperatures (TMin) and average annual temperature ranges (TRange) for a suite of interglacial sites in England spanning the Middle Pleistocene.
- To compare palaeoclimate reconstructions from the early and late Middle Pleistocene in order to determine whether a change in thermoclimatic variables is observable.
- To discuss the implications of these reconstructions for interglacial climates in Britain, within the broader context of European and global interglacial climate dynamics during the Middle Pleistocene.

1.4. Thesis Outline and Structure

In the next chapter (Chapter 2), a synthesis of relevant palaeoclimatic, palaeoecological and stratigraphic literature is provided. Next, Chapter 3 details the field, laboratory and analytical methods utilised throughout the thesis. Chapters 4, 5 and 6 present new in-depth palaeoenvironmental studies from West Runton, Pakefield and Brooksby, respectively. These include overviews of site stratigraphies and backgrounds, and new detailed investigations into local ecological characteristics and processes, climatic characteristics and implications for disturbance processes and hominin populations. In Chapter 7 a broad suite of reconstructions from Middle Pleistocene interglacial sites, based on coleopteran assemblages, is produced and used to test whether there is evidence for the MBT in Northwest Europe. Chapter 8 discusses the results of chapters

4 to 7 in the contexts of interglacial ecology, interglacial climates and the MBT, archaeological relevance, and potential areas for further research. Finally, Chapter 9 summarises the main findings of the thesis.

Chapter 2

Background

2.1. Introduction

The Middle Pleistocene encompasses Marine Oxygen Isotope Stages (MIS) 19 to 6 (*c.* 780-126 ka), and is defined at a global scale by the onset of climate cycles dominated by 100 kyr eccentricity cycles, an increase in global ice volume and normalised magnetic polarity (the Brunhes Chron) (Maslin & Ridgwell 2005; Pillans & Gibbard 2012) (Fig. 2.1). The early (*c.* 780-430 ka) and late (*c.* 430-126 ka) Middle Pleistocene represent the major subdivisions within this period, and are separated by the Mid-Brunhes Transition (*c.* 430 ka) (Fig. 2.1). This denotes a general transition from lower to higher amplitude glacial-interglacial cycles, recognised in records of Antarctic surface temperatures, greenhouse gases (CO_2 and CH_4), global ice volumes and global sea levels (Jansen *et al.* 1986; EPICA 2004; Lisiecki & Raymo 2005; Jouzel *et al.* 2007; Loulergue *et al.* 2008; Lüthi *et al.* 2008; Tzedakis *et al.* 2009; Lang and Wolff 2011; Berger *et al.* 2015). This tendency towards muted (i.e. lower amplitude) glacial-interglacial cycles, occurring with a 100 kyr periodicity, is a particular feature of the early Middle Pleistocene, and despite indications that some climatic parameters were unaffected in Britain (Candy *et al.* 2010; Candy & McClymont 2013), the influence of such boundary conditions on the climates and ecology of Northwest European interglacial environments has yet to be fully determined. The study of interglacial palaeoenvironments under different boundary conditions is fundamental to developing a full understanding of glacial-interglacial cycles, and their influence on local and regional climates and ecology (Lang & Wolff 2011; Seddon *et al.* 2014). Such 'palaeo-perspectives' are also valuable in assessing interactions between vegetation, herbivore activity, fire and other disturbance regimes under different boundary conditions and over long timescales (Willis & Birks 2006; Tzedakis *et al.* 2006; Seddon *et al.* 2014; Jeffers *et al.* 2015), exploring the repeatability, ubiquity and resilience of biological communities and fundamental ecological processes. Additionally, the early Middle Pleistocene is associated with the earliest robust evidence of hominin incursions into Northern Europe (Roberts *et al.* 1994; Parfitt *et al.* 2005, 2010; Hosfield 2011), for which the palaeoenvironmental and palaeoclimatic context is of the utmost importance (Candy *et al.* 2011).

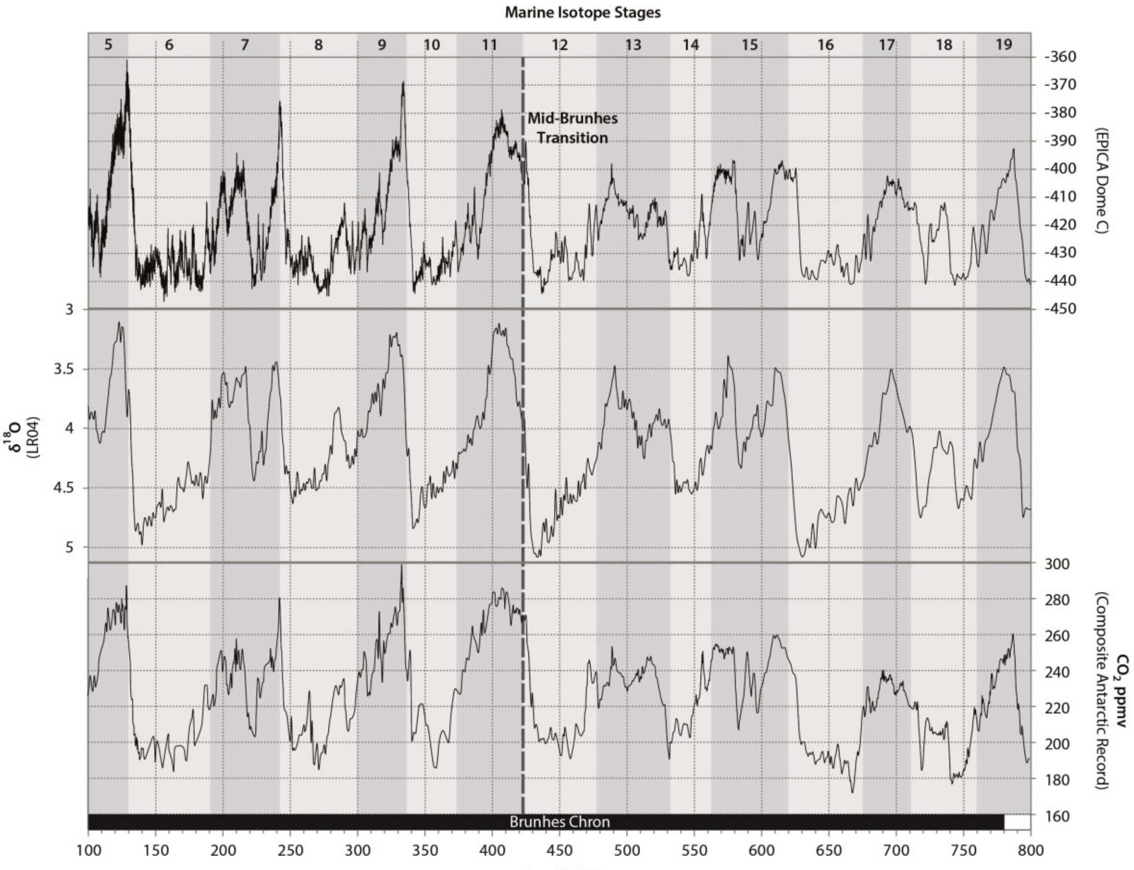


Figure 2.1 – Global climate change during the Middle Pleistocene (MIS 19-6) and MIS 5 (LR04 benthic $\delta^{18}O$ stack and chronology: Lisiecki & Raymo 2005, EPICA δD record and chronology: Jouzel et al. 2007, Antarctic CO_2 records: Petit et al. 1999; Pépin et al. 2001; Raynaud et al. 2005; Siegenthaler et al. 2005; Lüthi et al. 2008)

The following chapter will provide a review of global evidence for a transition in the intensity of glacial-interglacial cycles, and associated environmental changes, during the Middle Pleistocene. An overview of the Middle Pleistocene record of Britain is also presented, with a particular focus on the terrestrial record of the early Middle Pleistocene. Finally, a review of herbivory and other ecological processes in Quaternary palaeo-records is provided, and their applications and implications for Middle Pleistocene interglacials discussed.

2.2. The Mid-Brunhes Transition: Current Knowledge and Issues

2.2.1. Introduction

The last 1 Ma of Earth history were punctuated by two major climatic transitions, the Mid-Pleistocene Revolution (MPR) (*c.* 900 ka) and the Mid-Brunhes Transition (MBT) (*c.* 430 ka). The MBT, first recognised in the benthic $\delta^{18}O$ record by Jansen *et al.* (1986) and later validated by Antarctic ice core evidence (EPICA 2004; Jouzel 2007), is typically defined as a general shift in the relative amplitude of glacial-interglacial cycles, according to polar temperatures, greenhouse gas concentrations, ice volume, sea levels and sea surface temperatures (Jansen *et al.* 1986; EPICA 2004; Lisiecki & Raymo 2005; Jouzel *et al.* 2007; Loulergue *et al.* 2008; Lüthi *et al.* 2008; Tzedakis *et al.* 2009; Lang and Wolff 2011; Berger *et al.* 2015) (see Figure 2.1). It is also recognised that the amplitude of variation in orbital obliquity, a notable control on high latitude summer insolation (Yin & Berger 2012), is generally greater following the MBT (Berger *et al.* 2015). Consequently, variations in obliquity are often cited as being a potentially significant driver of this phenomenon (EPICA 2004; Jouzel *et al.* 2007; Yin & Berger

2010; Lang & Wolff 2011; Yin 2013; Berger *et al.* 2015). Interglacial duration, however, does not appear to be significant in this context, as both long (*c.* 28ka) and short (*c.* 13ka) interglacials occur prior to and following the MBT (Tzedakis *et al.* 2009, 2012).

Significant spatial complexity is recognised in MBT expression (Lang and Wolff 2011; Berger *et al.* 2015), and its relevance for mid and low latitude terrestrial environments is particularly uncertain. This stems from a lack of evidence in variables typically definitive of interglacial intensity at a regional level, such as summer temperatures in Northern Europe (Candy *et al.* 2010; Candy & McClymont 2013), arboreal pollen concentrations in the Mediterranean (Tzedakis *et al.* 2006, 2009) and tropical precipitation in Southeast Asia (Meckler *et al.* 2012). However, in an interglacial climate system characterised by unusually low temperatures (in the deep ocean and at high latitudes) and low greenhouse gas concentrations, a total absence of impact on mid to low latitude terrestrial environments seems unlikely. For these regions, two alternative hypotheses are proposed here: 1) climatic equifinality, in which comparable regional climates were produced throughout Middle Pleistocene interglacials, regardless of global boundary conditions, or 2) atypical response to such boundary conditions, expressed in climatic, ecological or landscape variables not generally characteristic of interglacial intensity.

The following sections will review evidence for a broadly synchronous global environmental transition occurring during the Middle Pleistocene (*c.* 780-126 ka), and evidence for the presence of unique or unusual conditions during early Middle Pleistocene (*c.* 780-430 ka) interglacials in particular. The focus of discussion in this chapter will be on the climatic, ecological and landscape changes associated with this transition, rather than its potential drivers (i.e. orbital conditions). The chronological uncertainty associated with many Middle Pleistocene records severely limits high-resolution temporal comparison at a global scale, but general patterns at glacial-interglacial scales can be discerned. Furthermore, there is no *a priori* reason to assume global sychroneity in the expression of a transition such as the MBT, and therefore seemingly asynchronous climatic and environmental transitions are discussed. Although this transition has been previously referred to as the Mid-Brunhes Event (e.g. EPICA 2004; Jouzel *et al.* 2007; Tzedakis *et al.* 2009; Candy *et al.* 2010; Lang & Wolff 2011), it is referred to as the Mid-Brunhes Transition here, following the suggestion of Yin (2013), as this carries fewer implications of rapidity or synchroneity. Rather, it simply implies a movement from one state to another, without implicit assumptions regarding the mode of transition.

2.2.2. Marine and Antarctic ice records

The MBT has been primarily demonstrated on the basis of marine and Antarctic ice records, which provide the firmest evidence of muted glacials and interglacials during the early Middle Pleistocene. This tendency was initially recognised by Jansen *et al.* (1986), with a strong emphasis on an oceanic signal derived from a number of biological, geochemical and sedimentological proxies obtained from a global array of sites, though significant complexity within this signal, including in terrestrial contexts, was also recognised. This signal has been further refined and corroborated through the production of the LR04 benthic δ^{18}O stack, based on 57 globally-distributed (though primarily Atlantic) records (Lisiecki & Raymo 2005), and reviews of marine, terrestrial and cryospheric records by Lang & Wolff (2011) and Berger *et al.* (2015). These demonstrate a general pattern of muted interglacials during the early Middle Pleistocene, which is reflected by similar patterns of inferred global ice volume and sea level fluctuations (Bintanja *et al.* 2005; Tzedakis *et al.* 2009; Elderfield *et al.* 2012; Shakun *et al.* 2015). However, there is a certain degree of complexity, and therefore uncertainty, associated with these records. For example, MIS 7 is broadly recognised as a ‘cool’ interglacial (or pair of interglacials, *cf.* Berger *et al.* 2015), despite being post-MBT (Tzedakis *et al.* 2009; Lang & Wolff 2011; Berger *et al.* 2015), emphasising the non-uniform nature of the trend in interglacial strength. Lang & Wolff (2011) also emphasise that owing to their stringent criteria for the inclusion of records in terms of temporal coverage and resolution, the quantity and spatial coverage of records is limited. Thus, although their conclusions may be treated as relatively robust, given the high quality of the data included, they are also necessarily somewhat broad. Furthermore, the LR04 benthic δ^{18}O stack (Lisiecki & Raymo 2005), whilst providing a useful global palaeoclimatic framework, has questionable direct relevance to terrestrial interglacial environments. This is because δ^{18}O change within the stack is primarily driven by global ice volume and deep water temperatures representative of global averages, thus giving little indication of regional complexities or terrestrial conditions (Lisiecki & Raymo 2005).

Ocean circulation patterns are major determining factors of the climatic characteristics of both marine and terrestrial environments, and there is evidence for distinctive, though highly complex, circulation patterns during early Middle Pleistocene interglacials. The Agulhas leakage is a transfer of heat and salinity from the Indian Ocean to the Atlantic Ocean, via the Cape of Good Hope, and is a source of heat and salinity for the northward surface currents of the Atlantic Meridional Overturning Circulation (AMOC) (Beal *et al.* 2011). This phenomenon was notably diminished during the early Middle

Pleistocene (Caley *et al.* 2012), which is potentially significant in the context of Northern Hemisphere climates, as they receive heat transported from southern latitudes via AMOC, through thermohaline convection (Rahmstorf 2007). This is complicated, however, by a strengthened positive mode of the Indian Ocean Dipole (higher temperatures and precipitation in the east Indian Ocean, and lower in the west Indian Ocean) during the early Middle Pleistocene (Gupta *et al.* 2010), which has been suggested to be linked to a strengthened Agulhas Current (Beal *et al.* 2011). This seemingly contradicts the suggestion of a diminished Agulhas leakage but it is likely that this aspect of the ocean system is not yet fully understood, particularly during this period.

Further complexity is added to this scenario when latitudinal gradients in sea surface temperatures (SSTs) in the North Atlantic are also considered. There is evidence, based on a range of planktonic and biomarker proxies, for interglacial SSTs to have been similar prior to and following the MBT in the mid-latitude North Atlantic (40-56°N), but cooler during pre-MBT interglacials in the high latitude North Atlantic (>56°N) (Candy & McClymont 2013). Therefore, latitudinal SST gradients in the North Atlantic were greater during early Middle Pleistocene interglacials. This implies enhanced poleward wind strength, and therefore surface water currents, which in turn implies enhancement of North Atlantic Deep Water (NADW) formation. This modulates the magnitude of heat transport away from the North Atlantic via thermohaline circulation, and is therefore a major component in the determination of AMOC strength (Rahmstorf 2007).

Collectively, this evidence suggests that ocean circulation during early Middle Pleistocene interglacials likely operated under a configuration with unknown analogues. The implications of this are unclear, given the apparently contrasting evidence from the

North and South Atlantic: potentially diminished heat and salinity transport to the South Atlantic (via the Agulhas leakage) suggests a weakening of AMOC, whilst enhanced NADW formation (as a product of increased latitudinal gradients in SST temperatures) suggests a strengthening of AMOC. This situation is clearly unusual, and further research will be required to fully understand it. However, it is possible that the late Middle Pleistocene shift towards generally more intense glacial-interglacial cycles may have been a result of (or modulated by) a change in ocean circulation patterns towards a configuration broadly more similar to the present.

The publication of the EPICA record from Antarctica has provided corroboration for the MBT signal observed in marine sediments, through the study of atmospherically-derived proxies of palaeoclimate (EPICA 2004; Jouzel *et al.* 2007; Lüthi *et al.* 2008; Loulergue *et al.* 2008). A measure of Antarctic mean annual surface air temperatures is provided by δD records, which exhibit more muted glacial-interglacial fluctuations prior to the MBT (Jouzel *et al.* 2007) (Fig. 2.1). In this context, the prominent theory of a 'bipolar seesaw' (Broeker 1998; EPICA 2006; Pedro *et al.* 2011), in which Arctic and Antarctic cooling occur out of phase, due to dominant directions of heat transport via AMOC, should be borne in mind. This hemispheric lag is typically suggested to occur on short timescales of 1000-2000 years during glacial periods, rather than during interglacials or on broader timescales (10,000-100,000 years). However, as AMOC appears to exhibit unusual characteristics during early Middle Pleistocene interglacials, it should not be assumed that associated phenomena, such as the bipolar seesaw, functioned in a manner equivalent to later periods, though its influence (or lack thereof) during this period is currently uncertain.

The pattern in Antarctic δD measurements is notably reflected in patterns of atmospheric CO_2 and CH_4 concentrations, derived from air inclusions within Antarctic ice cores (Lüthi *et al.* 2008; Lourlergue *et al.* 2008). Due to the rapid mixing of these gases in the atmosphere, and their relatively long lifetimes, these can be assumed to be globally representative records (Lang & Wolf 2011). Thus, it is particularly significant to note that pre-MBT CO_2 concentrations remained consistently below 'pre-industrial' levels (280 ppmv: see Figure 2.1) during early Middle Pleistocene interglacials (Lüthi *et al.* 2008), and that even Early Pleistocene records demonstrate that this is a specific characteristic of early Middle Pleistocene interglacials (Hönisch *et al.* 2009). Although the global relevance of proxies of other atmospheric conditions (e.g. air temperature) may be questioned, these greenhouse gas records provide unequivocal evidence for the existence of unique atmospheric conditions during early Middle Pleistocene interglacials at a global scale. This likely affected vegetation productivity, which may have led to further climatic feedbacks.

2.2.3. Non-European terrestrial records

Records discussed here have been selected on the basis of their temporal coverage (i.e. all or most of the Middle Pleistocene), and hence potential for detecting an MBT, as well as their relevance to terrestrial climates and environments. They have been drawn from all continental regions (except North America, where there is a paucity of records spanning the Middle Pleistocene) (see Figure 2.2), in order to provide a global context, for the British records.

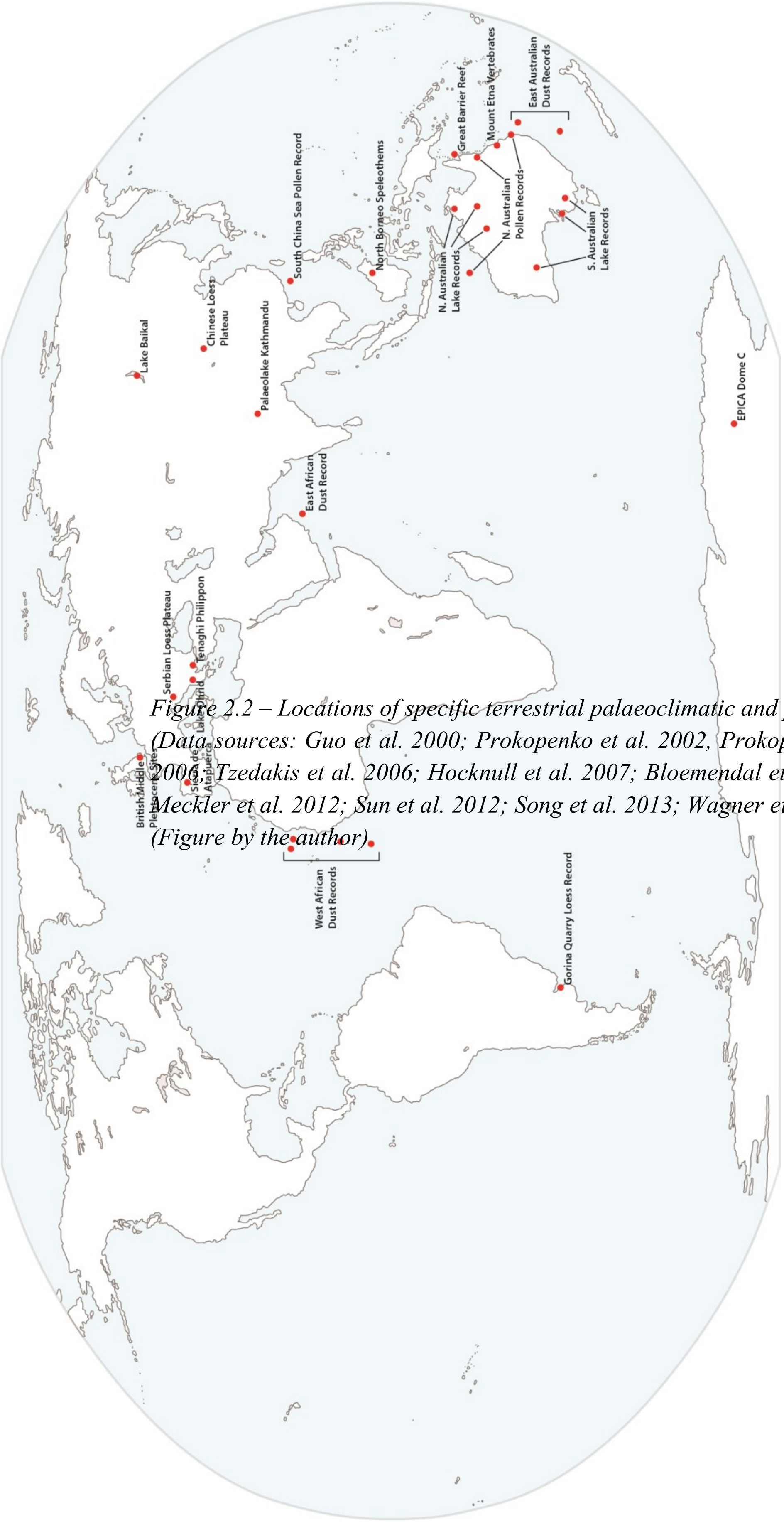


Figure 2.2 – Locations of specific terrestrial palaeoclimatic and palaeoenvironmental records
(Data sources: Guo et al. 2000; Prokopenko et al. 2002, Prokopenko et al. 2006; Sun et al.
2006; Tzedakis et al. 2006; Hocknull et al. 2007; Bloemendal et al. 2008; Candy et al. 2010,
Meckler et al. 2012; Sun et al. 2012; Song et al. 2013; Wagner et al. 2017)
(Figure by the author).

The major long-term records of Central Asia and Siberia, such as the Chinese Loess Plateau (CLP) and Lake Baikal, provide a complex view of the MBT. Several studies based on the CLP have shown an intensification of the East Asian summer monsoon during the Middle Pleistocene, based on a range of geochemical, sedimentological and palaeoecological features (e.g. Guo *et al.* 2000; Sun *et al.* 2006; Bloemendal *et al.* 2008; Sun *et al.* 2012). However, the signals appear to be asynchronous across the plateau, at the scale of marine oxygen isotope stages, though CLP chronologies are often orbitally tuned, and therefore their relative synchroneity is necessarily tentative. Contrary to the CLP, sedimentary and biological continental lake records from Siberia (Lake Baikal: Prokopenko *et al.* 2002, 2006; Lake El'gygytgyn: Melles *et al.* 2012) and Nepal (Palaeolake Kathmandu: Hayashi 2011) exhibit remarkable stability throughout the Middle Pleistocene. Diatom assemblages from Palaeolake Kathmandu do exhibit increased frequency of change in community composition, but not until approximately MIS 9 (Hayashi 2011), which could represent a lagged MBT, but may also be unrelated.

The apparent existence of a shift in East Asian summer monsoon intensity during the Middle Pleistocene, alongside apparent environmental stability in the extreme continental interior of Siberia (Lake Baikal), suggests that the MBT may have been a primarily ocean-propagated signal in this region. This would therefore explain the apparent lack of influence in Siberia, and possibly the Himalayas.

The evidence for environmental transitions during the Middle Pleistocene in Australasia and Southeast Asia is clear in parts, but spatially and temporally complex. In southern Australia there is firm evidence for a transition towards greater aridity, based on sedimentological changes in dune and lake systems, around *c.* 600-500 ka (e.g. Pillans & Bourman 2001; Hocknull *et al.* 2007). Furthermore, the initiation of tropical reef formation close to Australia's eastern coast, forming the modern Great Barrier Reef, occurred during MIS 13-11, suggesting a change in peak annual shallow marine temperatures in this region (Webster & Davies 2003). However, similarly to CLP records, the timing of this transition appears to be variable across the continent. In records of lake levels, faunal turnover, pollen and dust flux from northern Australia, increasing aridity is only registered after *c.* 300 ka (Hocknull *et al.* 2007). This demonstrates the existence of environmental transitions during the Middle Pleistocene in Australia, though whether these phenomena are connected remains to be seen.

The signal for an MBT further north, in Southeast Asia, is also complex. Meckler *et al.* (2012) suggest that MBT influence is absent from the region, based on a speleothem palaeoprecipitation record from Borneo, which indicates similar levels of precipitation from *c.* 550-200 ka. However, a long pollen record from the South China Sea, believed to range from MIS 29-1, does exhibit some mid-Brunhes changes, though it is far from conclusive, due to the relatively poor representation of interglacial periods (Sun *et al.* 2003).

There is a paucity of well-studied palaeoenvironmental records spanning MIS 19-5e in continental Africa and South America, but there is nevertheless some suggestion of a mid-Brunhes climatic transition. Jansen *et al.* (1986) suggested that subtropical Africa may have experienced drier conditions during the early Middle Pleistocene. However, this has been challenged by records suggesting an intense African monsoon during this period (Rossignol-Strick *et al.* 1998) and African dust records do not generally appear to record a notable shift in deposition rates during the Middle Pleistocene (deMenocal 2004). In South America, Argentinian loess deposits provide evidence for a notable increase in interglacial temperatures around 500 ka. This is based on a decrease in the amount of palaeosol goethite relative to hematite (Heil *et al.* 2010), and follows the pattern of the Antarctic MBT signal. However, deep sea records adjacent to tropical South America (e.g. Harris & Mix 1999) and lake records from Colombia (Torres *et al.* 2013) show no conclusive MBT signal, though interpreting the latter is complicated by biogeographical factors (Berger *et al.* 2015).

2.2.4. European records

There are several long European records spanning the Middle Pleistocene, but these give contrasting pictures of the mid-Brunhes. In the eastern Mediterranean, at Tenaghi Philippon, Greece no significant difference was found between pre- and post-MBT arboreal pollen values: a typical indicator of Mediterranean interglacial environments (Tzedakis *et al.* 2006). In the Balkans, however, a notable shift towards less humid, more steppic interglacial environments is recorded in the Brunhes Chron Serbian loess sequences (Fitzsimmons *et al.* 2012), though these are currently lacking chronological control. A shift towards warmer and less humid interglacials and glacials is also recorded at *c.* 300 ka at Lake Ohrid, FYROM/Albania (Wagner *et al.* 2017). Similarly, in Spain a decrease in annual precipitation, and an increase in interglacial warmth, following the MBT has been suggested (Blain *et al.* 2009, 2012), based on herpetofaunal mutual climatic ranges (MCR) (though this record is somewhat problematic, as species distributions beyond Iberia were not accounted for when determining climatic ranges).

In Northwest Europe, the interglacial climates and environments of the early Middle Pleistocene are of particular interest, as the earliest hominin dispersals into the region occurred during this period (Parfitt *et al.* 2005, 2010; Candy *et al.* 2011; Hosfield *et al.*

2011). However at present, the Northwest European expression of the MBT is unclear. Based on a range of palaeoecological proxies (primarily, 17 coleopteran Mutual Climatic Range records), Candy *et al.* (2010) demonstrated that the temperature of the warmest months during interglacials in Britain prior to the MBT was equivalent to that following the transition (Fig. 2.3). (Note that two records have been omitted from Figure 2.3, as they were lacking properly constrained warmest month (TMax) and coldest month (TMin) values.) This is a signal also borne out by mid-latitude North Atlantic SSTs (Candy & McClymont 2013). Unfortunately, limitations in palaeoclimatic reconstructions using Mutual Climatic Range (MCR) methods mean that such reconstructions can be problematically broad. For example, the reconstructed warmest month temperatures (TMax) from Bobbitshole, Suffolk (MIS 5e) (Coope 1974) and Sidestrand, Norfolk (*c.* MIS 13) (Preece *et al.* 2009) each have a potential range of 8°C, lying between 17°C and 25°C, and 16°C and 24°C, respectively (see Figure 2.3), and coleopteran MCR measurements often overestimate TMax (Atkinson *et al.* 1987; Elias *et al.* 1996; Elias & Matthews 2014). Conversely, whilst mid-latitude SSTs in the North Atlantic during this period appear to have been similar pre- and post-MBT, those of high latitudes were distinctly cooler, and the polar front more southerly, pre-MBT (Lang & Wolff 2011; Candy & McClymont 2013). Thus, the presence of an increased temperature gradient between mid and high latitudes, for at least part of the year, is indicated. This implies that although pre-MBT interglacial climatic conditions in mid-latitude Northern Europe appear to have been similar to those post-MBT with regards to summer temperatures (Candy *et al.* 2010; Candy & McClymont 2013), they are highly unlikely to be equivalent to those of other periods in all respects. They may have been distinctive in the context of other climatic variables, such as temperature seasonality (continentality), precipitation or storminess. Indeed, it has been suggested that early

Middle Pleistocene interglacials in Britain may have experienced enhanced seasonality, based on both modelling (Yin & Berger 2010) and empirical (Candy *et al.* 2006; Holmes *et al.* 2010; Candy & McClymont 2013) studies. However, this has yet to be fully tested using terrestrial records, as palaeotemperature reconstructions (particularly for winter temperatures) have lacked the required precision (see Figure 2.3).

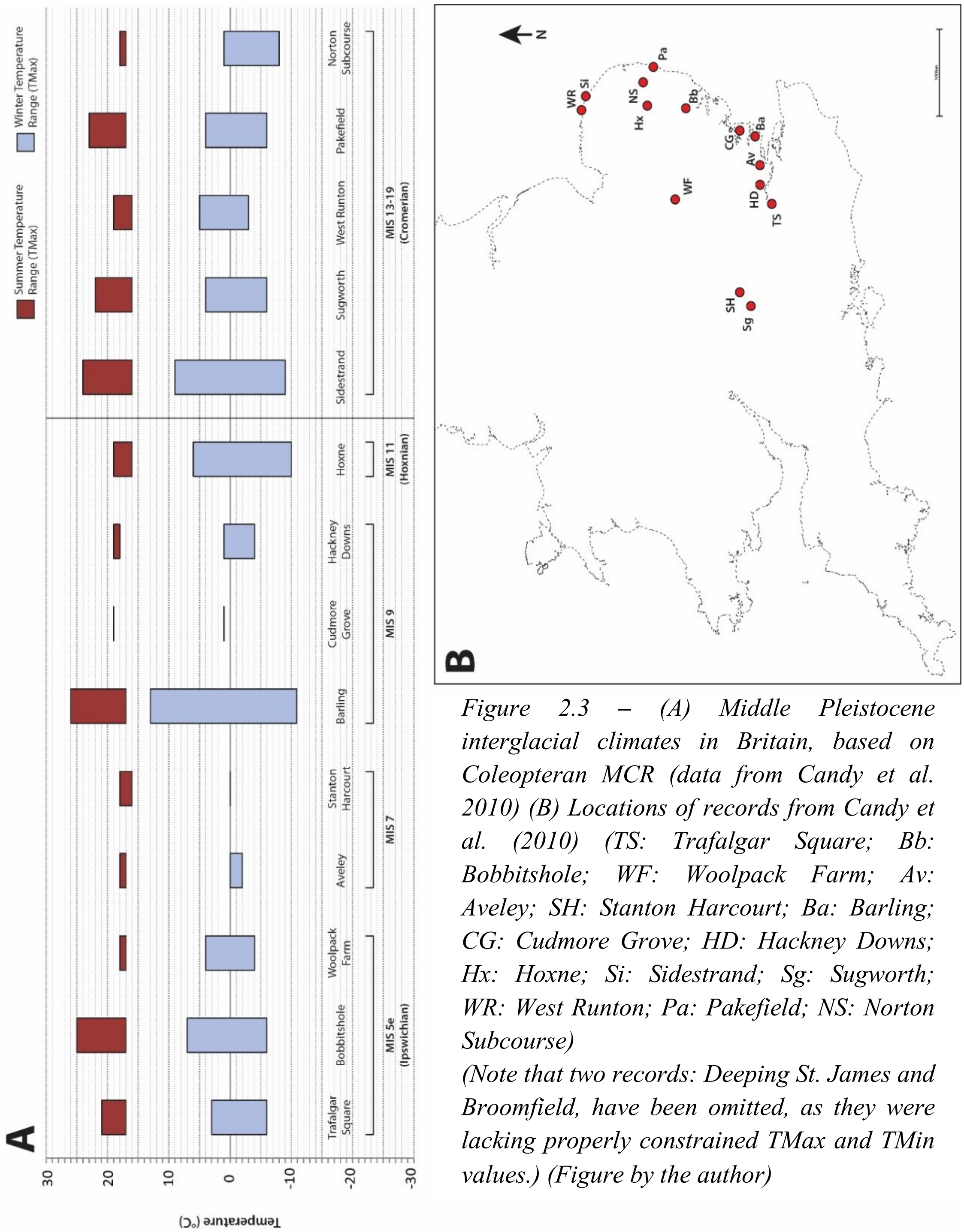


Figure 2.3 – (A) Middle Pleistocene interglacial climates in Britain, based on Coleopteran MCR (data from Candy et al. 2010) (B) Locations of records from Candy et al. (2010) (TS: Trafalgar Square; Bb: Bobbitshole; WF: Woolpack Farm; Av: Aveley; SH: Stanton Harcourt; Ba: Barling; CG: Cudmore Grove; HD: Hackney Downs; Hx: Hoxne; Si: Sidestrand; Sg: Sugworth; WR: West Runton; Pa: Pakefield; NS: Norton Subcourse)
(Note that two records: Deeping St. James and Broomfield, have been omitted, as they were lacking properly constrained TMax and TMin values.) (Figure by the author)

2.2.5. Summary

The above discussion demonstrates that there are reasonable grounds to suggest that the early Middle Pleistocene is climatically distinct in global terms, though much remains to be understood. The Antarctic and Atlantic MBT signals for muted interglacial conditions during this period are clear (e.g. Jansen *et al.* 1986; Jouzel *et al.* 2007; Lang & Wolff 2011; Berger *et al.* 2015), and form the basis of the classic definition of the MBT. There is also reasonable evidence for distinctive early Middle Pleistocene palaeoenvironments on the basis of ocean circulation patterns and terrestrial palaeoenvironments in predominantly climatic, but occasionally landscape or ecological, terms. Around the mid-Brunhes, Chinese loess deposits record an increase in the intensity of the East Asian summer monsoon (Guo *et al.* 2000; Sun *et al.* 2006; Bloemendal *et al.* 2008; Sun *et al.* 2012; Song *et al.* 2013), southern Australia underwent a transition to more arid and variable climates (Hocknull *et al.* 2007), Argentinian loess deposits exhibit an increase in interglacial temperatures (Heil *et al.* 2010), and there is evidence of a shift towards less humid interglacial environments in the Balkans (Serbia: Fitzsimmons *et al.* 2012; FYROM/Albania: Wagner *et al* 2017). Additionally, the Agulhas leakage was demonstrably weaker prior to the MBT (Caley *et al.* 2012), and a steep temperature gradient likely existed in the North Atlantic, for at least part of the year (Candy & McClymont 2013).

However, there are two primary factors hindering discussion of this phenomenon and its apparently variable expression. Firstly, there is a serious paucity of independently dated palaeoenvironmental archives relating to this period, resulting in a heavy reliance on orbital tuning, which introduces major issues in the temporal correlation of records (Blaauw 2012). This severely restricts any discussion of leads and lags in the spatial propagation of MBT influences. In spite of this, a general pattern of environmental transitions occurring around MIS 13-11 is recognisable in a number of terrestrial, marine and ice core records (e.g. Jansen *et al.* 1986; Hocknull *et al.* 2007; Jouzel *et al.* 2007; Heil *et al.* 2010; Lang & Wolff 2011; Caley *et al.* 2012; Fitzsimmons *et al.* 2012; Candy & McClymont 2013; Song *et al.* 2013; Berger *et al.* 2015). Secondly, in mid- to low-latitude regions, the potential for MBT expression in environmental variables other than those typically used to define interglacial strength has thus far been overlooked. For example, in Northwest Europe peak annual or summer temperatures typically define interglacial intensity (Tzedakis *et al.* 2009; Lang & Wolff 2011; Berger *et al.* 2015). However, there is a strong indication that early Middle Pleistocene interglacials in this region were characterised by distinctive ocean circulation patterns, due an increased SST temperature gradient (Candy & McClymont 2013), but consideration of a potential expression beyond summer temperatures has been limited. Climatic variables other than summer and peak annual temperatures, such as winter temperatures, temperature seasonality (continentality) and precipitation, may be significant in this context and therefore warrant further consideration. Additionally, differences in these variables may have consequences for landscape and ecological characteristics, which may be detectable in palaeoenvironmental records.

2.3. The Early Middle Pleistocene Record of Britain

2.3.1. Introduction

The study of long-term Middle Pleistocene palaeoenvironmental trends and signals in Northern Europe is hampered by the absence of long, continuous archives, necessitating the use of spatiotemporally fragmentary deposits (Turner 1996; Preece *et al.* 2009), albeit ones that are often extremely rich in palaeoenvironmental detail. In the absence of a continuous record, the early Middle Pleistocene deposits of East Anglia, in eastern England, present the most appropriate composite record in Northwest Europe. Here, a suite of early Middle Pleistocene deposits are regularly exposed on the coast, which yield valuable palaeoenvironmental information, the quality of which has long been recognised;

> *"The sections present, perhaps better than other sections in Europe, an opportunity for detailed palaeoecological reconstruction of the immediately pre-glacial period of time in northern Europe."* – RG West (1980a, p1)

This suite of deposits also possesses a number of properties that make them a viable focus for the present study (*cf.* Schreve & Candy 2010). Firstly, the record incorporates an extensive range of deposits, representing most, if not all, temperate episodes relevant to this study. Furthermore, the presence of an array of palaeoenvironmental proxies makes detailed palaeoclimatic and palaeoecological resonstructions possible. Their long history of study (see Preece & Parfitt 2012 for an overview) means that their chronostratigraphy is robust enough to facilitate conceptual relation to other long-term records. Additionally, as noted by Preece & Parfitt (2012), the accessibility of many of the deposits of southern and central England in open section is critical (contrasting the Dutch records, for example, *cf.* Turner 1996). This has aided the study of fossil groups such as insects, molluscs, ostracods and vertebrates in conjunction with pollen analysis (e.g. Shotton *et al.* 1993; Parfitt *et al.* 2005, 2010; Stuart & Lister 2010), alongside the recognition of hominin presence (e.g. Preece & Parfitt 2008). However, the records are not without significant issues, which limit the potential for a full understanding of within-interglacial variability. There is a severe paucity of applicable independent chronological techniques (*cf.* Rose 2009), and so chronologies are predominantly determined on a relative basis, according to magneto-, litho- morpho- and biostratigraphy (see Section *2.3.3.*). Substantial hiatuses are often involved (though the precise length is generally indeterminate), both within and between deposits, and deposits are typically representative of only relatively short periods of time or short-term events (Preece & Parfitt 2012). Additionally, they are biased in terms of the types of sedimentary environments represented: terrestrial deposits from temperate periods tend to be the result of floodplain or channel-fill processes.

The following section will provide a broad context for this suite of deposits in relation to palaeogeography, chronostratigraphy, palaeoenvironments and archaeology.

2.3.2. Palaeogeography

The palaeogeography of Northwest Europe was markedly different prior to the influence of the major mid-latitude lowland glaciation of the Anglian (correlated with MIS 12) (see Figure 2.4). Drainage was dominated by more extensive fluvial systems than at present: southern Britain and the English Midlands were drained by the Solent, Thames and Bytham catchments (Fig. 2.5) (though see Gibbard *et al.* 2013 for an alternative view), but most notable amongst these was the Baltic River, draining the area occupied by the present Baltic Sea (Fig. 2.4). This period precedes the formation of the Dover Strait, which formed as a result of catastrophic flooding from a pro-glacial lake in the southern North Sea basin, at the end of the Anglian, causing rapid erosion of the Weald-Artois anticline that formed a continuous landbridge between Britain and modern mainland Europe (Gupta *et al.* 2007). Therefore, prior to the Anglian glaciations, Britain was a permanent peninsula of Europe, allowing the free dispersal of terrestrial fauna and flora across the continent.

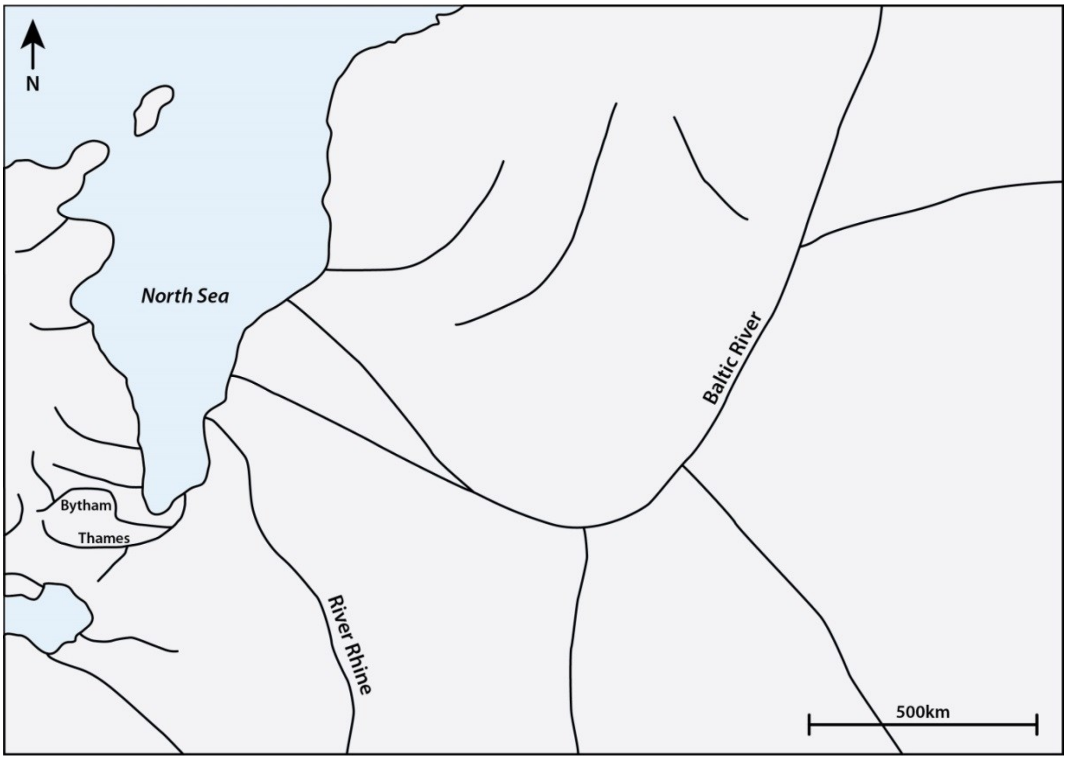


Figure 2.4 – Palaeogeography of Northern Europe during the early Middle Pleistocene (after Rose 2009, Fig. 12)

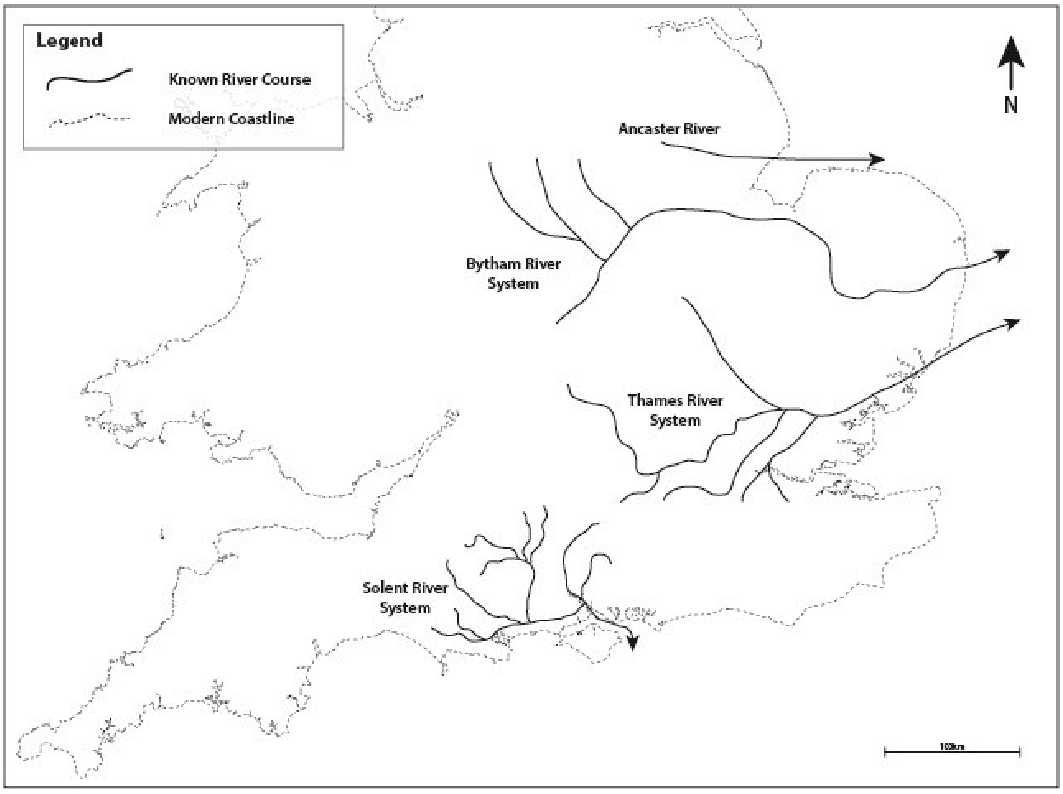


Figure 2.5 – Palaeogeography of early Middle Pleistocene Southern Britain (after Hosfield 2011, Fig. 1)

2.3.3. Chronostratigraphy

There is a paucity of applicable dating techniques for the Middle Pleistocene (*c.f.* Rose 2009), and so the construction of a coherent chronological model is complex and has involved a significant degree of debate, particularly with regards to the early Middle Pleistocene (e.g. Lee *et al.* 2004; Preece & Parfitt 2008, 2012; Preece *et al.* 2009). Despite these issues, a robust model based on a combination of magneto-, litho- morpho- and biostratigraphy, in conjunction with amino acid racemisation (AAR), has been successfully developed (e.g. Lee *et al.* 2004; Parfitt *et al.* 2005, 2010; Preece & Parfitt 2008, 2012; Preece *et al.* 2009; Rose 2009; Penkman *et al.* 2011, 2013) (see Figure 2.6 for a summary of early Middle Pleistocene chronostratigraphy in Britain). The resulting chronological framework allows comparison of the British record to other regional and global records, facilitating its inclusion in broader discussions of long-term palaeoclimatic, palaeoecological and palaeolandscape change.

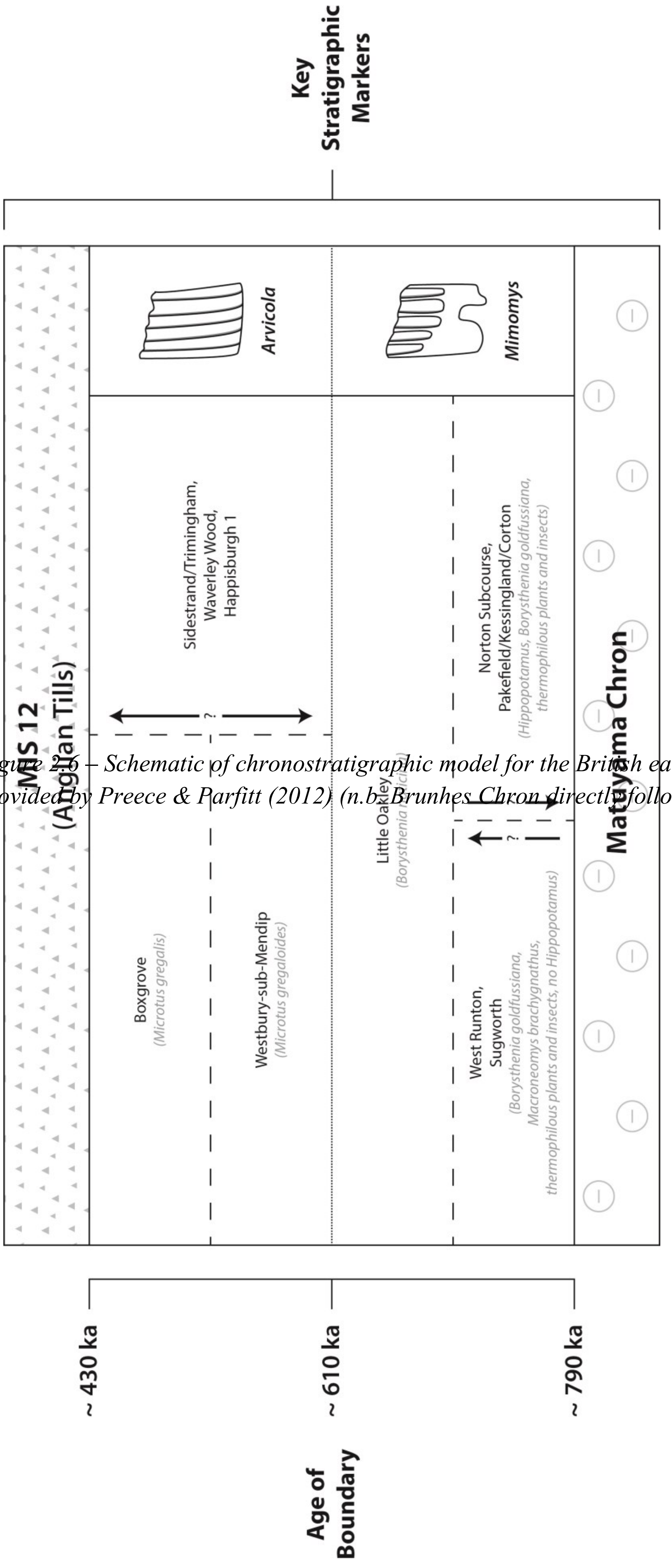


Figure 2.6 – Schematic of chronostratigraphic model for the British early Middle Pleistocene sho provided by Preece & Parfitt (2012) (n.b. Brunhes Chron directly follows Matuyama Chron)

The early Middle Pleistocene (*c.* 781-430 ka) is considered to be broadly equivalent to the 'Cromerian Complex' in Britain (Preece & Parfitt 2012). This encompasses a number of deposits previously attributed to a single interglacial stage: the 'Cromerian' (*sensu* West 1980a), which have since been recognised as being derived from several distinct temperate periods (Preece & Parfitt 2000, 2008, 2012; Preece 2001), and collectively re-termed the 'Cromerian Complex', following the Dutch model (*cf.* Zagwijn 1996a). In Britain, the early Middle Pleistocene is defined on the basis of boundaries provided by magneto- and lithostratigraphy (Preece & Parfitt 2012) (see Figure 2.6). The Brunhes-Matuyama magnetic reversal designates the lower boundary for the Middle Pleistocene at approximately 781 ka (Pillans & Gibbard 2012). This is convenient, due to the virtually ubiquitous applicability of magnetostratigraphy, but there remain two notable issues: (1) there is some suggestion that this reversal occurs later, at *c.* 770 ka (Dreyfus *et al.* 2008; Channell *et al.* 2010; Suganuma *et al.* 2010), and (2) it falls within an interglacial stage (MIS 19) (Channell *et al.* 2010; Pillans & Gibbard 2012). The upper boundary of the early Middle Pleistocene in Britain is provided by a series of Anglian (*c.* MIS 12) till deposits, though this is similarly not straightforward (Preece & Parfitt 2012). Firstly, the tills typically occur at erosional surfaces and are therefore separated from the underlying early Middle Pleistocene deposits by hiatuses of unknown length (Preece & Parfitt 2012). More significantly, although this suite of tills has classically been attributed to the Anglian glaciation (*c.* MIS 12) (Bowen *et al.* 1986), this view has been questioned in recent years with the proposal of the 'New Glacial Stratigraphy' (e.g. Lee *et al.* 2004; Hamblin *et al.* 2005). This suggested that these tills are attributable to a range of glacial stages between MIS 16 and 6, rather than just MIS 12. However, further research stimulated by this debate has since produced sufficient independent corroborating evidence to confirm the uniformly Anglian age of these deposits (e.g. Pawley *et al.* 2008; Preece & Parfitt 2008, 2012; Preece *et al.* 2009; Penkman *et al.* 2013). The Anglian tills therefore provide a convenient upper lithostratigraphical boundary in central and eastern England.

Subdivision within this framework has a primarily biostratigraphical basis, supported by aminostratigraphy. Early biostratigraphical subdivision of the early Middle Pleistocene in Britain was based on pollen zonation (e.g. Turner & West 1968; West 1980a) but this recognised only a single fully temperate stage within the period (the 'Cromerian' *sensu stricto*, with the stratotype at West Runton, Norfolk), characterised by a succession of pollen floras (see Table 2.1). Further study using other fossil groups has since revealed the presence of several warm stages within the 'Cromerian Complex' (e.g. Preece & Parfitt 2000; Preece 2001), and central to the current biostratigraphical age model is subdivision of sites into two groups on the basis of water vole evolution. During the early Middle Pleistocene, a transition from ancestral water voles with rooted molars (*Mimomys savini*) to those with continuously growing molars (*Arvicola terrestris*) took place (Bishop 1982; Preece & Parfitt 2000, 2008, 2012), allowing sites yielding rooted *Mimomys* teeth to be designated as older (see Figure 2.6). Although a transitional period during evolution is reasonable to assume, aminostratigraphical techniques unequivocally support the chronological separation of the two genera (Penkman *et al.* 2011; 2013), and the transition is thought to be synchronous across Europe (Stuart & Lister 2010). The age of this transition has been dated to MIS 15: ^{40}Ar/^{39}Ar dates at Isernia La Pineta, Italy have given ages of 610±10 ka BP and 606±2 ka BP (2σ error) (Coltorti *et al.* 2005), whilst a combination of Electron Spin Resonance (ESR) and U-series dating at Mauer, Germany have provided an age 609±40 ka BP (Wagner *et al.* 2010). The further separation of sites within this framework is principally based on vertebrate and molluscan palaeontology. These show distinctive assemblages, both in terms of taxonomic composition and morphometrics, indicating chronological separation, and evolutionary trends in particular taxa (e.g. in the molluscan genus, *Borysthenia*), providing relative ages. For example, *Mimomys* occur in pre-Anglian interglacial sediments at Pakefield, West Runton and Little Oakley, but at Pakefield the presence of *Hippopotamus antiquus* (hippopotamus) and *Mimomys* cf. *pusillus* (another species of archaic water vole) indicates a separation from West Runton, where these species are absent, despite similar depositional environments (Parfitt *et al.* 2005). Little Oakley is then separated from West Runton by the presence of *Borysthenia naticina* (a freshwater snail) (Preece 1990), as opposed to the ancestral *Borysthenia goldfussiana* found at Pakefield and West Runton, suggesting a younger age for Little Oakley (see Figure 2.6 and Preece & Parfitt 2012 for an overview).

Table 2.1 Summary of Turner & West's (1968) interglacial pollen zones

Turner & West (1968) Pollen Zone	**Vegetation Characteristics**
Post-temperate (IV)	*Pinus*-*Betula* dominated
Late-temperate (III)	Dense mixed deciduous-coniferous (including *Carpinus*, *Abies*)
Early-temperate (II)	Dense deciduous woodland (*Quercus*, *Corylus*, *Ulmus*, *Tilia*, etc)
Pre-temperate (I)	*Pinus*-*Betula* dominated

2.3.4. Palaeoenvironmental context

In southern Britain, the palaeoenvironmental record of the Middle Pleistocene is fragmentary, but well studied. It exists primarily in the form of fluviatile and shallow marine deposits (Bridgland & Schreve 2004; Rose 2009), supplemented by notable raised beach (e.g. Bates *et al.* 1997; Westaway *et al.* 2006), cave infill (e.g. Bishop 1982) and lacustrine (e.g. Turner 1970; Tye *et al.* 2012) sequences. The fluviatile deposits consist of the sands, gravels and organic-rich channel fills and flood deposits associated with the major rivers of the period, such as the Cromer Forest-bed Formation and the Thames and Bytham terrace sequences (e.g. Preece & Parfitt 2000, 2008; Bridgland & Schreve 2004; Rose 2009) (Table 2.2 provides a list of important examples, focussed on sites with palaeoentomological records). The marine sequences are dominated by the Wroxham Crag deposits of East Anglia (Rose *et al.* 2001). Reconstruction of the contemporary palaeoenvironments associated with these sediments has been achieved though the utilisation of a broad range of evidence, including biological proxies (e.g. pollen, plant macrofossils, insects, molluscs, vertebrates) (e.g. Shotton *et al.* 1993; Preece *et al.* 2009; Böhme 2010; Coope 2010a; Maul & Parfitt 2010), sedimentological features (e.g. ice-wedge casts, palaeosols) (e.g. Whiteman 2002; Lee *et al*. 2006) and stable isotopes (e.g. Candy *et al.* 2006), occasionally simultaneously (e.g. Stuart & Lister 2010: Tye *et al.* 2012), demonstrating the existence of a range of environmental conditions in Britain throughout the period.

Britain (MIS 19-5e) with palaeoentomological (predominantly coleopteran) records. Orange: pre-Anglian,
Ve: Vertebrates, Mo: Molluscs, Os: Ostracods, Fo: Foraminifera, Di: Diatoms, Cl: Cladocera , Br: Bryozoa,

Site/ Deposit Name	Latitude	Longitude	Interglacial (MIS)	Insects	Pollen	Archaeology	Other Proxies	Depositional Environment	References
Trafalgar Square	51°30'27"N	0°7'42"W	5e	Yes			PM, Ve, Mo	Fluviatile	Franks 1960; Preece 1999; Coope 2001, unpublished
Deeping St James	52°39'28"N	0°14'58"W	5e	Yes	Yes		Mo	Fluviatile	Keen *et al.* 1999
Bobbitshole	52°1'46"N	1°7'47"E	5e	Yes	Yes		PM, Ve, Mo	Lacustrine	Sparks 1957; West 1957; Coope 1974; Stuart 1979
Woolpack Farm	52°17'54"N	0°5'47"W	5e	Yes	Yes		Ve, Mo	Fluviatile	Gao *et al.* 2000
Itteringham	52°49'37"N	1°7'22"E	5e	Yes			Ve	Fluviatile/Lacustrine	Beesley 1988 (unpublished); Coope 2001
Shropham	52°29'56"N	0°54'56"E	5e	Yes			Ve	Fluviatile/Lacustrine	Coope 1995, 2001; Walkling 1996
Cassington	51°47'57"N	1°17'59"W	5e	Yes	Yes		Ve, Mo	Fluviatile	Maddy *et al.* 1998
Maxey	52°38'56"N	0°19'52"W	5e	Yes			Mo	Fluviatile	Davey *et al*. 1991
Stone Point	50°47'4"N	1°21'14"W	5e	Yes	?		PM	?	Reid 1893; Coope 2010a
Tattershall Castle	53°5'48"N	0°11'51"W	5e	Yes	Yes		PM, Ve, Mo, Os, Fo	Fluviatile	Girling 1980b; Holyoak & Preece 1985
Marsworth	51°49'5"N	0°39'0"W	5e/7	Yes	Yes		PM, Ve, Mo, Os	Fluviatile	Murton *et al.* 2001
Histon Road, Cambridge	52°13'32"N	0°6'35"E	5e/7	Yes	Yes		PM, Ve, Mo	Fluviatile?	Coope 2001; Boreham *et al.* 2010
Aveley	51°30'1"N	0°14'5"E	7	Yes	Yes	Yes	Ve	Fluviatile	West 1969; Coope 2001; Schreve 2001
Stanton Harcourt	51°44'22"N	1°24'17"W	7	Yes	Yes		PM, Ve, Mo	Fluviatile	Briggs *et al.* 1985; Buckingham *et al.* 1996; Coope unpublished
Stoke Goldington	52°7'25"N	0°44'43"W	7	Yes	Yes		PM, Ve, Mo, Os	Fluviatile	Green *et al.* 1996
Latton	51°40'2"N	1°53'3"W	7	Yes	Yes	Yes	PM, Ve, Mo	Fluviatile	Lewis *et al.* 2006
Tattershall Thorpe	53°7'45"N	0°9'36"W	7	Yes	Yes		PM, Mo, Os	Fluviatile	Coope 2001; Holyoak & Preece 1985
Selsey	50°43'23"N	0°47'14"W	7	Yes	Yes	Yes	PM, Ve, Mo	Fluviatile	West *et al.* 1960
Whittlesey	52°33'45"N	0°9'21"W	7	Yes	Yes		PM, Mo, Os	Fluviatile	Langford *et al.* 2007, 2014
Frog Hall Pit, Stretton-on-Dunsmore	52°21'26"N	1°23'32"W	7/9	Yes	Yes		PM, Mo, Os	Fluviatile	Keen *et al.* 1997; Gibbard *et al.* 2013
Barling	51°34'19"N	0°47'2"E	9	Yes		Yes	PM, Ve, Mo	Fluviatile	Bridgland *et al.* 2001
Cudmore Grove	51°47'24"N	0°59'34"E	9	Yes	Yes		PM, Di, Ve, Mo	Fluviatile	Roe *et al.* 2009
Hackney	51°32'60"N	0°3'0"W	9	Yes	Yes		PM, Ve, Mo	Fluviatile	Green *et al.* 2006
Hoxne	52°21'3"N	1°11'59"E	11	Yes	Yes	Yes	Ve, Mo	Lacustrine	West 1956; Coope 1993; Ashton *et al.* 2008a
Nechells, Birmingham	52°29'27"N	1°52'24"W	11	Yes			PM, Ve, Mo, Os, Zp, Br, Ar	Lacustrine	Shotton *et al.* 1965
Woodston	52°32'43"N	0°14'48"W	11	Yes	Yes		PM, Ve, Mo, Os	Estuarine	Horton *et al.* 1991, 1992
Quinton	52°27'24"N	2°0'7"W	*c.* 11	Yes	Yes		PM	Fluviatile	Coope & Kenward 2007
Waverley Wood	52°20'24"N	1°27'51"W	*c.* 13	Yes	Yes	Yes	PM, Ve, Mo, Os	Fluviatile	Shotton *et al.* 1993
Pool's Farm Pit	52°22'57"N	1°25'53"W	*c.* 13	Yes	Yes			Fluviatile	Osborne & Shotton 1968; Coope 1989; Maddy *et al.* 1994
Mathon	52°7'0"N	2°24'0"W	*c.* 13	Yes	Yes		PM	Fluviatile	Coope *et al.* 2002
Brooksby	52°44'31"N	1°0'6"W	*c.* 13	Yes		Yes		Fluviatile	Coope 2006, unpublished
Happisburgh 1	52°49'0"N	1°34'0"E	13-15	Yes	Yes	Yes	PM, Ve	Fluviatile	West 1980a; Coope 2006; Ashton *et al.* 2008b
Sidestrand	52°54'21"N	1°22'27"E	13-15	Yes	Yes		PM, Ve, Mo	Fluviatile	West 1980a; Preece *et al.* 2009
High Lodge	52°20'21"N	0°33'31"E	13-19	Yes		Yes		Fluviatile	Coope 1992
Broomfield	51°46'19"N	0°29'30"E	13-19	Yes	Yes		PM, Ve	Fluviatile	Gibbard *et al.* 1996; Coope 2010a
Ardleigh	51°55'51"N	0°58'49"E	13-19	Yes	?		?	Fluviatile	Coope 2010a
Sugworth	51°42'10"N	1°15'33"W	15-19	Yes	Yes		PM, Mo	Fluviatile	Gibbard & Pettit 1978; Osborne 1980; Shotton *et al.* 1980; West 1980a
West Runton	52°56'30"N	1°15'17"E	15-19	Yes	Yes		PM, Ve, Mo	Fluviatile	West 1980a; Coope 2000, 2010b
Pakefield	52°25'45"N	1°43'50"E	15-19	Yes	Yes	Yes	PM, Ve	Fluviatile	West 1980a; Parfitt *et al.* 2005; Coope 2006
Norton Subcourse	52°32'22"N	1°32'32"E	15-19	Yes	Yes		PM, Ve, Mo	Fluviatile	Lewis *et al.* 2004; Coope unpublished
Beeston	52°56'30"N	1°15'17"E	15-19	Yes	Yes		PM	Fluviatile	West 1980a; Coope 2000
Happisburgh 3	52°49'36"N	1°31'58"E	≥19	Yes	Yes	Yes	PM, Ve, Mo	Fluviatile	Parfitt *et al.* 2010

Interglacial environments in Britain are typically characterised by mild temperatures, moderate precipitation and the expansion of deciduous woodland and associated faunas. Turner & West (1968) developed a four-phase biostratigraphic model for interglacials in Northwest Europe, based on pollen zonation (see Table 2.1). Although the usefulness of this scheme as a chronological tool in modern Quaternary science is questionable (*cf.* Rose 2009), it remains valuable as a broad demonstration of the general characteristics of interglacial floras and ecosystems in Northwest Europe. Under peak interglacial conditions, these are typically dominated by deciduous taxa, such as *Quercus*, *Ulmus*, *Tilia* and *Corylus* (West 1980a, 1980b; Schreve & Candy 2010), and the study of the Cromer Forest-bed Formation has been instrumental in recognising these generalities (West 1980a). Cromer Forest-bed Formation sites such as West Runton and Pakefield have also yielded extensive faunal remains (vertebrates, molluscs and Coleoptera), which further corroborate floral evidence for temperate conditions (Stuart 1996; Stuart & Lister 2001; Coope 2006, 2010a; Stuart & Lister 2010; Kahlke *et al.* 2011; Preece & Parfitt 2012). These are discussed further in chapters 4 (West Runton) and 5 (Pakefield). Similarly to Turner & West's (1968) pollen zones, Gibbard & Lewin (2002) identified a general pattern of phases in lowland fluvial sedimentation and channel development during interglacials, summarised in Table 2.3, which can be broadly characterised by low seasonality in flow regimes, stable floodplains, reduced sedimentation rates and the deposition of fine-grained, fossiliferous material. This work further demonstrates the similarity between interglacial periods in terms of landscape processes.

Table 2.3 Summary of Gibbard & Lewin's (2002) lowland interglacial fluvial phases

Fluvial phase (Fph)	**Channel form and depositional mode**	**Sedimentology**	**Turner & West (1968) Pollen Zone**
Fph i	Multiple inherited channels. Stabilised banks. Deposition, vertical accretion.	Rapidly decreasing inorganic and increasing organic content.	I–Early II
	Infilling of depressions and channels.	Marls, tufas, organic muds, silts. Fossiliferous.	
Fph ii	Anastomosing channels. Channel avulsion. Deposition, vertical accretion.	High organic content.	II
	Infilling of depressions and channels. Sheet-like floodplains.	Detritus silt and clay muds, peats. Fossiliferous.	
Fph iii	Inactive meandering and anastomosing channels. Channel avulsion. Deposition, vertical accretion.	High organic content.	II–III
	Infilling of remaining depressions. Floodplains becoming planar.	Detritus silt and clay muds, peats. Fossiliferous.	
Fph iv	Multiple channels formed. Potential channel avulsion. Vertical accretion.	Decreasing organic and increasing inorganic content.	Late III–IV
	Planar floodplains.	Detritus silt and clay muds, peats. Less fossiliferous.	

In spite of broad climatic and environmental similarities between interglacials, much remains to be learned about interglacial climates and ecologies in Britain and Northwest Europe. Whilst general similarities in summer temperatures throughout Middle

Pleistocene interglacials have been emphasised (Candy *et al.* 2010; Candy & McClymont 2013), the concept of a 'typical' interglacial is not necessarily useful (Schreve & Candy 2010). For example, whilst MIS 7 and 11 exhibit climatic conditions similar to the Holocene (e.g. Murton *et al.* 2001; Candy *et al.* 2014), temperatures apparently warmer than this are known from MIS 5e, 9 and the interglacial represented at Pakefield (*c.* MIS 15/17) (Keen *et al.* 1999; Gao *et al.* 2000; Parfitt *et al.* 2005; Green *et al.* 2006; Roe *et al.* 2009; Coope 2010a). However, comparisons between these interglacials in Britain and Northwest Europe have largely been on the basis of differences in summer temperatures, compared to the modern day, and their faunal assemblages. This leaves much to be learned on the basis of other climatic variables (e.g. winter temperatures, temperature seasonality, precipitation, storminess, etc) and ecological factors (e.g. herbivory and disturbance processes, forest structure, biodiversity, nutrient cycling, etc). Although some progress has been made in these areas (e.g. Candy *et al.* 2006; Holmes *et al.* 2010; Kuneš *et al.* 2011, 2013), new methodological developments and approaches (e.g. Smith *et al.* 2010; Jackson & Blois 2015; Milne 2016) are expected to facilitate further advancements.

2.3.5. Archaeological context

During the early Middle Pleistocene, southern Britain represented the northwestern fringe of hominin geographical ranges. Evidence for this presence is primarily based on the occurrence of lithic tools (cores and flakes, handaxes) in sedimentary sequences (Ashton *et al.* 2011; Hosfield *et al.* 2011), complimented by several notable palaeontological finds (hominin fossils, cut-marked faunal remains) (Roberts *et al.* 1994; Stringer *et al.* 1998; Parfitt & Roberts 1999; Parfitt 2005) (see Hosfield 2011 for a review). Given their peripheral position, these populations were likely to have been extirpated during periods of adverse climatic conditions, resulting in only sporadic occupation, with southern Britain acting as a population ‘sink’. Different populations, or even species, of *Homo* may have contributed to each pulse of expansion and colonisation (Bridgland *et al.* 2006; Roebroeks 2006; Dennell *et al.* 2011; Ashton & Lewis 2012). These populations appear to have been predominantly, though not exclusively, present during periods of cool temperate climate, and inhabited mosaic ecotonal landscapes, which incorporated woodland, grassland and wetland habitats (Coope 2006; Holmes *et al.* 2009; Hosfield 2011). Environmental context is particularly pertinent in studying these northerly populations (Candy *et al.* 2011), and understanding of their ecology, adaptability and vulnerability will be enhanced by continued investigation into the climates and ecology of early Middle Pleistocene interglacials.

2.4. Low CO_2, Herbivory and Disturbance in Palaeoecology: Applications and Implications for Middle Pleistocene Interglacials

2.4.1. Introduction

Ecosystems are influenced by a suite of interacting biotic and abiotic variables, and changes in any one of them may result in a change in ecosystem characteristics or function, through either direct or cascading impacts. Thus, in the context of investigating the MBT and the distinctive nature of early Middle Pleistocene palaeoenvironments, the study of their ecosystems and associated communities provides a complimentary perspective to directly climatological lines of enquiry. Ecological differences between interglacials may be partially symptomatic of subtle differences in climate that have remained undetected. For early Middle Pleistocene interglacials, there is firm evidence for low atmospheric CO_2 (Lüthi *et al.* 2008), and some suggestion of enhanced seasonality, storminess and/or precipitation in Northwest Europe (Candy *et al.* 2006; Holmes *et al.* 2010; Candy & McClymont 2013). It is likely that these factors were ecologically influential, via (potentially interacting) impacts such as altered primary productivity, increased patchiness, altered growing season length and phenologies, increased moisture availability, altered precipitation seasonality, altered wildfire regimes and changes in susceptibility to disease, parasites, herbivory and other disturbance regimes (e.g. Bond & Midgley 2001; Dale *et al.* 2001; Spiller & Agrawal 2003; Gerhart & Ward 2010; Lindner *et al.* 2010; Fischer *et al.* 2013; Seidl *et al.* 2014; Stuart-Haëntjens *et al.* 2015). However, whether such ecological factors are significant, or even detectable, in the context of the early Middle Pleistocene interglacials and the MBT remains to be seen.

2.4.2. Low atmospheric CO_2: Physiological and ecological impacts

The low levels of atmospheric CO_2 during early Middle Pleistocene interglacials (max: ~260 ppmv: Lüthi *et al.* 2008) (see Figure 2.1) may have been ecologically significant. Atmospheric CO_2 distribution is broadly even across the globe, and hence its availability to plants is relatively uniform. It is the primary source of carbon for photosynthesis in plants, and determines rates of carbon assimilation, via internal leaf CO_2 concentrations. Thus, a reduction in CO_2 availability results in reduced net photosynthetic rates, and subsequent reduced biomass production (Ward 2005; Gerhart & Ward 2010; Temme *et al.* 2013, 2015). This has been experimentally demonstrated: biomass production, based on a range of indices, exhibits a clear positive correlation with ambient CO_2 concentrations in a broad variety of plant species, grown in otherwise optimal conditions (Fig. 2.7) (Gerhart & Ward 2010; Temme *et al.* 2013, 2015). This effect is even observed in differences of 10-20 ppmv (Gerhart & Ward 2010), which is equivalent to the differences in CO_2 concentrations between early and late Middle Pleistocene interglacials (see Figures 1 and 7). Thus, photosynthetic rates and biomass production are likely to have been lower during early Middle Pleistocene interglacials, resulting in plants with both lower growth rates and lower reserves of excess carbon and water. This may reduce the resilience of plants to other sources of stress, such as herbivory and other disturbance processes, nutrient limitation, moisture limitation and temperature, as well as altering competitive interactions (Cowling & Sage 1998; Cowling & Sykes 1999; Ward 2005; Temme *et al.* 2013, 2015). In a broader context, low atmospheric CO_2 in the past is known to be associated with lower net primary productivity, which may have a number of cascading impacts. On a continental and global scale, this may be associated with altered albedo, terrestrial carbon storage and net evapotranspiration, with resultant impacts on hydrological regimes and regional temperature (Crucifix & Hewitt 2005; Bonan 2008; Hoogakker *et al.* 2016). At a regional to local scale, this may also have resulted in limited tree cover, lower quantities of fuel available for burning (affecting the frequency and magnitude of wildfires), altered geomorphic regimes and altered nutrient cycles. Ecosystem carrying capacities would also be expected to be lower, resulting in lower faunal biomass across trophic levels. It seems likely, therefore, that ecological communities during early Middle Pleistocene interglacials were distinct from those of other periods, in terms of biomass, disturbance regimes, competitive interactions, and community structure and composition.

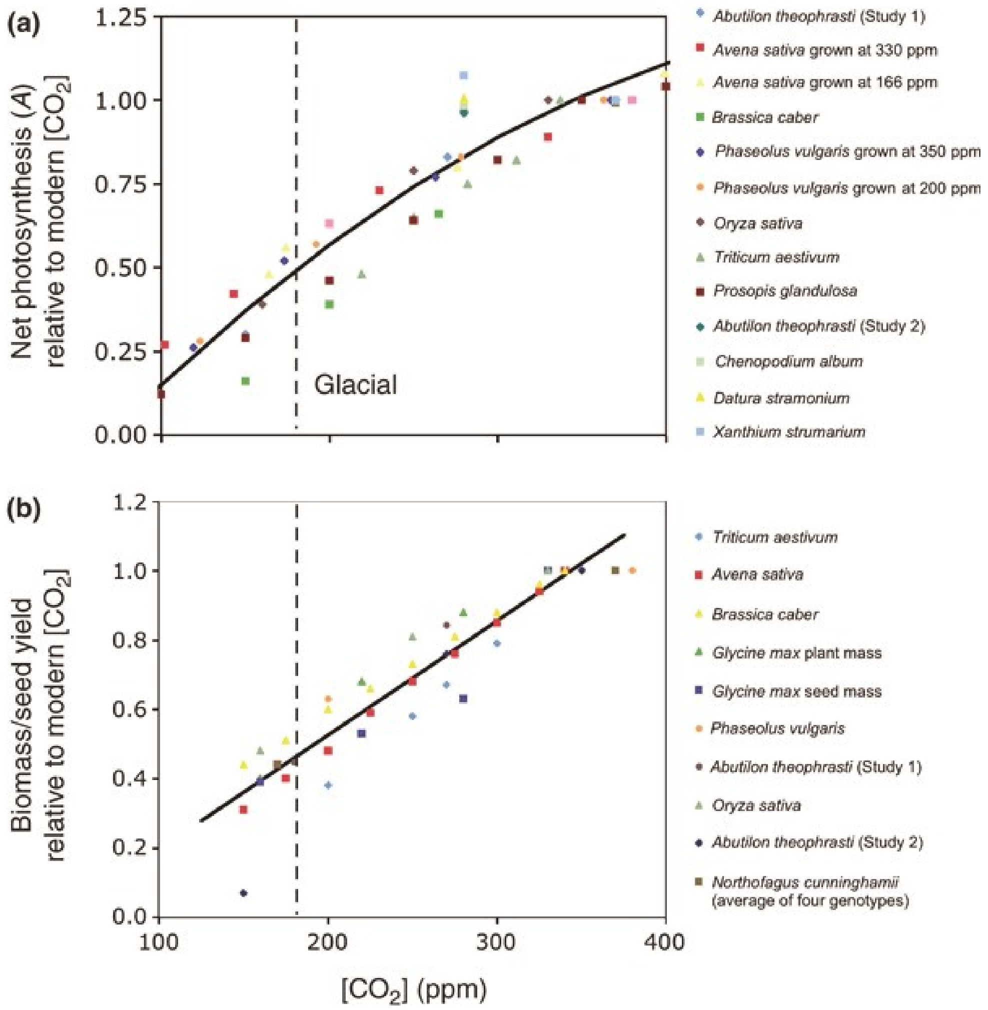


Figure 2.7 – (a) Relative net photosynthesis and (b) biomass production (or seed yield) for a variety of modern plants grown at atmospheric CO_2 levels ranging from glacial to modern levels (from Gerhart & Ward 2010)

2.4.3. Herbivory and disturbance regimes in palaeoecology

Disturbance is a fundamental ecological process, driving habitat heterogeneity, species diversity and temporal dynamism in ecosystems (Seidl *et al.* 2011, 2014; Fischer *et al.* 2013). In a terrestrial context, it may be broadly defined as any "discrete event in time that disrupts ecosystem structure, composition and/or processes by altering its physical environment and/or resources, causing destruction of plant biomass" (Seidl *et al.* 2011, p905). This may be derived from biotic (e.g. herbivory, disease) or abiotic (e.g. fire, flooding, wind, frost) agents. In palaeoecology, herbivory and other disturbance factors have garnered considerable interest, particularly in the context of debates around relative landscape openness (e.g. Vera 2000; Svenning 2002; Bradshaw *et al.* 2003; Davis *et al.* 2007; Power *et al.* 2008; Olsson & Lemdahl 2010; Smith *et al.* 2010; Whitehouse & Smith 2010; Baker *et al.* 2013; Kuneš *et al.* 2013; Gill 2014; Seddon *et al.* 2014). Novel approaches to the study of vegetation-herbivore interactions in the past have been developed accordingly, utilising dung-associated fungi (e.g. Davis 1987; Richardson 2001; van Geel 2001; Blackford & Innes 2006; Davis & Shafer 2006; Raper & Bush 2009; Baker *et al.* 2013, 2016; Wood & Wilmshurst 2013; Johnson *et al.* 2015) and insects (e.g. Robinson 1983; Whitehouse 2006; Smith *et al.* 2010, 2014; Whitehouse & Smith 2010; Sandom *et al.* 2014), as well as drawing on information from mammalian fossils (e.g. Bradshaw *et al.* 2003; Pushkina *et al.* 2014; Rivals & Lister 2016). These approaches have been used to explore the long-term ecological impacts of herbivore extinctions and introductions (e.g. Gill *et al.* 2009; Rule *et al.* 2012; Gill 2014; Wood *et al.* 2016), the interplay of herbivory with other disturbance factors and ecological processes (e.g. Gill *et al.* 2009; Rule *et al.* 2012) and the role of herbivores in archaeological landscapes (e.g. Blackford *et al.* 2006; Whitehouse 2006; Elias *et al.* 2009; Wood *et al.* 2011; Buckland *et al.* 2016). However, studies focussed on disturbance ecology have been primarily based on the Holocene and Lateglacial, with a few exceptions (e.g. Bradshaw *et al.* 2003; Kuneš *et al.* 2013; Sandom *et al.* 2014), but given the demonstrable utility of these approaches, they have much to offer in the study of Middle Pleistocene interglacials. In terms of the early Middle Pleistocene, there have been occasional inferences made regarding disturbance regimes (e.g. Field & Peglar 2010), but these are fairly limited in scope. Conversely, there is prolific evidence for extensive assemblages of large herbivores throughout early and late Middle Pleistocene interglacials, of greater diversity than Holocene assemblages (e.g. Bradshaw *et al.* 2003; Bridgland & Schreve 2004; Kahlke *et al.* 2011). This suggests that herbivory-induced disturbance was likely an influential factor in Middle Pleistocene palaeoenvironments, with potentially diverse impacts, warranting more in-depth research. Furthermore, as vertebrate communities and atmospheric characteristics vary between interglacials, there may even be potential to detect differences between interglacials in terms of disturbance processes, habitat structure or other ecological variables, and this may be extended to exploring the terrestrial expression of the MBT. This research is also valuable in terms of understanding disturbance processes and herbivore-vegetation relationships with a long-term perspective. Determining the repeatability of such natural 'experiments', by observing these processes under different conditions (such as those that vary between temperate stages), allows their ubiquity and flexibility to be observed. This advances understanding of the fundamental properties of such processes across time and space, leading to more in-depth knowledge of their potential influence and significance in past, present and future ecosystems.

2.5. Choice of Sites Investigated

Three sites have been chosen for primary investigations in this thesis: West Runton, Norfolk (Chapter 4), Pakefield, Suffolk (Chapter 5) and Brooksby, Leicestershire (Chapter 6) (Fig. 2.8). Early Middle Pleistocene interglacial deposits yielding pollen, insects and other organic remains are known from these sites (West 1980a; Coope 2006; Stephens *et al.* 2008; Stuart & Lister 2010), and each is derived from a distinct temperate stage (details of stratigraphical separation is provided in relevant chapters). Each site is also known to be associated with different climatic settings, allowing the exploration of local ecological dynamics under a range of different boundary conditions.

West Runton is associated with conditions broadly similar to the present (Coope 2010b; Stuart & Lister 2010), Pakefield is thought to be associated with warmer, seasonally-dry, temperate conditions (Candy 2006; Coope 2006), and the Brooksby deposits are thought to be derived from a cool temperate interval (Coope 2006; Stephens 2008). Additionally, prior research on the Cromer Forest-bed Formation at West Runton and Pakefield (particularly regarding coleopteran, pollen and vertebrate assemblages) provides valuable context for new studies focused on vegetation reconstructions and ecological processes, and reference may be made to other local ecosystem components. For example, the vertebrate record from West Runton is exemplary amongst early Middle Pleistocene sites in Northwest Europe (Stuart 1996), and includes a diverse range of large and small vertebrate herbivores and carnivores (Breda *et al.* 2010; Lewis *et al.* 2010; Lister *et al.* 2010; Maul & Parfitt 2010; Stewart 2010; Böhme 2010), which are likely to have had a mutually influential relationship with vegetation communities. The palaeoenvironmental and palaeoecological contexts for these sites will be discussed further in Chapters 4, 5 and 6.

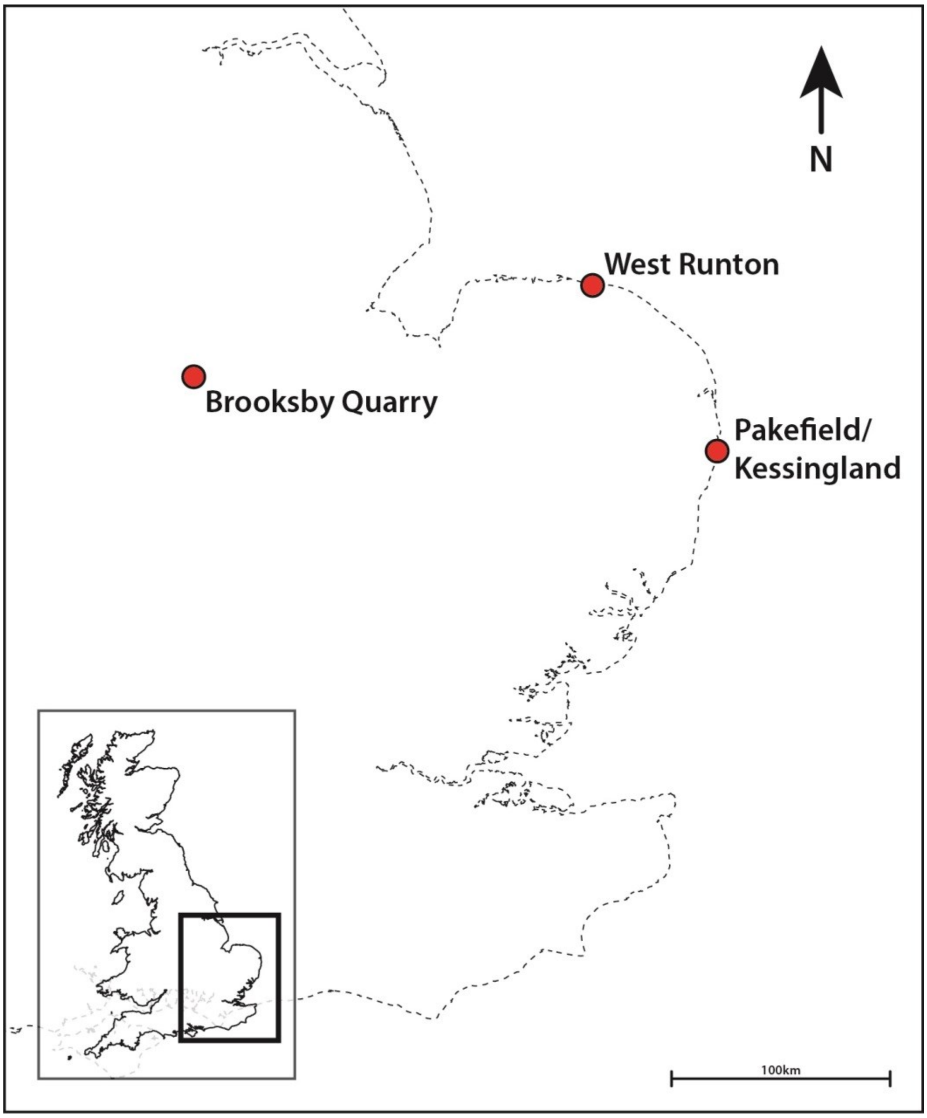


Figure 2.8 – Locations of case study sites used in the present thesis: West Runtong (Chapter 4), Pakefield/Kessingland (Chapter 5) and Brooksby (Chapter 6)

Chapter 3

General Methodology

3.1. Introduction

This chapter details the methodologies used in obtaining and preparing samples, and analysing data which are common between chapters. This includes the preparation of palynological and palaeoentomological samples, their identification and taxonomy, details of coleopteran Mutual Climatic Range (MCR) and functional group analyses, and multivariate analyses. Specific methodological details relating to particular chapters are provided therein.

3.2. Generic Field and Laboratory Procedures

3.2.1. Preparation of field sections

Prior to description and sampling, sedimentary sections at West Runton (Chapter 4) and Pakefield (Chapter 5) were cleaned. Weathered material and beach material were removed using shovels to reveal sedimentary structures and contacts which would be otherwise obscured, and to provide an even, vertical surface for sampling.

3.2.2. Description of field sections

Field sections were described qualitatively, as well as semi-quantitatively using the Troels-Smith method (Troels-Smith 1955). Sections were divided into sub-units, in accordance with sedimentary contacts and significant changes in composition and/or colour. Each sub-unit was then described in terms of overall composition (proportion of different sedimentary size classes, organic material, etc), colour, sedimentary structures present (e.g. lenses of coarser material), type of contact with adjacent sub-units, and changes of these properties within sub-units.

3.2.3. Field sampling procedure

Contiguous bulk samples were excavated for the extraction of sub-fossil Coleoptera. These samples were typically 5 cm in depth, and extended approximately 0.3-0.5 m backwards and horizontally. Sampling across sub-unit boundaries was avoided, and sample depth occasionally adjusted accordingly.

Monolith samples (10 cm wide, 6 cm depth, 50-100 cm length) were driven into the sediments directly adjacent to sections sampled for Coleoptera. These were then excavated, wrapped and transported to the laboratory to be sub-sampled for pollen, fungal spores and sedimentological analyses.

3.2.4. Laboratory sedimentological preparation and analyses

To determine changes in grain size, bulk organic matter and carbonate content, sub-samples for particle size analysis and loss-on-ignition (LOI) were taken from the monolith sequences at 1 cm resolution. Samples for particle size analysis were treated with H_2O_2 and sieved to 1 mm before laser diffraction analysis with a Malvern Mastersizer 2000. Loss-on-ignition (LOI) samples were initially oven-dried, before heating for four hours at 550°C to remove organic material, and for two hours at 950°C to remove carbonate content, following the recommendations of Heiri *et al.* (2001).

3.2.5. Pollen, fungal spores and microcharcoal

Pollen, fungal spore and microcharcoal samples were prepared in the laboratory simultaneously, using standard pollen extraction methods (Moore *et al.* 1991). This included acetolysis to remove organic material, and treatment with hydrofluoric acid (HF) to remove minerogenic clays, before mounting in silicon oil. Though HF treatment is aggressive, resulting pollen, spore and microcharcoal samples are known to be directly comparable to those prepared using less aggressive methods, such as density separation (Campbell *et al.* 2016). Acetolysis is known to degrade *Sordaria*-type spores, which can make diagnostic features more difficult to discern (van Asperen *et al.* 2016), but no such issues were encountered in the present work. A known quantity of an exotic marker spike (*Lycopodium* spore tablets) was added to facilitate calculation of concentration values (Stockmar 1971). Pollen, spores and microcharcoal were recorded on slides simultaneously Unless otherwise stated, a standard pollen sum of 500 terrestrial pollen grains was used for each sample. Aquatic taxa and fern spores were also counted, but not included in this sum. Percentages of these groups (aquatics and ferns) were calculated relative to the terrestrial pollen sum. Pollen grains were identified using Moore *et al.* (1991), Beug (2004) and a modern reference collection housed at Plymouth University, with taxonomy corresponding to Moore *et al.* (1991) and Beug (2004).

Three fungal spore types (*Sporormiella*-, *Podospora*- and *Sordaria*-type), which are demonstrably associated with dung (Baker *et al.* 2013), were recorded on the pollen slides. However, it should be noted that although *Sordaria*-type spores are generally associated with herbivore dung, they are not necessarily representative of obligate dung taxa (Newcombe *et al.* 2016). Also, the taphonomy of coprophilous fungal spores is not yet fully understood (though work is on-going, e.g. Raper & Bush 2009; Gill *et al.* 2013;

Baker *et al.* 2013, 2016), and so importance is not placed on individual 'spikes' in abundance, but rather on general trends and patterns. Their abundances are expressed as concentrations (spores cm^{-3}), calculated according to the exotic spike (*Lycopodium*) counts. This was chosen as the most appropriate method of quantification, as accumulation rates could not be calculated (due to lack of dating), and expression relative to pollen sums risks autocorrelation with vegetation affected by herbivory, preventing spores from being treated as a proxy independent from the pollen record (Baker *et al.* 2013).

Microscopic charcoal (microcharcoal) abundances were estimated by counting charcoal particles (shards) >10 μm (length) within view on pollen slides, a method often employed by palynologists (Patterson *et al.* 1987; Conedera *et al.* 2009). For the West Runton sequence (Chapter 4), this was carried out subsequently to pollen counting (using the same slides), and shards were counted until a standard number of *Lycopodium* spores had been encountered (23: the minimum number of *Lycopodium* spores associated with 500 terrestrial pollen grains in this sequence). For the Pakefield sequence (Chapter 5), shard counting was carried out simultaneously with pollen counting, and so shards were counted until 500 terrestrial pollen grains had been encountered. Microcharcoal abundances were expressed as concentrations (shards cm^{-3}) relative to the exotic spike (*Lycopodium*) counts, which is preferable to expression relative to pollen sums, as this may introduce autocorrelation (e.g. pollen sums may be affected as a result of fire damage to vegetation) (Mooney & Tinner 2011). Calculation of accumulation rates is generally considered preferable to expression as concentrations (Mooney & Tinner 2011), but this was not possible due to a lack of dating. Shard counts were not separated into size classes, as fragmentation of microcharcoal is a known issue (Weng 2005) which is likely to introduce heavy bias to smaller size classes, particularly given the physically and chemically aggressive nature of pollen sample preparation techniques (Moore *et al.* 1991).

Data were plotted using the R programming package ‘rioja’ (Juggins 2015).

3.2.6. Palaeoentomological methods

Coleopteran sub-fossil specimens were extracted in the laboratory using a standard procedure, broadly following that detailed by Coope (1986) and Elias (2010) (summarised in Figure 3.1). This method has been demonstrated to be efficient in concentrating sub-fossil insect remains from sedimentary samples (Rousseau 2009), and several sub-samples of residues were checked during processing, to ensure that this was also the case here. Specimens were primarily identified using a modern reference collection housed at Plymouth City Museum and Art Gallery. Exceptions include *Micropeplus caelatus* Er. (Chapter 4), for which identifaction was aided by material loaned from the Natural History Museum, London, and *Hallomenus binotatus* Quensel specimens (Chapter 5), which were identified using a collection housed at the Zoological Museum, University of Copenhagen. Coleopteran material which could not be identified to species level was identified to higher levels (genus, subfamily or family). Taxonomy follows Duff (2012), which includes species recorded as sub-fossils in British Pleistocene records.

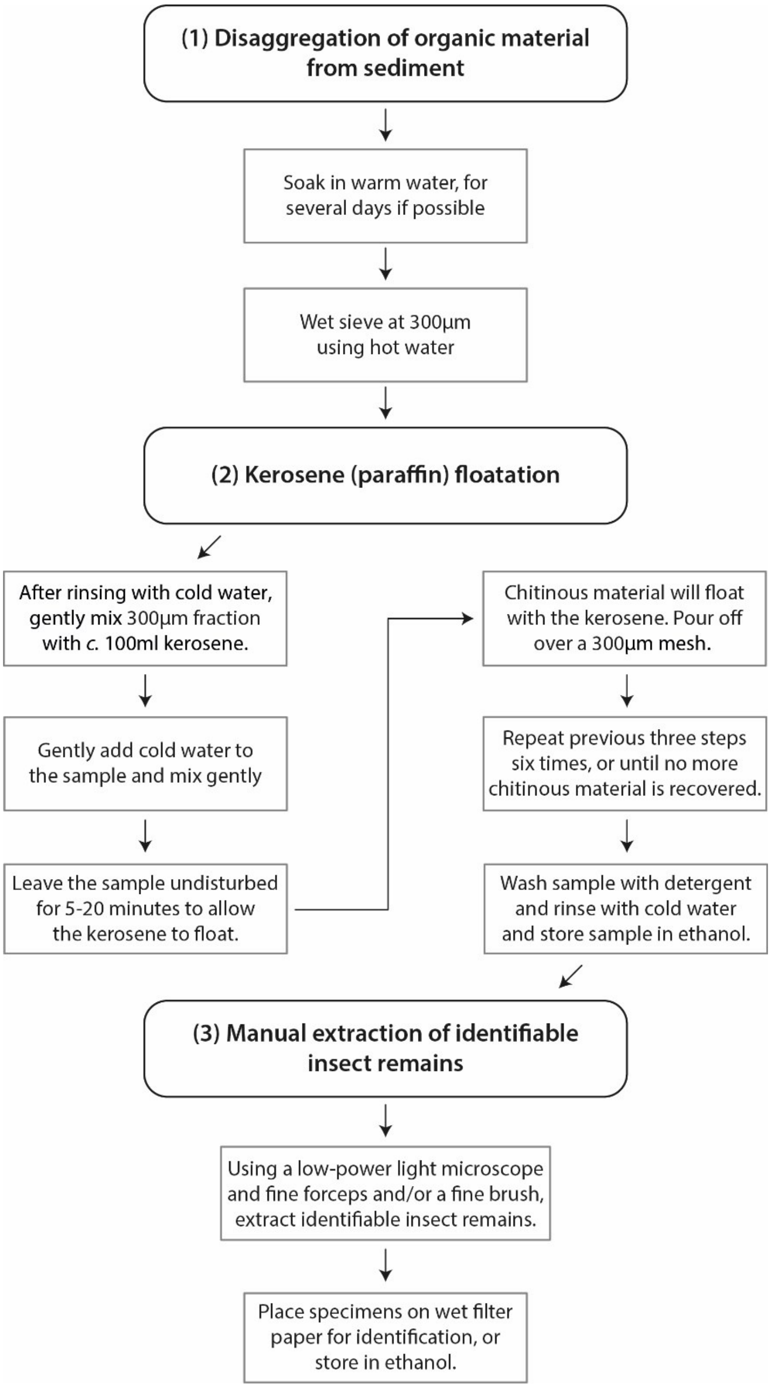


Figure 3.1 – Extraction of sub-fossil coleoptera from sediment samples (after Elias 2010)

3.3. Analytical Techniques

3.3.1. Coleopteran functional group analysis

Coleopteran functional group analysis provides a method of transforming unwieldy taxonomic data into more ecologically-meaningful semi-quantitative data, which can be incorporated into a variety of analyses. This approach was pioneered by Robinson (1981, 1983, 1991), and further developed by various authors (e.g. Whitehouse 2004; Buckland & Buckland 2006; Olsson & Lemdahl 2009; Smith *et al.* 2010; Mansell *et al.* 2014; Hill 2015). Each taxon in a fossil assemblage is assigned to a habitat category or functional group, based on knowledge of its modern ecological preferences. The designation of these groups is somewhat subjective, and they are typically assigned according to the particular focus of each individual study (Whitehouse 2004; Hill 2015). Both presences and abundances (minimum numbers of individuals) of taxa assigned to each category in any given sample may then be used to make inferences regarding the prevalence or importance of different habitat types in the palaeolandscape. The importance of different habitat types can be gauged using this approach (Smith *et al.* 2010; Hill 2015), though the relative proportions of each functional group in a sample should not be assumed to linearly reflect proportions of associated habitats (Whitehouse 2004).

In the present thesis, ecological information has largely been derived from literature contained within the BugsCEP database (Buckland & Buckland 2006). The categories used (see Table 3.1) are broadly based on those used by Olsson & Lemdahl (2009, 2010), Mansell *et al.* (2014), Hill (2015), and the BugsCEP database (Buckland & Buckland 2006). In a similar approach to Whitehouse (2004) and Hill (2015), wetland marginal and marshland taxa have been divided into separate categories here: Wetland Edge (WE), Riparian/Waterside (RW) and Hygrophilous (H) (this is in contrast to Olsson & Lemdahl (2009, 2010) and Mansell *et al.* (2014)). This allows distinction to be made between taxa associated with different components of the aquatic-terrestrial ecotone. Some level of overlap between categories is unavoidable (e.g. open/disturbed habitats may be riparian), and this is accounted for when discussing the datasets, and individual taxa in particular. Relative proportions of different functional groups are typically expressed as percentages relative to either the total fauna or total terrestrial/aquatic fauna (Hill 2015). In this thesis, the former approach is used, due to high proportions of aquatic-terrestrial ecotone beetles (WE, RW, H), many of which are difficult to categorise as either terrestrial or aquatic.

Table 3.1 - Coleopteran Functional Groups

Habitat Code	**Functional Group/ Habitat Category**	**Habitat Description**
AG	Aquatic (general)	Fully aquatic habitats of various types, including ponds, lakes, streams, rivers, ditches and temporary pools. (e.g. *Ochthebius minimus*)
AS	Aquatic (lentic)	Fully aquatic habitats with still, or very slow-flowing, water (e.g. ponds, fens and temporary pools). (e.g. *Helophorus strigifrons*)
AF	Aquatic (lotic)	Fully aquatic habitats with flowing water (e.g. streams and rivers). (e.g. *Oulimnius troglodytes*)
WE	Wetland Edge	Semi-aquatic habitats at wetland margins (e.g. areas of emergent vegetation; frequently flooded grassland). (e.g. *Plateumaris sericea*)
RW	Riparian/Waterside	Terrestrial habitats bordering rivers and wetlands. (e.g. *Elaphrus riparius*)
H	Hygrophilous (general)	A broad range of generally damp, and often shaded, habitats. (e.g. *Stenus circularis*)

(Continued overleaf)

Table 3.1 Continued

WTG	Woodland/Trees (general)	General woodland and arboreal habitats (e.g. leaf litter, dead wood, living trees) (e.g. *Otiorhynchus clavipes*)
WTD	Woodland/Trees (deciduous)	Deciduous woodland and arboreal habitats (e.g. leaf litter, dead wood, living trees). (e.g. *Scolytus multistriatus*)
WTC	Woodland/Trees (coniferous)	Coniferous woodland and arboreal habitats (e.g. needle litter, dead wood, living trees). (e.g. *Hylastes attenuatus*)
HP	Herbaceous Plants	Herbaceous (non-woody) plants in a variety of contexts. (e.g. *Phyllotreta nemorum*)
O	Open/Disturbed	Terrestrial habitats with low vegetation and/or exposed soil and sediments. (e.g. *Melanotus punctolineatus*)
DE	Decaying/Foul/Rotten (general)	Generally mouldy, decomposing and fetid habitats, including rotting vegetation, dung and carrion. (e.g. *Anotylus rugosus*)
DU	Dung	The faeces of vertebrates. (e.g. *Aphodius rufipes*)
UN	Uncategorised or Eurytopic	Specific habitat type undetermined, as a result of either low taxonomic resolution or eurytopic habits. (e.g. Carabidae indet.)

3.3.2. Assemblage zonations

For datasets in which assemblage change was evident, coleopteran and pollen assemblage zones were constructed on the basis of a constrained cluster analysis (CONISS, Grimm 1987), with a broken-stick model (Bennett 1996) used as a guide to determine a significant number of zones. For coleopteran records, this was applied to relative proportions of functional groups. These analyses were performed using the R package 'rioja' (Juggins 2015).

3.3.3. Coleopteran Mutual Climatic Range (MCR)

In the Mutual Climatic Range (MCR) method (Atkinson *et al.* 1987; Milne 2016), modern climate and species occurrence data are used to define species climatic niches (envelopes), and the overlap between the envelopes of co-occurring fossil taxa is used to reconstruct palaeoclimate (see Figure 3.2). Average warmest month temperatures (TMax) and average coldest month temperatures (TMin) are determined independently of each other, though each is dependent on annual average temperature range (TRange), as in Figure 3.2. Only macropterous species from the families Gyrinidae, Haliplidae, Dytiscidae, Carabidae, Hydrophilidae, Hydraenidae, Staphylinidae and Scarabaeidae are used in this context, as they tend not to be heavily dependent on specific vegetation types, and may readily colonise new areas (Milne 2016).

The original MCR method was developed by Perry (1986) and Atkinson *et al.* (1987), and subsequently described by Milne (2016) (though some details remain unclear). Species geographic ranges were determined based on distribution maps available at the time (e.g. Lindroth 1945). Average climatic values (average temperatures of the warmest and coldest months, *c.*1900-1980) were then determined within these ranges, based on data from 495 weather stations across the Palaearctic, or from an (unrecorded) atlas. Thermal limits were determined using a lapse-rate interpolation, though the precise details of this process are unclear (Milne 2016). Aside from sources of uncertainty generally associated with reconstructing past climates based on biological proxies (e.g. reconstructing macroclimate based on biota primarily affected by microclimate, Huntley 2012), this method had certain specific problems. In particular, the variable and often low-density pre-1980 coverage of meteorological stations outside of Western Europe meant that climate variance in other regions was poorly represented in the original MCR method (Bray *et al.* 2006; Milne 2016).

Secondly, the climatic tolerance ranges of some species are unlikely to be fully captured by available occurrence data, which may be lacking from poorly surveyed areas (e.g. remote regions) (Milne 2016).

The coleopteran MCR technique has recently been revised by Milne (2016). In this version, the underlying principles remain the same, but the species occurrence and modern climate data, from which species climate ranges are derived, have been altered. Species occurrence data are drawn from the Global Biodiversity Information Facility (GBIF) (GBIF 2016), and are cleaned to ensure that only accurately and precisely georeferenced and dated records are used. Whilst this ensures that only high quality data are included, without further input it does exclude potentially valuable occurrence data not present in GBIF. These data are then related to high-resolution (30 arc-second rasters) climate data, obtained from WorldClim (1950-2000) (www.worldclim.org, Hijmans *et al.* 2005) and the Intergovernmental Panel on Climate Change (IPCC) (1901-1950) (http://www.ipcc-data.org/observ/clim/cru_ts2_1.html, Mitchell & Jones 2005), to produce species climatic envelopes. The resulting species climate range estimates are generally overlapping (and therefore in agreement) with those obtained from the original method (Atkinson *et al.* 1987), but narrower. The palaeoclimatic reconstructions derived from these envelopes therefore tend to be significantly more precise (i.e. narrower Mutual Climatic Range estimates) than in the original method. This is particularly true for winter temperature estimates, which have been greatly improved in this regard (Milne 2016). Unless otherwise stated, the new ‘Milne method’ (Milne 2016) is used in the present thesis.

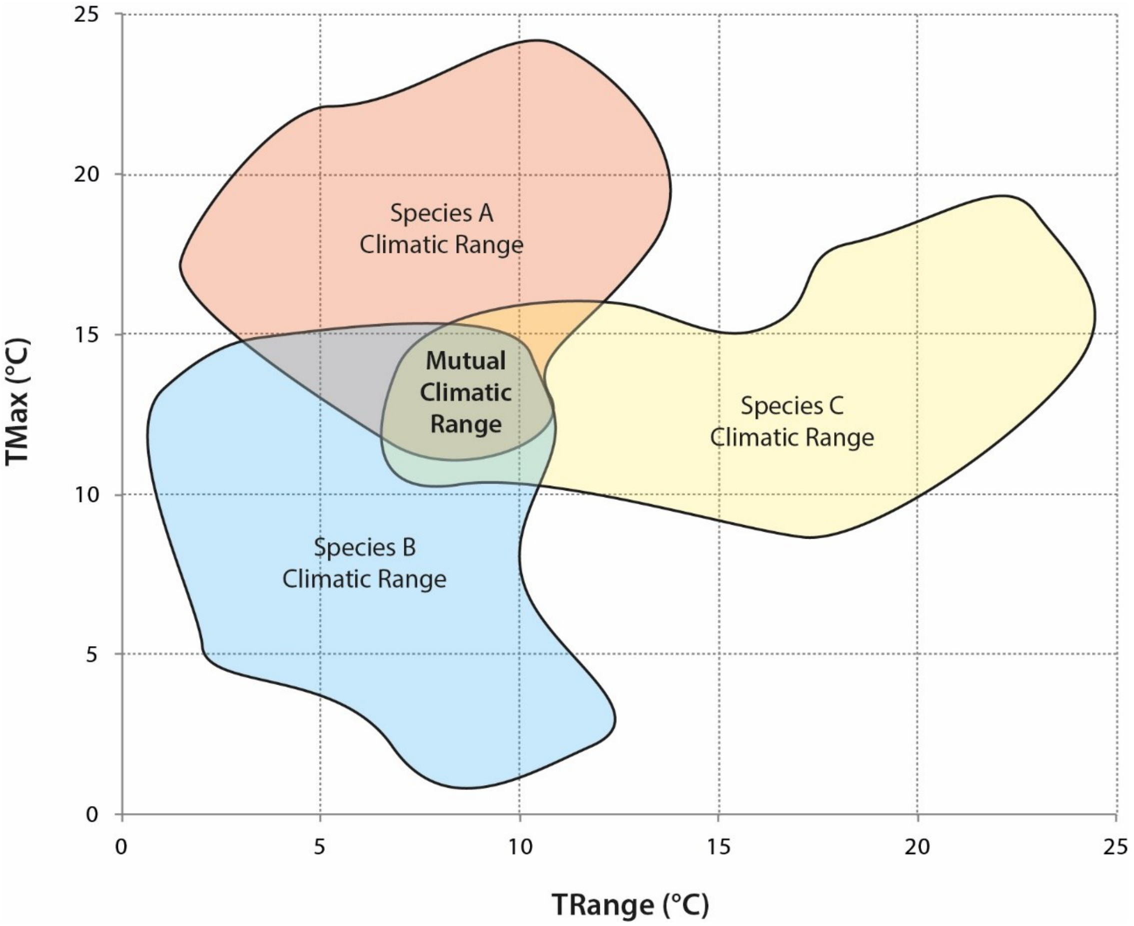


Figure 3.2 – The MCR method: A hypothetical example (after Atkinson et al. 1987)

In certain cases, the climatic envelopes for species within an assemblage may not overlap (e.g. Figure 3.3), for various reasons. For example, the thermal tolerance limits of a species may not be fully captured by its climate envelope, as its modern range may be incompletely sampled (or distributional data unavailable), different sub-populations of the same species may have different climatic and ecological tolerance ranges, its present distribution may not reflect its full range of tolerance or the climatic tolerance of a species may have changed through time. Alternatively, coarse sampling resolution of sedimentary records may give a false impression of temporal co-occurrence: a particular problem in sedimentary records spanning periods of rapid climate change. (*n.b.* The Milne (2016) method does not allow for the quantification of extent of overlap, as in BugsCEP (Buckland & Buckland 2006).)

In such cases, and when species cannot reasonably be excluded from analyses, palaeoclimatic range estimates are derived in the present thesis by treating each climatic variable (TMax, TMin, TRange) as independent, as in Figure 3.4 (as opposed to in Figures 3.2 & 3.3). However, this is undertaken cautiously. Whilst this may provide useful insights, particularly when applied to several species simultaneously, organisms do not experience July/January temperatures independently of annual temperature range. For example, in highly continental areas with intense summers and harsh winters, the favourable summer temperatures may compensate for cold winter temperatures, but in other areas increased survival during the winter months as a result of milder conditions may compensate for cooler summer temperatures (Huntley 2012).

Occasionally, when variables are treated independently, a lack of overlap may remain (e.g. TMax in Figure 3.4). For these situations in the present thesis, the upper and lower limits of range estimates are determined separately. This is illustrated by TMax in Figure 3.4: the lower limit has been determined using Species A and B (excluding Species C), and the upper limit has been determined using species B and C (excluding Species A). This ensures that no species are fully excluded and that the full breadth of potential climatic values is included in range estimates. Though this may introduce significant imprecision, the ‘true’ value may lie at any point within those ranges, and so broader range estimates are more likely to be accurate (i.e. include the ‘true’ value within the range). This is a pragmatic solution, and it is acknowledged that it is far from ideal to treat interdependent climatic variables as independent (*cf.* Huntley 2012).

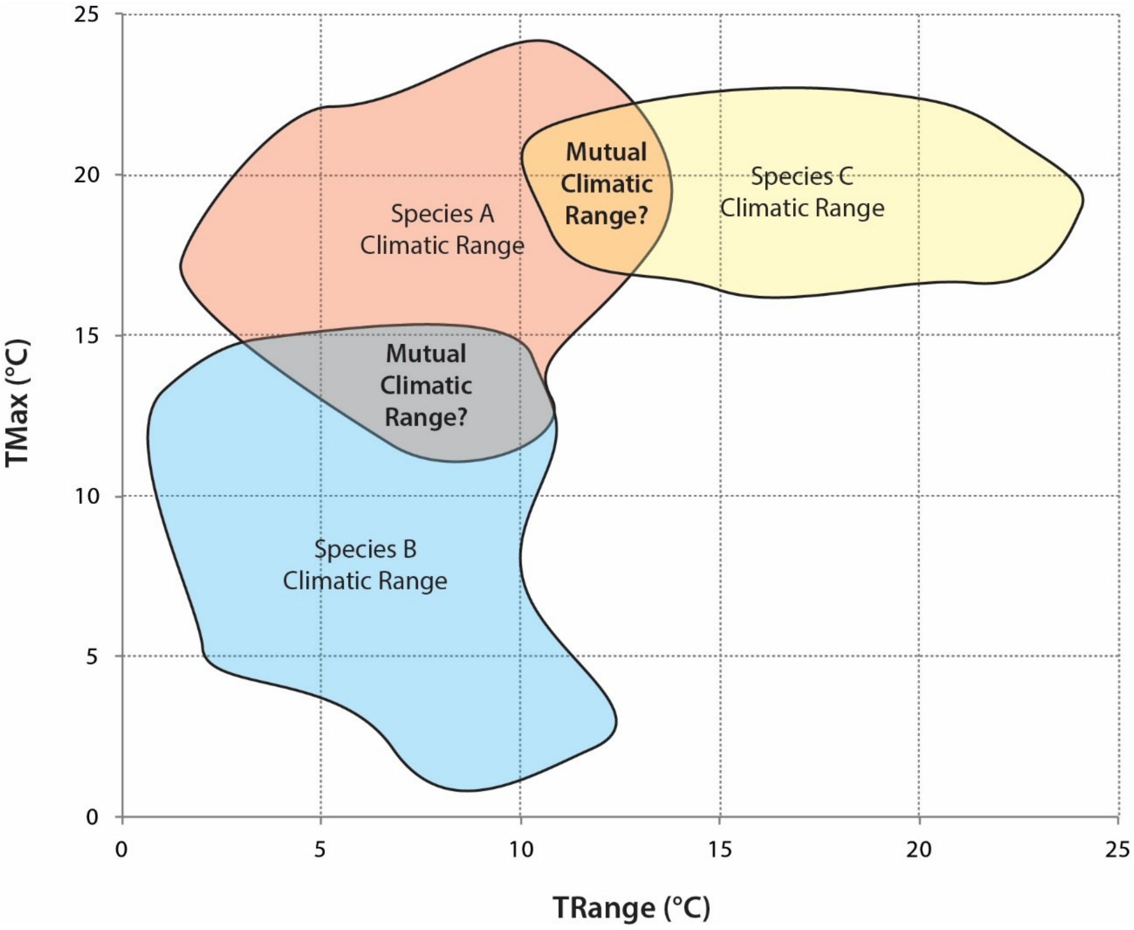


Figure 3.3 – The MCR method, with <100% overlap: A hypothetical example

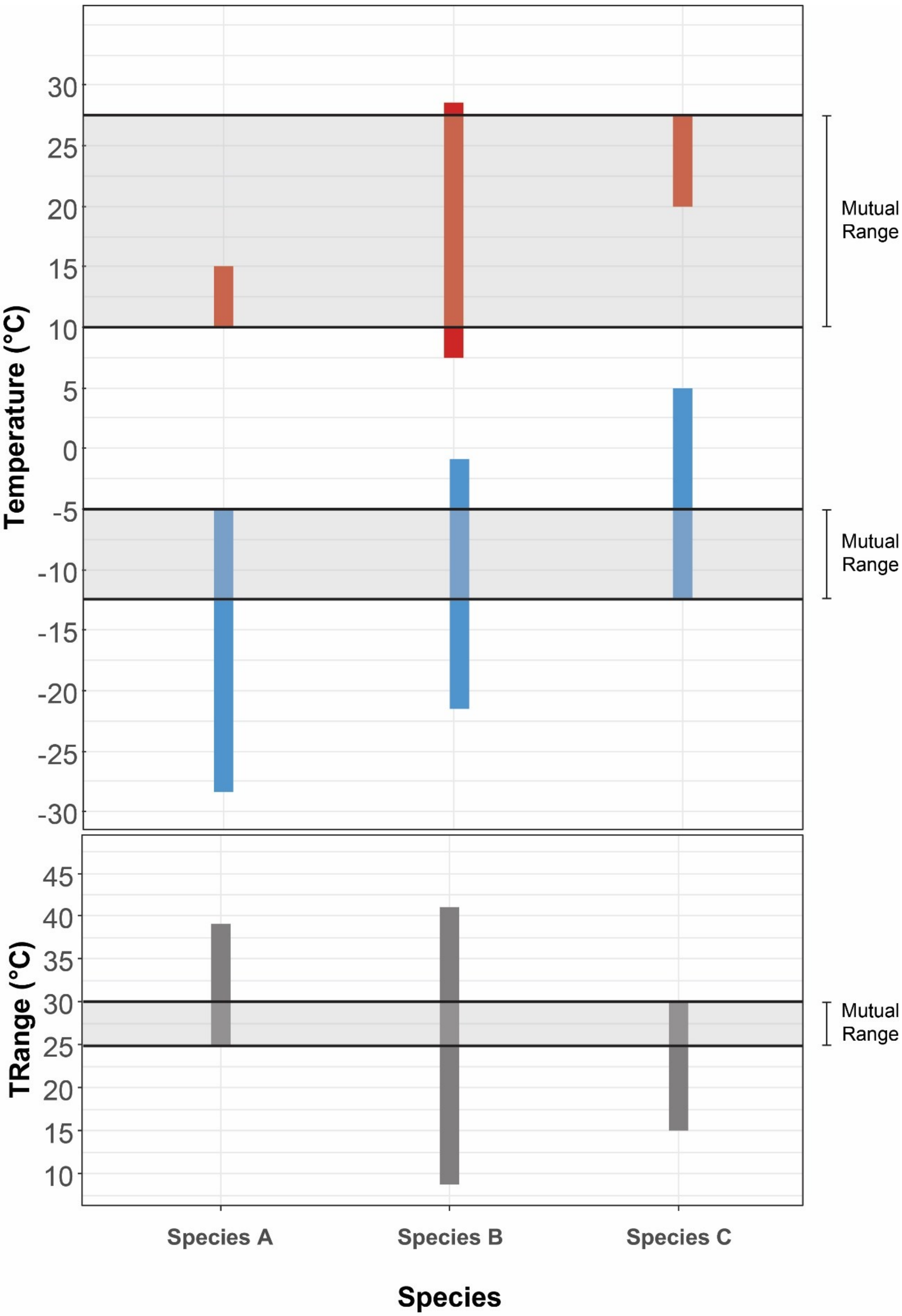


Figure 3.4 – The MCR method, with <100% overlap: A hypothetical example with variables treated independently. (red: average temperature of the warmest month (TMax), blue: average temperature of the coldest month (TMin), grey: average annual temperature range (TRange))

3.3.4. Multivariate analyses

Multivariate analyses are performed to explore ecological gradients and relationships between major taxa, coleopteran functional groups and environmental variables. Here, Principal Components Analysis (PCA) is used to explore trends in the composition of fossil pollen, spore and beetle assemblages within and between different sequences. This is particularly valuable in providing a graphical summary of the major patterns within a palaeoecological sequence (Legendre & Birks 2012), and is a useful compliment to traditional stratigraphic representations of these data (e.g. pollen diagrams). Canonical Correspondence Analysis (CCA) is used to gauge the relative importance of various environmental variables in structuring these communities, via palaeoenvironmental proxies (e.g. coprophilous fungi, microcharcoal). This is useful in assessing the response of past biological assemblages to environmental variables (Legendre & Birks *et al.* 2012). In order to explore the importance of different local ecological processes as fully as possible, all potential proxies of disturbance processes included in this study are utilised as environmental (explanatory) variables in this context. These are coprophilous fungal spores (herbivory), microcharcoal (wildfire) and grain size (hydrogeomorphic and sedimentary processes). Grain size classes (sand, silt clay) are expressed as percentages, and so autocorrelation is an issue (as with biological assemblages). However, all three size classes are included in CCAs, as the relative proportions of these classes are informative when characterising the energy of the sedimentary environment, and any fossil assemblages associated with distinct depositional modes. To fully explore the datasets, palynological and entomological assemblages were analysed both separately and together. These analyses are prefaced by exploratory correlation analyses of groups of taxa (e.g. deciduous tree pollen, fully aquatic Coleoptera) and environmental proxies (e.g. sedimentary organic content).

For Coleoptera, functional groups were used for multivariate analyses, rather than individual taxa. The low abundance and stochastic occurrence of most coleopteran taxa as sub-fossils here renders the datasets largely unsuitable for discerning ecological gradients on this basis. Analysis on the basis of functional groups alleviates this to some extent, decreasing the numbers of zeroes in the datasets, and allowing ecological (rather than taxonomic) patterns to be explored. However, it should be borne in mind that coleopteran sample MNI values are generally below those recommended for such quantitative analyses (e.g. Hill (2015) recommends at least 50 MNI per sample), and it is important that any conclusions drawn from these analyses are treated as provisional. Additionally, this also means (even when using functional groups, rather than taxa) that 'rarity' is the norm, and so down-weighting of rare species was not performed on these datasets. Coleopteran functional group abundances are not linearly related to the spatial extent of habitats they represent (Whitehouse 2004; Smith *et al.* 2010; Hill 2015) and therefore each group provides a different measure of landscape characteristics: this is analogous to (though not the same as) different units of measurement. Standardisation of the data is therefore necessary (Legendre & Birks *et al.* 2012), and these data were scaled according to unit variance (zero mean, variance of one). However, absolute abundances are also borne in mind when interpreting results, particularly given the low MNI values (<50: *cf.* Hill 2015) associated with most coleopteran samples.

For pollen and spore data in this thesis, rare taxa have generally been excluded when performing these analyses. This allows the broad trends and relationships between, and involving, major taxa to be explored, and to be disentangled from the abundances and occurrences of stochastically-occurring, rare pollen taxa, which have low statistical influence. Removing these taxa was chosen as an alternative to down-weighting approaches due to their combined low abundances and stochastic patterns of occurrence. These taxa are therefore unreliable as indicators of either plant taxon occurrence or abundance, particularly when these issues are comfounded by the non-linearity of pollen-vegetation relationships (Bunting 2008). The inclusion of these taxa was therefore considered unsuitable for analyses aimed at exploring the major patterns within the datasets. The basis for taxon exclusion varies between datasets, and so details of this are provided in relevant chapters. Pollen and spore data were also scaled according to unit variance (zero mean, variance of one), for similar reasons to beetle functional groups: pollen-vegetation relationships are also non-linear (Bunting 2008), but also because fungal spore abundances have been expressed in different units (concentrations, rather than abundance relative to total land pollen).

Multivariate analyses were carried out using the R Programming package ‘vegan’ (Okansen *et al.* 2015), and full details of the techniques applied to each dataset are given in the relevant chapters.

3.4. Further Methodological Considerations

The following section presents methodological considerations which are of particular importance to Chapter 7, but which also have some relevance to other chapters.

3.4.1. Rationale for Chapter 7 sites/records

In Chapter 7, a suite of interglacial coleopteran records spanning the Middle Pleistocene is analysed using the Milne (2016) MCR technique. This is to test whether the Mid-Brunhes Transition (MBT) has a detectable signal in thermoclimatic conditions associated with terrestrial environments in Britain. As discussed above (Section *3.3.3.*), this approach offers notable advantages over earlier iterations of the coleopteran MCR technique, particularly regarding reconstructions of winter temperatures and temperature seasonality.

The MBT is defined by a comparison of interglacial 'peaks' (see Chapter 2, Section *2.2.*), as observed in marine and polar records (e.g. Jansen *et al.* 1986; EPICA 2004; Lisiecki & Raymo 2005). Here, it is therefore necessary to utilise records which are also closely related to interglacial 'peaks' (i.e. deposited during interglacial climatic optima, *sensu lato*). However, interglacial stages incorporate significant climatic complexity (e.g. Tzedakis 2009; Berger *et al.* 2015), and in Britain are not limited to temperate conditions (i.e. warm summers, cool winters) (e.g. Shotton *et al.* 1993; Candy & Schreve 2007; Coope & Kenward 2007). Consequently, identifying climatic optima in the fragmentary British terrestrial record is far from straightforward. Criteria for identifying suitable records in this context are outlined here, though it should be acknowledged that this involves a certain level of pragmatism.

All records used must have assemblages of sub-fossil Coleoptera, with data accessible through publications and/or the BugsCEP database (Buckland & Buckland 2006). To facilitate comparisons between different interglacial stages, records should also be attributable to single marine isotope stages (MIS 19 to 5e) where possible (though this is considerably more difficult for early Middle Pleistocene records).

It is not possible to directly relate pre-Holocene terrestrial interglacial deposits in Britain to peaks in the marine or polar records, except in a few rare cases (e.g. Candy & Schreve 2007). For the purpose of Chapter 7, compromise is necessary, and records providing evidence for 'fully temperate' conditions (*sensu lato*) are deemed appropriate in this context. However, the definition and identification of 'fully temperate' conditions requires consideration. Firstly, evidence for such conditions must be independent of beetle records, to avoid circularity in subsequent analyses. A useful 'rule-of-thumb', applied by West (1980b), is that >50% arboreal pollen indicates fully-developed, mature deciduous woodland, and that this is representative of 'fully temperate' conditions. As acknowledged by West (1980b), this need not be strictly adhered to, as local conditions must also be accounted for (e.g. local openness within a densely wooded landscape), and *c.* 30-40% arboreal pollen (granted that deciduous taxa, such as *Quercus*, *Corylus*, *Ulmus*, *Alnus* and *Fraxinus*, are major components) seems a convenient and reasonable threshold to apply. However, whilst this is broadly applicable to the British Middle Pleistocene, it is not universally so. Interglacial temperate climates are occasionally associated with grassland-dominated environments (though not necessarily during climatic optima, *sensu stricto*), as in MIS 7 (Candy & Schreve 2007). In such cases, other lines of evidence (e.g. stable isotopes) are useful in providing independent confirmation of temperate conditions. Additionally, records which include arctic-alpine or boreal biota (e.g. Brooksby Sand and Gravel, Chapter 6) may be reasonably excluded. It should also be noted that though the majority of these records are derived from fluviatile sedimentary settings, a few are also based on records from lacustrine deposits (see Table 2.2). Whilst these are likely to differ in the representation of beetle remains, the assemblage-level climatic reconstructions carried out using the MCR method are unlikely to be affected.

Pragmatic decisions regarding the number of sites to include in analyses also must be made. Whilst including an exhaustive suite of potential interglacial records would be preferable, three to four per marine isotope stage is sufficient for the purpose of attempting to distinguish between pre- and post-MBT interglacials in Britain, as this allows the inclusion of within-interglacial variability. In this context, type sites (e.g. Hoxne, West 1956), other significant sites (e.g. Trafalgar Square, Franks 1960), and sites included in comparable multi-record studies (e.g. Candy *et al.* 2010) are given preference, assuming they conform to the above criteria.

Records selected on this basis for analysis in Chapter 7 are given in Figure 7.1 and Table 7.1.

3.4.2. Additional (non-coleopteran) thermophilous organisms

Following Candy *et al.* (2010), the presence of several organisms considered indicators of interglacial warmth, is used to supplement quantitative coleopteran MCR reconstructions (particularly Chapter 7). These include the aquatic plants *Trapa natans* L., *Salvinia natans* L. and *Najas minor* All., the molluscs *Belgrandia marginata* Michaud and *Unio crassus* Philipsson, the European pond tortoise (*Emys orbicularis* L.) and hippopotamus *(Hippopotamus amphibius/antiquus* L.). Each of these species is thought to represent conditions warmer than the present in Britain (e.g. Candy *et al.* 2010; Schreve & Candy 2010), either in terms of an apparent necessity for high summer temperatures (e.g. *T. natans*, *E. orbicularis*), or through intolerance to harsh winters (e.g. *Hippopotamus amphibius*). A brief review, based on available primary literature, of the utility of each as palaeoclimatic indicator species is provided here. However, the availability and specificity of literature varies from species to species. In particular, it should be noted that quantitative information regarding climatic requirements is not available for all species, or life stages of species. The climatic information which may be derived from each species is also rarely comparable to values derived from coleopteran MCR, as they typically represent different aspects of local or annual climate.

As such, they are generally used here to provide qualitative climatic context, rather than quantitative constraint.

Trapa natans L. (water chestnut) is a floating-leaved aquatic plant, which favours warm, shallow (≤1.5 m depth), nutrient-rich waters, and it has a current northern limit extending from central France, through Germany, Poland and into central Russia (Schofield & Bunting 2005). It is typically associated with interglacial thermal maxima, and often cited (e.g. Candy *et al.* 2010, 2015) as being indicative of July air temperatures in excess of 20°C, as a requirement for fruiting, based on Meusel (1978). However, the necessary length of exposure to such temperatures is unclear, but important in the context of its palaeoclimatic utility. For example, if only short-term (e.g. ≤1 week) exposure to >20°C is necessary, this could be achieved under average July air temperatures lower than 20°C. For germination, laboratory experiments have demonstrated that optimal water temperatures are more moderate: between 15°C and 20°C (Cozza *et al.* 1994). The presence of *T. natans* for several thousand years during the Holocene in Finland (Korhola & Tikkanen 1997) and Northern England (Schofield & Bunting 2005) has also been noted. This may partly be a result of warmer summers during the Holocene thermal maximum (*cf.* Davis *et al.* 2003; Seppä *et al.* 2009), but significant emphasis is also placed on the local availability of structurally and chemically favourable habitats (eutrophic standing water) during this period (Korhola & Tikkanen 1997; Schofield & Bunting 2005). Therefore, when other similarly thermophilous organisms are absent, caution should be exercised when using *T. natans* to infer enhanced summer warmth.

Salvinia natans L. is an annual aquatic fern, which occurs in low-energy shallow habitats. It is currently absent from Western and Northern Europe, including Britain, but present in Central and Eastern Europe, and the Mediterranean (Allen 2011). It is sensitive to spring temperatures: gametophyte development appears partly dependent on water temperatures around 16.5-19.5°C during spring months, during which time it is also highly vulnerable to ground frosts (Gałka & Szmeja 2013). Its presence in Pleistocene deposits may therefore be used to suggest mild spring temperatures.

Najas minor All. (brittle naiad) is present throughout Eurasia, and invasive in Eastern North America, but does not currently occur in Britain or Northern Europe (Lansdown 2014). *N. minor* exhibits plasticity in its realised niche (if not also its fundamental niche), and has an apparent propensity for invasiveness (Wang *et al.* 2017). However, its continued absence from Britain and Northern Europe in spite of this, suggests that conditions in these regions are not currently suitable for successful colonisation. This corroborates previous suggestions that its occurrence in Britain during interglacial periods corresponds to enhanced summer warmth (Aalbersbereg & Litt 1998; Candy *et al.* 2010).

Belgrandia marginata Michaud is a freshwater gastropod with a modern range largely restricted to southern France and northern Spain, which is also a frequent component of interglacial assemblages in Britain (Kerney 1977; Jones & Keen 1993; Preece 1999, 2001). On the basis of its modern distribution, it has long been interpreted as indicating enhanced warmth in previous interglacials, particularly the Ipswichian (Kerney 1977; Jones & Keen 1993; Candy *et al.* 2010; Schreve & Candy 2010). Despite being found in the deposits of large Pleistocene rivers in Britain, *B. marginata* is largely restricted to clear spring waters in modern contexts (Preece 1999), and it seems highly likely that its present distribution is controlled not only by climate, but also ecological (e.g. water quality) and biogeographic (dispersal ability) factors.

Unio crassus Philipsson is a freshwater mussel with a broad current range across Europe, extending into eastern Russia and the Middle East, but which is currently absent from the British Isles (Lopes-Lima 2014). It is frequently cited as an indicator of enhanced interglacial warmth (or least the absence of harsh climates) on the basis of this distribution (e.g. Briggs & Gilbertson 1980; Shotton *et al.* 1993; Candy *et al.* 2010). Laboratory experiments have demonstrated that water temperatures around 17°C are optimal for larval development (Taeubert *et al.* 2014). However, it should be noted that larval development also occurs at lower temperatures (12°C), albeit with reduced success and rapidity (Taeubert *et al.* 2014). The distribution of *U. crassus* is also thought to be driven by water quality, though its precise requirements are unclear (Denic *et al.* 2014). Caution should be exercised when using *U. crassus* to infer enhanced interglacial warmth in the absence of other similarly thermophilous organisms.

Emys orbicularis L. (European pond tortoise) is present throughout Central, Southern and Eastern Europe, with its northwestern limits in central France and northeast Germany (Stuart 1979; Schneeweiss 2004). It has also occurred in Britain and southern Scandinavia during the Holocene and previous interglacials (Stuart 1979; Sommer *et al.* 2007). It has a strongly climate-influenced distribution, and appears to require warmer, more continental-type summers than present-day Northwest Europe (Stuart 1979; Schneeweiss 2004; Sommer *et al.* 2007). This is likely related to within-nest microclimate control on embryonic sex determination, which results in all-female broods in cool conditions (<25°C) (Pieau & Dorizzi 1981). This combination of biogeographical and ecophysiological evidence suggests that *E. orbicularis* may be used as an effective indicator of enhanced interglacial warmth in Britain. However, given that the dependence is on nest microclimates, Stuart's (1979) oft-quoted 18°C average July air temperature threshold for *E. orbicularis* (e.g. Candy *et al.* 2010; Schreve & Candy 2010) should be viewed with caution.

Hippopotamus amphibius L. (hippopotamus) is currently restricted to sub-Saharan Africa, though was also been present in the Nile, Near East and Mediterranean until the Mid- to Late-Holocene (Horwitz & Tchernov 1990; Bunimovitz & Barkai 1996). However, during some interglacials it was more widespread in Eurasia, particularly during MIS 5e, with its most northerly occurrences in North East England (Teesside) (Schreve 2009). It is thought to be intolerant of freezing winter temperatures, and so is typically considered an indicator of mild winters in Northern Europe (e.g. Candy *et al.* 2010; Carrión *et al.* 2011), though this may need to be reassessed in light of Chapter 7.

Chapter 4

The West Runton Freshwater Bed

4.1. Introduction

This chapter presents a new palaeoecological record from the West Runton Freshwater Bed (West 1980a), combining Coleoptera, pollen, coprophilous fungal spores, microcharcoal and sedimentology. A single multi-proxy record, such as this, allows in-depth ecological and multivariate analyses of the assemblages, delivering detailed analyses of the communities, habitats and ecological processes associated with the site. Inferences are made regarding vegetation structure, interactions between taxa, and relationships with herbivore activity, wildfire, hydrogeomorphic processes and climate. This provides a novel and nuanced perspective of the Cromerian palaeolandscape at West Runton, its vegetation communities and the role of disturbance regimes in determining local-scale ecological characteristics.

4.2. Site Background

West Runton, on the north Norfolk coast, UK (01°15'E, 52°56'N, Fig. 4.1), is the type site for the Cromerian (West & Wilson 1966; West 1980a), and an internationally important early Middle Pleistocene site with a long history of study (e.g. Reid 1882; West 1980a; Rose *et al.* 2008; Stuart & Lister 2010).

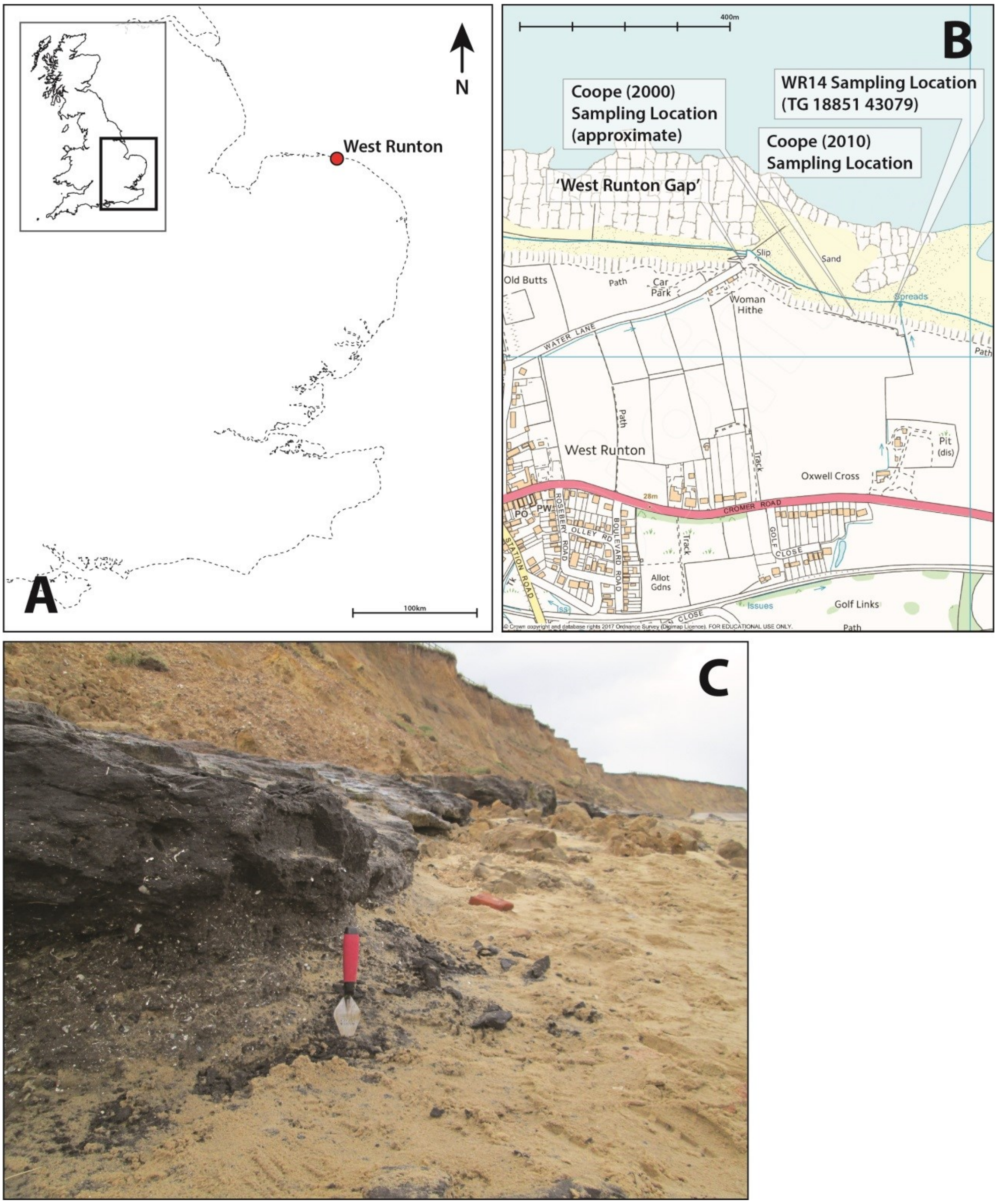


Figure 4.1 – Location maps (A: Regional location; B: Sampling locations; C: A typical exposure of the West Runton Freshwater Bed, n.b. Not the sampled section)

4.2.1. Chronostratigraphy

The Middle Pleistocene sequence exposed in the cliffs at West Runton is spatially complex, but contains four primary stratigraphic units (Rose *et al.* 2008) (summarised in Table 4.1). The shallow marine deposits of the Wroxham Crag Formation form the lowermost unit of the sequence, which is overlain unconformably by the silts, sands and clays of the West Runton Freshwater Bed. In turn, this is overlain by a large unit of cross-bedded shallow marine sands and gravels, which are capped by the uppermost unit: the glaciogenic Lowestoft Till. The Freshwater Bed is a member of the Cromer Forest-bed Formation (West 1980a), and is composed of a diverse sequence of silts and clays, typically 1-2 m in thickness, and contains visible wood, vertebrate remains and mollusc shells (West 1980a; Rose *et al.* 2008; Gibbard *et al.* 2010). It is horizontally and vertically heterogeneous, with numerous sub-units and lenses of coarse material. It is typically interpreted as having been deposited in either a lentic freshwater environment, which received periodic allochthonous lotic inputs (such as a cut-off channel, or a small lake or wetland adjacent to a river), or in a slow-moving lotic environment (e.g. West 1980a, Rose *et al.* 2008; Gibbard *et al.* 2010).

Table 4.1 Summary of primary stratigraphic units at West Runton (based on Rose *et al.* 2001, 2008; Lee *et al.* 2008a; Preece & Parfitt 2012)

Unit/Bed	**Formation**	**Climate/Environment**	**Age**
Lowestoft Till	Lowestoft Formation	Glacial	MIS 12
Mundesley Member	Wroxham Crag Formation	Shallow marine	MIS 17-12
West Runton Freshwater Bed	Cromer Forest-bed Formation	Interglacial, temperate	MIS 15-17
Dobbs Member	Wroxham Crag Formation	Predominantly shallow marine (both cold and temperate phases represented)	Early Pleistocene

A combination of litho-, magneto- and biostratigraphy determines the age of the West Runton Freshwater Bed. Its position underlying Anglian (*c.* MIS 12) glaciogenic sediments (Lowestoft Till) provides a minimum age of *c.* 430 ka BP (Preece & Parfitt 2012). The presence of *Mimomys savini* (an archaic water vole) and *Borysthenia goldfussiana* (a gastropod) implies an age early in the early Middle Pleistocene, possibly the equivalent of the Dutch Cromer II interglacial (Stuart & Lister 2001; Maul & Parfitt 2010; Preece & Parfitt 2012). The evolutionary transition from *M. savini* to *Arvicola terrestris cantiana* (which is thought to be synchronous across Europe (Stuart & Lister 2010)) has been placed at 610±10 ka BP, 606±2 ka BP (Coltorti *et al.* 2005) and 609±40 ka BP (Wagner *et al.* 2010): placing deposition in at least MIS 15, and MIS 17 has also been suggested (Maul & Parfitt 2010). A maximum age of *c.* 781 ka BP is provided by the normal magnetism of the Freshwater Bed, placing it within the Brunhes Chron (Gibbard *et al.* 2010; Pillans & Gibbard 2012). This gives a potential age range for deposition of *c.* 781-606 ka BP.

4.2.2. Palaeoenvironmental context

The West Runton Freshwater Bed has a rich history of research. Prior studies have proved influential in advancing both understanding of the Pleistocene history of eastern England (e.g. Reid 1882; Duigan 1963; West 1980a; Rose *et al.* 2008; Stuart & Lister 2010) and general theories of vegetation succession (e.g. West 1980b). As such a significant interglacial site, it is also a perennial component of multi-site review papers (e.g. Preece & Parfitt 2000, 2008, 2012; Preece *et al.* 2009; Rose 2009; Candy *et al.* 2010; Coope 2010a; Lister *et al.* 2010; Kahlke *et al.* 2011; Penkman *et al.* 2013; Rivals & Lister 2016). The seminal monograph by R.G. West (1980a) provided the basis of subsequent research, not least by establishing its site stratigraphy and regional context. This facilitated the inclusion of the West Runton Freshwater Bed into broader discussions of early Middle Pleistocene palaeoenvironments and stratigraphy, establishing its regional and international significance. West (1980a) also posited that the Freshwater Bed covered a major part of an interglacial stage, but this was challenged by Rose *et al.* (2008). They suggested that it accumulated rapidly and represents a brief interval, on the basis of pollen and stable isotopes providing little evidence of climatic change through the unit.

Prior studies on the West Runton Freshwater Bed provide a wealth of palaeoenvironmental information. The palaeobotanical and palaeontological work of Reid (1882), Duigan (1963), Stuart (1975), West (1980a) and others provides the broad context of a temperate interglacial environment, with characteristic flora and fauna. This includes deciduous trees (typically dominated by *Alnus*), a diverse vertebrate community incorporating an array of large and small herbivores and carnivores, and numerous floral and faunal wetland indicators. More recent work, in part catalysed by the discovery of the eponymous 'West Runton Mammoth' (*Mammuthus trogontherii*, Stuart & Lister 2010), has refined this and provided a considerably more detailed picture of the local environment. This has been achieved through further investigations of palaeobotany and palynology (Rose *et al.* 2008; Field & Peglar 2010), large mammals (Breda *et al.* 2010; Lewis *et al.* 2010; Lister *et al.* 2010), small mammals (Maul & Parfitt 2010), birds (Stewart 2010), ectothermic vertebrates (Böhme 2010), molluscs (Preece 2010), insects (Coope 2000, 2010b), sedimentology and taphonomy (Rose *et al.* 2008; Gibbard *et al.* 2010; Stuart & Larkin 2010), and chronostratigraphic properties (tephra: Brough *et al.* 2010; magnetostratigraphy: Gibbard *et al.* 2010; aminostratigraphy: Penkman *et al.* 2010). Collectively, these provide evidence of a diverse range of habitat types in the vicinity, including wetland, woodland and grassland, and a climate comparable to that of the region at present, though perhaps more continental in nature.

The West Runton Freshwater Bed remains a valuable resource for new and continuing research, due in part to the pre-existing wealth of data. However, flora and fauna from this site have rarely been subject to quantitative ecological analyses, or used to address explicitly ecological themes, such as the role of disturbance processes in structuring vegetation communities. Furthermore, new analyses may be readily supplemented with reference to other, well-documented floral and faunal records (e.g. West 1980a; Stuart & Lister 2010). For example, the remains of diverse assemblages of herbivores have been recorded from the site, ranging from the exceptionally large *Mammuthus trogontherii* (Lister & Stuart 2010) to small mammals (Maul & Parfitt 2010) and grazing waterfowl (Stewart 2010) (see Table 4.2). This offers the opportunity to explore specific inferences regarding herbivore-plant interactions at the site, adding to discussions of disturbance through herbivore activity, particularly given recent dietary analyses of part of the West Runton fauna, which give insights into local feeding behaviours (Rivals & Lister 2016). There is thus significant potential for new analyses to yield information around ecological function, habitat structure and heterogeneity, and disturbance processes. As a notable interglacial site, this has relevance beyond the Cromerian of East Anglia. Furthermore, recent advances in the coleopteran Mutual Climatic Range (MCR) method (Milne 2016) allow more refined palaeoclimatic estimates to be made, which can be incorporated into a broader discussion of the Mid-Brunhes Transition.

Table 4.2 Herbivores recorded from the West Runton Freshwater Bed ([1]Lister & Stuart 2010; [2]Lister *et al.* 2010; [3]Breda *et al.* 2010; [4]Maul & Parfitt 2010; [5]Stuart 1975; [6]Stewart 2010; [+]extinct taxa), with notes on ecology ([7]Rivals & Lister 2016; [8]Kahlke & Kaiser 2011)

Order	**Species**	**Common Name**	**Notes on Ecology**[4,5,6,7]
Proboscidea	*Mammuthus trogontherii*[1]	Steppe mammoth[+]	Browse-dominated
Perissodactyla	*Equus* cf. *suessenbornensis*[2]	Large stenonid horse[+]	Graze-dominated
	Equus cf. *altidens*[2]	Small stenonid horse[+]	Graze-dominated
	Stephanorhinus hundsheimensis[3]	Rhinoceros[+]	Mixed feeder[8]
	Stephanorhinus sp.[3]	Rhinoceros[+]	Mixed feeder[8]
Artiodactyla	*Sus scrofa*[2]	Wild boar	Woodland omnivore
	Dama sp.[2]	Fallow deer[+]	Browser
	Praemegaceros verticornis[2]	Giant deer[+]	Browse-dominated
	Megaloceros savini[2]	Giant deer[+]	Browse-dominated
	Cervalces latifrons[2]	Broad-fronted elk[+]	Wetland grazer
	Cervus elaphus[2]	Red deer	Mixed feeder
	Capreolus capreolus[2]	Roe deer	Browser
	Bison cf. *schoetensacki*[3]	Bison[+]	Graze-dominated
Lagomorpha	*Lepus* sp.[5]	Hare	Grassland
Rodentia	*Sciurus whitei*[5]	Squirrel[+]	Woodland
	Castor fiber[4]	Eurasian Beaver	Wetland
	Trogontherium cuvieri[5]	Giant Beaver[+]	Wetland
	Cricetulus migratorius[5]	Grey Dwarf Hamster	Dry grassland
	Cricetus runtonensis[4]	Hamster[+]	Grassland
	Clethrionomys hintonianus[4]	Red-backed Vole[+]	Woodland

(Continued overleaf)

Table 4.2 Continued

	Pliomys episcopalis[4]	Forest Vole[+]	Woodland
	Mimomys savini[4]	Water Vole[+]	Wetland/ Grassland
	Microtus arvalinus[4]	Meadow Vole[+]	Grassland
	Microtus ratticepoides[4]	Meadow Vole[+]	Grassland
	Microtus gregaloides[4]	Meadow Vole[+]	Grassland
	Microtus arvalidens[4]	Meadow Vole[+]	Grassland
	Apodemus cf. *sylvaticus*[4]	Wood Mouse	Woodland/ Grassland
Anseriformes	*Anser* sp. [6]	Goose	Wetland/ Grassland

4.3. Site-specific Methodology

4.3.1. Sampling and sub-sampling

Field sampling was undertaken between 25th March and 3rd April 2014, when the West Runton Freshwater Bed was exposed laterally for approximately 274 m. Ten sections along the length of the exposure were logged and described qualitatively and semi-quantitatively, using the Troels-Smith method (Troels-Smith 1955). One section, 263 m east of 'West Runton Gap' was selected for sampling, on the basis that it provided the longest record of relatively undisturbed sediments (Fig. 4.2). Thirty-one contiguous bulk sediment samples were excavated for Coleoptera at 5 cm resolution (except where it appeared that a sub-unit boundary would be crossed), from a cleaned open section. A 169 cm overlapping monolith sequence (two monoliths, 10 cm wide, 6 cm depth, 100 cm length) was excavated directly adjacent to this for palynological and sedimentological analyses.

Sub-samples for pollen and spores were taken from the monolith sequence at 4 cm intervals between 0 and 169 cm, utilising both monoliths. Sub-samples for sedimentological (loss-on-ignition and particle size) analyses were taken at 1 cm resolution from the same sequence. No sediment was recovered from the monolith sequence between 40 cm and 45 cm, as they were friable and lost during field sampling. Details of laboratory processes are outlined in Chapter 3 (*Section 3.2.1.*).

4.3.2. Assemblage zonations

Faunal (beetle) and pollen assemblage zones were constructed using constrained cluster analysis (CONISS, Grimm 1987), with a broken-stick model (Bennett 1996) used as a guide to determine a significant number of zones. Analyses were performed using the R package ‘rioja’ (Juggins 2015).

4.3.3. Multivariate analyses

A preliminary detrended correspondence analysis (DCA) applied to the pollen and spore data produced gradient lengths of <2.5 (DCA1: 1.92, DCA2: 1.70), and therefore principal components analysis (PCA) was selected as the most appropriate technique (as per recommendation by Legendre & Birks 2012). Only those pollen and spore taxa with >1% maximum abundance (throughout the sequence) and more than 15 occurrences were included in these analyses. This allowed the broad trends and relationships between, and involving, major taxa to be explored, and to be disentangled from the abundances and occurrences of rare pollen taxa, though it is acknowledged that the >1% maximum abundance limit still includes some low abundance taxa (e.g. *Nuphar*). A preliminary DCA applied to the coleopteran data also produced gradient lengths <2.5 (DCA1: 1.61, DCA2: 1.63) and a PCA was also carried out on this dataset.

Following this, canonical correspondence analysis (CCA) was carried out on pollen and coleopteran datasets separately, using coprophilous fungal spore concentrations, charcoal concentrations and sedimentological properties (organic content, $CaCO_3$ content and particle size) as ‘environmental variables’, and major pollen taxa as ‘species’ or ‘response’ variables. *Podospora*-type spores were excluded, as they occurred too infrequently to be influential.

Palynological and entomological datasets were also combined for simultaneous analysis, to explore potential covariance between major pollen and beetle functional groups. As the pollen sequence is higher resolution, it was occasionally necessary to combine several samples (by averaging abundance and concentration values) for this analysis, in order to create a composite biological dataset with equivalent samples. The monolith sequence from which pollen samples were derived was taken *c.* 20 cm to the left (East) of the coleopteran sequence, but equivalent samples in the composite dataset are derived from the same sedimentary subunits (Fig. 4.2). A preliminary DCA of this composite dataset produced gradient lengths of 2.05 (DCA1) and 1.90 (DCA2), and so a PCA was selected as a reasonable indirect ordination technique to apply. CCA was not applied to this composite dataset, as beetle assemblages were shown to be largely unrelated to the environmental proxies (discussed in Section *5.3.5.*).

Ordination was also used to compare the new coleopteran sequence presented here (WR14) with Coope’s (2000, 2010b) West Runton assemblages (see Figure 4.1 for relative locations). A preliminary DCA of these data produced gradient lengths of <2.5 (DCA1: 2.09, DCA2: 1.42), and so a PCA was selected as a reasonable indirect ordination technique to apply.

4.4. Results

4.4.1. Sedimentology and stratigraphy

Sediments were composed of generally upward-fining dark grey to black clayey silts, with some sand and visible fragmentary and whole mollusc shells (full details of field-recorded stratigraphy in Figure 4.2). (Further details, including Troels-Smith codes and section photograph, provided in Appendix 1.)

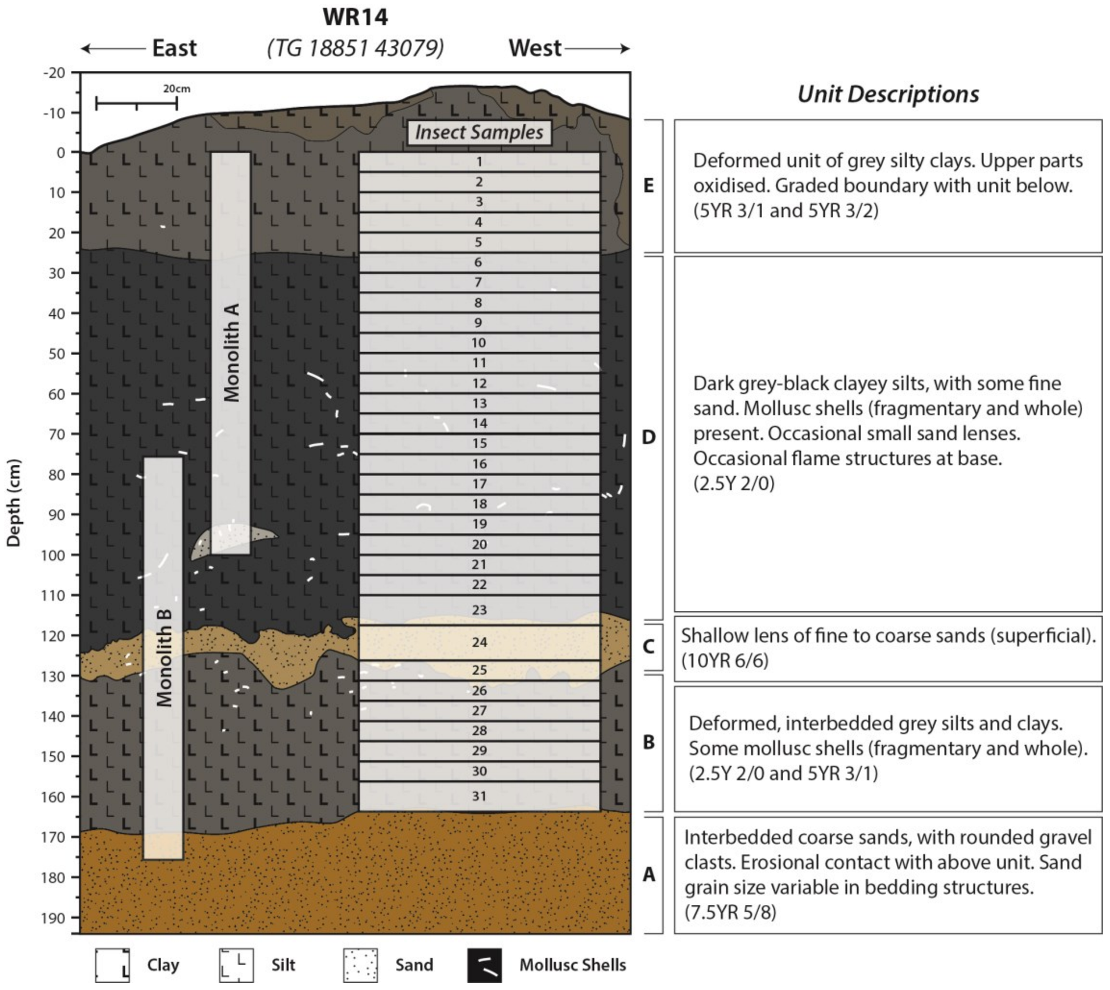


Figure 4.2 – West Runton Freshwater Bed sampling log and sub-unit descriptions (WR14) (see Figure 4.1 for section location)

The LOI data (Fig. 4.3) indicate an upward trend towards increasing organic content and decreasing calcium carbonate ($CaCO_3$) content. Organic matter remains low throughout the sequence, with a mean value of 8.14% and a maximum of 22.93% but variations are noted and the record can be divided into four sections (Fig. 3.1). Firstly, from the base to approximately 100 cm, it fluctuates between *c.* 4-9%, followed by a section of greater stability until about 50 cm, during which it fluctuates from *c.* 7-9%. After this, it exhibits a sharp increase over about 20 cm, and peaks at 22.93% at 29 cm, before decreasing rapidly, though unevenly, over the following 20 cm. In the uppermost 10-15 cm of the sequence, organic matter fluctuates between *c.* 6-12%. Calcium carbonate content ($CaCO_3$) exhibits a broadly opposite trend to that of organic matter, whether measured either relative to the total sample or to the mineral fraction, because the samples are predominantly minerogenic (Fig. 4.3). In the basal 10-15 cm, $CaCO_3$ rises sharply to a peak of *c.* 26-28% at 155 cm, before falling over the subsequent 25 cm to reach a period of stable fluctuation between approximately 14-18%. At *c.* 85 cm, $CaCO_3$ content begins to decrease, before reaching low levels (*c.* 2-4%) and relative stability around 30 cm. Neither organic content nor $CaCO_3$ appear to bear any relation to changes in gross sediment characteristics recorded in the field (see Figure 4.2).

Particle size analysis reveals an overall trend towards fining upward in the sequence, with alternations between two modes of deposition superimposed on this pattern (Fig. 4.3). Mean grain size ranges from approximately 3 phi (125 μm, fine sand) at the base, to 6 phi (16 μm, silt) at the top, illustrating the fining trend. Variations in modal grain size demonstrate an oscillation between deposition dominated by silt-sized particles (*c.* 4.5- 5.5 phi), with a more skewed distribution, and one dominated by medium to fine sands (*c.* 1.5-3 phi), with lower skewness. From *c.* 60 cm, the silt-dominated mode of deposition is amplified. Similarly to the LOI data, these particle size data also do not appear to bear any particular relation to gross sediment characteristics recorded in the field (see Figure 4.2).

The above sedimentological descriptions and analyses are broadly consistent with West's (1980a) beds 'f' to 'g', and Gibbard *et al.*'s (2010) units 'iv' to 'vi'.

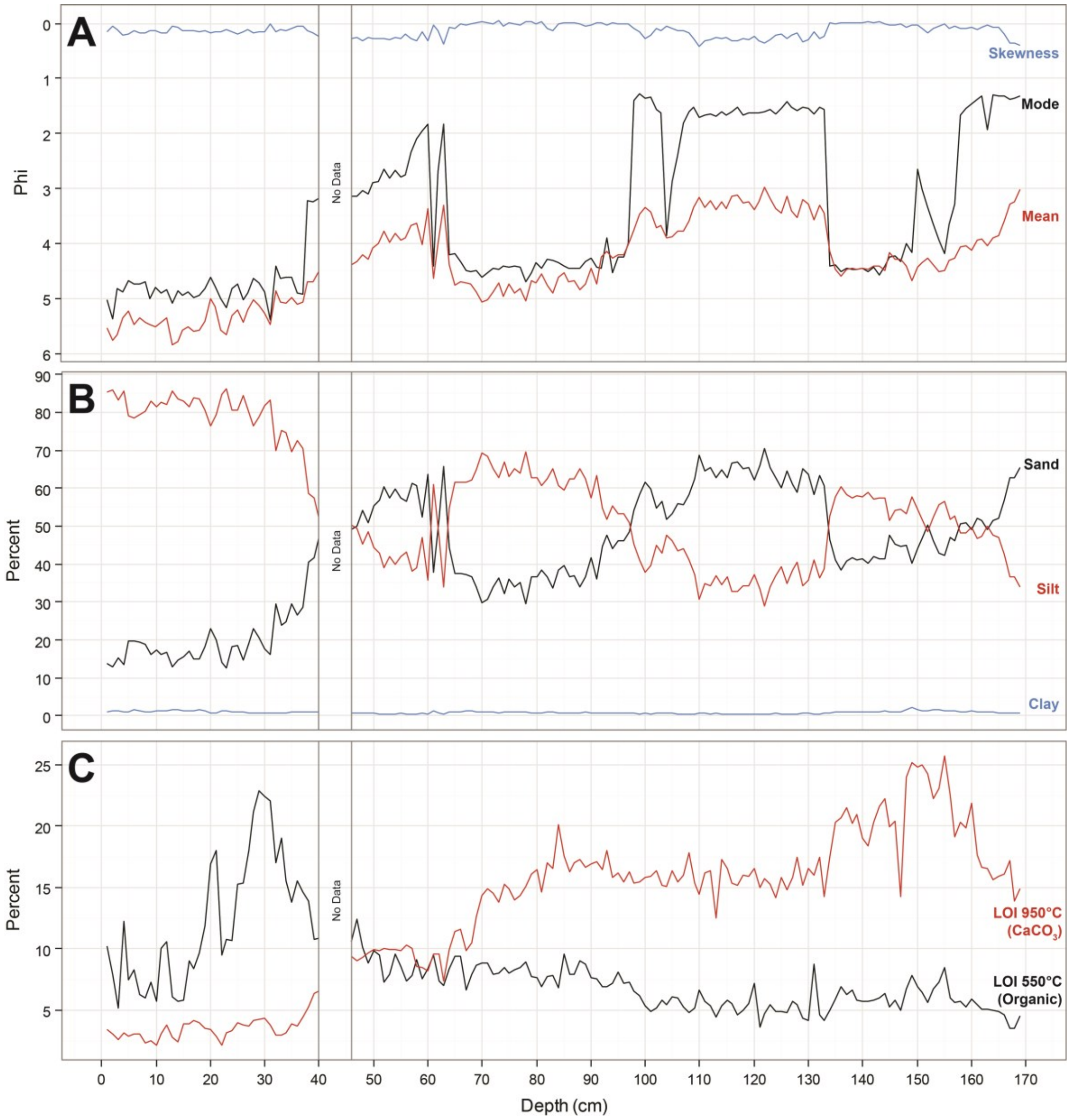


Figure 4.3 – WR14 (Fig. 4.2) loss-on-ignition and particle size data. A: average grain size; B: relative contributions of grain size classes; C: carbonate ($CaCO_3$) and organic content inferred from loss-on ignition

4.4.2. Palynostratigraphy

4.4.2.1. Introduction

A variety of arboreal, herbaceous and aquatic pollen taxa are present in the sequence, alongside pteridophyte and fungal spores (Figs. 4.4, 4.5 and 4.6). Proportions of tree and shrub taxa range from 28.5% to 65.8% (46.3% mean). Amongst these, *Alnus* and

Pinus pollen are most numerous, but occur alongside varying proportions of others, such as *Corylus*, *Ulmus* and *Abies*. Herbaceous pollen percentages range from 34.2% to 71.5% (53.7% mean), and are composed of both generalists (e.g. Apiaceae, *Galium*) and taxa of open, semi-open and disturbed habitats (e.g. *Filipendula*, *Plantago*, *Ranunculus acris*). Aquatics include those associated with lentic, relatively eutrophic environments (e.g. *Nuphar, Potamogeton*). A number of minor taxa are also present (Fig. 4.5), some occurring relatively frequently, though at very low abundances (e.g. Ericaceae, *Juniperus*, *Viscum*, *Solanum*, *Pteridium*, *Myriophyllum verticillatum*), and others more disparately (e.g. *Cornus*, *Tsuga*, *Lythrum*, *Pinguicula*, Rosaceae). Fungal spores associated with herbivore dung are present throughout (total coprophilous fungal spores: 0 spores cm^{-3} to 4848 spores cm^{-3} range, 884.7 spores cm^{-3} mean) (Figs. 4.4 & 4.6). All three fungal spore types identified by Baker *et al.* (2013) as dung-obligate (*Sporormiella*-type, *Podospora*-type) or strongly dung-associated (*Sordaria*-type) are present (Fig. 4.6). Low to moderate concentrations of microscopic charcoal are also present (8080 shards cm^{-3} to 79184 shards cm^{-3}). The taxonomic composition of the assemblages is relatively stable throughout the record, but there are some notable changes, detailed below.

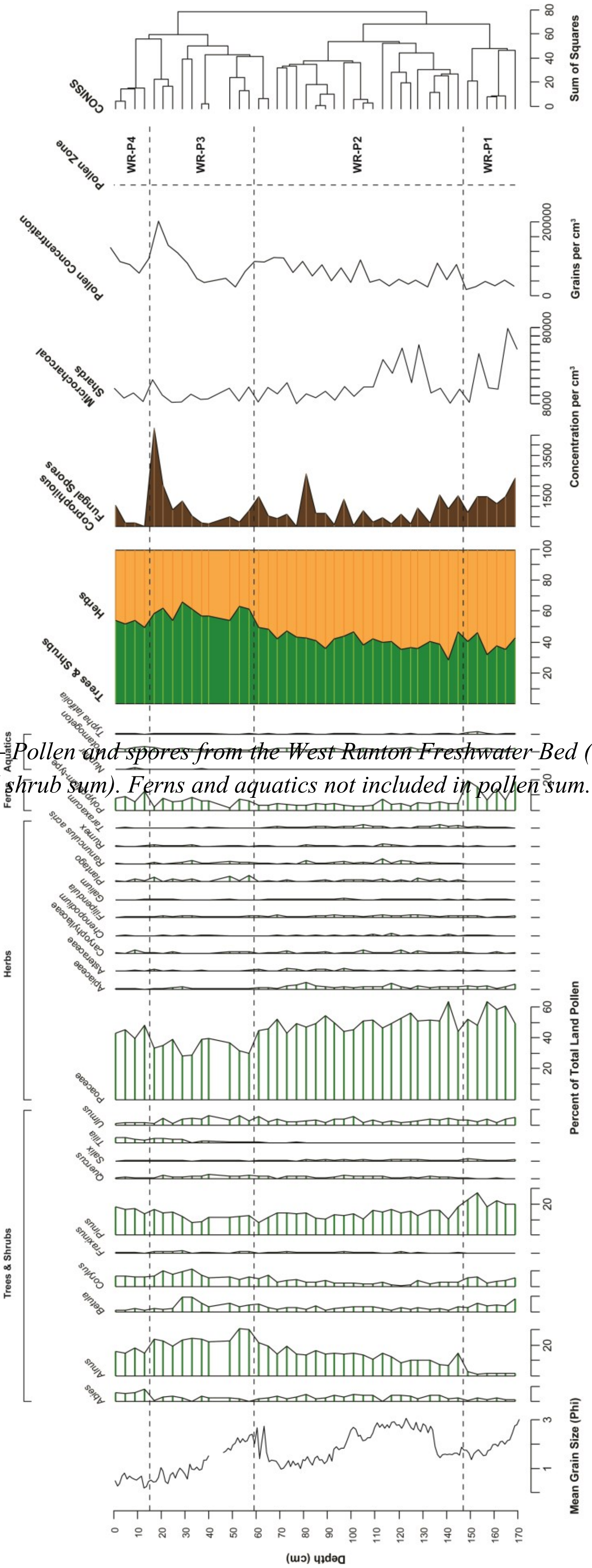


Figure 4.4 – Pollen and spores from the West Runton Freshwater Bed (WR14, Fig. 4.2) (major taxa) (
the tree and shrub sum). Ferns and aquatics not included in pollen sum. Total land pollen per sample:

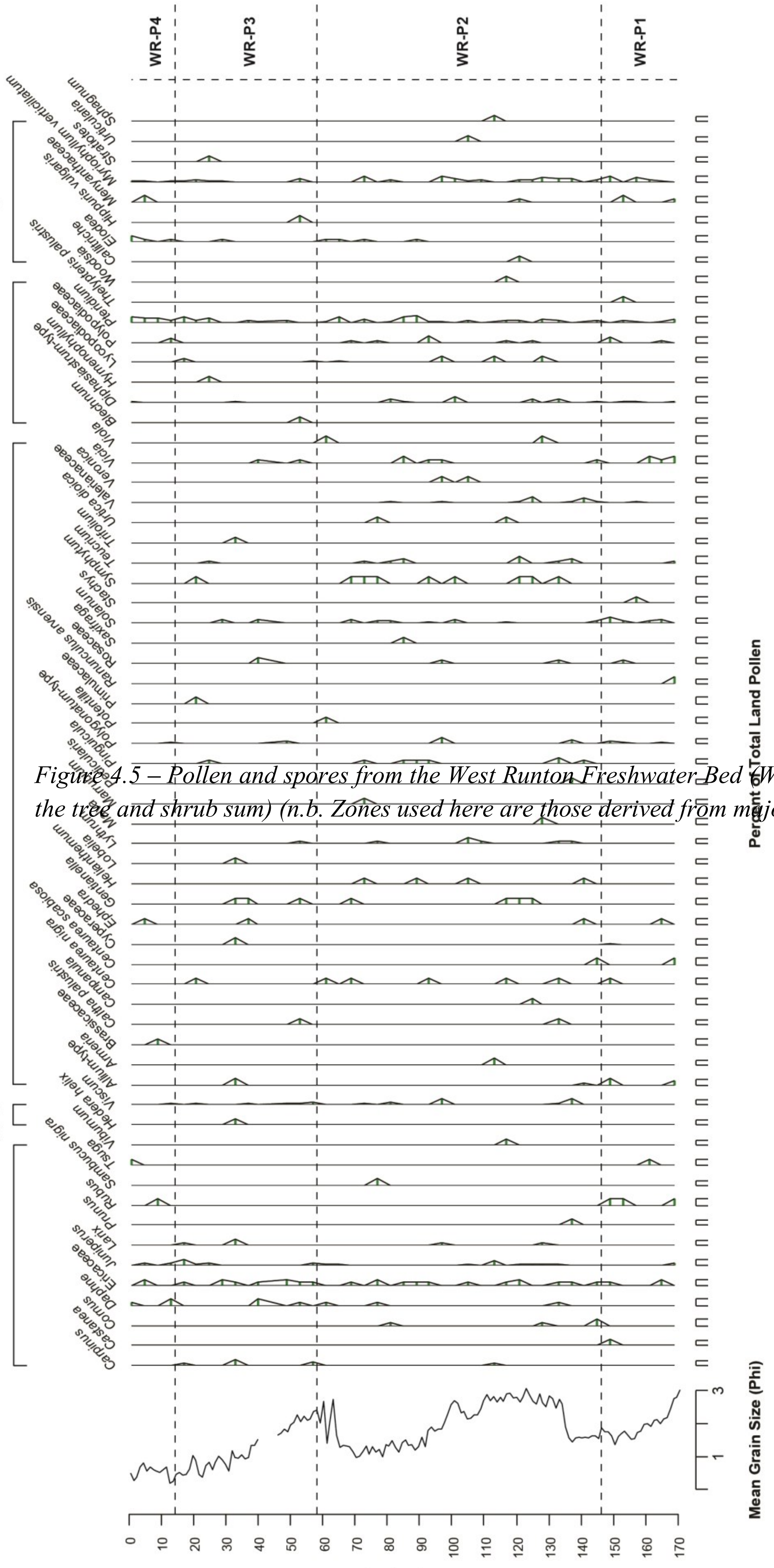


Figure 4.5 – Pollen and spores from the West Runton Freshwater Bed (WR14, Fig. 4.2) (minor

the tree and shrub sum) (n.b. Zones used here are those derived from major pollen taxa, Figure

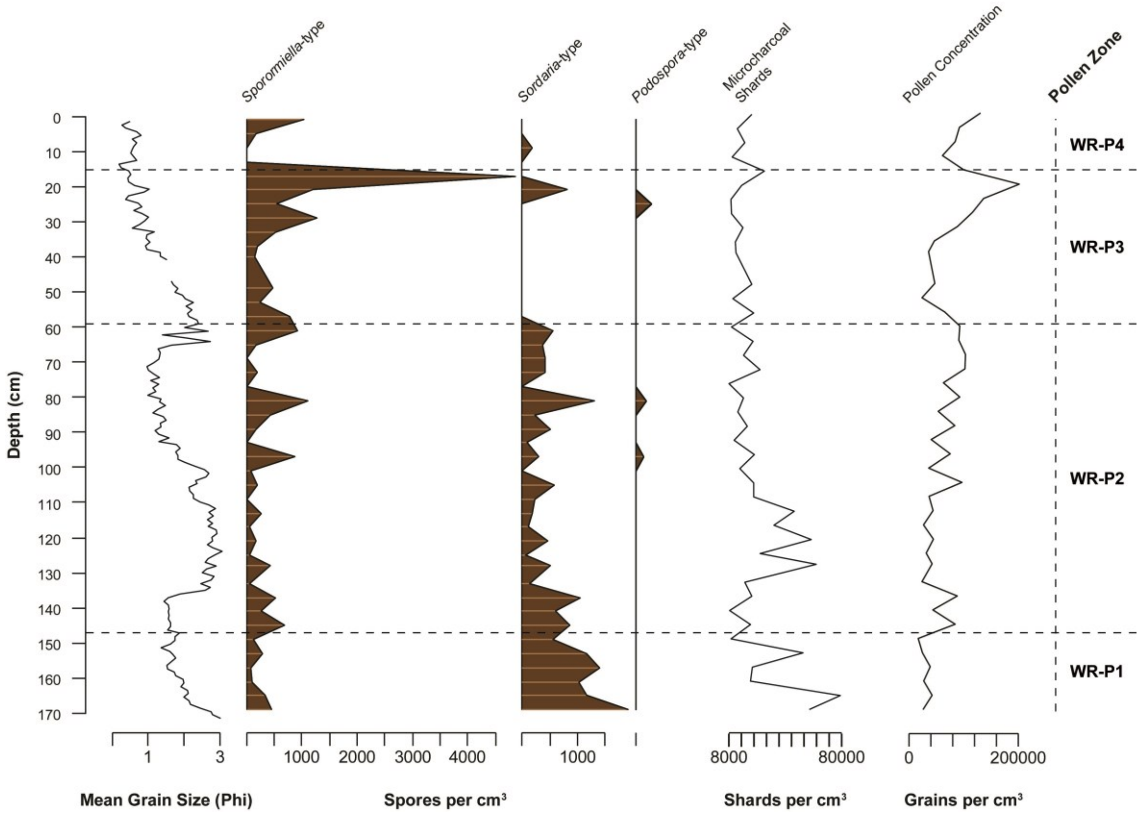


Figure 4.6 – Coprophilous fungal spores from the West Runton Freshwater Bed (WR14, Fig. 4.2)

4.4.2.2. Pollen assemblage zones

Pollen Zone WR-P1 (169-147 cm)

In the basal section of the record (zone WR-P1, 169-147 cm, Fig. 4.4) Poaceae and *Pinus* are the dominant taxa (55.3% and 21.8% means, respectively). *Sordaria*-type spores are also conspicuously abundant (1203.8 spores cm^{-3} mean) (Fig. 4.6), *Polypodium*-type spores are at their greatest abundance (13.5% mean) and charcoal concentrations are relatively high (79184 shards cm^{-3} maximum). Despite being a dominant taxon throughout the remainder of the sequence, *Alnus* pollen remains at <3% in this section. This is paralleled by *Plantago* pollen which, although present, is also rare. Mean herbaceous pollen abundance is 61.0%, and mean tree and shrub abundance is 39.0%. The dominance of Poaceae pollen in this zone indicates a relatively open landscape, though several deciduous tree taxa (e.g. *Betula*, *Corylus*, *Ulmus*) were evidently present at low densities, and *Pinus* was present in the broader landscape. Disturbance (burning, herbivory) is indicated by microcharcoal and *Sordaria*-type spores. Modal grain size indicates a significant sand component in this zone, but this decreases (Fig 4.3), reflecting initially higher energy conditions, and potentially greater disturbance as a result of hydrogeomorphic processes in the riparian zone.

Pollen zone WR-P2 (147-59 cm)

Pollen zone WR-P2 (147-59 cm, Fig. 4.4) comprises the most substantial portion of the sequence. Poaceae and *Pinus* remain as dominant taxa in this section, in addition to *Alnus* (49.6%, 13.6% and 13.5% means, respectively), which becomes roughly equivalent to *Pinus*. This is also the first point at which *Fraxinus* appears, and *Quercus*, *Plantago* and *Ranunculus acris* all exhibit subtle increases. Though both remain present, *Sordaria*-type spores (Fig. 4.6) and *Polypodium*-type are diminished relative to pollen zone WR-P1, and coprophilous fungi are, on average, lower (Figs. 4.4 & 4.6). *Tilia* appears for the first time in the record at 76-77 cm. Charcoal shard concentrations are briefly elevated between 128 cm and 113 cm, but drop to low concentrations (less than *c.*30000 shards cm^{-3}) following this. Mean herbaceous pollen abundance is 58.8%, and mean tree and shrub abundance is 41.2%. This represents little change in ratios of arboreal to non-arboreal pollen from the previous zone, but changes in the composition of arboreal pollen assemblages here suggest a slight increase in tree cover. The appearance of *Tilia* is particularly notable in this context, as *Tilia* are entomophilous (insect-pollinated) and typically underrepresented in pollen records relative to other trees (Pigott & Huntley 1980). It is therefore highly likely that they became established locally during the period represented by this zone, suggesting a slight increase in local tree cover. Grain size is variable in this zone, indicating variable energy conditions, and sedimentary $CaCO_3$ exhibits a stepwise decreasing trend (Fig. 4.3).

Pollen Zone WR-P3 (59-15 cm)

In zone WR-P3 (59-15 cm, Fig. 4.4), Poaceae, *Pinus* and *Alnus* continue to be the dominant taxa (34.1%, 12.3% and 24.3% means, respectively), with *Alnus* pollen becoming more abundant than *Pinus*. *Corylus* pollen abundance is also elevated in this section of the record (7.4% mean here, as opposed to 2.6% mean in WR-P2) and *Tilia* pollen exhibits a slight increase (mean: 1.6%), whilst *Betula* pollen decreases towards the top. Amongst the herbaceous taxa, abundances of Apiaceae are diminished and *Plantago* pollen exhibits a slight amplification. From this zone, tree and shrub pollen (59.3% mean) becomes more abundant than herbaceous pollen (40.7% mean), which occurs with a decrease in Poaceae abundance. Charcoal concentrations remain relatively low (mean: 16442 shards cm^{-3}). Notably, *Sordaria*-type spores become almost absent, whilst *Sporormiella*-type spores exhibit a dramatic, but very brief, peak of 4848.0 spores cm^{-3} at 16-17 cm. The numerical dominance of tree and shrub taxa indicates decreasing openness in the landscape, relative to the previous zone. The increase in *Alnus* pollen (and concurrent decrease in *Pinus* pollen) likely reflects the local importance of wet woodland habitats (e.g. alder carr), and the increase in *Tilia* suggests increasing tree cover in drier parts of the local landscape. The shift in coprophilous fungal spore types is interesting, as this suggests a change in the character of local herbivory (this is discussed further in Section *4.5.2.*). This zone is also coincident with a shift towards more organic, silt-dominated sediments (Fig. 4.3), suggesting lower fluvial influence and greater autochthonous deposition. Such a change in local catchment dynamics may also have influenced the representation of different spore types in this zone.

Pollen Zone WR-P4 (15-0 cm)

In the uppermost part of the record (zone WR-P4, 15-0 cm, Fig. 4.4) Poaceae, *Pinus* and *Alnus* remain the most abundant taxa, though Poaceae and *Pinus* increase slightly, whilst *Alnus* is decreased (44.0%, 16.6% and 15.8% means, respectively). There is a noticeable decline in *Ulmus* pollen (mean: 1.4%), alongside an increase in *Abies* pollen, and charcoal concentrations continue to remain relatively low. Despite the slight resurgence in Poaceae, tree and shrub abundances remain higher than those of herbaceous taxa: 52.4% and 47.6% means, respectively. In spite of this, the increase in Poaceae pollen perhaps represents a slight opening of the canopy during this period. The increase in *Abies* is also interesting, as this is thought to be a late-establishing taxon in British interglacials (Turner & West 1968), perhaps suggesting deposition within the latter half of an interglacial. The sedimentary environment appears to have stabilised in this zone (high silt content), and organic content is diminished, but erratic (Fig. 4.3). This suggests diminished fluvial influence, perhaps as a result of channel migration away from the site of deposition. Sediment stabilisation may also be reflective of local terrestrialisation at the site of deposition. Indeed, aerial exposure of the sediments is indicated by the oxidisation of the upper portion of this zone (Fig. 4.2).

4.4.3. Coleoptera

The following section presents the results of the extraction and analysis of coleopteran remains from the sedimentary sequence, and ecological interpretations. Thirty-one samples were analysed over a depth of 162 cm, with mean volume of approximately 9.2

litres and mean weight of 15.51 kg (see Table 4.3). In total, 722 MNI (minimum number of individuals) were extracted and identified from this sequence, with individuals from 16 families and 48 genera, 60 of which were identified to species-level.

Table 4.3 Summary of West Runton (WR14, Fig. 4.2) Coleopteran Samples

Sample Number	Depth (cm)	Approximate Volume (litres)	Weight (kg)	Total MNI	Taxon Richness
1	0-5	11	18.33	9	9
2	5-10	8	13.21	5	3
3	10-15	8	12.8	8	7
4	15-20	9	15.35	8	7
5	20-25	13	20.89	8	7
6	25-30	13	21.75	26	17
7	30-35	13	18.4	40	19
8	35-40	9	16.16	37	12
9	40-45	13	19.3	53	17
10	45-50	11	17.45	28	15
11	50-55	12	20.11	62	15
12	55-60	9	14.66	26	16
13	60-65	9.5	16.2	46	21
14	65-70	9.5	15.21	64	14
15	70-75	15	23.54	36	16
16	75-80	9.5	15.74	32	17
17	80-85	10.5	17.32	14	13
18	85-90	9	13.69	10	8
19	90-95	7	11.2	10	8

(Continued overleaf)

Table 4.2 Continued

20	95-100	7	11.46	11	7
21	100-105	8	14.23	25	20
22	105-110	7.5	12.63	14	13
23	110-117	9	17.26	36	18
24	117-125	7	14.23	14	10
25	125-130	7	13.29	12	11
26	130-135	6	10.65	6	6
27	135-140	9.5	13.49	17	15
28	140-145	6	10.78	6	6
29	145-150	6	10.56	22	15
30	150-155	9	14.39	16	12
31	155-162	5	10	21	14

4.4.3.1. Coleoptera: Limitations and caveats

The coleopteran record presented here is informative, but certain caveats should be noted. First of these is the low abundance of sub-fossil material. Mean total MNI per litre of sediment is 2.48 (min: 0.62, max: 6.74), and so despite large sample sizes (mean: 9.23 litres) the mean MNI per sample was just 23.29 (min: 5, max: 64). Underrepresentation of typically low abundance groups of beetles (e.g. bark beetles) is unavoidable in this context. This likely contributes to the apparently stochastic occurrence of taxa from particular habitat categories (e.g. woodland and tree categories), which may have been persistently present in the landscape, but only occasionally incorporated into the sediments of the Freshwater Bed. Additionally, such low abundance samples can lead to underrepresentation in proportional terms when one taxon becomes abundant.

Secondly, the sub-fossil material recovered was often fragmentary and degraded, meaning that for many specimens only genus-level identification was possible. The habitat preferences of individual species are often not consistent within a genus, necessitating the classification of some genera as 'uncategorised or eurytopic' (UE). This is particularly true of diverse genera in this record, such as *Pterostichus* (Carabidae) or *Otiorhynchus* (Curculionidae). Many genera are able to provide some ecological information, though a lack of species-level identification limits the potential level of detail. A pertinent example is provided by *Aphodius* (Scarabaeidae), which occurred frequently throughout the record, but was often only identifiable to genus. *Aphodius* species occur in a range of foul and rotten environments, and many are associated with herbivore dung, providing useful evidence of the local presence of large herbivores (Smith *et al.* 2014). However, a number of species (e.g. *Aphodius plagiatus*) are saprophagous, rather than coprophaghous or coprophilous, and so genus-level identifications of *Aphodius* must be assigned to the foul and rotten category (DE), rather than the more specific dung-obligate (DU) category.

4.4.3.2. Coleoptera: Landscape and Ecology

The coleopteran sequence has been divided, from the base, into three zones: WR-C1 (162-85 cm), WR-C2 (85-20 cm) and WR-C3 (20-0 cm) (Table 4.4, Fig. 4.7). Throughout the sequence, the assemblages are dominated by wetland-associated and aquatic Coleoptera, though a range of terrestrial habitat types are also represented, including both woodland and open habitats.

from the West Runton Freshwater Bed (WR14, Fig. 4.2)
uatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG:
: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed;
ral); DU: Dung; UN: Uncategorised or Eurytopic)

Family	Species	Habitat Category	Median Sample Depth (cm) and Faunal Zone																														
			158.5	152.5	147.5	142.5	137.5	132.5	127.5	121	113.5	107.5	102.5	97.5	92.5	87.5	82.5	77.5	72.5	67.5	62.5	57.5	52.5	47.5	42.5	37.5	32.5	27.5	22.5	17.5	12.5	7.5	2.5
			WR-C1														WR-C2													WR-C3			
Gyrinidae																																	
	Gyrinus sp.	AG	1						1																								
Dytiscidae																																	
	Dytiscidae indet.	AG																				1							1				
Carabidae																																	
	Notiophilus biguttatus (F.)	WTG																		1													
	Notiophilus palustris (Duftschmid)	H																															1
	Notiophilus sp.	UN	1	1									1					1				1	1		1		1	1		1	1		
	Elaphrus sp.	RW							1	1														1	1		1						
	Dyschirius sp.	RW																			1												
	Bembidion spp.	RW			1	1	2			2	2		1				1		3								1						
	Pterostichus nigrita (Payk.)	RW																						2									
	Pterostichus strenuus (Panz.)	H										1																					
	Pterostichus sp.	UN									1										1	1	2										
	Agonum sp.	RW																										1					
	Carabidae indet.	UN		1	2				1		1		1						1														
Helophoridae																																	
	Helophorus cf. *dorsalis* (Marsh.)	AS										1																					
	Helophorus fulgidicollis (Mots.)	AS						1																									
	Helophorus strigifrons (Thoms.)	AS		2			1			1									1		1												
	Helophorus sp.	AG			1								1		1		1						1	1	1			1					
	Helophorus spp.	AG																			2												
Histeridae																																	
	Margarinotus ventralis (Mars.)	DE															1																
Hydraenidae																																	
	Hydraena britteni (Joy)	AG																4			5					1							
	Hydraena gracilis (Germ.)	AF									1	1						1			4												
	Hydraena palustris (Er.)	AS									2							1															
	Hydraena pygmaea (Water.)	AF																										3					
	Hydraena riparia (Kug.)	AG	4	3	7	1	2		2		11	1	3				1	5	11	39	5	3	36	4	20	14	13	2					
	Hydraena sp.	AG								3				1		1																	
	Ochthebius minimus (F.)	AG					1												1					1									

(Continued overleaf)

Table 4.4 Continued

Family	Species	Habitat Category	Median Sample Depth (cm) and Faunal Zone																														
			158.5	152.5	147.5	142.5	137.5	132.5	127.5	121	113.5	107.5	102.5	97.5	92.5	87.5	82.5	77.5	72.5	67.5	62.5	57.5	52.5	47.5	42.5	37.5	32.5	27.5	22.5	17.5	12.5	7.5	2.5
			WR-C1														WR-C2													WR-C3			
Staphylinidae																																	
	Arpedium brachypterum (Grav.)	H																1															
	Omaliinae indet.	UN																				1				1							
	Micropeplus caelatus (Er.)	RW																							1								
	Micropeplus sp.	UN											1																				
	Atheta sp.	UN			1																												
	Anotylus fairmairei (Pandellé)	DU																1															
	Anotylus rugosus (F.)	DE			1						1		1						1			1						1					
	Anotylus sculpturatus (Grav.)	DE											1																				
	Anotylus tetracarinatus (Block)	DE		1																													
	Anotylus sp.	DE								1					1		1				1				1	1	1						
	Platystethus nodifrons (Mann.)	RW											1																	1			
	Bledius subniger (Schneid.)	RW										1																					
	Bledius femoralis (Gyll.)	RW																										1					
	Carpelimus rivularis (Mots.)	RW																			1												
	Carpelimus sp.	H																1															
	Stenus circularis (Grav.)	H											1					1				1	2	1									
	Stenus clavicornis (Scop.)	H																					1										
	Stenus juno (Payk.)	RW																								2							
	Stenus spp.	H	1	1							1				1		1	1	1		1		1		2		2					1	
	Rugilus sp.	H							1																								
	Neobisnius procerulus (Grav.)	RW																															1
	Aleocharinae indet.	DE					1				2																						
	Staphylinidae indet.	UN													2													1					
Scarabaeidae																																	
	Aphodius rufipes (L.)	DU			1						1									1													
	Aphodius coenosus (Panz.)	DU							1												1										1		
	Aphodius subterraneus (L.)	DE					1																										
	Aphodius niger (Ill.)	RW				1											1																
	Aphodius plagiatus (L.)	RW											1				1						1										
	Aphodius sp.	DE			1	1		1	1	1			1		1			1						1			1			1		1	1
	Aphodius spp.	DE																	2			2											
Elmidae																																	
	Elmis aenea (Müller)	AF													1						1												
	Normandia nitens (Müller)	AF														1				1					1								
	Oulimnius troglodytes (Gyll.)	AF					1																										
	Oulimnius sp.	AF		1																													
	Elmidae indet.	AF																									1						
Dryopidae																																	
	Dryops sp.	AF			1		1								1																		
Elateridae																																	
	Agrypnus murinus (L.)	O									1																						
	Melanotus punctolineatus (Pelerin)	O					1																										
Coccinellidae																																	
	Chilocorus renipustulatus (Scriba)	WTD																									1						

(Continued overleaf)

Table 4.4 Continued

Family	Species	Habitat Category	Median Sample Depth (cm) and Faunal Zone																														
			158.5	152.5	147.5	142.5	137.5	132.5	127.5	121	113.5	107.5	102.5	97.5	92.5	87.5	82.5	77.5	72.5	67.5	62.5	57.5	52.5	47.5	42.5	37.5	32.5	27.5	22.5	17.5	12.5	7.5	2.5
			WR-C1														WR-C2													WR-C3			
Chrysomelidae																																	
	Donaciinae indet.	WE	2																									1					
	Donacia cinerea (Hbst.)	WE	1		1																												1
	Donacia clavipes (F.)	WE										1																					
	Donacia crassipes (F.)	WE	1		1						1		1																				
	Donacia dentata (Hoppe)	WE												1						1	1												
	Donacia impressa (Payk.)	WE																	1														
	Donacia marginata (Hoppe)	WE	1																														
	Donacia semicuprea (Panz.)	WE										1						1						3									
	Donacia simplex (F.)	WE									1										1												
	Donacia sparagnii (Ahrens)	WE				1														1	1												1
	Donacia thalassina (Germ.)	WE					1												1	2			1		1	1	1						
	Donacia spp.	WE	3	1				1				2	3			1	1		2					1		1	4	1	1				
	Plateumaris bracata (Scop.)	WE														1						2	1				1	1					
	Plateumaris discolor (Panz.)	WE																							1								
	Plateumaris rustica (Kunze)	WE							1		3	1	2				1	2		2	3	2	2	4	1	3			1	1			
	Plateumaris sericea (L.)	WE	1		1		1		1	2	1	1	1	3	2	3		3	3	5	4	3	5	4	6	6	3	4		2	1		1
	Plateumaris spp.	WE		2		1		1				1	1	3															2		2	3	
	Phaedon sp.	H																													1		
	Phyllotreta sp.	HP										1																					
	Crepidodera sp.	WTD																										1					
	Chrysomelidae indet.	UN																									1						
Apionidae																																	
	Apion sp.	HP	1											1			1																1
Erirhinidae																																	
	Notaris acridulus (L.)	WE	1				1	1	1		1					1		1	2	1	4	2	1	1			1	1	1				
	Tanysphyrus lemnae (Payk.)	AS			1		1		1	1	4	1	1	1		1	2	6	4	7	5	3	6	2	11	5	4	2	1				1
Curculionidae																																	
	Orchestes sp.	WTD					1																		1	1							
	Bagous sp.	WE	1		1					1			1			1			1	1	2	1	1	1			1	1	1	1	1		
	Ceutorhynchus sp.	HP					1																		1								
	Graptus triguttatus (F.)	O																								1							
	Otiorhynchus clavipes (Bonsd.)	WTG																1															
	Otiorhynchus rugifrons (Gyll.)	O																		1													
	Otiorhynchus sp.	UN		1						1							1				1	1					1						
	Phyllobius sp.	UN																	1					1									
	Phyllobius/Polydrusus sp.	UN		1																											1		
	Magdalis phlegmatica (Hbst.)	WTC																									1						
	Curculionidae indet.	UN	2	1	1			1			1		1	1								1			2			3		1			1
Scolytidae																																	
	Scolytus multistriatus (Marsh.)	WTD																		1													
	Scolytus sp.	WTD																							1								
		Taxon Richness	14	12	15	6	15	6	11	10	18	13	20	7	8	8	13	17	16	14	21	16	15	15	17	12	19	17	7	7	7	3	9
		Total MNI	21	16	22	6	17	6	12	14	36	14	25	11	10	10	14	32	36	64	46	26	62	28	53	37	40	26	8	8	8	5	9

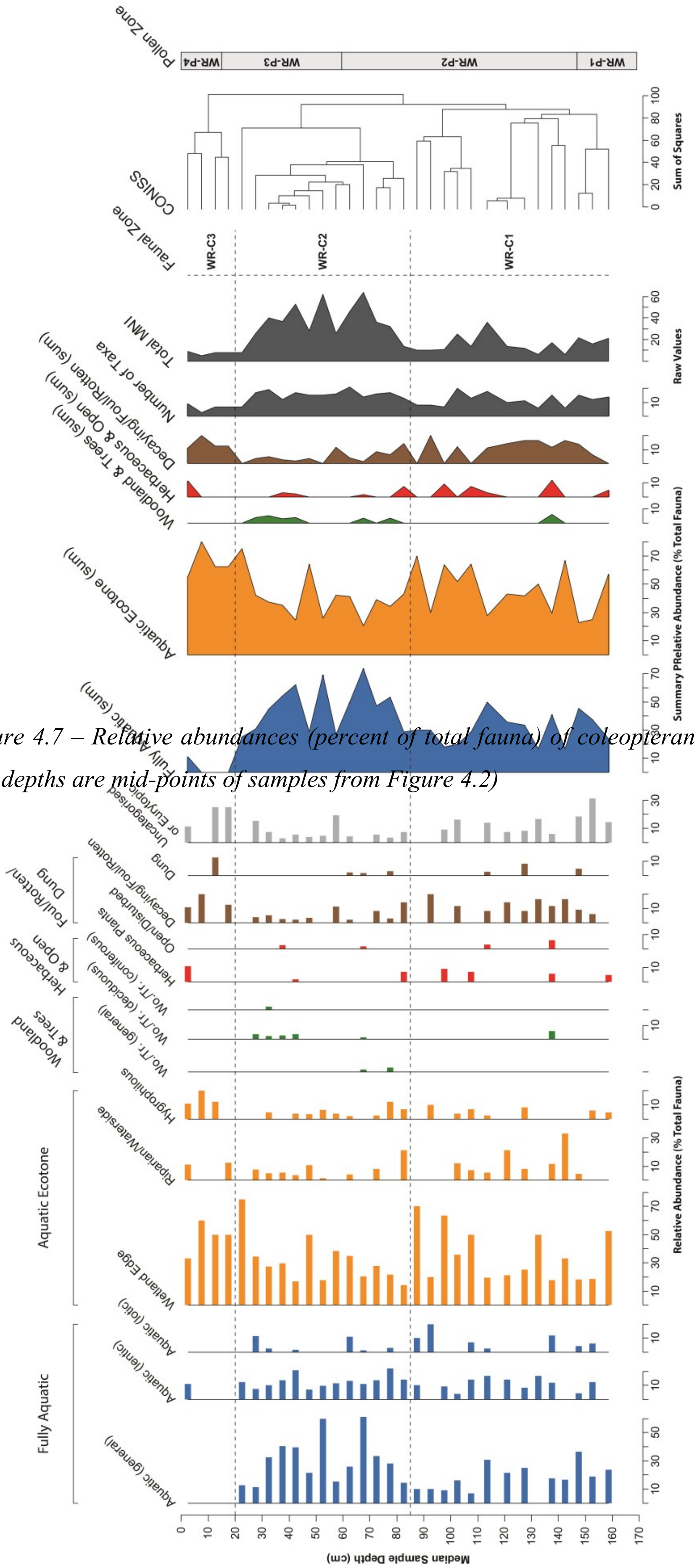


Figure 4.7 – Relative abundances (percent of total fauna) of coleopteran habitat groups from t
that depths are mid-points of samples from Figure 4.2)

Coleopteran Zone WR-C1 (162-85 cm)

In the lowermost zone (WR-C1: 162-85 cm), which comprises roughly half of the record (Table 4.4, Fig. 4.7), aquatic ecotone groups are the most abundant (50.7% mean), and of these, wetland edge taxa (WE) are the most numerous (35.4% mean). These are primarily represented by diverse assemblages of Donaciinae, a semi-aquatic Chrysomelid subfamily, which are associated with plants growing in or beside water, and undergo larval and pupal stages on, or inside, submerged plant tissues (Harde 1984). Of these, *Plateumaris sericea*, which is found on the margins of both flowing and still wetland types, associated with *Carex* spp., *Sparganium* spp. and other emergent macrophytes (Koch 1992; Cox 2007), occurs most frequently. Other Donaciinae include *Donacia cinera*, which feeds on *Typha*, *Phragmites*, *Sparganium* and *Carex* (Koch 1992), *D. crassipes*, which is found on Nymphaeaceae (Hyman 1992; Koch 1992), and *Plateumaris rustica*, which is oligophagous on *Carex* spp. (Koch 1992). The weevils, *Bagous* sp. and *Notaris acridulus*, are present alongside these taxa and inhabit similar areas. *Bagous* sp. may be semi-aquatic, living on various aquatic macrophytes at wetland edges (Harde 1984) and *N. acridulus* is oligophagous on *Glyceria* spp. (Koch 1992). The abundance and diversity of this group suggests extensive marsh and reedbed-type habitats in the local vicinity.

Riparian and waterside (RW) and hygrophilous (H) taxa are less abundant (12.2% and 3.1% means, respectively), but suggest that both shaded and exposed habitats were present adjacent to the wetland. The most frequently occurring riparian taxon is *Bembidion* spp., which are generally associated with waterside locations (Harde 1984). Amongst the Staphylinids, *Platystethus nodifrons* is typically found in fen and marsh habitats (Koch 1989a; Hyman 1994), whereas *Bledius subniger* is a coastal and saltmarsh species (Koch 1989a; Lott 2009). The closely related *Aphodius niger* and *A.*

plagiatus are saprophagous Scarabids, both found in open habitats on the margins of ponds, lakes and rivers (Koch 1989a; Mann & Garvey 2014). Hygrophilous taxa in this zone are limited to *Stenus* spp., and single occurrences of *Pterostichus strenuus* and *Stenus circularis*. *P. strenuus* is found on clayey soils on shaded sites, both in woodlands and open habitats (Lindroth 1986), and *S. circularis* is a hygrophilous generalist (Hyman 1994).

Fully aquatic functional groups are of lesser significance than wetland marginal taxa in WR-C1 (162-85 cm), but still important (30.5% mean). Of these, aquatic generalists (AQg) are the most abundant (17.3% mean), with *Hydraena riparia* the most numerous (Table 4.4), which inhabits both lentic and lotic environments (Hansen 1987; Koch 1989a). *Ochthebius minimus* is similarly generalist (Hansen 1987), though occurs only once in this zone. *Gyrinus* sp. may also be associated with either still or flowing water, though most species are found in calm conditions (Friday 1988). Eutrophic lentic habitats are represented by several species, including *Helophorus strigifrons* and *Hydraena palustris*, which are inhabitants of vegetated ponds and pools (Koch 1989a). Nutrient-rich standing water is also indicated by the frequently occurring weevil *Tanysphyrus lemnae*, which is oligophagous on *Lemna* spp. (duckweed) and other small floating-leaved plants (Koch 1992). Interestingly, *Helophorus fulgidicollis*, an obligate species of saltmarshes and brackish pool (Koch 1989a; Foster 2000), is also present in this zone, suggesting proximity to saltmarsh or estuarine environments. Lotic Coleoptera are also present, though not abundant (4.5% mean), indicating low fluvial influence. These are predominantly represented by 'riffle beetles' (Elmidae, Dryopidae); *Elmis aenea*, *Oulimnius troglodytes*, *Normandia nitens* and *Dryops* sp., though the former two may also be found at the edges of large lakes (Koch 1989b). Collectively, these taxa indicate deposition in a broadly lentic environment, with low fluvial influence, which may have been tidally-influenced or in close proximity to the coast. This is likely to have been a marsh or fen-type environment, in the vicinity of a river mouth or estuary, which is consistent with the variable energy regime indicated by sedimentological analyses (i.e. alternating sand- and silt-dominated sediments, Fig. 4.3).

The relative abundances of herbaceous plant (HP) and open and disturbed habitat (O) Coleoptera are generally low (1.9% mean and 0.6% mean, respectively), though they reach their maximum combined relative abundance in this zone (11.8%, 137.5 cm) (Fig. 4.7). Beetles associated with herbaceous plants were unfortunately not identifiable to species-level, but provide some information. *Phyllotreta* sp. mostly feed on Brassicaceae species, and may be agricultural pests in a modern context, whilst *Apion* sp. and *Ceutorhynchus* sp. feed on various herbaceous taxa (Harde 1984). Open and disturbed habitat beetles are more informative, indicating the presence of dry, open habitats. *Agrypnus murina* is found in an array of dry, open environments (Koch 1989b), and *Melanotus punctolineatus* develops at the roots of grasses in dry, sandy soils (Koch 1989b; Hyman 1992). Deciduous trees or shrubs were evidently locally present, but not necessarily abundant, as the woodland and tree fauna in this zone is represented by a single occurrence of *Orchestes* sp. which feed on a variety of deciduous taxa (Harde 1984).

Decaying, foul and rotten habitat (DE) and dung-obligate (DU) taxa collectively reach their highest proportional abundance in this zone (20% maximum, 9.9% mean), primarily represented by *Anotylus* and *Aphodius* species (Table 4.4). They indicate the presence of herbivores and generally rotten habitats (e.g. flood refuse, plant debris), in both shaded and open contexts. *Anotylus sculpturatus* and *A. tetracarinatus* are eurytopic species of foul and rotten environments, including carrion, dung and plant debris, and *A. rugosus* has similar habits, but often in waterside contexts (Koch 1989a; Anderson 1997). *Aphodius subterraneus*, is similarly polyphagous, but with a noted preference for open habitats (Lane & Mann 2016). Both *Aphodius rufipes* and *A. coenosus* are coprophilous on the dung of various herbivores, but *A. rufipes* tends to be associated with shaded habitats, whilst *A. coenosus* has a preference for exposed, sandy areas (Koch 1989b).

Coleopteran Zone WR-C2 (85-20 cm)

In zone WR-C2 (85-20 cm) (Table 4.4, Fig. 4.7) fully aquatic beetles are generally slightly more abundant than aquatic ecotone groups (45.7% and 43.0% means, respectively), though wetland edge taxa (WE) remain the most significant individual group (31.5% mean). Species representative of wetland edge habitats in this zone are broadly similar to those in WR-C1: an array of Donaciinae, accompanied by *Bagous* sp. and *Notaris acridulus*. *Plateumaris sericea* remains the most abundant taxon in this context, though the frequency and abundance of *P. rustica* increase. *Donacia impressa* and *P. discolor*, which were absent from WR-C1, each occur singly in this zone. *D. impressa* feeds on various Cyperaceae, and *P. discolor* is found on a range of marshland plants, often in more acidic wetlands (Cox 2007).

The relative abundances of riparian and waterside taxa (RW) are generally lower than in the previous zone (7.9% mean), though the group includes several additional taxa. *Pterostichus nigrita*, a marshland species typically found close to freshwater (Lott 2003; Luff 2007), is present in this zone alongside several non-specific waterside Carabids (e.g. *Bembidion* spp.). The Staphylinid representatives of this group in WR-C2 are generally hygrophilous species with a preference for waterside habitats. *Micropeplus caelatus* is found in marshes and alluvial environments (Koch 1989a), as well as on wet moorlands (Lott 2003). Both *Bledius femoralis* and *Carpelimus rivularis* have a preference for exposed sediments (Lott 2003), though *C. rivularis* may also be found amongst alluvial plant debris and in alder carrs (Koch 1989a), and *Stenus juno* is a eurytopic wetland species (Lott & Anderson 2011). *Aphodius niger* and *A. plagiatus* remain present, indicating open habitats adjacent to the wetland. More generalist hygrophilous species (H) are present in similar abundances to the previous zone (3.6% mean). These include *Arpedium brachypterum*, which is broadly eurytopic (Koch 1989a), and *Stenus circularis* and *S. clavicornis*: eurytopic hygrophilous species, which tend to inhabit damp, but not wet, habitats (Lott & Anderson 2011).

Assemblages of fully aquatic functional groups exhibit only minor changes in taxonomic composition, indicating stability in the general characteristics of wetland habitats. However, some changes in abundances are noted, perhaps signifying changes in the relative importance of different aquatic habitats. Amongst the fully aquatic functional groups, aquatic generalists (AG) remain most significant (30.5% mean) (Table 4.4, Fig. 4.7). This is primarily driven by high abundances of *Hydraena riparia*, though Dytiscidae indet., *Helophorus* sp., *Hydraena britteni* and *Ochthebius minimus* are also present. *H. britteni* is generally an inhabitant of pools and ponds, but is also found in lotic contexts (Hansen 1987). Lentic specialists (AS) in WR-C2 are represented by the same taxa as in WR-C1 (with the exception of the halophilous *Helophorus fulgidicollis*, which is absent in this zone), but their proportional abundance is greater (12.8% mean). This appears to be largely driven by increased abundances of *Tanysphyrus lemnae* in this zone. Relative abundances of lotic specialists (AF) are slightly lower than in the preceding zone (2.4% mean), and continue to be represented by *Elmis aenea* and *Normandia nitens*, in addition to *Hydraena pygmaea*, which is found amongst mossy stones in streams and rivers (Koch 1989a; Foster 2000). This combination of lentic and lotic taxa is consistent with the variable energy regime indicated by sedimentological analyses (i.e. alternating sand- and silt-dominated sediments, Fig. 4.3).

Occurrences of beetles associated with herbaceous plants (HP) and open and disturbed habitats (O) in WR-C2 remain sporadic, and in low abundances (Table 4.4, Fig. 4.7). The former group is represented by the same taxa as in WR-C1, with the exception of *Phyllotreta* sp. However, whilst open and disturbed habitat beetles were represented by Elateridae (*Agrypnus murinus*, *Melanotus punctolineatus*) in WR-C1, in this zone they are represented by the weevils (Curculionidae) *Graptus triguttatus* and *Otiorhynchus rugifrons*. These are both polyphagous herbivores with a preference for plants growing in relatively dry, open habitats (Koch 1992). *Graptus triguttatus* also has a reported preference for *Plantago lanceolata* (Koch 1992). Thus, despite taxonomic change in the fossil assemblage, the representation of dry, open disturbed habitats remains constant from WR-C1 to WR-C2.

Woodland and tree taxa (WTG, WTD, WTC) in this sequence are primarily confined to WR-C2 (85-20 cm), represented by eight taxa from four families (Carabidae, Coccinellidae, Chrysomelidae, Curculionidae) (Table 4.4, Fig. 4.7). The bark beetle (Scolytinae) *Scolytus multistriatus* is primarily associated with *Ulmus* spp., and the weevil *Magdalis phlegmatica* is oligophagous on *Pinus* spp. (Bullock 1993; Koch 1992), indicating the local presence of these tree taxa. *Scolytus* sp. and *Orchestes* sp. may be associated with various deciduous trees (Harde 1984), and *Chilocorus renipustulatus* is a eurytopic predator of Coccidae (Hemiptera) on deciduous trees (Majerus 1991). *Notiophilus biguttatus*, whilst not an obligate woodland species, has a noted preference for light woodland environments, and is often found amongst leaf litter (Lindroth 1985; Luff 2007). Similarly, *Crepidodera* sp. are generally associated with *Populus* spp. and *Salix* spp. (Cox 2007), but may also be associated with other plants (Harde 1984). Similarly, *Otiorhynchus clavipes* is polyphagous on herbs, shrubs and trees often, but not exclusively, in a woodland context (Koch 1992; Morris 1997). Collectively, these taxa indicate that woodland habitats were locally present in this section of the record, but were likely to have been relatively light.

The proportional abundance of beetles associated with decaying, foul and rotten habitats (DE) and dung (DU) decreases notably in zone WR-C2 (85-20 cm) (4.3% mean and 0.5% mean, respectively) (Table 4.4, Fig. 4.7). However, they exhibit little change in absolute abundances and are broadly stable in terms of taxa, though *Anotylus sculpturatus*, *A. tetracarinatus* and *Aphodius subterraneus* are not present (Table 4.4). The Histerid *Margarinotus carbonarius*, which inhabits dung, rotting vegetation and fungi (Koch 1989a) occurs singly in WR-C2. Similarly, *Anotylus fairmairei*, which is a eurytopic coprophile (Koch 1989a; Hyman 1994), occurs once in this zone. Collectively, these taxa indicate little functional change from the previous zone.

Coleopteran Zone WR-C3 (20-0 cm)

In the uppermost zone (WR-C3, 20-0 cm) (Table 4.4, Fig. 4.7), absolute abundances of sub-fossil Coleoptera are particularly low (7.5 mean total MNI). The zone is also notable for an almost total lack of species representing fully aquatic habitats, with the exception of a single occurrence of *Tanysphyrus lemnae*. However, wetland habitats are still represented, and wetland edge beetles (WE) are the most abundant group in this zone (48.3% mean). This group is taxonomically impoverished relative to previous zones, but still contains *Donacia cinera*, *D. sparganii*, *Plateumaris rustica*, *P. sericea* and *Bagous* sp. A single occurrence of *Apion* sp. represents the herbaceous plant-associated taxa (HP) in this zone, and there are no occurrences of either open and disturbed habitat taxa (O) or woodland and tree taxa (WTG, WTD and WTC). However, decaying, foul and rotten habitat (DE) and dung-obligate (DU) taxa remain present (14.0% combined mean), represented by *Aphodius* sp. and *A. coenosus*, respectively. The absence of certain groups in this zone is more likely related to taphonomic change, rather than ecological change, given the accompanying decreased total MNI. Indeed, sedimentological analyses (Fig. 4.3) indicate sediment stabilisation in this section of the record, which may indicate terrestrialisation at the sampling site, and diminished fluvial inputs. Thus, it is difficult to draw inferences regarding ecological change on the basis of this zone, though a change in the taphonomic environment signals some local landscape change. This may be related to terrestrialisaton of the depositional basin, fluvial channel migration or avulsion away from the site, or post-depositional weathering.

5.4.3.3. Coleoptera: Climatic inferences

Coleopteran mutual climate range (MCR) estimates provide evidence for a temperate climate throughout the sequence (Fig. 4.8, Table 4.5). Range estimates vary between samples, providing broad (e.g. 0-5 cm: 9.1°C to 30.5 summer, -13.4°C to 8.5°C winter) and more constrained (e.g. 100-105 cm: 15.25°C to 20.25°C summer, -5.5°C to 4.1°C winter) estimates, but as these ranges overlap through the entirety of the sequence, they provide no evidence of changes in climatic conditions. The area of overlap between range estimates for all samples provides an estimate of climate comparable to the region at present: average warmest month temperatures of 15.25°C to 20.25°C, average coldest month temperatures of -5.5°C to 2.45°C and average annual temperature range of

15.5°C to 22.3°C (Figure 4.8). All species used in producing these estimates (see Table 4.6) are currently present in Britain, though *Arpedium brachypterum* and *Aphodius subterraneus* have not been recorded in East Anglia, and the latter is somewhat rare across Europe (GBIF 2016; NBN 2016).

It is worth noting that the narrowest estimates within this sequence (100-105 cm, 80-85 cm, 50-55 cm) are largely constrained by the presence of *Aphodius plagiatus*. The georeferenced records used in the construction of its climate envelope are drawn from Britain, southern Scandinavia and southern Central Europe (GBIF 2016), but this represents only part of its full distribution. *Aphodius plagiatus* is known to be present throughout Europe (excluding the extreme north) and the Palaearctic, as well as North Africa (Tunisia) (Pivotti *et al.* 2011; Akhmetova & Frolov 2014), though the extent of its altitudinal distribution across this range is not known. This wide distribution suggests that *A. plagiatus* is tolerant of a broader range of climatic regimes than those contained within its MCR climate envelope, and therefore its 'real' climate envelope is likely to be broader. This is a recognised issue with certain species when using the MCR method (Milne 2016).

Table 4.5 Mutual Climatic Range (MCR) estimates for the new West Runton fauna (WR14, Fig. 4.2) presented here, based on new (Milne 2016) MCR methods

Sample Number	**Median Sample Depth (cm)**	**TMax (°C)**	**TMin (°C)**	**TRange (°C)**	**Number of Species**
1	2.5	9.1 to 30.5	-13.4 to 8.5	9.3 to 37.5	1
2	7.5	n/a	n/a	n/a	0

(Continued overleaf)

Table 4.5 Continued

3	12.5	n/a	n/a	n/a	0
4	17.5	14.25 to 25.5	-15.5 to 4.1	12.2 to 32	1
5	22.5	n/a	n/a	n/a	0
6	27.5	12.4 to 27.5	-16.5 to 7	8.4 to 40	2
7	32.5	12.4 to 28.5	-16.5 to 9	8.4 to 35	1
8	37.5	12.4 to 28	-14.3 to 6.5	9.1 to 33	3
9	42.5	12.4 to 28.5	-16.5 to 9	8.4 to 35	1
10	47.5	13 to 25.5	-16.5 to 7	9.6 to 35	3
11	52.5	14 to 20.25	-5.5 to 5	10.5 to 22.3	3
12	57.5	12.4 to 27.5	-16.5 to 7	8.4 to 40	2
13	62.5	12.4 to 25.5	-13.6 to 8	8.9 to 33	4
14	67.5	12.4 to 27	-13.6 to 8.75	8.7 to 30.8	3
15	72.5	13 to 25.5	-13.75 to 7	9.1 to 35	4
16	77.5	12.4 to 25.5	-14.6 to 5	11.3 to 33	4
17	82.5	14 to 20.25	-5.5 to 5	10.5 to 22.3	2
18	87.5	n/a	n/a	n/a	0
19	92.5	n/a	n/a	n/a	0
20	97.5	n/a	n/a	n/a	0
21	102.5	15.25 to 20.25	-5.5 to 4.1	12.25 to 22.3	5

(Continued overleaf)

Table 4.5 Continued

22	107.5	12.5 to 25.45	-14.36 to 2.45	12.2 to 33	3
23	113.5	12.4 to 26.9	-13.6 to 7	9.1 to 30.8	4
24	121	11.25 to 25.5	-14 to 8.5	8.75 to 38.5	1
25	127.5	12.4 to 28.5	-16.5 to 9	8.4 to 35	1
26	132.5	n/a	n/a	n/a	0
27	137.5	13.5 to 25.5	-10 to 5.5	15.5 to 32.75	4
28	142.5	12.4 to 28.5	-16.5 to 9	8.4 to 35	1
29	147.5	12.4 to 27	-13.6 to 7	9.1 to 31.8	3
30	152.5	12.4 to 25.5	-13.8 to 8.5	8.75 to 35	2
31	158.5	12.4 to 28.5	-16.5 to 9	8.4 to 35	1
Total Fauna	-	15.4 to 20.25	-5.5 to 2.2	16.1 to 22.3	18

(Continued overleaf)

Table 4.6 Species utilised in WR14 (Fig. 4.2) Mutual Climatic Range (MCR) reconstructions

MCR Species	TMax (°C)	TMin (°C)	TRange (°C)	Sample Presence (Sample Nos.)
Notiophilus biguttatus (F.)	8.85 to 28.5	-21.5 to 10.2	8.65 to 41	14
Notiophilus palustris (Duftschmid)	9.1 to 30.5	-13.45 to 6	9.3 to 37.5	1
Pterostichus nigrita (Payk.)	11.35 to 25.5	-19.5 to 3.35	8.65 to 40	10
Pterostichus strenuus (Panz.)	9.65 to 25.5	-14.5 to 7	12.2 to 38.5	22
Helophorus strigifrons (Thoms.)	11.25 to 25.5	-14 to 6.45	8.75 to 38.5	13, 15, 24, 27, 30
Hydraena britteni (Joy)	11.15 to 25.5	-16.5 to 8.5	8.7 to 35	8, 13, 16
Hydraena gracilis (Germ.)	10.35 to 28	-15.55 to 8	8.55 to 31.5	13, 16, 22, 23
Hydraena riparia (Kug.)	12.4 to 28.5	-16.5 to 9	8.4 to 35	6-17, 21-23, 25, 27-31
Ochthebius minimus (F.)	13 to 30.5	-24.5 to 9	8.8 to 40	10, 14, 27
Arpedium brachypterum (Grav.)	7.45 to 25.5	-25 to 5	11.35 to 41.5	16
Anotylus rugosus (F.)	9.95 to 27.5	-19.5 to 0	9.05 to 40	6, 12, 15
Anotylus sculpturatus (Grav.)	12.1 to 30.5	-7.5 to 5	9.3 to 33	21

(Continued overleaf)

Table 4.6 Continued

Platystethus nodifrons (Mann.)	13 to 30.5	-24.5 to 9	8.8 to 40	4, 21
Stenus clavicornis (Scop.)	9.35 to 27	-24.5 to 2.8	9.3 to 41.5	11
Stenus juno (Payk.)	9.55 to 30.5	-24.5 to 10	9.05 to 41.5	8
Aphodius rufipes (L.)	4.3 to 27.35	-14.25 to 12.25	8.7 to 30.8	14, 23, 29
Aphodius subterraneus (L.)	13.25 to 30.5	-10 to 8	15.45 to 33	27
Aphodius plagiatus (L.)	13.95 to 20.3	-5.45 to 4.95	10.5 to 22.35	11, 17, 21

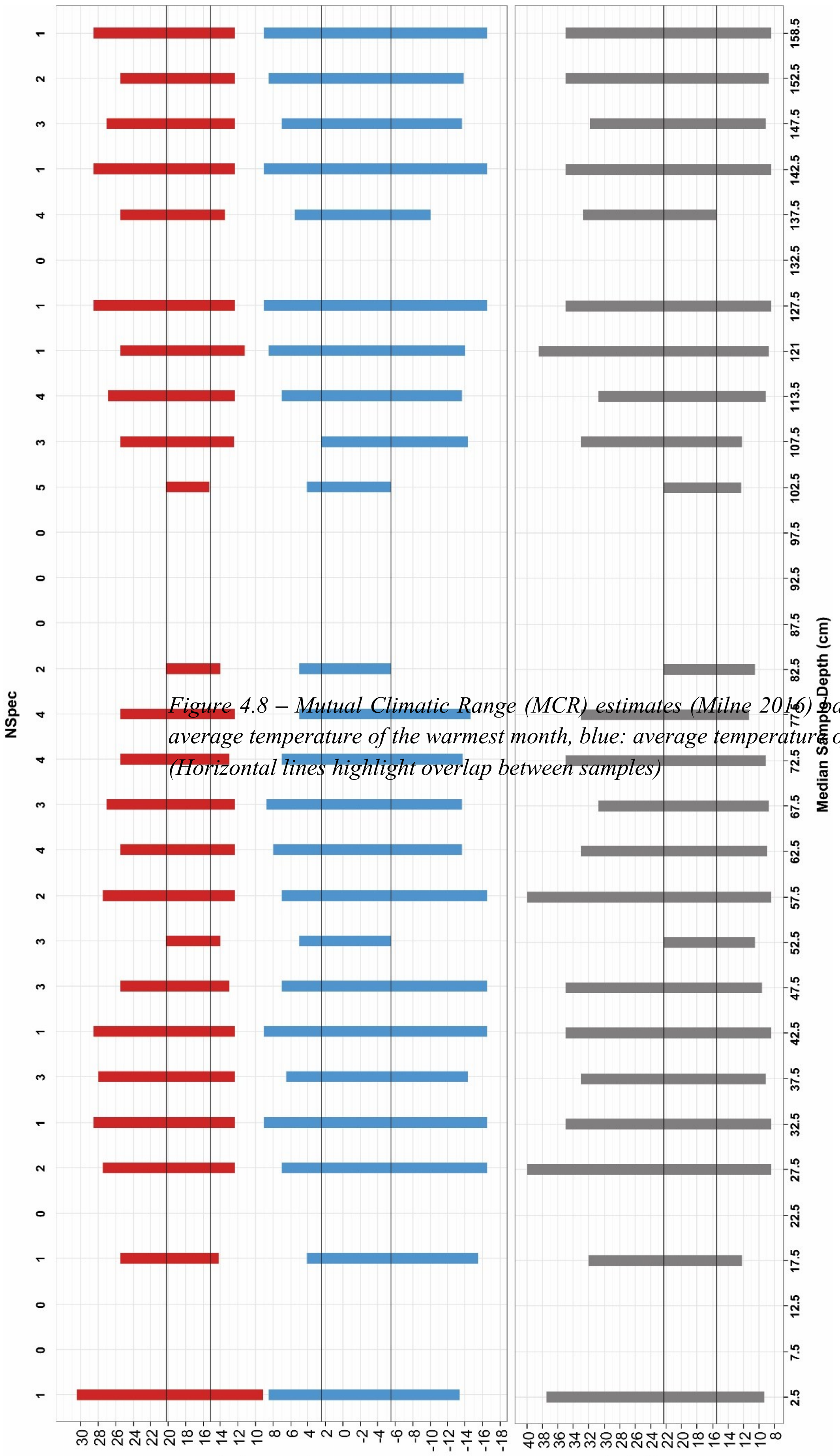


Figure 4.8 – Mutual Climatic Range (MCR) estimates (Milne 2016) based on coleoptera f average temperature of the warmest month, blue: average temperature of the coldest month (Horizontal lines highlight overlap between samples)

4.4.4. Coope's West Runton Coleoptera

This section presents beetle assemblages from the West Runton Freshwater Bed published by Coope (2000, 2010b) (see Figure 4.1 for sampling locations), re-analysed using a functional group approach (Table 4.7; Fig. 4.9) and Milne (2016) MCR (Fig. 4.10, Table 4.8). This gives emphasis to important aspects of the fauna in an ecological context, provides more accurate climatic reconstructions and facilitates comparison with the new coleopteran record from West Runton presented in this chapter (WR14: Section *5.4.3.*). Taxonomy has been updated according to Duff (2012).

Table 4.7 Sub-fossil Coleoptera from the West Runton Freshwater Bed (Coope 2000, 2010b) (AG: Aquatic (general); AS: Aquatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG: Woodland/Trees (general); WTD: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed; DE: Decaying/Foul/Rotten (general); DU: Dung; UN: Uncategorised or Eurytopic)

Family	**Species**	**Habitat Category**	**Median Sample Depth (cm) and Faunal Zone**												**Bulk (Coope 2000)**
			145	135	125	115	105	95	85	75	65	55	45	35	
			Co-C1						**Co-C2**						
Gyrinidae															
	Gyrinus sp.	AG		1	1	1	1								1
Dytiscidae															
	Agabus sp.	AG									1				1
	Ilybius sp.	AG		1											1
	Rhantus grapii (Gyll.)	AS				1		1							
Carabidae															
	Carabus sp.	UN					1								
	Elaphrus riparius (L.)	RW				1	1								1
	Loricera pilicornis (Fab.)	H													1
	Clivina fossor (L.)	H				2									
	Trechus secalis (Payk.)	H			1	1									
	Trechus obtusus (Er.)	H		1		1									1
	Bembidion clarkii (Dawson)	RW		1											
	Bembidion doris (Panz.)	RW			1	1	1								
	Bembidion guttula (Fab.)	RW		1		1							1		1
	Bembidion spp.	RW				2	1	1							5
	Patrobus atrorufus (Strøm)	WTD		1		1									1
	Pterostichus melanarius (Ill.)	O						1							
	Pterostichus gracilis (Dejean)	RW		1	1	1									1
	Pterostichus nigrita (Payk.)	RW		1		1		1							
	Pterostichus diligens (Sturm)	H				1			1						
Helophoridae															
	Helophorus nanus (Sturm)	AS		1											
	Helophorus sp.	AG	1	1											2
Histeridae															
	Histerinae indet.	DE				1		1						1	

(Continued overleaf)

Table 4.7 (continued)

Family	**Species**	**Habitat Category**	**Median Sample Depth (cm) and Faunal Zone**												**Bulk (Coope 2000)**
			145	135	125	115	105	95	85	75	65	55	45	35	
			Co-C1						**Co-C2**						
Hydrophilidae															
	Hydrobius fuscipes (L.)	AS		1		1									1
	Laccobius sp.	AG			1										
	Cercyon ustulatus (Preys.)	RW			1										2
	Cercyon convexiusculus (Steph.)	DE	1	1	2	1	2								
	Cercyon sternalis (Sharp)	DE				1									
	Cercyon tristis (Ill.)	RW													3
	Sphaeridium scarabaeoides (L.)	DU				1									
Hydraenidae															
	Hydraena sp.	AG	6	12	7	6	4	1							94
	Ochthebius bicolon (Germ.)	AG			1										
	Ochthebius minimus (Fab.)	AG					1								1
Leiodidae															
	Anisotoma sp.	WTG	1			1									
Staphylinidae															
	Olphrum fuscum (Grav.)	H				1									
	Micropeplus caelatus (Er.)	RW				1									1
	Brachygltua fossulata (Reich.)	H													1
	Tachinus rufipes (L.)	DE													1
	Tachyporus sp.	H													1
	Gymnusa sp.	H													1
	Aleocharinae indet.	DE	1		1		1	1							8
	Anotylus rugosus (Fab.)	DE		1	2	2	1	1							4
	Carpelimus sp.	H		1											2
	Stenus juno (Payk.)	RW			1			1							
	Stenus spp.	H				1		1							5
	Lathrobium sp.	H			1			1	1						1
	Gyrohypnus punctulatus (Payk.)	DE				1									
Scarabaeidae															
	Aphodius porcus (Fab.)	DU					1		1				1		
	Aphodius sp.	DE			1	3	2	1		1	1	1			1
	Serica brunnea (L.)	O			1										1
Scirtidae															
	Scirtidae indet.	RW													1
Dascillidae															
	Dascillus cervinus (L.)	O		1	1	1	1	1							
Buprestidae															
	Trachys sp.	UN					1								
Dryopidae															
	Dryops sp.	AF													1
Elateridae															
	Agrypnus murinus (L.)	O				1	1	1							
Ptinidae															
	Anobium cf. *punctatum* (De Geer)	WTG					1	1	1						
Coccinellidae															
	Coccinella septempunctata (L.)	O						1							
	Corylophus cassidoides (Marsh.)	H													3
Anthicidae															
	Anthicus sp.	O													1
Chrysomelidae															
	Donacia cinerea (Hbst.)	WE			1	1	1	1					1		
	Donacia clavipes (F.)	WE	1		1		1	1					1		1
	Donacia semicuprea (Panz.)	WE			2	1	1	1	1					2	3
	Donacia sparagnii (Ahrens)	WE													1
	Donacia thalassina (Germ.)	WE				1									
	Donacia sp.	WE			1										
	Plateumaris bracata (Scop.)	WE			1				1	1					
	Plateumaris rustica (Kunze)	WE	1	1	2	4	1	1	1	1	1	1	1		3
	Plateumaris sericea (L.)	WE						1							2
	Phaedon tumidulus	HP													1

(Continued overleaf)

Table 4.7 (continued)

Family	**Species**	**Habitat Category**	**Median Sample Depth (cm) and Faunal Zone**												**Bulk (Coope 2000)**
			145	135	125	115	105	95	85	75	65	55	45	35	
			Co-C1						**Co-C2**						
Apionidae															
	Apion sp.	HP			2	1		1	2	1					1
Erirhinidae															
	Notaris acridulus (L.)	WE		1	5	10	3	5	1	2	1	1	1	1	2
	Notaris scirpi (Fab.)	WE	1	1	1		1	1							
	Tanysphyrus lemnae (Payk.)	AS	1		4	3	2	1	1						13
Curculionidae															
	Curculio nucum (L.)	WTD													1
	Curculio venosus (Grav.)	WTD							1						1
	Mecinus pyraster (Hbst.)	HP								1					
	Bagous sp.	WE			1	1	2		1						2
	Limnobaris dolorosa (Goeze)	WE													1
	Micrelus ericae (Gyll.)	O											1		1
	Phytobius sp.	RW				1		1							1
	Graptus triguttatus (Fab.)	O					2	2							
	Otiorhynchus ligustici (L.)	O			1										
	Polydrusus sp.	WTD		1			1				1				1
	Tropiphorus sp.	UN						1	1						
	Pissodes pini (L.)	WTC			1										
	Orobitis cyaneus (L.)	HP			1										
	Scolytus intricatus (Ratz.)	WTD													1
	Scolytus multistriatus (Marsh.)	WTD				1									1
	Polygraphus poligraphus (L.)	WTC			1										
		Taxon Richness	9	20	31	38	26	28	13	6	5	3	7	3	50
		Total MNI	14	31	49	62	36	33	14	7	5	3	7	4	187

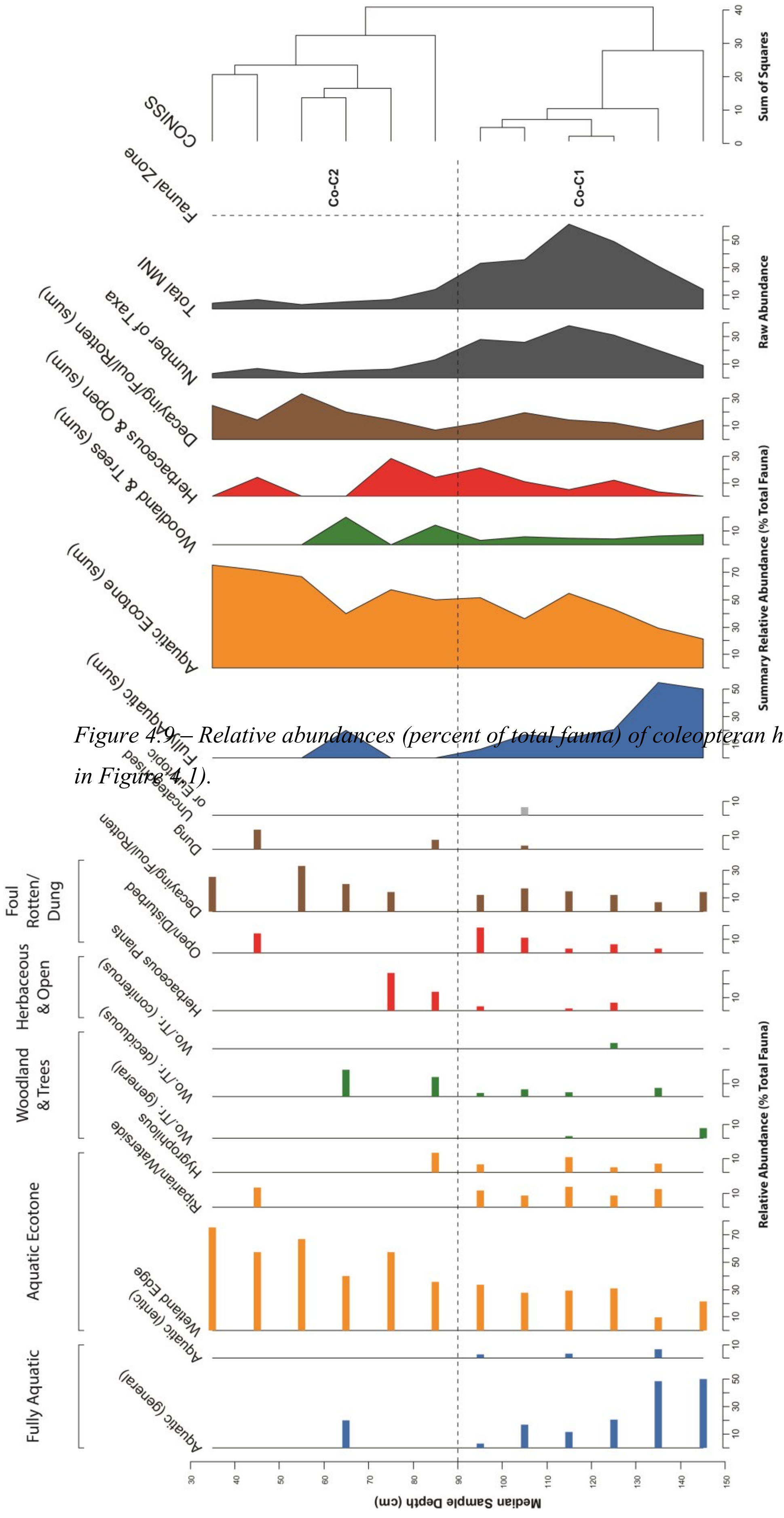


Figure 4.9 – Relative abundances (percent of total fauna) of coleopteran habitat groups from West Ru in Figure 4.1).

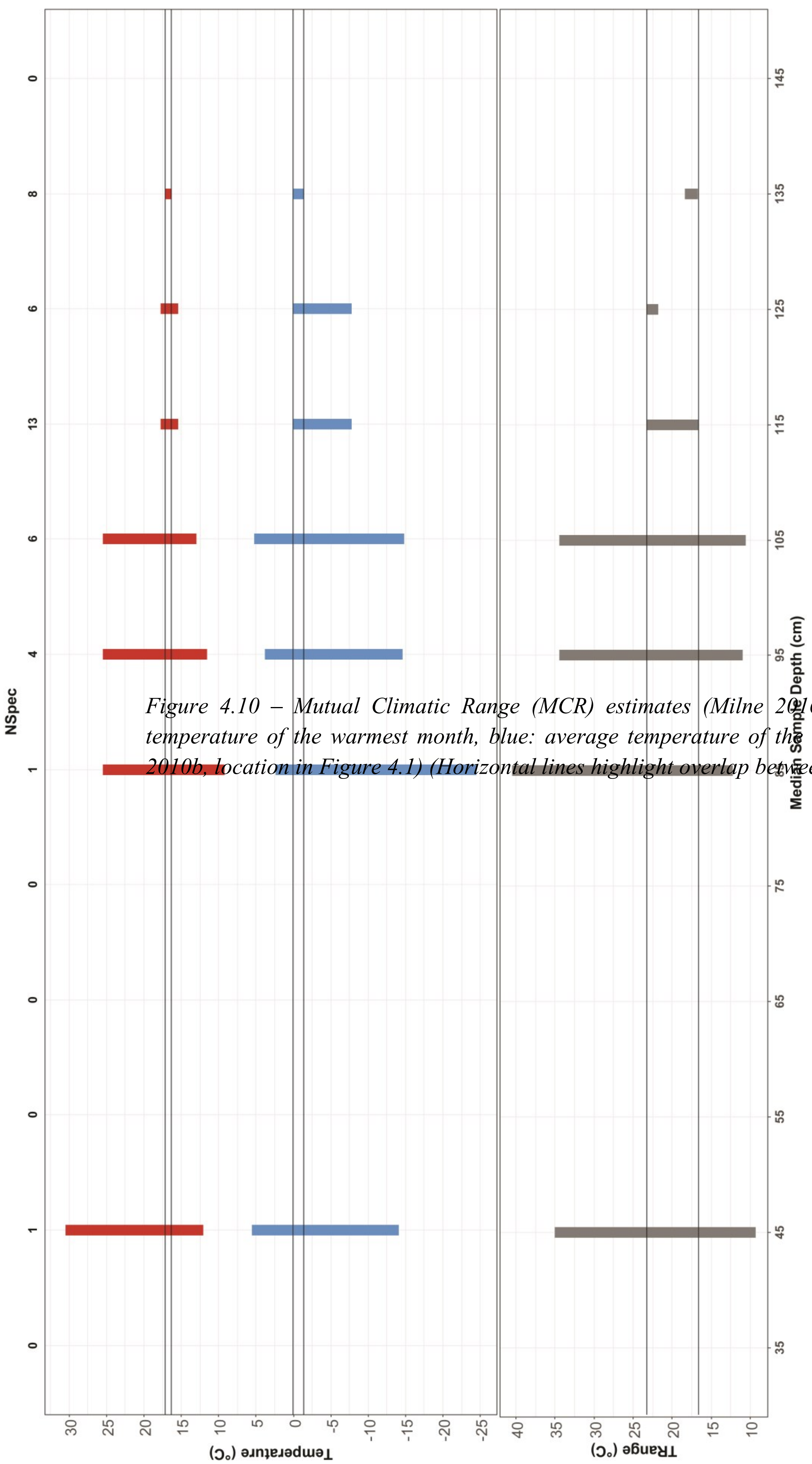


Figure 4.10 – Mutual Climatic Range (MCR) estimates (Milne 2016) based on coleopt
temperature of the warmest month, blue: average temperature of the coldest month, grey:
2010b, location in Figure 4.1) (Horizontal lines highlight overlap between samples)

Table 4.8 Mutual Climatic Range (MCR) estimates for the Coope (2000, 2010b) (location in Figure 4.1) West Runton fauna, based on new (Milne 2016) MCR methods

Sample Number	Median Sample Depth (cm)	TMax (°C)	TMin (°C)	TRange (°C)	Number of Species
55	35	n/a	n/a	n/a	0
56	45	12.1 to 30.5	-14.1 to 5.5	9.3 to 35	1
57	55	n/a	n/a	n/a	0
58	65	n/a	n/a	n/a	0
59	75	n/a	n/a	n/a	0
60	85	9.25 to 25.5	-24.5 to 2.4	12.2 to 40.5	1
61	95	11.6 to 25.5	-14.6 to 3.8	10.95 to 34.5	4
62	105	13 to 25.5	-14.8 to 5.3	10.6 to 34.5	6
63	115	15.45 to 17.8	-7.8 to 0.1	16.65 to 23.3	13
64	125	15.5 to 17.8	-7.8 to 0.1	21.8 to 23.3	6
65	135	16.4 to 17.2	-1.35 to 0.1	16.7 to 18.4	8
66	145	n/a	n/a	n/a	0
Total Fauna (Coope 2010b)		16.35 to 17.2	-1.35 to 0.1	16.7 to 18.4	19
Bulk Sample (Coope 2000)		15.5 to 17.8	-7.8 to 0.1	16.7 to 23.3	8

4.4.4.1. Coope's West Runton Coleoptera: Landscape and ecology

The coleopteran sequence has been divided into two zones: Co-C1 (150-90 cm) and Co-C2 (90-30 cm) (Table 4.7; Fig. 4.9). The assemblages are principally dominated by wetland-associated and aquatic Coleoptera, though a range of terrestrial habitat types are also represented, including both woodland and open habitats.

Coleopteran Zone Co-C1 (150-90 cm)

The lower of the two zones (Co-C1: 150-90 cm) is characterised by declining proportions of fully aquatic taxa, which range from 54.8% to 6.1% relative abundance (27.1% mean) (Table 4.7; Fig. 4.9). These are almost exclusively taxa assigned to 'aquatic generalists' (AG), with occasional occurrences of lentic taxa (AS). Lotic taxa (AF) are absent from both assemblage zones. Taxa classified as aquatic generalists in this zone are largely those with genus-level identifications, for which finer taxonomic resolution is necessary to determine whether they are derived from lentic or lotic environments (e.g. *Gyrinus* sp., *Illybius* sp., *Hydraena* sp.), though also includes *Ochthebius bicolon* and *O. minimus*. Both of these species may be found in either flowing or still conditions (Koch 1989a), though *O. bicolon* exhibits some preference for low-energy edges of flowing water habitats (Hansen 1987). Lentic specialists include *Rhantus grapii*, an inhabitant of vegetated, often shaded, pools (Koch 1989a; Foster & Friday 2011), *Helophorus nanus*, which has an apparent preference for temporary ponds (Foster 2000) and *Tanysphyrus lemnae*, which is oligophagous on *Lemna* spp. (duckweed) and other small floating-leaved plants (Koch 1992). Together, these taxa indicate the presence of a low-energy waterbody, perhaps with seasonally fluctuating margins creating temporary habitats and potentially low-level fluvial input. However, the relative importance of these habitats appears to decline.

Relative abundances of wetland edge (WE) Coleoptera increase gradually through this zone (min: 9.7%, max: 33.3%, mean: 25.3%), and are derived from Donaciinae (Chrysomelidae), Erirhinidae and Curculionidae (Table 4.7; Fig. 4.9). They indicate that aquatic habitats were fringed with abundant semi-aquatic grasses and sedges. *Plateumaris rustica*, which is oligophagous on *Carex* spp. (Koch 1992), is the most frequently occurring reed beetle (Donaciinae). Others include *Donacia cinera*, which feeds on *Typha*, *Phragmites*, *Sparganium* and *Carex* (Koch 1992) and *D. semicuprea*, which is monophagous on *Glyceria* spp. (Koch 1992). The weevil, *Notaris acridulus* also typically feeds on *Glyceria* spp. and occurs frequently throughout Co-C1, whilst *N. scirpi* feeds on *Scirpus*, *Carex* and *Typha* (Koch 1992). *Bagous* sp. are semi-aquatic, living on various aquatic macrophytes at wetland edges (Harde 1984).

Riparian and waterside taxa (RW) are relatively consistent in this zone (9.3% mean relative abundance), and provide evidence of both shaded and exposed waterside habitats. *Bembidion clarkii* and *Pterostichus gracilis* are typically found on marshy sites, with abundant vegetation, the former often in a woodland or reedbed context (Lindroth 1985), and the latter amongst grasses and sedges (Lindroth 1985). *Cercyon ustulatus* and *Micropeplus caelatus* may both be associated with wet plant debris and flood refuse (Koch 1989a; Foster *et al.* 2014b), and in this context are likely part of the reedbed fauna. However, *Elaphrus riparius* is confined to areas with unshaded, exposed sediments (Lindroth 1985), suggesting that vegetation cover was somewhat discontinuous. Other taxa present which are typically associated with waterside habitats (e.g. *Bembidion doris*, *Stenus juno*) are broadly eurytopic in this context, and may also inhabit bogs (Koch 1989a).

Generalist hygrophilous taxa (H) are less consistent in their presence, and occur in slightly lower abundances than riparian and waterside taxa (4.6% mean). Some of the hygrophilous taxa present, such as *Pterostichus diligens* and *Olophrum fuscum*, are eurytopic in damp habitats (Koch 1989a). *Clivina fossor* is also broadly eurytopic, though requires some low vegetation (Lindroth 1985). *Trechus secalis* is more specialist, and has a preference for moist, shaded habitats, particularly in woodlands (Lindroth 1985). *Corylophus cassidoides* is also a specialist, of damp grasslands and reedbeds (Koch 1989a). Together, these taxa indicate the presence of damp microhabitats in both open and shaded areas.

Coleoptera associated with trees and woodland habitats (WTG, WTD, WTC) are present throughout Co-C1 (150-90 cm) (Table 4.7; Fig. 4.9). These are primarily deciduous specialists, but woodland generalists and coniferous specialists are also represented, together comprising 5.2% (mean relative abundance) of assemblages in this zone. These groups include species associated with dead and decaying wood, such as *Anobium punctatum* (woodworm), which is found in dry wood, from both deciduous and coniferous trees (Harde 1984; Koch 1989a), and *Anisotoma* sp., which are saprophagous on various types of wood-associated fungi (Harde 1984; Koch 1989a). Bark beetles (Scolytinae), which attack old and dying trees include *Scolytus multistriatus*, which is primarily associated with *Ulmus* spp., and *Polygraphus poligraphus*, which feeds on various conifers (Koch 1992; Bullock 1993). Similarly, the weevil, *Pissodes pini*, is specific to *Pinus* spp., but targets older trees (Koch 1992; Bullock 1993). *Polydrusus* sp. occur on various deciduous trees and shrubs (Harde 1984). The Carabid, *Patrobus atrorufus*, is a woodland litter species typically found in deciduous floodplain and fen woodlands (Koch 1989a). These species are indicative of the presence of well-established woodland habitats, incorporating both deciduous and coniferous trees.

Decaying, foul and rotten habitat (DE) and dung-obligate (DU) taxa collectively account for 13.2% (mean relative abundance) of assemblages in zone Co-C2 (Table 4.7; Fig. 4.9). Amongst decaying, foul and rotten habitat species, *Cercyon convexiusculus* and *Anotylus rugosus* are the most numerous, and are both broadly eurytopic, but often associated with waterside habitats (Koch 1989a). *Gyrohypnus punctulatus* is eurytopic in decaying plant matter (Harde 1984). Scarabaeidae are largely represented by *Aphodius* sp., which are assigned to 'DE' as this genus includes both coprophagous and saprophagous species. However, *Aphodius porcus* is recognised, which is a relatively eurytopic dung-obligate species, with some preference for grassland habitats (Lane & Mann 2016).

Coleopteran Zone Co-C2 (90-30 cm)

The upper zone, Co-C2 (90-30 cm) is characterised by a general absence of fully aquatic, riparian and waterside, and hygrophilous taxa (Table 4.7; Fig. 4.9). This zone is also notably characterised by low total MNI throughout (6.7 mean minimum individuals per sample), which may partially account for low representation of these groups and should be borne in mind. Wetland edge (WE) taxa are dominant in this zone, comprising 55.3% of assemblages on average. Species composition within this group is similar to the preceding zone, with *Plateumaris rustica* and *Notaris acridulus* occurring most frequently. This suggests that marshy and reedbed-type habitats may have expanded locally in this part of the record, but that their characteristics (e.g. composition of vegetation assemblages) remained relatively constant. The accompanying lack of fully aquatic taxa (with the exception of a single occurrence of *Agabus* sp.) suggests that the expansion of these habitats may have been a result of wetland terrestrialisation. Riparian and waterside (RW) and hygrophilous (H) taxa are equally scarce in this zone, each represented by single individuals: the former by *Bembidion guttula*, a eurytopic hygrophilous riparian species, and the latter by *Pterostichus diligens*, which is similarly catholic in its preferences.

Coleoptera associated with deciduous woodland and trees continue to be present, though not consistently. They are represented by two weevils (Curculionidae): *Polydrusus* sp., which feed on various deciduous trees and shrubs (Harde 1984), and *Curculio venosus*, which is oligophagous on *Quercus* spp. (Koch 1992; Bullock 1993). These taxa demonstrate the continued presence of deciduous trees in the local vicinity.

Beetles associated with herbaceous plants and open habitats have a similarly inconsistent presence in this zone. *Mecinus pyraster* is oligophagous on *Plantago* spp., and *Micrelus ericae* feeds on various Ericaceae (Koch 1992; Bullock 1993), together indicating the presence of dry, open disturbed areas. *Apion* sp., which feed on various herbaceous plants (Harde 1984), are also present.

In spite of the low MNI per sample in zone Co-C2 (90-30 cm), Coleoptera associated with decaying, foul and rotten habitats, and dung, occur consistently throughout (Table 4.7; Fig. 4.9). With the exception of one Histerinae indet. specimen, these are exclusively either *Aphodius porcus* or *Aphodius* sp. Histerinae species are predatory and occur in a range of contexts, including dung, carrion and decaying plant matter (Harde 1984). *Aphodius* sp. may be found in a similar range of contexts, and are often dung-associated. *Aphodius porcus*, a relatively eurytopic coprophile (Lane & Mann 2016), provides firm evidence of continued herbivore presence in this zone.

These assemblages are broadly similar, in functional terms, to WR14 assemblages (Section *4.4.3.*), though there are some differences. The most notable distinguishing characteristic between the two records is in the relative proportions and diversity of full aquatic and woodland functional groups, respectively. The WR14 assemblages are notably richer (in terms of number of species and relative abundance) in both lentic (e.g. *Helophorus strigifrons*, *Hydraena palustris*) and lotic (e.g. *Hydraena gracilis*, *Normandia nitens*) specialist aquatic taxa. Coope's (2010b) assemblages, on the other hand, are most notably richer in specialist (as opposed to generalist) arboreal and woodland taxa (e.g. *Patrobus atrorufus*, *Curculio venosus*, *Pissodes pini*, *Polygraphus poligraphus*). This is discussed further in Section *4.5.3.*

4.4.4.2. Coope's West Runton Coleoptera: Climate

New climatic reconstructions based on Coope's (2000, 2010b) coleopteran assemblages provide evidence of temperate conditions, with little suggestion of substantial climate change (Fig. 4.10, Table 4.8). This is in broad agreement with Coope's (2010b) prior assessments, albeit with a greater level of detail. All of the beetle taxa utilised are currently present in Britain, and most are eurythermic species with broad distributions (e.g. *Ochthebius minimus*, *Anotylus rugosus*). In the lower part of the record (150-110 cm), these taxa are accompanied by less eurytopic species, with more restricted distributions: *Bembidion clarkii* and *Pterostichus gracilis*. These species provide more constrained climatic estimates (e.g. 140-130 cm: 16.4°C to 17.2°C summer, -1.4°C to 0.1°C winter). The former, *B. clarkii*, is largely restricted to oceanic and coastal areas of Northwest Europe (Lindroth 1985; GBIF 2016), which have relatively low seasonality, cool summers and mild winters. *P. gracilis* has a broader distribution, and is present throughout Europe (below *c.*60-61°N) (Lindroth 1985; GBIF 2016), as well as in western and southwestern Siberia and Central Asia (Kryzhanovskij *et al.* 1995). Whilst the eastern range of *P. gracilis* (in Siberia and Central Asia) is not included in GBIF (GBIF 2016) (the distributional data used to construct climate envelopes, see Section *3.3.1.*), this is compensated for by the inclusion of the majority of its range across Western, Central and Northern Europe (extending from Western Ireland to Finland, as well as including Germany and Austria, GBIF 2016). The distribution of *B. clarkii* in GBIF appears to be relatively comprehensive in coverage of its full range. Thus, the distributions of both species as recorded in GBIF (GBIF 2016) are sufficient to give reasonable estimates of their thermal tolerance.

The upper part of the record (110-30 cm) lacks species with more constrained climatic envelopes, and climatic estimates are correspondingly broader (e.g. 100-90 cm: 11.6°C to 25.5°C summer, -14.6°C to 3.8°C winter) (Fig. 4.10, Table 4.8). These estimates are based on species such as *Patrobus atrorufus*, *Anotylus rugosus* and *Bembidion guttula*, which have broader distributions than *B. clarkii* and *P. gracilis*, (GBIF 2016) and have broader thermal tolerance ranges. However, given that the absence of less eurythermic species (e.g. *B. clarkii*) coincides with declining overall abundances of sub-fossil beetle remains in the record (see Figure 5.9) this should not be taken as evidence for climatic change. Rather, their absence from the record is more likely related to taphonomic changes.

These reconstructions are broadly similar to those based on WR14 assemblages, giving no evidence of climatic distinction between different records. Assemblages from both sequences provide evidence for deposition in temperate conditions, broadly similar to the region at present. This is discussed further in Section *4.5.3.*

4.4.5. Multivariate Analyses

The results of ordination analyses (principal components analysis, canonical correspondence analysis) applied to pollen and coleopteran datasets are presented in this section. These analyses aim to identify underlying co-variance between taxa, functional groups and environmental proxies, explore relationships between beetle and pollen records, and to provide a more nuanced perspective of assemblages than possible with just a stratigraphic diagram. As discussed in Chapter 3, multivariate analyses of Coleoptera assemblages use functional groups, rather than taxa, to compensate for the stochastic occurrences of individual species/genera and to facilitate ecologically-based interpretations.

4.4.5.1. Correlation analysis

The correlation matrix (Fig. 4.11) demonstrates statistical relationships between various groups of taxa and proxies of environmental variables in the WR14 sequence. A number of the more significant paired relationships are between deciduous tree pollen ('Decidu') and other variables, including with Poaceae pollen ('Poacea') (r=-0.89), *Sordaria*-type spores ('Sordari') (r=-0.73), organic content ('Organic') (r=0.81) and $CaCO_3$ content ('$CaCO_3$') (r=-0.81). Deciduous pollen is also weakly correlated with *Sporormiella*-type spores ('Sporor') (r=0.44). Poaceae pollen exhibits some weaker relationships with other variables, including *Sporormiella*-type spores (r=-0.58), *Sordaria*-type spores (r=0.64), organic content (r=-0.71) and $CaCO_3$ content (r=0.71).

Coleopteran functional groups generally do not exhibit strong relationships with other variables (Fig. 4.11), though the correlation between charcoal ('Charco') and fully aquatic Coleoptera ('FullyAq') is a notable exception (r=-0.81). Aquatic ecotone Coleoptera ('AqEcot') exhibit weak correlations with charcoal (r=0.51), fully aquatic

Coleoptera (r=-0.47) and organic content (r=0.43). Coleoptera associated with herbaceous plants and open/disturbed habitats also exhibit a weak correlation with organic content (r=-0.42), and Coleoptera associated with foul/rotten habitats and dung exhibit a weak positive relationship with herbaceous pollen (r=0.53).

Collectively, these correlations indicate the particular significance of deciduous trees and grasses (Poaceae) in the palaeolandscape, and suggest potential interactions between herbivory (indicated by *Sporormiella*-type and *Sordaria*-type spores) and vegetation, which are investigated further in the following sections. Whilst paired relationships involving coleopteran functional groups are generally weak, they are not entirely negligible, and further multivariate investigation remains worthwhile. The exception is the relatively strong negative relationship (r=-0.81) between charcoal and fully aquatic Coleoptera, potentially suggesting that fire was more prevalent when wetland habitats were more limited (i.e. when the immediate landscape was drier), though this may also reflect a taphonomic signal.

Figure 4.11 – Paired correlations between biotic (groups of pollen types and coleopteran functional groups) and abiotic variables (sedimentary properties, charcoal) from the WR14 (Fig 4.2) West Runton sequence.

(Decidu: deciduous tree and shrub pollen; Conifer: coniferous tree and shrub pollen; Poacea: Poaceae pollen; Herbs: non-grass herbaceous pollen; Aquatic: aquatic pollen; Ferns: fern spores; Sporor: Sporormiella-type spores; Sordari: Sordaria-type spores; Charco: charcoal; FullyAq: fully aquatic Coleoptera; AqEcot: aquatic ecotone Coleoptera; WoTre: woodland/tree Coleoptera; HerbOp: herbaceous plant and open/disturbed habitat Coleoptera; FoRuDu: Foul/Rotten/Dung-associated Coleoptera; PhiMea: average grain size; Organic: organic content; $CaCO_3$: calcium carbonate content

4.4.5.2. Ordinations of palynological assemblages

The PCA of major pollen and spore taxa (Fig. 4.12) provides an ecological perspective of pollen assemblages more nuanced than possible with just a stratigraphic diagram. The first axis (PC1) accounts for 21.1% of variability within the sequence, and the second (PC2) accounts for 14.8%. Therefore, 64.1% of variability in the sequence is unaccounted for in Figure 4.12.

The first axis (PC1, explaining 21.1% of variability) is strongly influenced by *Alnus* pollen abundances (Fig. 4.12). These exhibit negative covariance with a number of taxa, including Poaceae, *Sordaria*-type spores, *Pinus*, *Abies* and *Chenopodium*, which are drawn from a range of relative source areas. *Sordaria*-type spore source areas are highly local (<10 m, Baker *et al.* 2016), *Abies* pollen is likely to be derived from within 50-100 m of the sampling site (Poska & Pidek 2010) and *Pinus* may be drawn from within several kilometres (Poska & Pidek 2010).This suggests that the negative co-variance between these taxa and *Alnus* may represent a landscape-scale gradient. *Alnus* abundances are also positively associated with taxa such as *Fraxinus*, *Plantago* and *Sporormiella*-type spores. This may be indicative of a wetness gradient, as *Alnus* generally tolerate wetter conditions than *Abies* and *Chenopodium*, but this is complicated by Poaceae, which is a broad family and may represent either dry-ground or wetland taxa (or more likely, both), and *Pinus* which may grow in both saturated and well-drained edaphic conditions (Bunting 2008). The second axis (PC2, explaining 14.8% of variation) suggests negative covariance between *Potamogeton* (and other aquatic taxa, such as *Typha latifolia* and *Nuphar*, though less significantly) and an array of dry-ground, predominantly herbaceous, taxa. These include *Ranunculus acris*, Caryophyllaceae, Asteraceae, *Rumex*, *Galium* and *Filipendula*, in addition to *Ulmus*. This more clearly suggests a discrete wetness gradient, and that moisture levels are influential in determining vegetation community structure. However, the relative source areas of aquatic and dry-ground taxa are important to note here, as proportions of dry-ground pollen may also be influenced by patterns of in-washing, whereas aquatic pollen is more likely to be derived from *in situ* macrophytes.

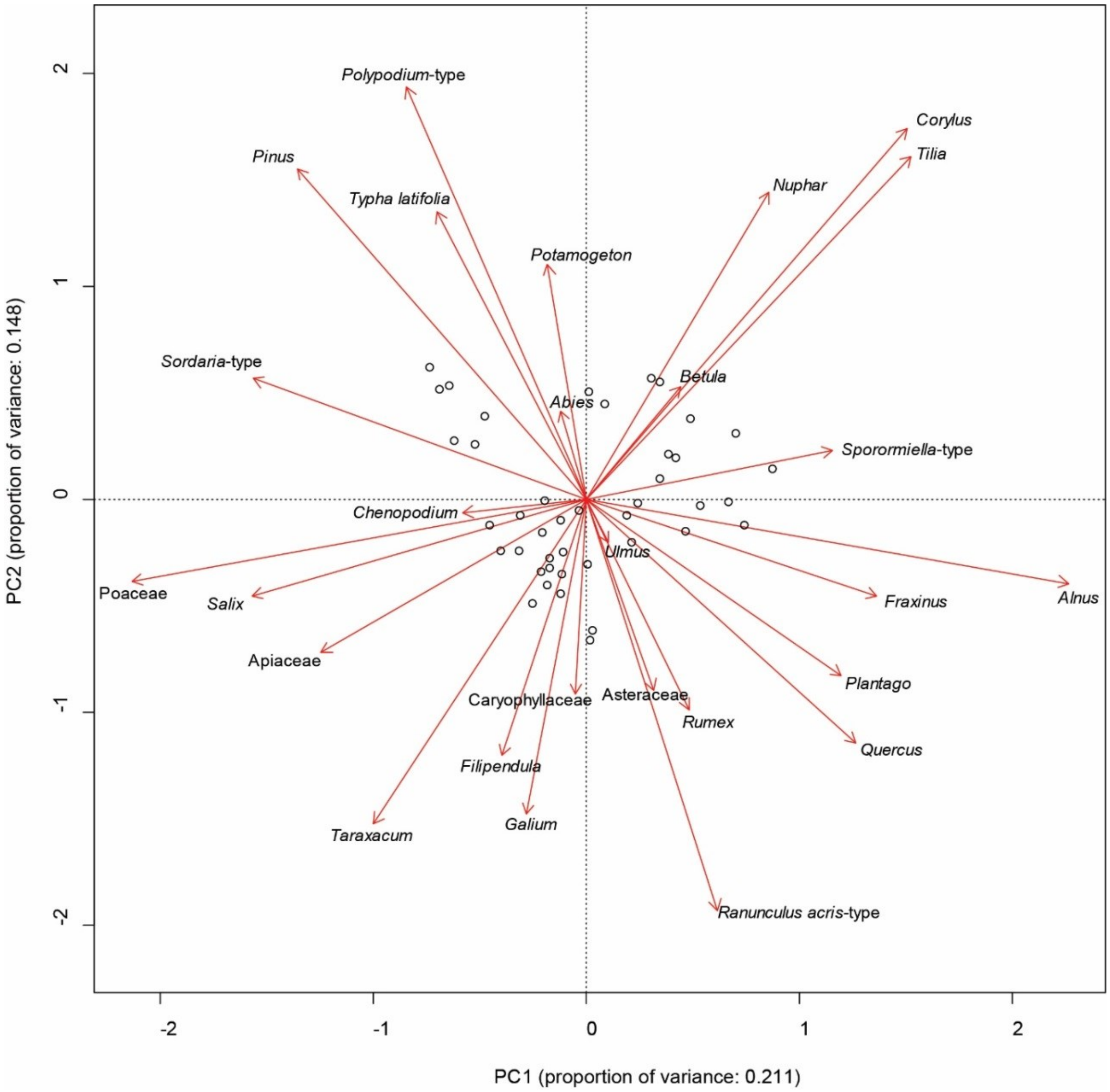


Figure 4.12 – PCA of major pollen and spore taxa from the West Runton Freshwater Bed (WR14, Fig. 4.2) (Circles represent samples)

Figure 4.13 demonstrates the extent to which relative abundances of major pollen and fern spore taxa co-vary with concentrations of coprophilous fungal spore taxa, concentrations of microcharcoal shards and sedimentological variables. Thirty point seven percent of variance is explained by the first axis (CCA1), and the second (CCA2) accounts for 13.4%. This CCA indicates two distinct modes of deposition in the sequence (silt-dominated and sand-dominated), each associated with characteristic pollen and spore assemblages. However, 55.9% of variability amongst major pollen taxa is unaccounted for in Figure 4.13, and this should be borne in mind in the following discussion.

Sporormiella-type concentrations are closely related to the primary axis (CCA1), and also to sedimentary organic and silt content (Fig. 4.13), in accordance with coincident shifts in each of these variables at *c.* 60 cm (Figs. 4.3 & 4.6). A diverse range of taxa is also associated with negative values on CCA1 (the left side of the biplot), including *Alnus*, *Tilia*, *Fraxinus*, *Plantago*, *Corylus* and *Nuphar*. (*n.b.* Abundances of *Nuphar* are typically <1% and its covariance with other taxa should be interpreted very cautiously.) Samples plotting with positive values on CCA1 (the right side of the biplot) are associated with more sandy, carbonate-rich sediments, and higher charcoal concentrations. These are associated with taxa such as Poaceae, *Salix*, Apiaceae and *Pinus*. The association between more sand-dominated sediments and microcharcoal is likely to partially reflect some deposition of charcoal via alluvial and fluvial processes, and pollen assemblages may have been similarly affected (*cf.* Brown *et al.* 2008), though the precise nature of these effects cannot be determined. Collectively, this indicates that herbivory is an influential factor in structuring vegetation communities, but suggests that they are also influenced by wildfire and hydrogeomorphic processes (e.g. alluvial deposition and erosion). Throughout the sequence, a positive correlation (p=0.404) may also be found between *Pinus* and microcharcoal. The lack of covariance between *Sporormiella*- and *Sordaria*-type spores, previously demonstrated in Figure 4.11, is also emphasised here. This highlights the distinct autecological characteristics of these fungal types, as they appear to be associated with separate components of the vegetation community.

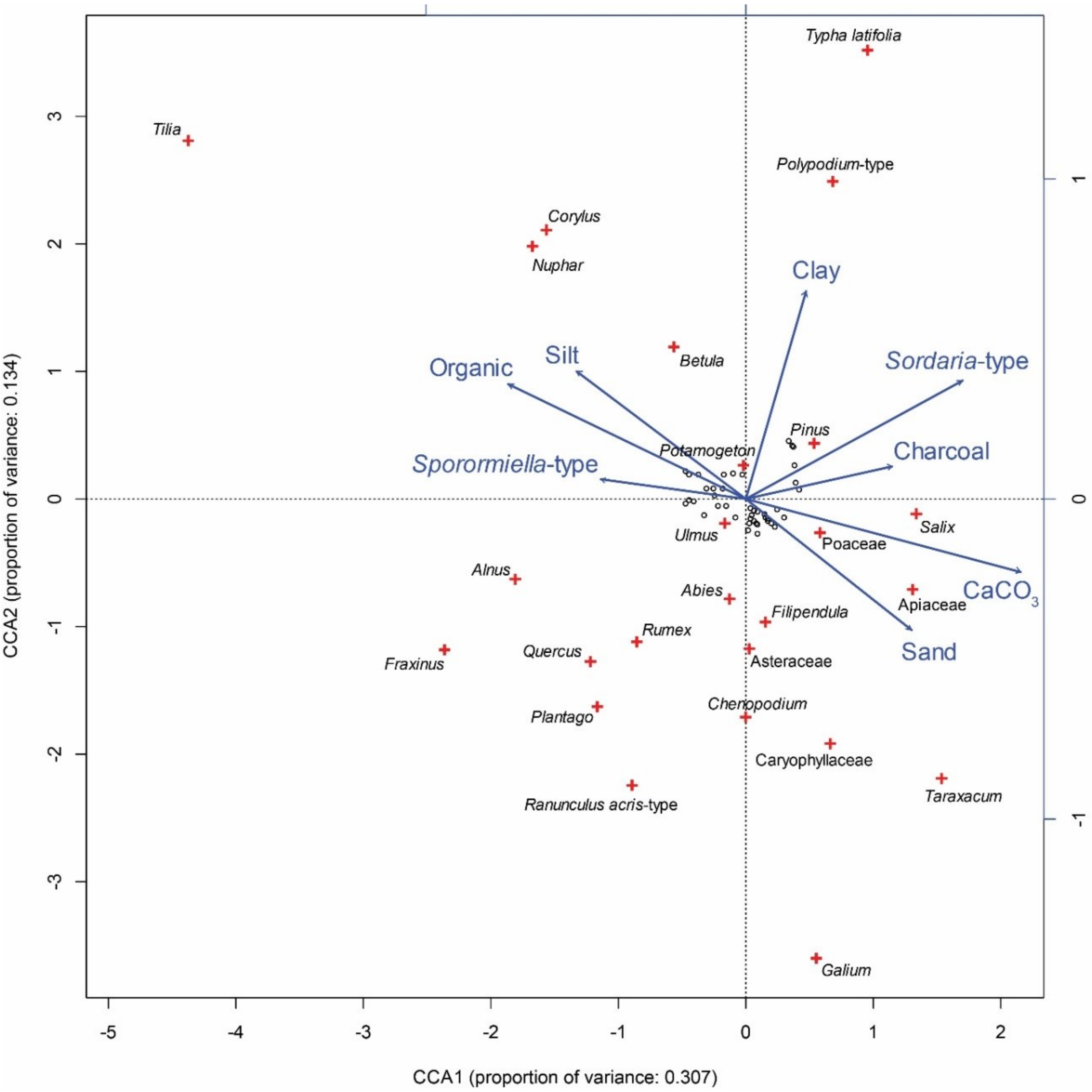


Figure 4.13 – CCA of major pollen and spore taxa with environmental proxies from the West Runton Freshwater Bed (WR14, Fig. 4.2) (Circles represent samples)

4.4.5.3. Ordinations of coleopteran assemblages

As with pollen assemblages, PCA of Coleopteran functional groups (Fig. 4.14) provides insights into numerical relationships, which are complimentary to qualitative stratigraphic analyses. The first axis (PC1) accounts for 19.4% of variability in the sequence, and the second (PC2) accounts for 14.4%. Therefore, 66.2% of variability in the sequence is unaccounted for in Figure 4.14. As noted in Chapter 3 (Section *3.3.4.*), the low MNI values (<50, *cf.* Hill 2015) for many of the coleopteran samples render conclusions drawn from these analyses (PCA and CCA) tentative.

The first axis appears to be associated with relative abundances of wetland marginal taxa (WE), which are predominantly Donaciinae, and uncategorised or eurytopic taxa (UN). Aquatic generalist (AG) and lentic taxa (AS) exhibit negative covariance with these groups, reflecting the abundance of *Hydraena riparia* and *Tanysphyrus lemnae* in WR-C2 (Tables 4.3 & 4.4, Fig 4.7). This is also true of lotic taxa (AF), though their presence in the record is more sporadic, and they occur in lower abundances. This suggests a gradient in the prevalence of different habitats within the wetland. Beetles from open and disturbed habitats (O) and deciduous woodland and tree habitats (WTG) also appear to be negatively associated with wetland marginal taxa, suggesting a wetness gradient, similar to pollen assemblages (Fig. 4.12), though the more intermittent occurrence of these groups makes interpretations more tentative. The second axis is strongly aligned with the relative abundances of riparian and waterside taxa (RW), which positively co-vary with foul and rotten habitat taxa (DE) and taxa from herbaceous plants (HP), all of which appear to be more prevalent in WR-C1 (Fig. 4.7). Both dung-obligate (DU) and generalist woodland and tree taxa (WTG) negatively covary with riparian and waterside taxa, but these are groups with discontinuous distributions in the sequence. The negative relationship between foul and rotten, and dung-obligate taxa is more likely to be a result of taphonomy than ecology. The major contributors to both of these groups in this sequence are species of *Aphodius*. When preservation is such that they are identifiable to species, *Aphodius* are often assigned to 'DU', whereas genus-level identifications are assigned to 'DE', as discussed (*4.3.3.*

Coleoptera: Landscape and Ecology), leading to an apparent disconnect between 'DU' and 'DE' groups.

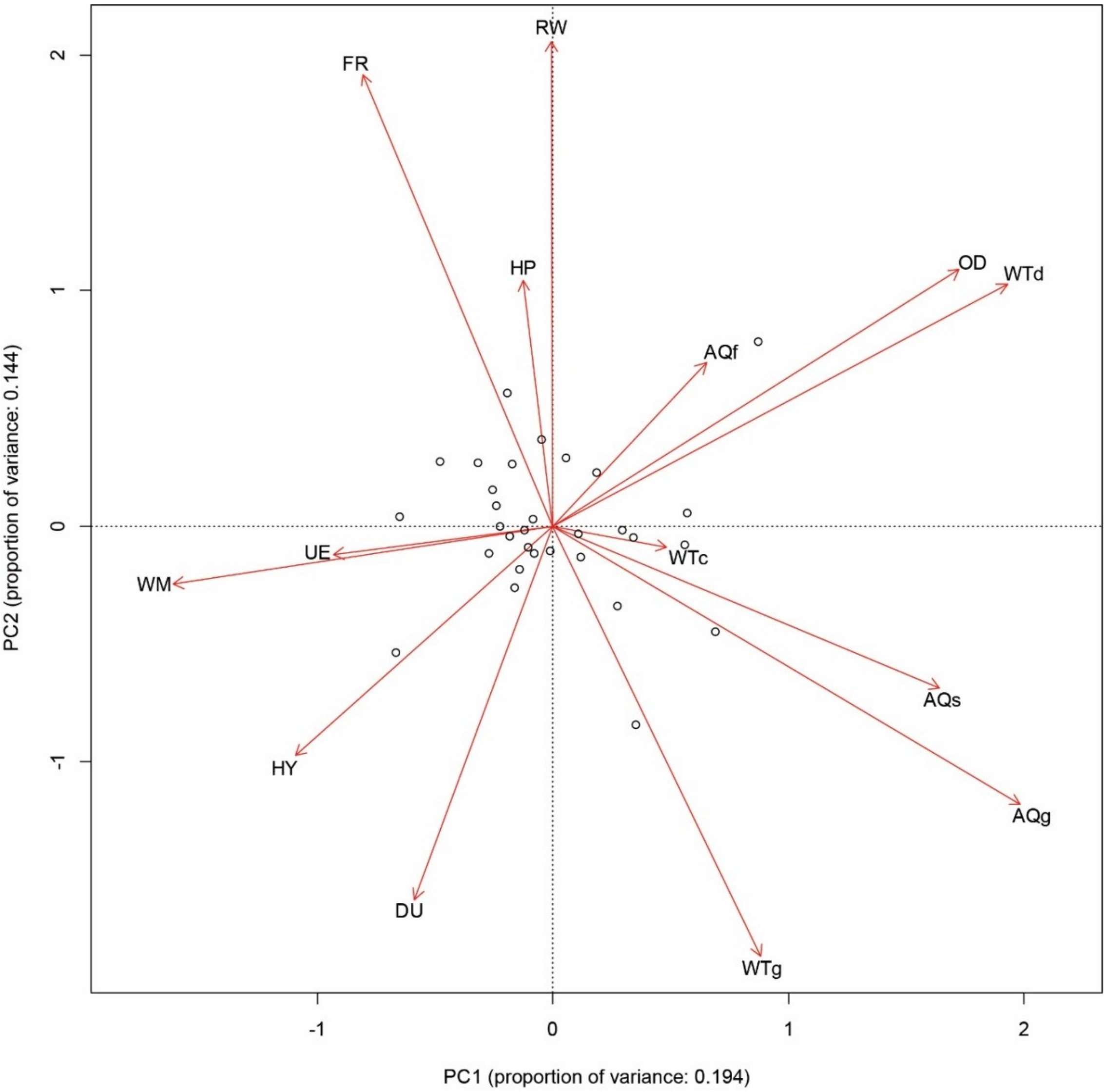


Figure 4.14 – PCA of coleopteran habitat groups from the West Runton Freshwater Bed (WR14, Fig. 4.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

The extent to which relative abundances of coleopteran functional groups co-vary with concentrations of coprophilous fungal spore taxa, concentrations of microcharcoal shards and sedimentological variables is demonstrated in Figure 4.15. Fourteen percent of variance is explained by the first axis (CCA1), 7.1% is explained by the second (CCA2). Therefore, 78.9% of variability is unaccounted for in Figure 4.15.

Generally, coleopteran groups do not appear to be related to the environmental proxies (fungal spores, charcoal, sedimentological properties) here, and although several do exhibit some association, ecological explanations for these associations are not necessarily straightforward (Fig. 4.15). Some covariance between riparian and waterside taxa (RW), many of which have preferences for disturbed riparian environments (e.g. various *Bledius* species), and *Sordaria*-type spores may be the result of herbivores creating disturbed waterside habitats, though this may also reflect a preference for moisture in *Sordaria*-type. However, the stronger association of lotic aquatic taxa (AF) with *Sordaria*-type spores is more difficult to explain in ecological terms, though as discussed, its stochastic distribution adds to this difficulty, and renders analyses of covariance rather tentative. Similarly, the occurrence of open and disturbed taxa (O) is too discontinuous to attach particular meaning to its apparent covariance with $CaCO_3$. Conversely, whilst an association between hygrophilous beetles (H) and clay content may be meaningful, reflecting the prevalence of damp terrestrial habitats in the vicinity of standing water bodies, clay content is actually relatively low and broadly consistent through the sequence. Given that almost 80% of variance is not represented by the first two axes, and few meaningful relationships can be discerned between coleopteran functional groups and environmental proxies, it appears that the environmental variables represented exert little direct influence on coleopteran assemblages here.

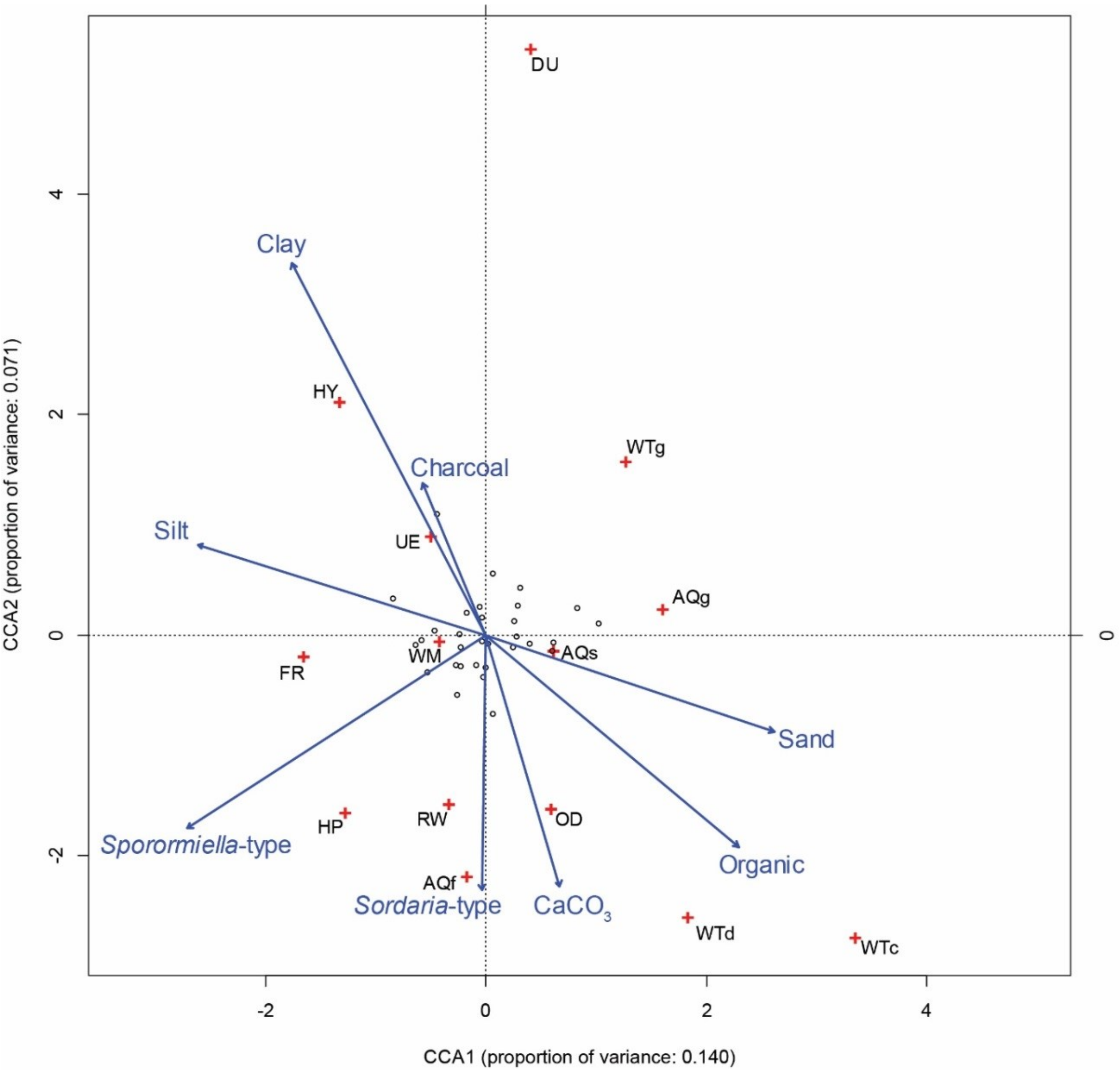


Figure 4.15– CCA of coleopteran habitat groups and environmental proxies from the West Runton Freshwater Bed (WR14, Fig. 4.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

4.4.5.4. Ordinations of combined palynological and coleopteran assemblages

Principal components analysis of palynological and coleopteran assemblages simultaneously (Fig. 4.16) allows relationships between the datasets to be explored, elucidating potential links between vegetation and beetle assemblages. As in the previous section, the low MNI values (<50, *cf.* Hill 2015) for many of the coleopteran samples render conclusions drawn from these analyses tentative. The first axis (PC1) represents 16.8% of variance, and the second (PC2) represents 13.1%, and so 70.1% of variance is unaccounted for here. Interestingly, when the palynological and entomological datasets are subjected to PCA independently (Figs. 4.12 & 4.14), the combined eigenvalues of PC1 and PC2 are greater than the combined eigenvalues in Figure 4.16.

Associations between pollen taxa in Figure 4.16 are broadly consistent with those in Figure 4.12. The first axis (PC1) is closely correlated with *Alnus* and *Fraxinus* abundances, which strongly exhibit distinct negative covariance and with Poaceae, *Sordaria*-type spores and *Salix*, perhaps suggesting the occurrence of *Sordaria*-type spores in more open habitats. As in Figure 4.12, the second axis (PC2) indicates negative covariance between wetland (e.g. *Nuphar*, *Potamogeton*) and herbaceous (e.g. *Ranunculus acris*-type, *Filipendula*, *Taraxacum*) taxa. Similarly, covariance between coleopteran functional groups is relatively consistent with Figure 4.14, and the primary gradient in these assemblages is between wetland marginal (WE) and hygrophilous (H) taxa, and aquatic generalist and lentic (AG, AS) taxa on the second axis in Figure 4.16. This axis appears to represent a moisture gradient in pollen assemblages, but interestingly, fully aquatic beetles (AG, AS, AF) are associated with the dryland and herbaceous pollen taxa, whilst wetland marginal (WE) and hygrophilous (H) taxa are associated with fully aquatic plant types (*Nuphar*, *Potamogeton*). This appears counterintuitive, but it is well-documented that sub-fossil pollen and beetles are drawn from differently-sized catchments (Kenward 2006; Smith *et al.* 2010; Hill 2015), and so each may represent different aspects of local ecology and landscape.

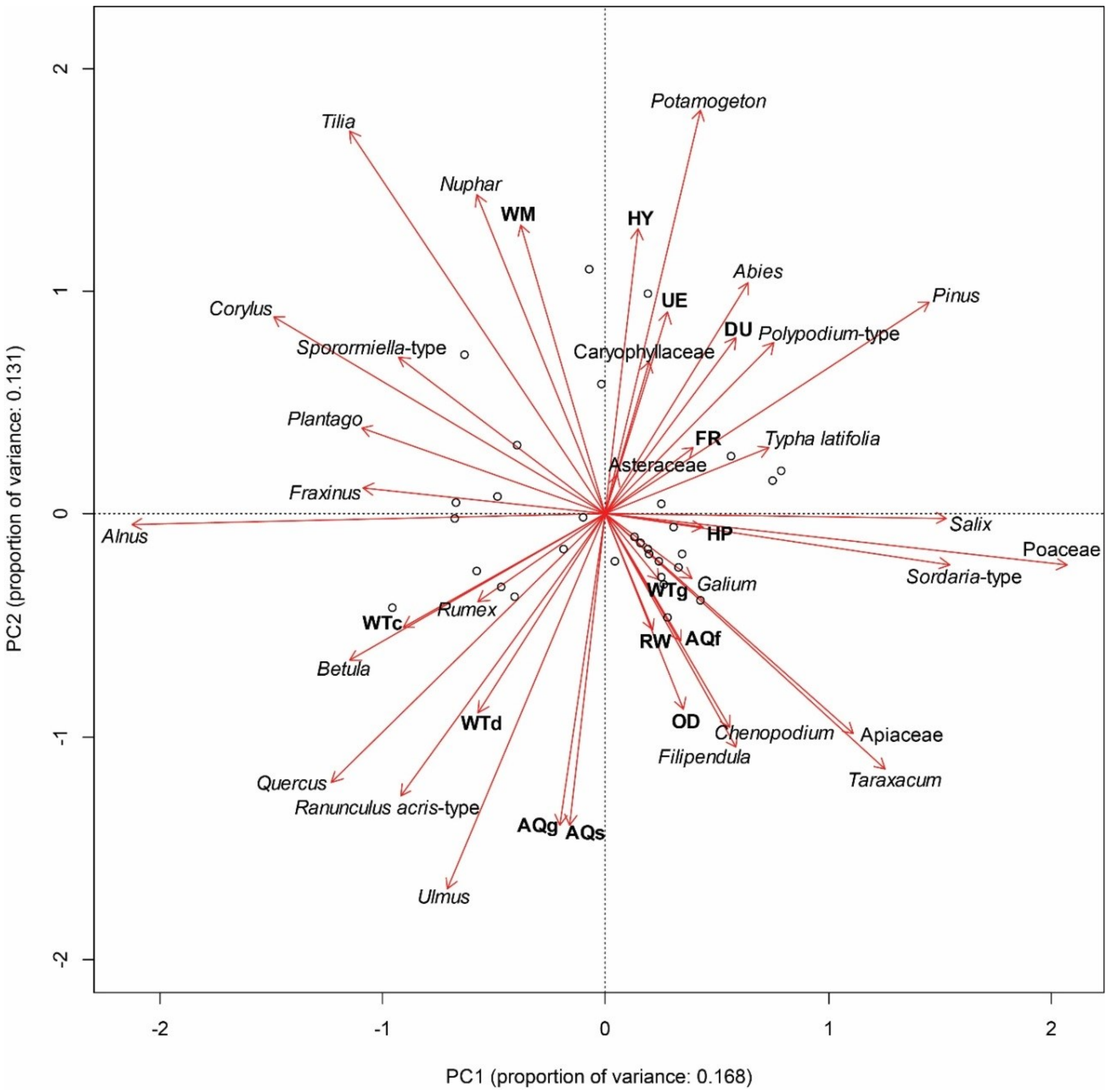


Figure 4.16 – PCA of major pollen and spore taxa, and coleopteran habitat groups from the West Runton Freshwater Bed (WR14, Fig. 4.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

4.4.5.5. Ordination of new (WR14) and Coope (2000, 2010b) coleopteran assemblages

Figure 4.17 presents the results of PCA used to compare new coleopteran assemblages from West Runton (WR14, presented in this chapter) with those of Coope (2000, 2010b). This is performed on a functional group basis, in order to compare the ecological characteristics of each sequence, and again the low MNI values (<50, *cf.* Hill 2015) for many of the coleopteran samples render conclusions drawn from these analyses tentative.

The first axis (PC1) represents 16.2% of total variance, and the second (PC2) represents 12.6%. Therefore, 71.2% of variance is not represented (Fig. 4.17). Samples are clearly separated on the basis of the sequence from which they are drawn, and differentiated by the relative abundances of several functional groups. However, samples from each sequence remain closely related, indicating that whilst distinct differences may be noted, their overall characteristics are broadly comparable. The new coleopteran assemblages presented in this chapter (WR14) have a greater proportion of both lotic (AS) and lentic (AF) aquatic specialists, as well as uncategorised taxa (UN), than Coope's (2000, 2010b) assemblages. The latter assemblages have greater proportions of decaying foul and rotten taxa (DE), open and disturbed habitat taxa (O), and both deciduous (WTD) and coniferous (WTC) tree and woodland taxa. This demonstrates that terrestrial habitats are better represented in Coope's (2000, 2010b) assemblages, and aquatic habitats are better represented in the WR14 assemblages. These differences appear to be driven by whole assemblages of taxa within these groups, rather than by particular species. For example, the WR14 sequence contains 13 lotic and lentic specialist aquatic taxa (Table 4.4), whereas Coope's (2000, 2010b) assemblages contain only five (Table 4.7). Conversely, Coope's (2000, 2010b) assemblages contain nine indicators of open and disturbed habitats (Table 4.7), whereas WR14 assemblages contain only four (Table 4.4). This is likely related to the relative local importance of aquatic and terrestrial habitats in each record. However, wetland edge (WE) taxa, dung-obligate taxa (DU), aquatic generalists (AG) and woodland and tree generalists (WTG) appear to be of similar importance in both sequences. Given that wetland edge and aquatic generalist taxa are generally the most abundant functional groups in both sequences (Figs. 4.7 & 4.9) this highlights the level of similarity between the sequences, despite some subtle differences in local ecology. It seems likely that differences between WR14 and Coope (2000, 2010b) records may be a result of their distinct locations within the palaeolandscape (sampling locations given in Figure 4.1), the representation of different periods of time (within the same temperate stage), or both.

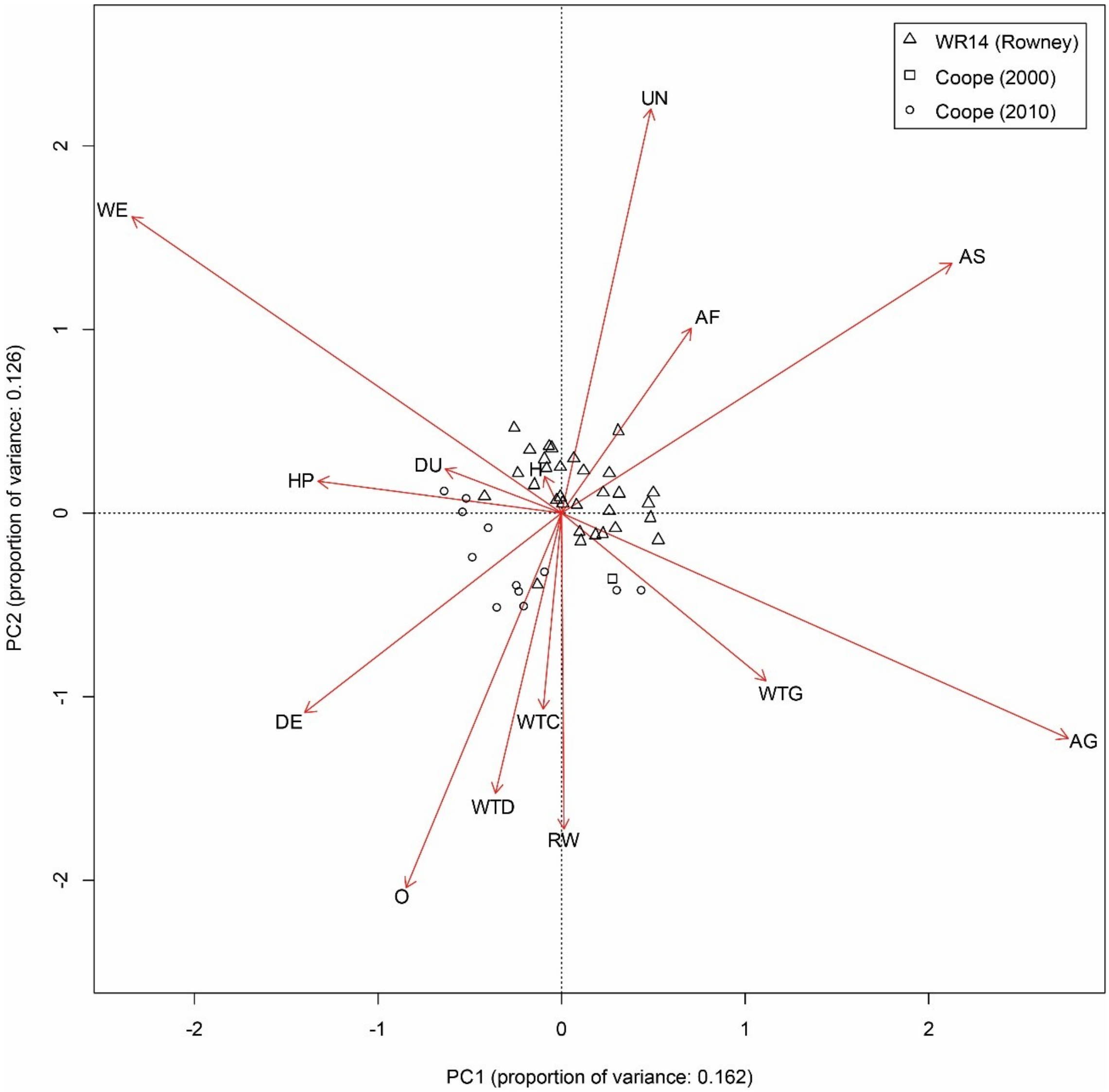


Figure 4.17– PCA of coleopteran habitat groups from WR14 (Fig. 4.2) Coope (2000) and Coope (2010b) records from the West Runton Freshwater Bed (See Table 3.1 for habitat group abbreviations) (Circles, triangles and squares represent samples) (See Figure 4.1 for relative locations)

4.5. Local Palaeoenvironmental Summary

This section summarises the key features of local palaeoenvironments, and notable changes, inferred from pollen and beetle assemblages, and sedimentological properties.

A brief comparison of the new records presented here with previous records is also given. Disturbance regimes and vegetation dynamics are discussed in detail in Chapter 8, alongside records from Pakefield (Chapter 6) and Brooksby (Chapter 7).

4.5.1. Depositional Environment

Sedimentological analyses (Fig. 4.3), supplemented with palaeoentomological data (Table 4.4, Fig. 4.7), provide a reconstruction of the depositional environment of the West Runton Freshwater bed, broadly consistent with previous interpretations (Rose *et al.* 2008; Gibbard *et al.* 2010; Preece 2010). Particle size analyses indicate a low-energy environment, with pulses of higher energy inputs superimposed on an overall trend of upward fining. This combination of lower- and higher-energy inputs is mirrored in the beetle fauna (Table 4.4, Fig. 4.7), which contains species from both lentic (e.g. *Helophorus strigifrons*, *Tanysphyrus lemnae*) and lotic (e.g. *Normandia nitens*, *Dryops* sp.) environments. Loss-on-ignition data generally vary independently of grain size: they indicate an initial phase of high $CaCO_3$ deposition (*c.* 22-26%), which decreases in a step-wise manner, whilst organic content is increasing, though this remains relatively low throughout (maximum 22.9%). However, a marked change is observed in both LOI data and grain size data from *c.* 60 cm, indicating a subtle shift in the mode of sedimentation.

Collectively, these data suggest deposition in a well-vegetated low energy (lentic) environment, with predominantly minerogenic, and therefore allochthonous, sedimentation, (e.g. a floodplain fen-type environment) throughout the sequence. The LOI data indicate a proportionally decreasing minerogenic component (i.e. increasing organic content), suggesting an increase in either autochthonous organic productivity or biomass in the surrounding environment, particularly from *c.* 60 cm. These hypotheses are consistent with the upward-fining trend in grain size, which could also be induced by increasingly dense local vegetation cover, either through the terrestrial retention of minerogenic material, or by increased supply of allochthonous organic material (though this organic component may also be autochthonous). Given the absence of nearby hillslopes, the pulses of higher energy inputs likely indicate proximity to a periodically flooding river, which supplied coarser inputs through overbank sedimentation. Indeed, this may be the primary mode of deposition throughout, and the variation in grain size may be indicative of variation in flood severity or channel proximity. This can result in variability in sedimentary pollen and spore concentrations, and possibly the extent of source areas (Brown *et al.* 2008). This is consistent with previous interpretations of the West Runton Freshwater Bed as having been deposited in a lentic environment in close proximity to an active channel, or which is fed by an active channel (e.g. Rose *et al.* 2008). An alternative interpretation is that the Freshwater Bed accumulated in a broad, complex channel system, which was heterogeneous at the mesohabitat-scale, incorporating both low- and high-energy habitats. For example, in-channel lentic conditions may be created by the dense growth of *Typha latifolia* and other emergent vegetation, whilst shallower, more gravelly areas may produce the more energetic conditions favoured by Elmids and Dryopids.

4.5.2. Local palaeoenvironment: Vegetation, landscape and climate

The analyses presented in this chapter indicate that the West Runton Freshwater Bed was deposited in a wetland environment, set within a complex mosaic landscape, under temperate climatic conditions. Palynological and entomological assemblages each exhibit some notable changes, though the taxonomic consistency of the pollen assemblages (Fig. 4.4), and relative consistency of beetle functional groups present (Fig.

5.7), suggest that the major vegetation and habitat characteristics are broadly continuous throughout the sequence. A summary of the major features of the WR14 record is therefore given here, before evidence for landscape and ecological change is outlined.

Significant wetland structural diversity at the meso-habitat scale is demonstrated by the presence of lentic (e.g. *Nuphar, Helophorus strigifrons*) and lotic (e.g. *Hydraena gracilis*, *Normandia nitens*) taxa, as well as marshland species (e.g. various Donaciinae, *Typha latifolia*). This wetland appears to have been set within a broader wooded landscape, incorporating a range of arboreal taxa, including both deciduous (e.g. *Alnus*, *Betula*, *Corylus*, *Quercus*, *Ulmus*) and coniferous taxa (e.g. *Abies*, *Pinus*), and occasional occurrences of arboreal and saproxylic beetles (e.g. *Magdalis phlegmatica*, *Scolytus multistriatus*) demonstrate that some of these trees were growing in close proximity to the wetland. However, any immediately wetland-proximal woodland habitats are unlikely to have included *Abies*, which prefer drier edaphic conditions (Mauri *et al.* 2016). Habitats in the immediate vicinity of the wetland seem to have been maintained as being at least semi-open, and subject to persistent disturbance regimes, as indicated by an array of floral (e.g. *Plantago*, *Taraxacum*), faunal (e.g. *Aphodius plagiatus*, *Melanotus punctolineatus*) and fungal (e.g. *Sporormiella*-type) taxa. These may have been dominated by *Alnus*, which is light-demanding and adapted to waterlogged conditions (Houston Durrant *et al.* 2016). Background levels of dung fungi (Fig. 4.6), which have limited dispersal ability (Davis & Shafer 2006; Raper & Bush 2009; Baker *et al.* 2016), and occurrences of dung beetles (*sensu* Smith *et al.* 2010; e.g. *Anotylus fairmairei*, *Aphodius rufipes*) indicate that herbivore activity was a component of the landscape close to the wetland. Quantitative palaeoclimatic reconstructions indicate that this was set within a temperate, stable climate (Fig 4.8, Table 4.5) (at least regarding temperature), and in combination with the general taxonomic stability of pollen assemblages, this indicates that no major environmental changes took place during the period of deposition. This suggests that this sequence is not representative of a major part of an interglacial, but rather that it represents a ‘snapshot’ record. It is not possible to determine the precise length of time represented, but this is at least consistent with the suggestions of Rose *et al.* (2008) and Rose (2009) that the West Runton Freshwater Bed was deposited rapidly, on a scale of 10^2, rather than 10^3, years. The presence of *Abies* may be considered significant here, as in British interglacial records it is often considered a ‘late immigrant’ and thought to indicate deposition during late successional (‘late temperate’) stages (*cf.* Turner & West 1968; West 1980a, b). However, such suggestions should be made cautiously, given that regional Cromerian successional patterns have been inferred from discontinuous, fragmentary pollen records with little independent chronological control (West 1980a; Rose 2009).

In the lower half of the record, in coleopteran zone WR-C1 (162 cm-85 cm: Table 4.4, Figure 4.7), extensive reed bed-type habitats are indicated, particularly by the presence of various Donaciinae species, as well as *Notaris acridulus* and *Bagous* sp., accompanied by *Typha latifolia* pollen (Fig. 4.4). These habitats, and others at the aquatic-terrestrial ecotone, were perhaps more extensive than fully aquatic habitats during this period: aquatic beetle species (e.g. *Hydraena riparia*, *Tanysphyrus lemnae*) are present throughout the zone, but generally in lower abundances than species associated with the ecotone. Terrestrial habitats are less well represented by coleopteran assemblages, but open and disturbed habitats were evidently present close to the wetland during this period: WR-C1 contains the only occurrences of the Elaterids, *Agrypnus murinus* and *Melanotus punctolineatus*, which inhabit dry grassland-type habitats (Koch 1989b), and there are several occurrences of the weevils, *Apion* sp. and

Ceutorhynchus sp., which feed on various herbaceous plants (Harde 1984). There is little evidence for the presence of trees in close proximity to the wetland during this phase, asides from a single occurrence of *Orchestes* sp., further suggesting openness in the riparian zone.

In spite of the relative consistency of the beetle assemblages during the lower half of the record (Zone WR-C1: 162-85 cm), pollen and spore assemblages exhibit distinct change, particularly in the relative importance of wet woodland habitats. In zone WR-P1 (169 cm-147 cm: Figs. 4.4 to 4.6), pollen assemblages are distinctively low in *Alnus*, contain elevated proportions of *Pinus*, *Polypodium*-type and *Sordaria*-type and are associated with the highest levels of $CaCO_3$ deposition and charcoal concentrations (Figs. 4.3 & 4.4). The rarity of *Alnus* in this zone suggests that the wetland margins were less wooded, and that woodland habitats were drier, likely aiding the preponderance of *Pinus* and ferns (*Polypodium*-type), and possibly the occurrence of fire. Heightened concentrations of both charcoal (Fig. 4.4) and *Sordaria*-type spores (Fig. 4.6) indicate more intensive disturbance regimes (wildfire and herbivore activity) than in the subsequent phase, which is corroborated by the presence of click beetles (Elateridae). Whilst this could be a taphonomic signal, given the coarser grain size at this point of the record, the coherence of the pollen assemblages suggests otherwise. Whilst part of the *Pinus* signal may be far-travelled, this combination of factors may have favoured the local growth of *Pinus*, which are known to benefit from drier conditions, and the removal of competitors and upper soil layers as a result of wildfire and other disturbance factors (Nuñez *et al.* 2003; Hille & den Ouden 2004). Though speculative, it may be suggested that greater seasonality in precipitation (and/or temperature) regimes played a role in promoting local conditions conducive to occasional wildfire in this part of the record. The combination of faunal disturbance, low deciduous tree abundances and somewhat drier conditions (which may be promoted through grazing) may have resulted in lower sediment stability in the catchment, and therefore greater erosive potential, thus promoting allochthonous sedimentation, derived from fluvial and alluvial inputs. Indeed, greater $CaCO_3$ deposition is noted in this part of the record (Fig. 4.3), which may be a result of greater allochthonous minerogenic inputs, particularly given the region's chalk bedrock, though some level of autochthonous biogenic $CaCO_3$ deposition (algae and/or molluscs) cannot be discounted.

Following WR-P1, a significant increase in *Alnus*, and decrease in *Polypodium*-type spores, indicate an expansion of wet woodland, and possibly an expansion of the wetland margins, which is not reflected in the beetle assemblages. This is accompanied by a fall in $CaCO_3$ deposition suggesting increased stabilisation of catchment sediments (i.e. less allochthonous minerogenic input). Some burning is suggested early in this phase by heightened charcoal concentrations, though this may partially result from the deposition of remobilised material. Vegetation then appears to remain broadly stable during WR-P2 (147-59 cm: Figs. 4.4 to 4.6), and there is little notable change in the pattern of sedimentation (Fig. 4.3). However, one notable detail is the appearance of *Tilia* in this zone, albeit at very low abundances (<1%). *Tilia* tend to grow in well-drained soils (Pigott & Huntley 1978; Eaton *et al.* 2016), and are typically underrepresented in pollen assemblages (Pigott & Huntley 1980), and so this may indicate the beginnings of woodland assemblage turnover in drier parts of the local landscape. The disparity between beetle and pollen assemblages in the lower half of the record (169-85 cm) (i.e. relative stability in the coleopteran assemblages, and notable change in the pollen assemblages) likely reflects the differently-sized catchments of sub-fossil beetles and pollen (*c.f.* Smith *et al.* 2010; Hill 2015), which therefore represent different components of the landscape.

The most prominent change in the coleopteran assemblages occurs at approximately 85 cm: the beginning of WR-C2 (85 cm to 20 cm: Fig. 4.7, Table 4.5). The most notable aspect of this is an increase in fully aquatic taxa, driven in particular by increased abundances of *Hydraena riparia* and *Tanysphyrus lemnae*. This is unlikely to be a taphonomic signal, because other aquatic taxa (derived from the same environments) do not show an appreciable increase in abundance. Rather, it is more likely that the wetland expanded at this point and populations of *H. riparia* and *T. lemnae* expanded in response. The increased frequency of woodland, arboreal and saproxylic beetle occurrences in WR-C2 suggests that trees were also becoming more common in the areas directly surrounding the wetland. These include species potentially associated with a range of different deciduous trees (*Chilocorus renipustulatus*, *Crepidodera* sp., *Orchestes* sp., *Otiorhynchus clavipes*, *Scolytus multistriatus*, *Scolytus* sp.), as well as *Pinus* (*Magdalis phlegmatica*).

The most prominent change in the pollen sequence occurs during WR-C2, at the start of pollen zone WR-P3 (59 cm to 15 cm: Figs. 4.4 to 4.6). Arboreal pollen becomes more abundant than herbaceous (primarily Poaceae) pollen (Fig. 4.4), *Sordaria*-type spores become almost absent (Fig. 4.6), and there is a simultaneous increase in the silt fraction and sedimentary organic content (Fig. 4.3). In conjunction with the increase in the frequency of arboreal and saproxylic beetles (Fig. 4.7), it is evident that woodland habitats, including alder carr, were increasingly encroaching upon the wetland margins and semi-open habitats, as demonstrated by an increase not only in the relative proportion of *Alnus*, but also proportions of *Corylus* and *Tilia*. This expansion does not appear to have been restricted to wetland-marginal woodlands, as the increase occurs in tree taxa typical of both waterlogged (*Alnus*) and well-drained (*Tilia*) conditions. The encroachment of alder carr in particular may have facilitated the greater deposition of organic material, due to greater terrestrial biomass in close proximity to the wetland. Intriguingly, and in spite of the virtual disappearance of *Sordaria*-type spores, this is also accompanied by a slight increase in both *Sporormiella*-type spores and *Plantago*, though there is no discernible change in assemblages of dung beetles (*sensu* Smith *et al.* 2010), in terms of absolute abundances (Table 4.4). The ecological niches of the fungal taxa represented by these spores are similar, but not interchangeable (Baker *et al.* 2013; van Asperen *et al.* 2016); thus, it is implicit that whilst herbivory-associated disturbance is a constant feature of the landscape, its characteristics changed. The precise differences between the ecologies of *Sporormiella*- and *Sordaria*-type spores are incompletely known, and their taxonomies relatively broad, and so the exact nature of this shift is unclear. Different species of coprophilous fungi have demonstrated preferences for the dung of particular herbivores, though none appear to be obligate to specific herbivore types (Richardson 2001). Those typically preserved and recorded in palaeo-sequences (*Sporormiella*-, *Sordaria*-, *Podospora*-types) tend to be more prevalent in the dung of hind-gut fermenters (Proboscidea, Perissodactyla) (van Asperen *et al.* 2016). However, these spore types are taxonomically coarse and species-level fungal assemblage change is not detectable, though may be an important factor in this record. *Sporormiella*-type abundances have also been tentatively linked to local moisture levels (Wood & Wilmshurst 2012), which may be an additional factor, perhaps related to increased shading and alder carr expansion. Consequently, the shift in spore types at 59 cm (Fig. 4.6) may be linked to a change in the herbivore types (functional and/or taxonomic) locally prevalent, local moisture levels, the habitats utilised by herbivores, or a combination of these factors. It should also be noted that differential taphonomy may play a role in this shift in spore types. Current understanding of coprophilous fungal spore taphonomy is primarily based on modern analogue studies from either lakes (e.g. Baker *et al.* 2016) or non-aquatic contexts (e.g. Gill *et al.* 2013), whereas the present record is partly derived from fluvial processes.

In the uppermost part of the sequence (WR-C3, 20 cm to 0 cm, Fig. 4.7; WR-P4, 13 cm to 0 cm, Figs. 4.4 to 4.6), changes in entomological and palynological assemblages are roughly coincident. Coleopteran zone WR-C3 (20 cm to 0 cm) marks a sharp decrease in overall beetle abundance, with an almost total disappearance of beetles representing fully aquatic habitats, with the exception of a single occurrence of *Tanysphyrus lemnae*. Beetles of reedbed-type and marshland habitats (e.g. various Donaciinae and Staphylinidae) remain (Table 4.4), suggesting a distinct contraction of fully aquatic habitats, likely associated with terrestrialisation of the wetland. A reduction in standing water also provides a convenient explanation for the decrease in beetle fossil abundance, as this would reduce the area conducive to their accumulation and preservation. The change marked by pollen zone WR-P4 (13 cm to 0 cm), though more subtle, appears to represent the beginning of a shift in arboreal assemblages. The increase in *Abies*, slight decreases in *Alnus* and *Ulmus*, and low *Betula* suggests the continuation of turnover in the woodland community, first indicated by the appearance of *Tilia* at 77 cm in Zone WR-P2 (147-59 cm). Both *Abies* and *Tilia* are relatively poor pollen dispersers (Pigott & Huntley 1980; Poska & Pidek 2010), which grow on well-drained soils (Pigott & Huntley 1978; Mauri *et al.* 2016). Therefore, this may be an indication of a local trend towards drier edaphic conditions and consequent encroachment of drier woodland types into previously aquatic and marshy areas: the latter stages of localised wetland terrestrialisation. As *Abies* is often considered a ‘late immigrant’ in British interglacials (Turner & West 1968; West 1980a, b), its expansion in this part of the record may also be interpreted as a reflection of regional-scale successional patterns and transition into a 'late temperate' interglacial substage (Turner & West 1968). However, as previously noted, such suggestions should be made cautiously, given that regional Cromerian successional patterns have been inferred from discontinuous, fragmentary pollen records with little independent chronological control (West 1980a; Rose 2009).

4.5.3. Broader landscape context: Comparison with previous records

The spatial heterogeneity in the palaeolandscape, implicit in the pollen and beetle records presented here, is further emphasised by comparison with other, existing records from the Freshwater Bed (West 1980a; Coope 2000, 2010b; Rose *et al.* 2008; Field & Peglar 2010). These sequences have typically been excavated from open sections at different points of the Freshwater Bed, and so vary correspondingly in terms of depth and sedimentary characteristics. The West Runton Freshwater Bed spans *c.*300 m laterally, and is regularly eroded backwards to reveal new sections, suggesting that its past and present extent occupies a broad area. Thus, there is no *a priori* reason to assume simultaneous deposition across this area or that sediment compaction and rates of deposition were spatially homogenous. Furthermore, each sequence is likely to represent a different location within the palaeolandscape. Consequently, each individual sedimentary record may be distinct in terms of age, length of time represented and landscape context.

Previous coleopteran records from the West Runton Freshwater Bed (WR14; Coope 2000, 2010b) (Fig. 4.1), whilst exhibiting some level of difference, are demonstrated as being broadly similar in functional terms. The primary distinction is in the relative proportions of terrestrial and specialist (as opposed to generalist) aquatic assemblages.

The WR14 assemblages are notably richer in both lentic (e.g. *Helophorus strigifrons*, *Hydraena palustris*) and lotic (e.g. *Hydraena gracilis*, *Normandia nitens*) specialist taxa, whilst Coope's (2000, 2010b) assemblages are richer in specialist (as opposed to generalist) arboreal and woodland taxa (e.g. *Patrobus atrorufus*, *Curculio venosus*, *Pissodes pini*, *Polygraphus poligraphus*), and taxa associated with dry open and disturbed habitats (e.g. *Dascillus cervinus*, *Graptus triguttatus*). However, the relative proportions of the most important functional groups (aquatic generalists and wetland edge taxa) are similar in both records. This strongly suggests that these records are broadly contemporary, but spatially distinct, representing different locations within the palaeolandscape. The WR14 assemblages are likely to represent a more central location within the wetland, with greater input of autochthonous aquatic beetle remains, whilst Coope's (2000, 2010b) assemblages appear to be more influenced by allochthonous deposition of terrestrial beetle remains. The differences in the relative proportions of lotic taxa (indicative of relative fluvial influence, Smith & Howard 2004) may also result from different phases of wetland development, contemporaneous wetland complexity, or a combination of both.

Palaeoclimatic reconstructions based on WR14 and Coope (2000, 2010b) are also similar, giving no evidence of distinct differences in climatic terms. Assemblages from both sequences provide evidence for deposition in temperate conditions, similar to the region at present. Whilst estimates based on Coope's (2000, 2010b) assemblages are more constrained than those derived from the WR14 assemblages, due to the presence of species such as *Bembidion clarkii* and *Pterostichus gracilis*, their absence from WR14 is unlikely to be indicative of climatic distinction. They are rare species in Coope's (2000, 2010b) assemblages, and so it is likely that their absence from WR14 assemblages results from the low probability of being incorporated into sedimentary records as identifiable fossils, rather than from 'genuine' absence.

In previous pollen records from the West Runton Freshwater Bed (West 1980a; Rose *et al.* 2008; Field & Peglar 2010), *Alnus* and *Pinus* typically dominate arboreal assemblages, and both occur with a range of deciduous taxa, including *Betula*, *Fraxinus*, *Quercus* and *Tilia*, but the relative abundances of these taxa vary significantly between records. This variability is also evident amongst herbaceous pollen assemblages. Poaceae abundances, in particular, range from the high abundances of the present record (28.19% to 63.32%, Fig. 4.4) to a virtual absence in others (Rose *et al.* 2008), and other taxa, such as Cyperaceae, *Plantago*, *Filipendula* and *Taraxacum*, also vary considerably. In West's (1980a) pollen records, this variation between sequences appears related to sedimentological sub-units of the Freshwater Bed, but these are not necessarily representative of distinct time periods, as previously thought (*cf.* West 1980a). As stated here, each record may be distinct in spatial contexts, as well as temporal. Thus, this variability between pollen records is likely to be at least partly related to landscape-scale heterogeneity in vegetation and soil conditions. The pattern of variability between pollen records is consistent with modern analogue studies from alder carr woodlands (Binney *et al.* 2005; Waller *et al.* 2005). In these studies, the representation of both arboreal and herbaceous taxa in pollen samples varies according to sampling location, relative to different habitat types. For example, proximity to 'dry woodland' results in higher proportions of *Quercus*, *Betula* and *Fraxinus* (Binney *et al.* 2005), and although generally underrepresented, understorey taxa also exhibit spatial relationships (Waller *et al.* 2005).

Herbivore activity (grazing, browsing, trampling), wildfire and hydrogeomorphic processes are identified here as influential disturbance processes, whereas thermal climate appears stable (Fig. 4.8). Therefore, the spatial and temporal heterogeneity in vegetation communities inferred are likely to be driven by local and regional ecological processes, rather than regional climatic changes.

Herbivore activity is an evidently persistent feature of the West Runton Freshwater Bed: coprophilous fungal spores are virtually ubiquitous in this sequence, *Aphodius* and other dung-associated beetles occur frequently, and diverse herbivore assemblages are well documented (see Table 4.2). These include an array of large herbivores with both browse-dominated (e.g. *Mammuthus trogontherii*, various Cervidae) and graze-dominated (e.g. *Equus* spp., *Bison* cf. *schoetensacki*) diets, alongside mixed feeders (e.g. *Stephanorhinus* spp.) and numerous smaller herbivores (e.g. *Castor fiber*, *Trogontherium cuveri*, *Microtus* spp., *Anser* sp.). Interestingly, analyses of tooth-wear patterns of large herbivores from West Runton indicate that none were exclusively grazers, and that even taxa such as *Equus* were actively browsing to some extent (Rivals & Lister 2016). This suggests that shrubs and young trees may have been under particular pressure from herbivory. Furthermore, correlation and multivariate analysis of the pollen and spore data presented here infers a quantitative relationship between herbivory and vegetation assemblages (Figs. 4.11 and 4.13). However, this appears to be more complex than a simple model of grazing pressure driving local vegetation openness. Whilst *Sordaria*-type spores are positively related to Poaceae abundances, which could be interpreted as evidence of herbivory driving openness, *Sporormiella*-type spores exhibit closer relationships with deciduous trees (Figs 4.12 & 4.13). This may be related to herbivore types (functional and/or taxonomic) favoured by fungal taxa, local moisture levels, the habitats utilised by herbivores, taphonomy, or a combination of these factors. Regardless of the precise scenario, herbivore activity appears to have exerted some level of influence on vegetation communities. This elaborates on Stuart's (1975, p.69) early postulation that "The browsing and grazing of herbivorous mammals and the tree-felling activities of beavers no doubt contributed to the locally open nature of the vegetation cover [at West Runton]".

In the present record, the simultaneous upward-fining of the sediments and increasing proportions of arboreal pollen (Fig. 4.4) and covariance of silt content with various deciduous tree taxa in (Fig. 4.13) suggest that hydrogeomorphic processes are also influential. Alluvial processes can both prevent and facilitate plant colonisation and growth (through periodic flooding and sediment deposition, respectively), whilst vegetation growth may stabilise banks and enhance sedimentation, but also instigate flooding and alter channel forms via the deposition of large woody debris (Viles *et al.* 2008). Periodic flooding likely contributed to maintaining local vegetation openness, but encroaching alder-dominated woodland at the wetland edges may also have served to stabilise banks, enhancing sediment storage and thus reducing sediment supply. The combination of lentic (e.g. *Helophorus strigifrons, Tanysphyrus lemnae*) and lotic (e.g. Elmidae, Dryopidae) beetle taxa, and species associated with exposed riparian sediments (e.g. *Bledius* species, *Neobisnius procerulus*, *Aphodius plagiatus*) (Table 4.3, Fig. 4.7), is consistent with this type of energetically variable regime.

The presence of microcharcoal shards throughout the sequence demonstrates the occurrence of wildfire at West Runton. Charcoal concentrations are elevated in Zone WR-P1 in particular (Fig. 4.4). In this zone, *Pinus* and *Polypodium*-type ferns are abundant, whilst *Alnus* is rare, indicating drier, more flammable vegetation. The flammability of *Pinus* and its association with wildfire regimes are known from both neo- (e.g. Agee 1998; Tanskanen *et al.* 2005) and palaeoecology (e.g. Whitehouse 1997, 2000; Olsson *et al.* 2010; Grant *et al.* 2014), and its relative abundance in WR-P1 (21.8%) may partly be a product of this relationship. Tentatively, it may also suggest drier summers, conducive to wildfire, during the period represented by WR-P1. Speculatively, covariance between charcoal and sand content (Fig. 4.13) may allude to an opportunistic response of *Pinus* to both hydrogeomorphic processes and wildfire. *Pinus* is often favoured by sandy, disturbed habitats (Hille & den Ouden 2004), and such areas may have been created close to the wetland by a combination of wildfire, alluvial erosion and alluvial deposition (increased hydrogeomorphic activity is implied by higher sand content). However, it should also be noted that this covariance is likely also likely to reflect the concentration of microcharcoal (and potentially *Pinus* pollen) through sedimentary in-washing from the broader landscape, through fluvial and alluvial processes. Pyrophilous insects have been recorded with other evidence for burning in Holocene contexts (Whitehouse 1997, 2000; Olsson & Lemdahl 2009, 2010; Olsson *et al.* 2010), but are absent from the present record. Speculatively, this could be used to suggest that the frequency and/or intensity of burning events were low, and insufficient to support populations of pyrophilous insects. This is discussed further in Chapter 8 (Section *8.2.2.*).

Chapter 5

The Cromer Forest-bed Formation at Pakefield

5.1. Introduction

This chapter presents a new palaeoecological record from the Cromer Forest-bed at Pakefield Cliffs, combining Coleoptera, pollen, coprophilous fungal spores, microcharcoal and sedimentology. Inferences are made regarding vegetation structure, interactions between taxa, and relationships with herbivore activity, wildfire, hydrogeomorphic processes and climate. This provides a novel and nuanced perspective of the Cromerian palaeolandscape at Pakefield, its vegetation communities and the role of disturbance regimes in determining local-scale ecological characteristics.

5.2. Site Background

The cliffs between Pakefield and Kessingland, on the Suffolk coast, UK (*sensu* 'Pakefield Cliffs', 01°44'E, 52°26'N, Fig. 5.1), are a site of international significance for the early Middle Pleistocene. They have long been recognised for their palaeontological and palaeoenvironmental value (e.g. Blake 1890; West 1980a; Stuart & Lister 2001; Candy *et al.* 2006; Lee *et al.* 2008b; Parfitt 2008), and more recently for yielding some of the earliest evidence of hominins in Northern Europe (Parfitt *et al.* 2005).

5.2.1. Chronostratigraphy

The Middle Pleistocene sequence at Pakefield Cliffs is complex, and its interpretation has been a source of debate (*cf.* Lee *et al.* 2006, 2008c; Gibbard *et al.* 2008), but several primary stratigraphic units have been identified (Lee *et al.* 2008b) (see Table 5.1). Shallow marine deposits of the Wroxham Crag Formation form the lowermost unit of the sequence and are overlain by the silts and clays of the Cromer Forest-bed Formation. This is overlain by a second unit of the Wroxham Crag, which, in turn, is overlain by deep deposits of fluvial and glaciofluvial outwash sands. Finally, these are overlain by a third shallow marine deposit and capped by the glaciogenic Lowestoft Till. The Cromer Forest-bed at Pakefield is typically divided into three subunits (*cf.* West 1980a; Candy *et al.* 2006; Lee *et al.* 2008b): the dark grey to brown silts and clays of the 'Rootlet Bed', the shelly sands and gravels of the '*Unio* Bed', and a unit of light grey laminated silts and clays. Together, these range from *c.* 0.5-2 m in thickness, contain various indicators of a warm temperate climatic episode (West 1980a; Stuart & Lister 2001; Parfitt *et al.* 2005; Candy *et al.* 2006), and are typically interpreted as being derived from alluvial deposition on an aggrading floodplain (West 1980a; Candy *et al.* 2006; Lee *et al.* 2008b).

Table 5.1 Summary of primary stratigraphic units at Pakefield/Kessingland (based on Lee *et al.* 2008b, but see Gibbard *et al.* 2008 for an alternative view). Chronostratigraphy based on Gibbard *et al.* (2008), Preece & Parfitt (2012) and this chapter.

Unit/Bed	Formation	Climate/Environment	Age
Lowestoft Till	Lowestoft Formation	Glacial	MIS 12
Pakefield Member	Wroxham Crag Formation	Shallow marine, interstadial/interglacial	MIS 12

(Continued overleaf)

Table 5.1 Continued

Leet Hill Sand and Gravel; Corton Sand	Happisburgh Formation	Glaciofluvial	MIS 12
Timworth Terrace Member	Bytham River	Fluvial (glacial stage)	MIS 12
How Hill Member	Wroxham Crag Formation	Shallow marine, temperate	MIS 12-15
'Rootlet Bed'; '*Unio* Bed'; 'Laminated Muds'	Cromer Forest-bed Formation	Interglacial, temperate	MIS 15-17
How Hill Member	Wroxham Crag Formation	Shallow marine, temperate	>MIS 17

A similar combination of litho-, magneto- and biostratigraphy to West Runton (Chapter 4) determines the age of the Cromer Forest-bed at Pakefield. Its position underlying the Anglian-age (*c.* MIS 12) Lowestoft Till provides a minimum age of *c.* 430 ka BP. The presence of two *Mimomys* species (archaic water voles) and *Borysthenia goldfussiana* (a gastropod) implies an age early in the early Middle Pleistocene, possibly the equivalent of the Dutch Cromer II interglacial (Stuart & Lister 2001; Preece & Parfitt 2012). As discussed (Chapter 2, Section *2.3.3.*, Chapter 4, Section *4.2.1.*), the evolutionary transition from *M. savini* to *Arvicola terrestris cantiana* has been dated to 610±10 ka BP, 606±2 ka BP (Coltorti *et al.* 2005) and 609±40 ka BP (Wagner *et al.* 2010), placing deposition in at least MIS 15. Furthermore, the Cromer Forest-bed at Pakefield is normally magnetised, placing it within the Brunhes Chron (Lee *et al.* 2006; Pillans & Gibbard 2012), thus providing a lower boundary. Like West Runton, this gives a potential age range for deposition of *c.* 781-606 ka BP.

Despite this similarity in age, a range of evidence suggests that Pakefield represents a distinct temperate stage from that represented at West Runton. Firstly, the sediments at Pakefield have yielded remains of *Hippopotamus antiquus* (= *H. major*)

(Stuart & Lister 2001), and a range of distinctive beetles (e.g. *Cybister lateralimarginalis*, *Valgus hemipterus*) (Parfitt *et al.* 2005; Coope 2006) and plants (e.g. *Trapa natans*, *Salvinia natans*) (West 1980a) that are absent from West Runton (see Chapter 3, Section *3.4.2.* for a discussion of the climatic preferences of some of these taxa); these are accompanied by pedological and stable isotope evidence for a Mediterranean-type precipitation regime (Candy *et al.* 2006). Collectively, this suggests the presence of a distinctively warm climate at Pakefield, implying deposition during a different temperate phase to West Runton (Preece & Parfitt 2012). However, the precise chronological relationship between Pakefield and West Runton is unclear. Typically, the Cromer Forest-bed at Pakefield is thought to pre-date the West Runton Freshwater Bed, on the basis of the presence of another archaic water vole, *Mimomys* aff. *pusillus* (Parfitt *et al.* 2005; Preece & Parfitt 2012). This species, otherwise known from the Early Pleistocene and early Middle Pleistocene of Eastern Europe pre-MIS 16 (suggesting a *c.*MIS 17 age for Pakefield), has been thought to precede *M. savini* (Maul & Markova 2007), implying an older age for Pakefield *Mimomys* populations, although the presence of both species at Pakefield suggests that the former cannot be the ancestor of the latter. Conversely, recent aminostratigraphic work has suggested that Pakefield may be slightly younger than West Runton (Penkman *et al.* 2011, 2013). Regardless of their precise chronological relationship, it is at least clear that the Cromer Forest-bed at Pakefield and West Runton each represent distinct temperate-climate phases.

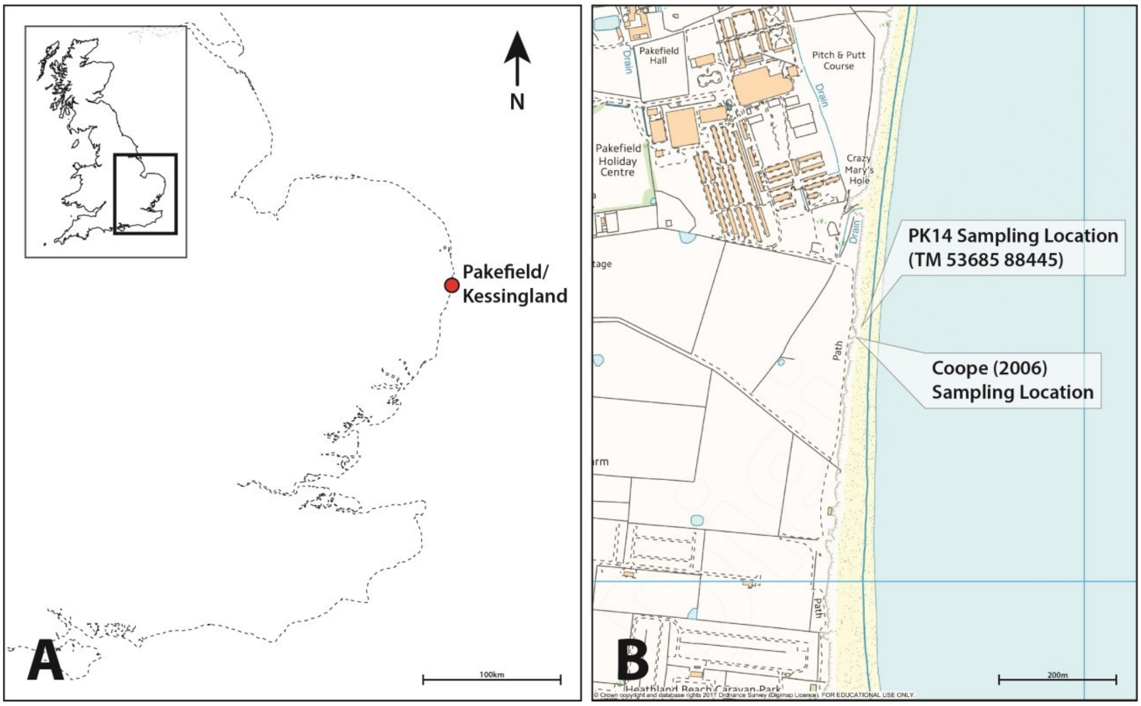


Figure 5.1 – Location Maps (A: Regional Location; B: Sampling Locations)

5.2.2. Palaeoenvironmental and archaeological context

The Cromer Forest-bed at Pakefield has a long history of research, comparable to that of West Runton. Its study has contributed to the understanding of the Pleistocene history of Eastern England (e.g. Blake 1890; West 1980a; Lee *et al.* 2008b) and its archaeological context (Parfitt *et al.* 2005; Coope 2006; Ashton *et al.* 2011), as well as being regularly incorporated into palaeoecological, palaeoclimatological and stratigraphic multi-site review papers (e.g. West 1980b; Preece & Parfitt 2000, 2008, 2012; Preece *et al.* 2009; Rose 2009; Candy *et al.* 2010; Coope 2010a; Kahlke *et al.* 2011; Penkman *et al.* 2013; Rivals & Lister 2016). As discussed, Pakefield is characterised by evidence for warmer climatic conditions than the region at present, distinct from the cooler temperate climate at West Runton (Stuart & Lister 2001; Parfitt *et al.* 2005; Candy *et al.* 2006 Coope 2006, 2010a). Several thermophilous beetles with predominantly Southern distributions are known from this site, including *Cybister* *lateralimarginalis*, *Oxytelus opacus* and *Valgus hemipterus*, which are unknown or rare in other Cromerian deposits (Coope 2010a). On the basis of the Mutual Climatic Range (MCR) method applied to sub-fossil assemblages, Coope (2006) estimated that mean warmest month temperatures were between 17°C to 23°C, and that mean coldest month temperatures were between -6°C to 4°C. Pollen assemblages from Pakefield also typically have greater relative abundances of arboreal pollen than West Runton, representing diverse tree communities including deciduous (e.g. *Alnus*, *Betula*, *Carpinus*, *Quercus*, *Tilia*, *Ulmus*) and coniferous (e.g. *Pinus*, *Picea*) taxa. These are accompanied by pollen and macrofossil evidence for heathers (Ericaceae), various dry and damp ground herbaceous taxa, and rich aquatic assemblages (West 1980a). Mammals recorded from the Cromer Forest-bed at Pakefield, and the closely-correlated site of Corton, are similarly suggestive of a heterogeneous landscape, incorporating wetland, woodland and open habitats (Stuart & Lister 2001) (see Table 5.2). Likewise, insect assemblages also demonstrate the presence of diverse wetland and terrestrial habitats (Coope 2006).

Lower Palaeolithic assemblages of worked flints (Mode 1, core and flake), documented *in situ* from throughout the Cromer Forest-bed at Pakefield (Parfitt *et al.* 2005), are amongst the earliest evidence for hominins in Northern Europe (Ashton *et al.* 2011; Hosfield *et al.* 2011). As discussed in Chapter 2 (Section *2.3.5*), the environmental context for these peripheral hominin populations is of central importance in developing a full understanding of their ecology, adaptability and vulnerability (Candy *et al.* 2011).

Table 5.2 Herbivores recorded from the Cromer Forest-bed at Pakefield/Kessingland (Stuart & Lister 2001; Parfitt *et al.* 2005; $^+$extinct taxa), with notes on ecology (Kahlke & Kaiser 2011; Rivals & Lister 2016). (Graze/Browse-dominated is used to signify a primarily, but not exclusively, grazing/browsing diet.)

Order	**Species**	**Common Name**	**Notes on Ecology**
Proboscidea	*Mammuthus trogontherii*	Steppe mammoth$^+$	Grazer
	Palaeoloxodon antiquus	Straight-tusked elephant$^+$	Mixed feeder
Perissodactyla	*Equus altidens*	Small stenonid horse$^+$	Grazer
	Equus sp.	Large stenonid horse$^+$	Grazer
	Stephanorhinus hundsheimensis	Rhinoceros$^+$	Mixed feeder
Artiodactyla	*Hippopotamus antiquus*	Hippopotamus	Grazer
	Sus scrofa	Wild boar	Woodland omnivore
	Praemegaceros verticornis	Giant deer$^+$	Browse-dominated
	Megaloceros savini	Giant deer$^+$	Browse-dominated
	Megaloceros dawkinsi	Giant deer$^+$	Browse-dominated
	Dama dama	Fallow deer	Browser
	Cervus elaphus	Red deer	Mixed feeder
	Bison sp.	Bison$^+$	Graze-dominated
Rodentia	*Mimomys savini*	Water Vole$^+$	Wetland/Grassland
	Mimomys cf. *pusillus*	Water Vole$^+$	Wetland/Grassland
	Castor fiber	Eurasian Beaver	Wetland
	Trogontherium cuvieri	Giant Beaver$^+$	Wetland

Pakefield remains a valuable focus for continuing research, for much the same reasons as West Runton. The floral and faunal assemblages from this site have rarely been used in quantitative ecological analyses, or utilised in addressing explicitly ecological ideas. The data provided by existing research allow new analyses to be readily supplemented with reference to other components of the palaeoecosystem (e.g. West 1980a; Stuart & Lister 2001). For example, although less extensive than at West Runton, a range of mammalian herbivores has been recorded from the site (Stuart & Lister 2001). These are primarily the remains of large herbivores, such as elephantids (*Mammuthus trogontherii*, *Palaeoloxodon antiquus*), *Stephanorhinus*, *Hippopotamus* and giant deer species (e.g. *Megaloceros* spp.), though medium-sized (e.g. *Dama dama*, *Trogontherium cuvieri*) and small (e.g. *Mimomys savini*) herbivores have also been recorded (see Table 5.2). This allows more specific inferences to be made regarding herbivore-plant interactions at the site than would be possible with palynological and entomological information alone, particularly given recent dietary analyses of part of the Pakefield fauna (Rivals & Lister 2016). New analyses at Pakefield have the capacity to yield insights into ecological function, habitat structure and heterogeneity, and disturbance processes during early Middle Pleistocene interglacials, especially in the context of comparison with the West Runton record presented here (Chapter 4). Given the archaeological significance of the site, such analyses have broader relevance in the context of Lower Palaeolithic hominin ecology. Furthermore, recent advances in the coleopteran MCR method (Milne 2016) allow more accurate palaeoclimatic estimates to be made, which can be incorporated into a broader discussion of the Mid-Brunhes Transition.

5.3. Site-specific Methodology

5.3.1 Sampling and sub-sampling

Field sampling was undertaken on 2nd November 2014. The Cromer Forest-bed Formation is known to extend for several hundred metres between Pakefield and Kessingland (Parfitt 2008) (see Figure 5.1), but only a small exposure (*c.* 5 m laterally) was visible and accessible at this time (grid reference: TM 53685 88445). The exposure was logged and described qualitatively and semi-quantitatively, using the Troels-Smith method (Troels-Smith 1955). Seven contiguous bulk sediment samples were excavated for Coleoptera from a cleaned open section (28-75 cm), and a 50 cm monolith sequence (31-80 cm) was excavated directly adjacent to this for palynological and sedimentological analyses.

Sub-samples for pollen and spores were taken from the monolith sequence at 4 cm intervals between 31 and 80 cm. Given the general lack of pollen assemblage change through most of the sequence (see Section *5.4.2.*), finer resolution sub-sampling was deemed unnecessary. Sub-samples for sedimentological (loss-on-ignition and particle size) analyses were taken at 1 cm resolution from the same sequence. Details of laboratory processes are given in Chapter 3.

5.3.2. Assemblage zonations

Pollen assemblage zones were constructed using constrained cluster analysis (CONISS, Grimm 1987), with a broken-stick model (Bennett 1996) used to determine the most significant number of zones. Given the low number of Coleoptera samples in the present sequence, faunal (coleopteran) assemblage zones were determined qualitatively by assessing changes in faunal assemblages. These analyses were performed using the R package 'rioja' (Juggins 2015).

5.3.3. Multivariate analyses

A preliminary detrended correspondence analysis (DCA) applied to the pollen and spore data produced gradient lengths of <2.5 (DCA1: 1.09, DCA2: 0.72), and therefore principal components analysis (PCA) was selected as the most appropriate technique. Only those pollen and spore taxa with three or more occurrences (of any abundance) were included in these analyses. A preliminary DCA applied to the coleopteran data also produced gradient lengths >2.5, but <4 (DCA1: 3.39, DCA2: 1.76) and so a PCA was also carried out on this dataset. Following this, canonical correspondence analysis (CCA) was carried out on pollen (excluding rare taxa) and coleopteran datasets separately, using coprophilous fungal spore concentrations, charcoal concentrations and sedimentological properties (organic content, $CaCO_3$ content and particle size) as 'environmental variables', and major pollen taxa as 'species' or 'response' variables.

Palynological and entomological datasets were combined for simultaneous analysis, to explore potential covariance between major pollen and beetle functional groups. As the pollen sequence is higher resolution, it was necessary to combine several samples (by averaging abundance and concentration values according to sample depths) for this analysis, in order to create a composite biological dataset with equivalent samples (n=7). Whilst pollen and Coleoptera were not drawn from the same sequence *sensu stricto*, they were derived from directly adjacent bulk sample (Coleoptera) and monolith (pollen, spores, sedimentology) sequences (see Figure 5.2). A preliminary DCA of this composite dataset produced gradient lengths <2.5 (DCA1: 2.03, DCA 2: 1.13), and so a PCA was selected as a reasonable indirect ordination technique to apply. CCA was also applied to the composite dataset, with 'environmental variables' also averaged across samples to correspond to the lower-resolution coleopteran data.

Ordination was also used to compare the new coleopteran sequence presented here (PK14) with Coope's (2006) Pakefield sequence. A preliminary DCA of these data produced gradient lengths of 3.62 (DCA1) and 1.91 (DCA2), and so a PCA was selected as a reasonable indirect ordination technique to apply.

As discussed below (see Sections *5.4.2.* and *5.4.3.*), little ecological change is qualitatively discernible in the sequences presented here. This is partly a result of apparent stability in vegetation communities (see Section *5.3.2.*), but also the relative paucity of coleopteran material (see Section *5.4.3.*). Therefore, observed co-variance between taxa and environmental variables in ordinations is not representative of strong ecological gradients in the datasets. However, such techniques remain potentially valuable in elucidating subtle co-variance which would otherwise be difficult to discern, and so are employed here, albeit with due caution.

5.4. Results

5.4.1. Sedimentology and stratigraphy

Sediments were generally composed of clayey silts and silty clays, indistinctly stratified. A summary of field-recorded sedimentological properties is given in Figure 5.2. (Further details, including Troels-Smith codes and section photograph, provided in Appendix 2.)

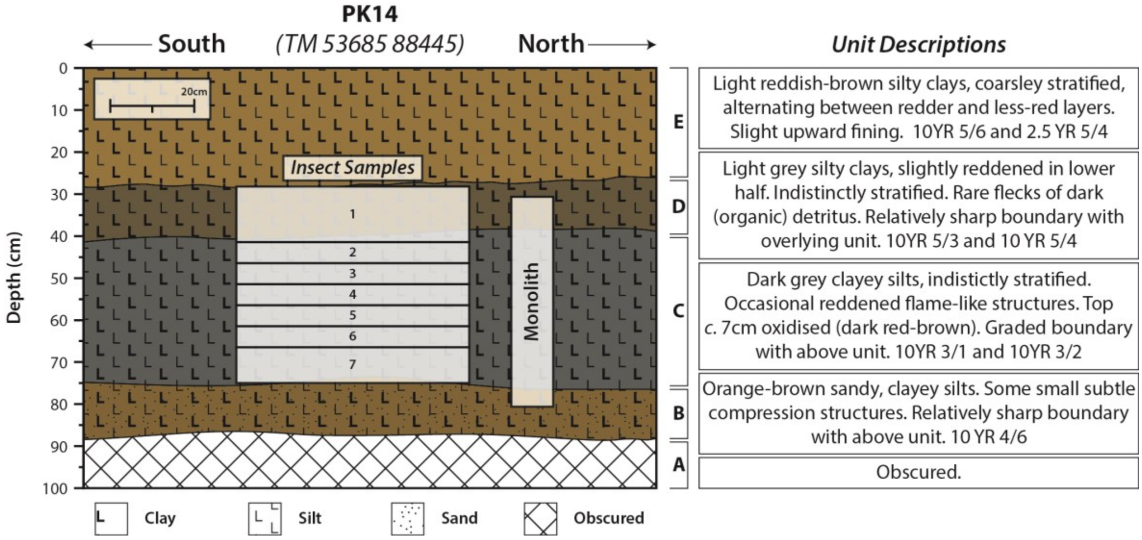


Figure 5.2 – Pakefield Cliffs sampling log and sub-unit descriptions (PK14) (see Figure 5.1 for section location)

The LOI data (Fig. 5.3) indicate low organic and calcium carbonate ($CaCO_3$) content throughout the sequence, though this is not without change. Organic matter has a mean value of 7.97% and a maximum of 12.51%, and can be divided into several phases. The lowermost 11 cm (80-69 cm) comprise the initial phase, in which organic matter rises sharply from *c.* 3% to *c.* 11-12%. Then follows a phase of relative stability, until 54-51 cm when organic matter decreases to approximately 7%. It then remains relatively stable until 40 cm, when it begins a general decrease towards approximately 3% at the top of the sequence.

Calcium carbonate content ($CaCO_3$) is less variable than organic matter, and changes little throughout the sequence, though it does exhibit some slight variations. Similarly to organic matter, $CaCO_3$ rises in the basal 3 cm, from *c.* 2% to *c.* 4%. Following this, it shows a general declining trend, towards *c.* 2% at the top of the sequence.

Neither organic content nor $CaCO_3$ appear to bear any relation to changes in gross sediment characteristics recorded in the field (see Figure 5.2).

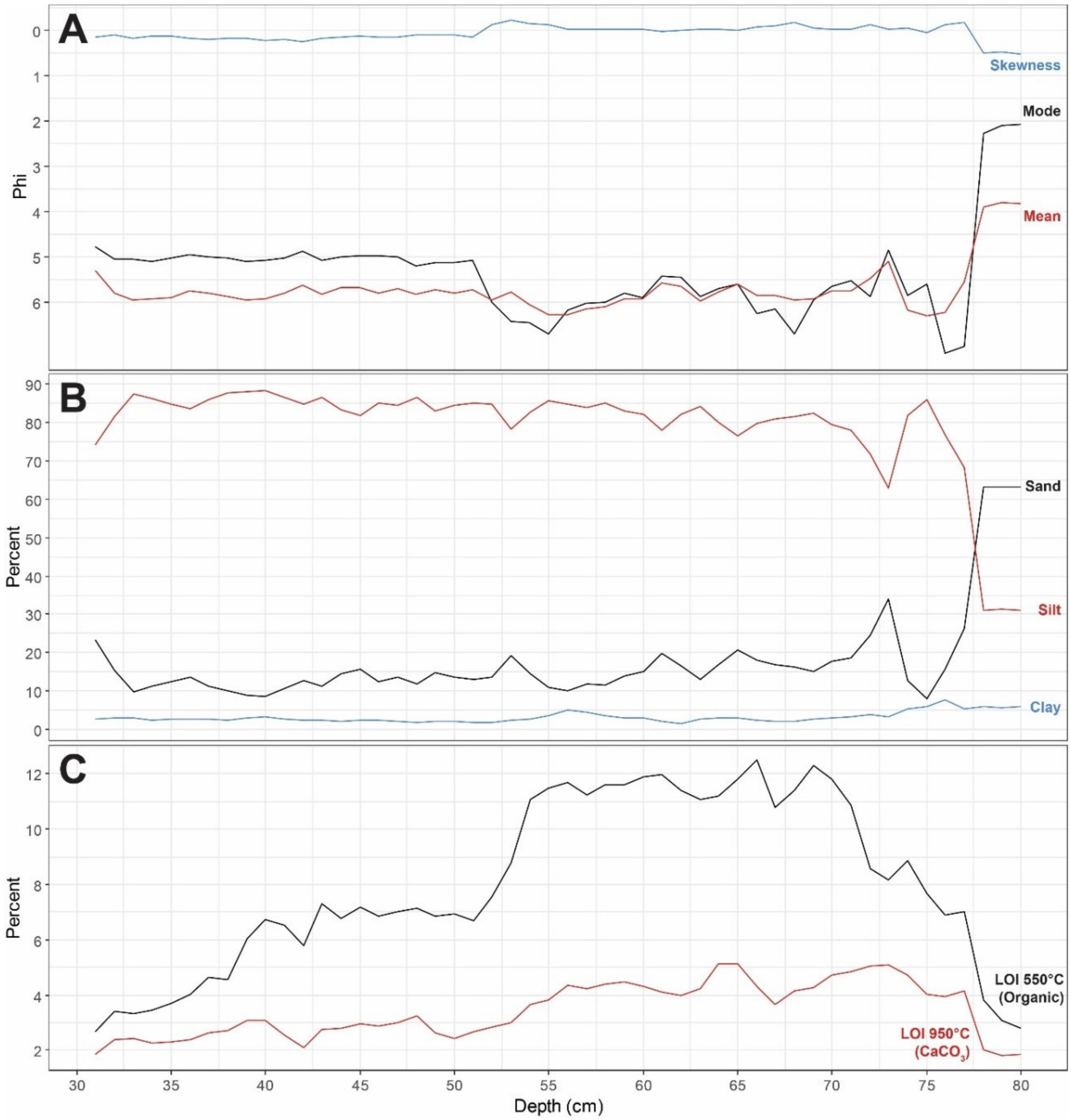


Figure 5.3 – PK14 (Fig. 4.2) loss-on-ignition and particle size data. A: average grain size; B: relative contributions of grain size classes; C: carbonate ($CaCO_3$) and organic content inferred from loss-on-ignition

Particle size analysis demonstrates that the sediments are dominated by fine and very fine silts and sand, with some clay, and though broadly stable in terms of grain size throughout the sequence, there are some notable changes (Fig. 5.3). These are particularly noticeable in modal grain size, which ranges from 2.08 phi (250 µm, fine sand) to 7.12 phi (8 µm, very fine silt). The basal 4 cm of the sequence exhibit rapid fining, encompassing the range from 2.08 phi to 7.12 phi in modal grain size, after which grain size is relatively stable by most measures (Fig. 5.3). However, modal grain size exhibits two distinct phases following the initial decrease: between 76 cm and 52 cm, this fluctuates between approximately 7 phi (8 µm, fine silt) and 5.5 phi (*c.*23 µm medium silt), and between 52 cm and 31 cm it is stable at approximately 5 phi (31 µm, coarse silt).

Similarly to the LOI data, these particle size data also do not appear to bear any particular relation to sedimentary sub-units recorded in the field (Fig. 5.2).

The above sedimentological descriptions and analyses are broadly consistent with West's (1980a) bed 'g' and Lee *et al.*'s (2008b) unit 'PaC'.

5.4.2. Palynostratigraphy

Assemblage change in the present sequence is limited, and only two significant assemblage zones are identified: PK-P1 (80-36 cm) and PK-P2 (36-31 cm) (Fig. 5.4).

Pollen Zone PK-P1 (80-36 cm)

The lowermost zone (PK-P1: 80-36 cm), which comprises the majority of the sequence, is dominated by a range of arboreal taxa, which are present alongside an array of herbaceous and aquatic taxa, as well as pteridophyte and fungal spores (Fig. 5.4). Proportions of tree and shrub pollen generally remain above 60% and range from 39.0% to 77.6% (68.87% mean). *Alnus* and *Pinus* pollen are the most abundant, and occur alongside diverse assemblages of both deciduous and coniferous taxa. These include consistently present pollen such as *Abies*, *Carpinus*, *Corylus*, *Quercus*, *Tilia* and *Ulmus*, and more rarely occurring pollen such as *Juglans* and *Prunus*. These may be derived from a range of catchments and habitats, and are unlikely to represent a spatially homogeneous mixture of tree taxa. For example, *Pinus* pollen may be derived from several kilometres away, but *Abies* and *Tilia* are poor pollen dispersers and are likely to have been growing relatively locally (<100 m) (Pigott & Huntley 1980; Poska & Pidek 2010). Additionally, whilst *Alnus* often grow in riparian and waterlogged situations (Houston Durrant *et al.* 2016), *Abies* prefer drier edaphic conditions (Mauri *et al.* 2016), and these taxa were unlikely to be growing together. This assemblage of tree pollen (particularly *Abies* and *Carpinus*) is indicative of mature, well-established woodland and is typical of Turner & West's (1968) 'late temperate' interglacial substage. Herbaceous pollen percentages range from 16.8% to 50.9% (26.7% mean), though they generally remain below 30%. Ericale pollen (especially *Calluna vulgaris*) also occurs throughout the sequence (4.5% mean), alongside occasional occurrences of *Juniperus*. *Calluna vulgaris* is a light-demanding species (Gaudio *et al.* 2011), and its consistent presence suggests a light canopy, the persistent occurrence of gaps in tree cover, or both. Herbaceous assemblages are dominated by Poaceae (20.9% mean), consistently accompanied by Cyperaceae, *Filipendula*, Apiaceae and *Solanum* pollen, further suggesting persistent openness within the landscape. Herbaceous taxa associated with disturbed habitats (*Plantago*, *Rumex*, *Taraxacum*) are also present, but less frequently, and a number of taxa occur only occasionally (e.g. *Artemisia*-type, *Galium*, *Lythrum*, *Symphytum*, Valerianaceae). Pteridophyte spores are common throughout the sequence, ranging from 12.2% to 27.9% (17.9% mean) (relative to total land pollen). Aquatic taxa also occur throughout in low abundances (5.2% mean, relative to total land pollen), including emergent (e.g. *Sparganium*, *Typha latifolia*), floating-leaved (e.g. *Nuphar*) and submerged (e.g. *Potamogeton*, *Myriophyllum*) taxa. Coprophilous fungal spores are rare in this sequence, with only two occurrences of individual *Sordaria*-type spores at 68 cm (432.2 spores cm^{-3}) and 40 cm (254.6 spores cm^{-3}), respectively. Low to moderate concentrations of microcharcoal shards are present throughout, with some variability, ranging from 5584.2 shards cm^{-3} to 43650.8 shards cm^{-3} (22779.0 shards cm^{-3} mean). Grain size is relatively consistent during this zone, asides from the basal 4 cm of the sequence which exhibit rapid fining (Fig. 5.3). The lowermost pollen sample (80 cm) is therefore derived from sand-dominated sediments, and may be more influenced by fluvial in-washing of pollen than the rest of the sequence, in which sediments are silt-dominated.

Pollen Zone PK-P2 (36-31 cm)

From 36-31 cm (PK-P2), the proportion of Poaceae increases, and most arboreal pollen types decrease proportionally (Fig. 5.4). Most notably, the abundance of pteridophyte spores increases considerably at this point (max: 438.8%, relative to total land pollen). However, it must be noted that pollen concentrations also significantly decrease, from 128306.0 grains cm^{-3} at 40 cm, to 3700.2 grains cm^{-3} at 36 cm (as a result, pollen counts at 36 cm and 32 cm were limited to 134 and 59 grains, respectively). This indicates a distinct change in the taphonomic and/or depositional conditions at this point in the sequence, leading to poor recovery of pollen grains in the laboratory. This suggests that although palynological change is recorded, this may not be a direct result of vegetation change. There is also a minor coarsening of the sediments in this zone (Fig. 5.3), which is consistent with a change in deposition conditions.

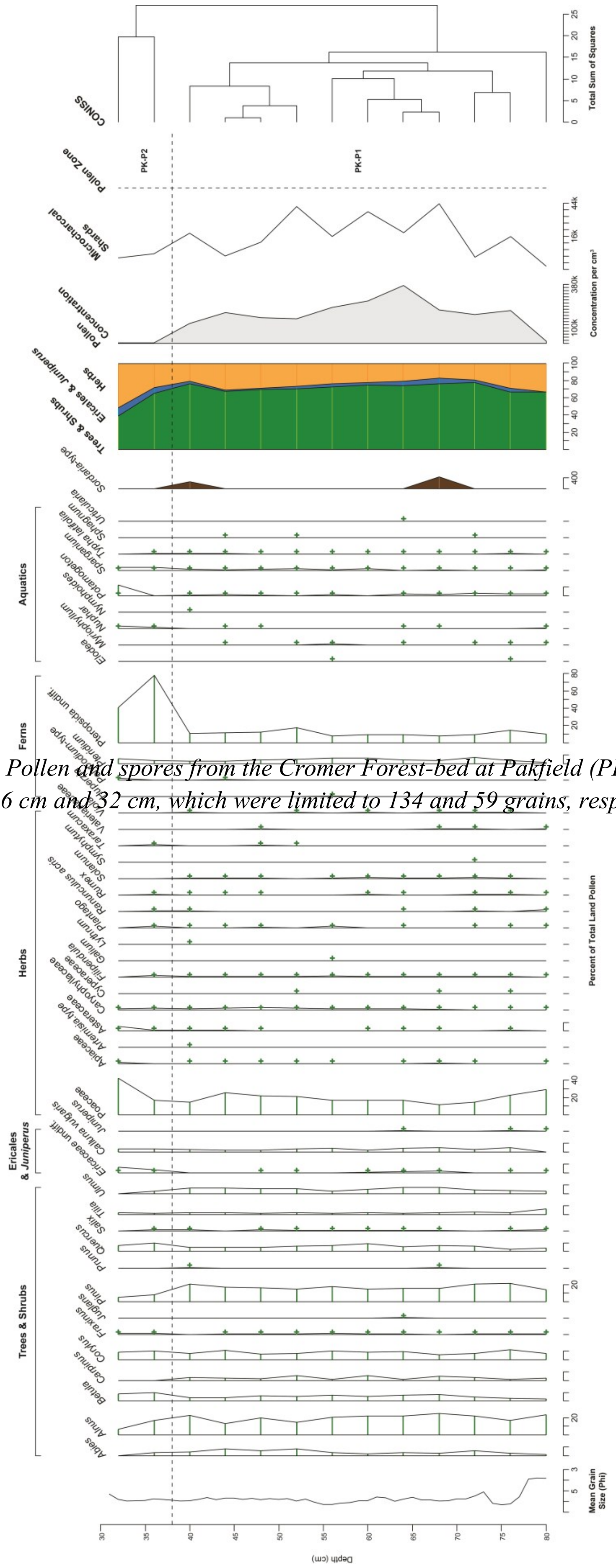


Figure 5.4 – Pollen and spores from the Cromer Forest-bed at Pakfield (PK14, Fig. 5.2) Total land polle
samples at 36 cm and 32 cm, which were limited to 134 and 59 grains, respectively.

5.4.3. Coleoptera

The following section presents the results of the extraction and analysis of coleopteran remains from the sedimentary sequence, and ecological interpretations. Seven samples were analysed over a depth of 47 cm, with mean volume of approximately 9 litres and mean weight of 15.20 kg (see Table 5.3). In total, 40 MNI (minimum number of individuals) were extracted and identified from this sequence, with individuals from 14 families and 23 genera, eight of which were identified to species-level.

Table 5.3 Summary of Pakefield (PK14, Fig. 5.2) Coleopteran Samples

Sample Number	**Depth (cm)**	**Approximate Volume (litres)**	**Weight (kg)**	**Total MNI**	**Taxon Richness**
1	28-41	14	24.86	2	2
2	41-47	10	16.17	3	3
3	47-52	7	12.94	10	10
4	52-57	6	11.41	2	2
5	57-62	7	10.99	6	6
6	62-67	7	12.05	7	7
7	67-75	12	17.98	10	6

5.4.3.1. Coleoptera: Limitations and caveats

The coleopteran record presented here provides valuable palaeoenvironmental information, but certain caveats should be borne in mind. Firstly, sub-fossil insect material is of particularly low abundance in this sequence: mean total MNI per litre of sediment is 0.67 (min: 0.14, max: 1.43), and so despite large sedimentary sample sizes (mean: *c.* 9 litres) the mean MNI per sample is just 5.71 (min: 2, max: 10). Underrepresentation of typically low abundance groups of beetles (e.g. bark beetles) is unavoidable in this context, and their absence in the fossil record should not be interpreted as absence in the palaeolandscape. Additionally, such low abundance samples can also lead to underrepresentation in proportional terms when one taxon becomes abundant.

Secondly, the condition of much of the sub-fossil material meant that for the majority of specimens only genus-level identification was possible. This limits the specificity of the ecological information which can be derived from these specimens, as the habitat preferences of individual species are often not consistent within a genus. Few in the present sequence were classified as ‘uncategorised or eurytopic’ (UN), though several were necessarily assigned to comparatively broad categories. For example, whilst certain species of *Cercyon* and *Aphodius* have specific requirements for herbivore dung, this is not true of the whole genera, and so these genus-level identifications are assigned to ‘Decaying/Foul/Rotten’ (DE) habitats, rather than the more specific ‘Dung’ (DU) category.

5.4.3.2. Coleoptera: Landscape and ecology

The coleopteran sequence has been divided into two assemblage zones, primarily on the basis of the presence (PK-C1: 75-47 cm) and absence (PK-C2: 47-28 cm) of riffle beetles (Elmidae, Dryopidae) (Table 5.4, Fig. 5.5).

Coleopteran Zone PK-C1 (75-47 cm)

The lower zone (PK-C1: 75-47 cm), contains a generally greater concentration of sub-fossil material, and more diverse assemblages. In the lower samples of this zone (75-57 cm), aquatic taxa are typically the most abundant. Of these, several are associated with lotic habitats: riffle beetles (Elmidae, Dryopidae) are generally associated with flowing water conditions, and the species *Oulimnius tuberculatus* is often associated with stony-bottomed streams and rivers (Holland 1972), though is occasionally found at lake edges (Holland 1972; Koch 1989b). The occurrence of the weevil *Tanysphyrus lemnae*, an oligotroph of *Lemna* spp. (duckweed) and similar small floating-leaved plants (Koch 1992), indicates the presence of lentic conditions. *Hydraena* sp. and *Ochthebius* sp. are more general aquatic taxa, though species within these genera may have preferences for specific conditions. Taxa associated with the terrestrial-aquatic ecotone (wetland edge, riparian/waterside and hygrophilous taxa) are consistently present through this zone, in similar abundances to fully aquatic taxa. Wetland edge species in this sequence are exclusively Donaciinae, assigned to *Plateumaris sericea*, *Plateumaris* sp. and Donaciinae indet. Species in this subfamily are semi-aquatic: they are associated with plants growing in or beside water, and undergo larval and pupal stages on, or inside, submerged plant tissues (Harde 1984). *P. sericea* is found on the margins of both flowing and still wetland types, associated with *Carex* spp., *Sparganium* spp. and other emergent macrophytes (Koch 1992; Cox 2007). The presence of *Bledius* sp., which burrow into exposures of soft sediments and feed on algae (Harde 1984), suggests that the wetland was also bordered by banks or disturbed areas. *Bembidion* sp. and *Stenus* sp. are also generally associated with waterside habitats. The rove beetle *Anotylus rugosus* is another frequent inhabitant of waterside habitats, though with a preference for rotten or foul material in this context (Koch 1989a; Anderson 1997). The presence of *Aphodius* sp. also indicates foul and rotten habitats, and potentially the presence of dung, though this genus is not exclusively coprophilous.

Drier habitats within PK-C1 are represented by arboreal and grassland species. *Melanotus punctolineatus* develops at the roots of grasses in dry, sandy soils (Hyman 1992; Koch 1989b), suggesting the presence of open, disturbed habitats. Some species of *Agriotes* are found in similar contexts, but not exclusively. The mycophagous *Hallomenus binotatus* is primarily found on fungal fruiting bodies on dead and decaying deciduous and coniferous wood (Koch 1989b), suggesting that woodland habitats were also present locally, and were mature and well-established. The bark beetle, *Hylastes attenuatus* is exclusively associated with *Pinus* spp. (Alexander 2002), confirming the local presence of these trees.

Table 5.4 Sub-fossil Coleoptera from the Cromer Forest-bed at Pakefield (PK14, Fi.g 5.2)

(AG: Aquatic (general); AS: Aquatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG: Woodland/Trees (general); WTD: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed; DE: Decaying/Foul/Rotten (general); DU: Dung; UN: Uncategorised or Eurytopic)

Family	**Species**	**Habitat Category**	**Median Sample Depth (cm) and Faunal Zone**						
			71	64.5	59.5	54.5	49.5	44	34.5
			PK-C1					**PK-C2**	
Dytiscidae									
	Dytiscidae indet.	AG							1
Carabidae									
	Bembidion sp.	RW		1			1		
	Pterostichus sp.	UN					1		
Hydrophilidae									
	Cercyon sp.	DE					1		
Hydraenidae									
	Hydraena spp.	AG	2						
	Ochthebius sp.	AG			1			1	
Staphylinidae									
	Anotylus rugosus (F.)	DE		1					
	Bledius sp.	RW					1		
	Stenus sp.	H			1				
	Lobrathium multipunctum (Grav.)	RW							1
	Aleocharinae indet.	DE					1		
Scarabaeidae									
	Aphodius sp.	DE	1				1		

(Continued overleaf)

Table 5.4 (continued)

Family	**Species**	**Habitat Category**	**Median Sample Depth (cm) and Faunal Zone**						
			71	64.5	59.5	54.5	49.5	44	34.5
			PK-C1					**PK-C2**	
Elmidae									
	Oulimnius tuberculatus (Müller)	AF	4		1				
	Oulimnius sp.	AF		1					
	Elmidae indet.	AF					1		
Dryopidae									
	Dryops sp.	AF	1						
Elateridae									
	Agriotes sp.	UN			1				
	Melanotus punctolineatus (Pelerin)	O		1	1		1	1	
Tetratomidae									
	Hallomenus binotatus (Quensel)	WTG	1			1			
Coccinelidae									
	Coccinelidae indet.	UN		1					
Chrysomelidae									
	Donaciinae indet.	WE	1						
	Plateumaris sericea (L.)	WE			1		1		
	Plateumaris sp.	WE		1		1		1	
Erirhinidae									
	Tanysphyrus lemnae (Payk.)	AS		1					
Curculionidae									
	Hylastes attenuatus (Er.)	WTC					1		
		Taxon Richness	6	7	6	2	10	3	2
		Total MNI	10	7	6	2	10	3	2

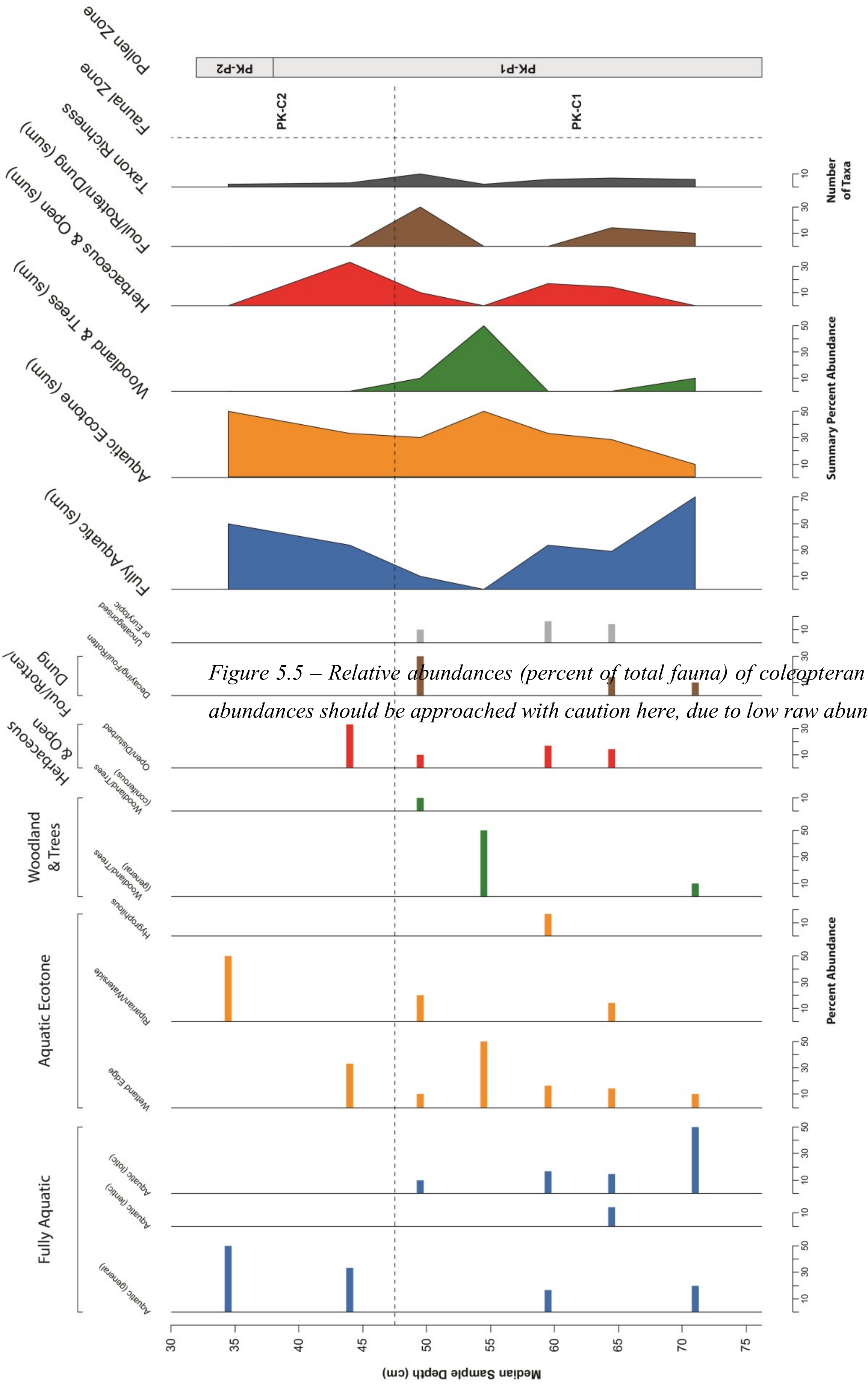


Figure 5.5 – Relative abundances (percent of total fauna) of coleopteran habitat gro

abundances should be approached with caution here, due to low raw abundances (see

Coleopteran Zone PK-C2 (47-28 cm)

The upper unit of this sequence (PK-C2: 47-28 cm) contains very low concentrations of sub-fossil insect material (Table 5.4, Fig. 5.5) and so contains few taxa, despite comprising a substantial part of the sedimentary sequence. Notably, no riffle beetles (Elmidae, Dryopidae) were found in this zone, though aquatic habitats are represented by Dytiscidae indet. and *Ochthebius* sp., both of which contain subordinate taxa which may be associated with a range of aquatic conditions, including both lentic and lotic habitats. The continued presence of *Plateumaris* sp. indicates that wetland margins remained vegetated in this zone. *Lobrathium multipunctum* may be associated with a range of riparian habitats, often on fine-grained sediment substrates (Koch 1989a; Lott & Anderson 2011), suggesting the continued presence of the exposed sediment habitats favourable to *Bledius* sp. Dry, grassland-type habitats are again indicated by *Melanotus punctolineatus*. Taxa associated with foul and rotten habitats or woodlands and trees are absent from this zone, but given the low concentration of material, their absence in the palaeolandscape cannot be inferred.

This coleopteran fauna (Table 5.4, Fig. 5.5) is somewhat limited, but indicates the local presence of various aquatic and terrestrial micro-, meso- and macrohabitat types. Wetland-associated and aquatic taxa are the most common groups in these assemblages, and are indicative of a freshwater habitat, fringed with emergent macrophytes and some exposed banks. The silt-dominated sedimentology (Fig. 5.3) indicates that this was a low-energy environment, but the presence of Elmidae and Dryopidae in PK-C1 is a clear indication of fluvial influence in at least part of the record. This implies input from a periodically flooding stream or river nearby, or feeding into the lentic environment, meaning that some of the coleopteran remains may not have been derived from the immediately local landscape. Both woodland-type and open grassland-type habitats were evidently present in the drier parts of the local landscape, and both were evidently persistent and well-established. Whilst there is no conclusive evidence for frequent herbivore presence in this landscape from the beetle fauna, the occurrence of *Aphodius* sp. is at least suggestive of this.

5.4.3.3. Coleoptera: Climate

Climatic inferences based on the PK14 fauna are limited by the paucity of the sub-fossil assemblages. Quantitative estimates of climate were only able to be derived from *Anotylus rugosus*, which gives estimates of mean warmest month temperatures between 10°C and 27.5°C, and mean coldest month temperatures between -19.5°C and 7°C. All species in the assemblage are currently present in Britain, though not all are present in East Anglia. *Melanotus punctolineatus* and *Hylastes attenuatus* have predominantly southern distributions in Britain (GBIF 2016), suggesting mild winters and/or warm summers.

5.4.4. Coope's Pakefield Coleoptera

This section presents beetle assemblages from the Cromer Forest-bed at Pakefield published by Coope (2006) (see Figure 5.1 for sampling location), re-analysed using a functional group approach (Table 5.5; Fig. 5.6) and Milne (2016) MCR (Table 5.6). This gives emphasis to important aspects of the fauna in an ecological context, provides more accurate climatic reconstructions and facilitates comparison with the new coleopteran record from Pakefield presented in this chapter (PK14: Section *5.4.3.*). The greater diversity and abundance of sub-fossil Coleoptera in Coope's (2006) Pakefield record, relative to the PK14 record, also allows more reliable inferences to be drawn on the basis of relative abundances. Taxonomy has been updated according to Duff (2012).

Table 5.5 Sub-fossil Coleoptera from the Cromer Forest-bed at Pakefield (Coope 2006) (Sample 1: Upper; Sample 2: Middle; Sample 3: Lower)

(AG: Aquatic (general); AS: Aquatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG: Woodland/Trees (general); WTD: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed; DE: Decaying/Foul/Rotten (general); DU: Dung; UN: Uncategorised or Eurytopic)

Family	**Species**	**Habitat Category**	**Sample**		
			1	2	3
Gyrinidae					
	Gyrinus sp.	AG		1	
	Orectochilus villosus	AF	2		
Dytiscidae					
	Ilybius sp.	AS		1	
	Dytiscus sp.	AS	1		
	Cybister lateralimarginalis	AS	1		
Carabidae					
	Carabus violaceus	WTG		1	
	Trechus secalis	H	3	1	
	Tachys bistriatus	RW	1	1	
	Bembidion gilvipes	RW	1		
	Pterostichus diligens	H		1	
	Pterostichus strenuus	H	1		
	Calathus fuscipes	O	1		
	Amara infima	O	1		
	Bradycellus ruficollis	O		1	
	Paradromius longiceps	RW	1		
	Syntomus foveatus	O	1	1	
Helophoridae					
	Helophorus sp.	AG	1		

(Continued overleaf)

Table 5.5 (continued)

Family	Species	Habitat Category	Sample 1	Sample 2	Sample 3
Hydrophilidae					
	Hydrobius fuscipes	AS	1		
	Limnoxenus niger	AS		1	
	Hydrophilus sp.	AS		1	
	Laccobius sp.	AG	1	1	
	Coelostoma orbiculare	AS	1		
	Cercyon convexiusculus	DE	1	1	
	Cercyon sternalis	DE	1		
Histeridae					
	Hister sp.	DE			1
Hydraenidae					
	Hydraena riparia	AG	5	1	
	Ochthebius sp.	AG	2	1	
Staphylinidae					
	Olophrum sp.	H		1	
	Micropeplus staphylinoides	DE	1		
	Bryaxis sp.	H	1		
	Pselaphaulax dresdensis	H	1	1	
	Tachinus rufipes	DE	1		
	Aleocharinae indet.	DE	1	1	1
	Anotylus nitidulus	DE		1	
	Oxytelus opacus	DE	1		
	Bledius sp.	RW	2	2	
	Carpelimus sp.	H	2		
	Stenus juno	H		1	
	Stenus spp.	H	2	1	
Ptiliidae					
	Acrotrichis sp.	DE	1		
Scirtidae					
	Scirtidae indet.	RW	1	1	
Buprestidae					
	Agrilus sp.	WTD		1	

(Continued overleaf)

Table 5.5 (continued)

Family	Species	Habitat Category	Sample		
			1	2	3
Lucanidae					
	Dorcus parallelipipedus	WTD		1	
Scarabaeidae					
	Aphodius spp.	DE	1	1	
	Onthophagus sp.	DU	1		
	Valgus hemipterus	WTD	1		
	Cetonia aurata	WTD	1		
Elmidae					
	Esolus parallelepipedus	AF	27	7	2
	Limnius volckmari	AF	2		
	Macronychus quadrituberculatus	AF	2	1	
	Normandia nitens	AF	1		
	Oulimnius troglodytes	AF	3	5	1
	tuberculatus	AF	11	1	
	Riolus cupreus	AF	1		
	Stenelmis canaliculata	AF	1		
Dryopidae					
	Pomatinus substriatus	AF	1	1	
Elateridae					
	Agrypnus murina	O	1	1	
	Agriotes sp.	UE	1		
Dermestidae					
	Dermestes murinus	DE		1	
Ptinidae					
	Xestobium rufovillosum	WTD	1		
Nitidulidae					
	Epuraea sp.	WTG	1	2	
Monotomidae					
	Rhizophagus bipustulatus	WTD	1		

(Continued overleaf)

Table 5.5 (continued)

Family	Species	Habitat Category	Sample		
			1	2	3
Silvanidae					
	Airaphilus elongatus	H	1		
Laemophloeidae					
	Notolaemus unifasciatus	WTD	1		
Phalacridae					
	Phalacrus sp.	DE	1	1	
Corylophidae					
	Corylophus crassidoides	DE	4		
Chrysomelidae					
	Bruchus/Bruchidius sp.	HP	1		
	Macroplea appendiculata	AG	2		
	Donacia bicolora	WE	1		
	Donacia cinerea	WE	1	1	
	Donacia clavipes	WE	1		
	Donacia crassipes	WE	1		
	Donacia semicuprea	WE		1	
	Plateumaris bracata	WE	1	1	
	Plateumaris affinis	WE	1		
	Plateumaris sericea	WE	1	1	1
	Phaedon cochleariae	HP	1		
	Phaedon tumidulus	HP	1		
	Plagiodera versicolora	WTD	1		
	Agelastica alni	WTD	1	1	
	Altica sp.	UN	1		
Apionidae					
	Apion sp.	HP	1	2	
Dryophthoridae					
	Dryophthorus corticalis	WTD	1		
Erirhinidae					
	Notaris scirpi	WE	1	1	
	Tanysphyrus lemnae	AS	4	2	1

(Continued overleaf)

Table 5.5 (continued)

Family	**Species**	**Habitat Category**	**Sample**		
			1	2	3
Curculionidae					
	Curculio venosus	WTD	1	1	
	Orchestes quercus	WTD	1	2	
	Orchestes sp.	WTD	1		
	Bagous sp.	WE	1	2	
	Limnobaris dolorosa	WE	1		

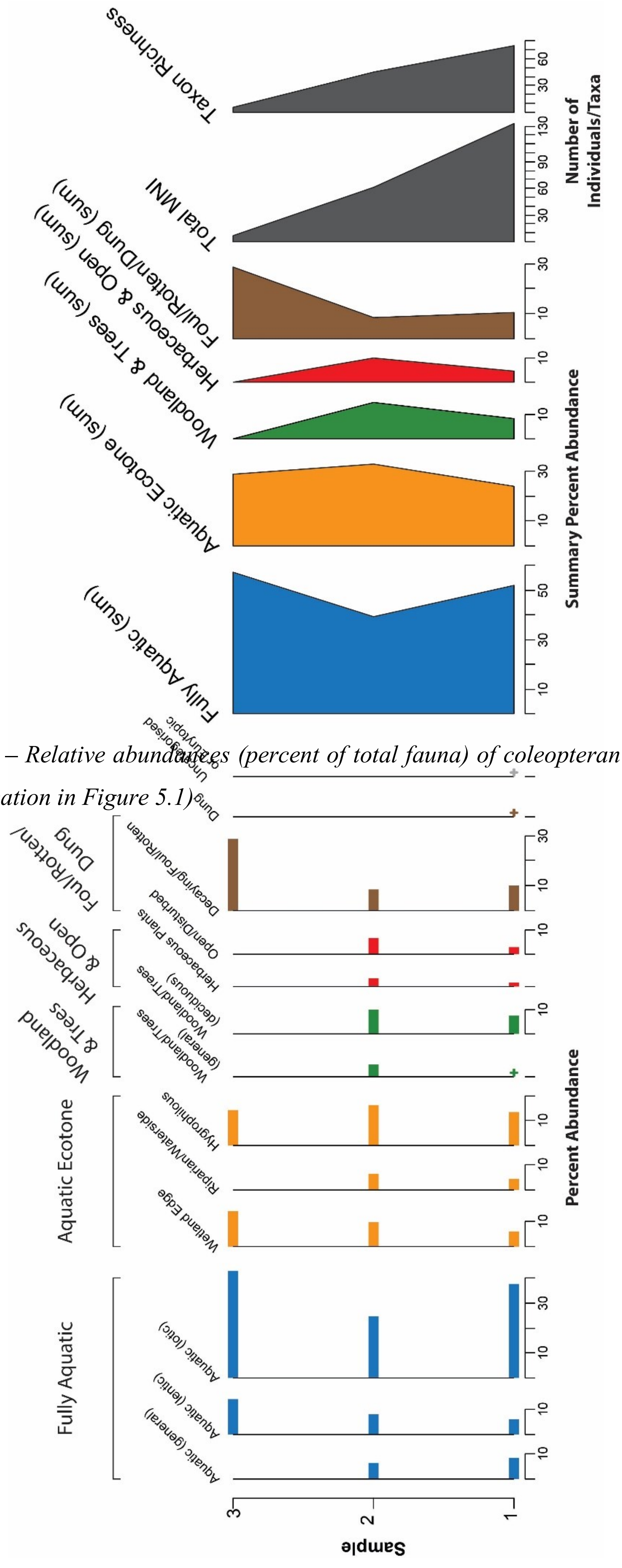


Figure 5.6 – Relative abundances (percent of total fauna) of coleopteran habitat groups from the Cro
(2006), location in Figure 5.1)

Table 5.6 Mutual Climatic Range (MCR) estimates for Coope's (2006) Pakefield fauna (sampling location in Figure 5.1), based on BugsCEP (Buckland & Buckland 2006) and new (Milne 2016) MCR methods

Sample	**BugsCEP MCR**		**New MCR**		**Number**
	TMax (°C)	**TMin (°C)**	**TMax (°C)**	**TMin (°C)**	**of Species**
1	18 to 22	-6 to 1	15.5 to 20	-5.5 to 2.5	12/11*
2	15 to 24	-12 to 9	14 to 25	-5.5 to 2.25	7
3	n/a	n/a	n/a	n/a	0
All	18 to 22	-6 to 1	15.75 to 20	-5.5 to 2.25	18/17*

**Oxytelus opacus* excluded from new MCR due to paucity of data

A quantitative functional group approach provides a reconstruction of the local palaeolandscape broadly in agreement with that given by Coope (2006), but with additional emphasis and detail regarding certain aspects of the fauna. Aquatic beetles are the most important group, comprising 39.3% to 51.9% of assemblages (Fig. 5.6). As emphasised by Coope (2006), lotic taxa are the most significant contributor to this (24.6% to 42.86% of the total fauna), due to the abundance and diversity of 'riffle beetles' (Elmidae, Dryopidae). Of these, *Esolus parallelepipedus*, a species typical of energetic stony-bottomed streams and rivers (Holland 1972; Elliott 2008), is particularly notable for its abundance (Table 5.5). Coope (2006, p1750) suggested that this abundance and diversity of riffle beetles indicated that "a substantial river existed in the vicinity [of the deposit]"; this is confirmed by the quantitative treatment of this data, which provide percentage abundances of lotic taxa consistent with other sub-fossil assemblages associated with high-energy fluvial environments (Smith & Howard 2004). As noted in the original publication, deposition cannot have taken place in high-energy conditions, but rather in a backwater or cut-off channel. Accordingly, the lotic taxa are accompanied by species associated with lentic conditions (AS) (e.g. *Cybister lateralimarginalis*, *Hydrobius fuscipes*), shown here to comprise 6.0% to 14.3% of the fauna, and species which inhabit reedbed-type habitats (WE) (e.g. *Donacia* & *Plateumaris* species, *Limnobaris dolorosa*), which comprise 6.0% to 14.3% of the assemblages (Fig. 5.6).

Coope (2006) also suggested the presence of open woodland habitats in the local area, based on the presence of a number of arboreal, deadwood and leaf litter species. Here, it is demonstrated that obligate woodland and arboreal taxa account for 8.3%, 14.8% and 0% of the total fauna in samples 1, 2 and 3, respectively (Fig. 5.6). Excluding fully aquatic species, these percentage abundances become 17.5%, 22.5% and 0%, respectively. With the exception of the latter sample, which has a low total MNI (Table 5.5), these values are consistent with relative abundances of woodland and arboreal taxa associated with low-density woodland habitats in modern analogue (Smith *et al.* 2010) and Holocene (Whitehouse & Smith 2010) studies. Many of these species are associated with living deciduous trees, and several, such as *Dorcus parallelipipedus*, *Valgus hemipterus* and *Xestobium rufovillosum*, are associated with deadwood habitats (Harde 1984). Additionally, *Trechus secalis*, though designated here as 'hygrophilous', also exhibits some preference for shaded, moist woodland microhabitats (Lindroth 1985), and the riffle beetle *Macronychus quadrituberculatus* is an inhabitant of deadwood submerged in rivers (Foster 2000). In combination, these species suggest that local woodland habitats were mature, well-established and deciduous-dominated.

The presence of a small number of taxa associated with open and disturbed grassland-type habitats, in conjunction with woodland species, further suggests that local woodland habitats were not characterised by a dense a canopy. Coleoptera associated with open and disturbed habitats are not abundant in these assemblages, accounting for just 3.0%, 6.6% and 0% in samples 1, 2 and 3, respectively (Fig. 5.6), but give additional insights nonetheless. Ground beetle (Carabidae) assemblages include several species associated with relatively dry habitats, with sparse or low vegetation. *Amara infima* and *Bradycellus ruficollis* both have a preference for habitats with abundant *Calluna* (Lindroth 1974), *Syntomus foveatus* typically inhabits dry, sandy open habitats, such as coastal grasslands and dunes (Koch 1989a [Okologie 1]) and *Calathus fuscipes* may be found in a range of relatively open, disturbed habitats (Koch 1989a). The click beetle (Elateridae), *Agrypnus murina* is also found in an array of dry, open environments (Koch 1989b). Together, these suggest the presence of sandy heath-type habitats.

Beetles associated with a variety of decaying and rotten microhabitats are shown here to comprise between 8.2% and 28.6% of assemblages (mean: 15.5%) (Fig. 5.6), and are therefore a significant aspect of the fauna. However, they received limited attention in Coope (2006). Many of these taxa are generalists, found amongst rotten vegetation and plant debris in a variety of contexts, but a number are particularly associated with such microhabitats in riparian, marsh and fen environments. The most numerous of these is *Corylophus crassidoides* (Table 5.5), which is found amongst fen vegetation and flood debris (Bowestead 1999), and is accompanied by *Cercyon convexiusculus* and *C. sternalis* which have similar habits (Koch 1989a). As noted by Coope (2006), specifically dung-obligate taxa, indicating the presence of herbivores, are rare in these assemblages: they are represented by a single occurrence of *Onthophagus* sp. However, the presence of the carrion-feeding *Dermestes murinus* (Koch 1989b) provides some additional suggestion of the availability of vertebrate-associated habitats (i.e. carcasses).

As previously noted by Coope (2006, 2010a), several species in this assemblage are rare or absent in the British Isles at present. For example, *Cybister lateralimarginalis* and *Valgus hemipterus* are both generally absent from Britain at present, though the former is occasionally recorded (Foster & Friday 2011). They also have no records for the Holocene, but were present in several Middle Pleistocene interglacials (Coope 2010a). *Airaphilus elongatus*, whilst absent from Britain at present, has been recorded at several Early Holocene sites in Britain, including in northern England (e.g. Howard *et al.* 2000). The presence of these species at Pakefield has been used to infer a warm temperate climate (e.g. Parfitt *et al.* 2005; Coope 2006, 2010a). Indeed, northwest continental Europe and southern Scandinavia are the most proximal areas to Britain that these species currently inhabit (GBIF 2016), suggesting that their successful establishment in Britain may be partly related to warmer summers and greater climatic continentality during certain interglacials. However, their apparent absence from Britain during other interglacials, including the Holocene, is unlikely to be solely determined by climate. The failure to establish populations in Britain may also be related to other factors, such as relative habitat availability, competitive exclusion or inability to disperse across the English Channel from mainland glacial refugia during post-Anglian interglacials. It should be noted that whilst they are absent in the PK14 record (Table 5.4), given the low abundances of fossil material in this sequence, this should not be treated as evidence of absence: the possibility remains that these are not a 'true' absences, but instead reflects a lack of detection.

This new analysis does not re-write Coope's (2006) original reconstruction, but rather provides an additional level of clarity and detail. The inferred presence of a "substantial river in the vicinity" (Coope 2006 p1751) is strengthened by relative abundances of lotic taxa, which are consistent with the local presence of a high-energy fluvial environment (Smith & Howard 2004). Coope (2006) also inferred that mature, well-established trees were present in the landscape, and the quantification of woodland and tree-associated beetles presented here add to this by comparison with more recent studies (e.g. Smith *et al.* 2010; Whitehouse & Smith 2010). In combination with species associated with open, disturbed and heathland-type habitats, they suggest that woodland-type habitats were locally prevalent, but were likely relatively open, without a dense canopy. Though given limited attention by Coope (2006), a suite of taxa associated with decaying and mouldy vegetation was also prevalent in the beetle fauna, particularly those associated with marsh and wetland vegetation. This suggests that abundant plant debris was available in the riparian zone, possibly as a result of flood deposition.

5.4.5. Multivariate analyses

The results of ordination analyses (principal components analysis, canonical correspondence analysis), applied to pollen and coleopteran datasets, are presented in this section. These analyses aim to identify underlying co-variance between taxa, functional groups and environmental proxies, to provide a more nuanced perspective of assemblages than possible with just a stratigraphic diagram, as another perspective is given on the same data. As discussed in Chapter 3, multivariate analyses of coleopteran assemblages use functional groups, rather than taxa, to compensate for the stochastic occurrences of individual species/genera and to facilitate ecologically-based interpretations. Interpretations drawn from analyses involving the PK14 coleopteran samples (Fig. 5.2) should be approached with caution and viewed as strictly tentative, given the low MNI values and number of samples (n=7).

5.4.5.1. Correlation analysis

The correlation matrix (Fig. 5.7) demonstrates statistical relationships between various groups of taxa and proxies of environmental variables in the PK14 sequence. Given that datasets were harmonised according to the coleopteran sequence, the resulting number of samples is low (n=7), and correlations here should therefore be approached with caution. Several variables, such as woodland/tree-associated Coleoptera ('WoTre') and *Sordaria*-type spores ('Sordari') have very limited occurrences within these samples (see Figures 5.4 and 5.5), and correlation coefficients for such variables are especially unlikely to represent meaningful trends.

Several of the more significant paired relationships are between deciduous tree pollen ('Decidu') and other variables, including with Poaceae pollen ('Poacea') (r=-0.68), charcoal ('Charco') (r=-0.68), organic content ('Organic') (r=0.96) and $CaCO_3$ content ('$CaCO_3$') (r=0.71). Deciduous pollen is also weakly correlated with coniferous pollen ('Conifer') (r=-0.46), aquatic pollen ('Aquatic') (r=-0.57) and mean grain size ('PhiMea') (r=0.46). Ericale pollen exhibits weaker relationships with coniferous pollen ('Conifer') (r=-0.61), *Sordaria*-type spores (r=0.58) and Coleoptera associated with herbaceous plants and open/disturbed habitats (r=-0.70). Poaceae pollen exhibits negative correlations with organic content (r=-0.64) and $CaCO_3$ content (r=-0.93). Other herbaceous pollen ('Herbs') is positively correlated with fern spores ('Ferns') (r=0.61) and aquatic ecotone Coleoptera (r=0.84), and negatively correlated with $CaCO_3$ content (r=-0.71). Aquatic pollen is negatively correlated with charcoal (r=-0.86), which may represent a taphonomic signal.

Coleopteran functional groups exhibit some noteworthy correlations with other variables (Fig. 5.7), though these should be approached with particular caution, given the low MNI values of the coleopteran samples. Fully aquatic Coleoptera ('FullyAq') are positively correlated with *Sordaria*-type spores (r=0.81), though this is unlikely to represent a meaningful relationship given the low number of occurrences of *Sordaria*-type spores (Fig 5.4). Aquatic ecotone Coleoptera ('AqEcot') are correlated positively with herbaceous pollen (r=0.84), and negatively with Coleoptera associated with foul/rotten habitats and dung ('FoRoDu') (r=-0.76) and $CaCO_3$ content (r=-0.73). Coleoptera associated with herbaceous plants and open/disturbed habitats exhibit negative correlations with both ericale pollen (r=0.70) and Coleoptera associated with woodlands and trees (r=-0.62).

These correlations highlight the significance of deciduous trees, ericales and grasses (Poaceae) in the palaeolandscape, and suggest potential interactions between fire (charcoal) and vegetation, which are investigated further in the following sections. Paired relationships involving coleopteran functional groups are tentative, and though some are intuitively logical (e.g. the negative relationship between woodland/tree Coleoptera and Coleoptera associated with herbaceous plants and open/disturbed habitats), caution should continue in the following multivariate investigations for the reasons previously stated.

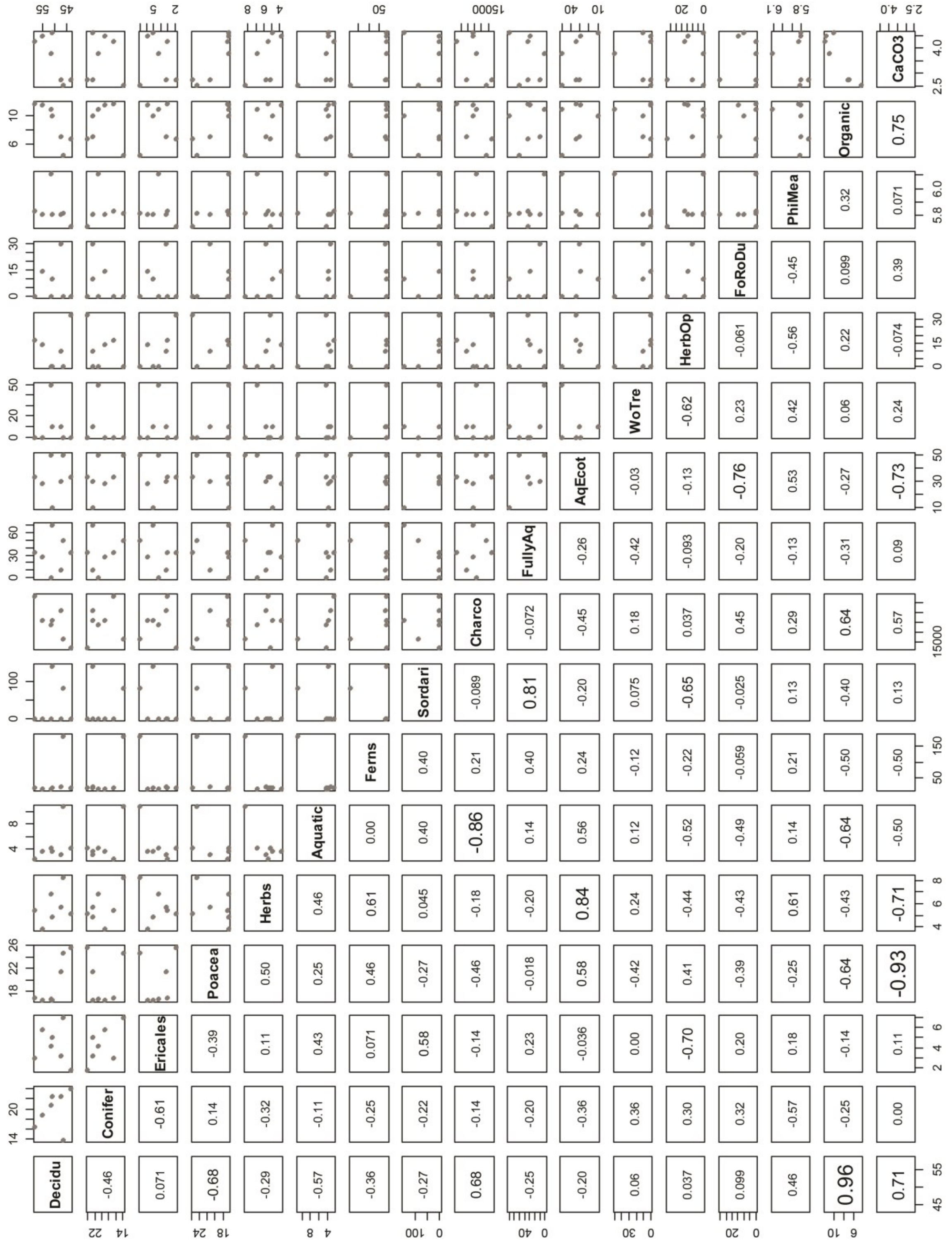


Figure 5.7 – Paired correlations between biotic (groups of pollen types and coleopteran functional groups) and abiotic variables (sedimentary properties, charcoal) from the PK14 (Fig 5.2) Pakefield sequence.

(Decidu: deciduous tree and shrub pollen; Conifer: coniferous tree and shrub pollen; Ericales: ericale and Juniperus pollen; Poacea: Poaceae pollen; Herbs: non-grass herbaceous pollen; Aquatic: aquatic pollen; Ferns: fern spores; Sordari: Sordaria-type spores; Charco: charcoal; FullyAq: fully aquatic Coleoptera; AqEcot: aquatic ecotone Coleoptera; WoTre: woodland/tree Coleoptera; HerbOp: herbaceous plant and open/disturbed habitat Coleoptera; FoRuDu: Foul/Rotten/Dung-associated Coleoptera; PhiMea: average grain size; Organic: organic content; $CaCO_3$: calcium carbonate content

5.4.5.2. Ordinations of palynological assemblages

Figure 5.8 presents the result of a PCA applied to pollen and spore assemblages. The first axis (PC1) accounts for 28.7% of variability within the sequence, and the second (PC2) accounts for 16.5% (54.8% of variability is unaccounted for in this figure). The first axis is primarily influenced by relative abundances of *Alnus* and *Pinus*, and to a lesser extent, Cyperaceae, *Viola*, *Sphagnum*, *Ulmus* and *Solanum*. They exhibit negative covariance with Ericaceae undiff., *Nuphar*, *Fraxinus* and *Sparganium*. There is also a distinct separation of samples on this axis, with those from the uppermost 6 cm of the sequence (32 cm and 36 cm) plotting on the left of this axis (highlighted in Figure 5.8). This may indicate a distinction between more wooded habitats (with greater abundances of *Alnus* and *Pinus*) and more open habitats (with greater abundances of Ericaceae undiff.). However, given the notably low pollen concentrations at 32 cm and 36 cm (see Figure 5.4), changing taphonomic conditions, may also be an important factor. The second axis is influenced by low-abundance taxa, such as *Calluna vulgaris*, *Salix*, *Rumex*, *Filipendula*, *Plantago*, *Taraxacum*, *Ranunculus acris* and *Tilia*. The abundances of these taxa have a particularly low range of variability, and so differences in their relative abundance are minor and unlikely to represent significant palaeoenvironmental differences.

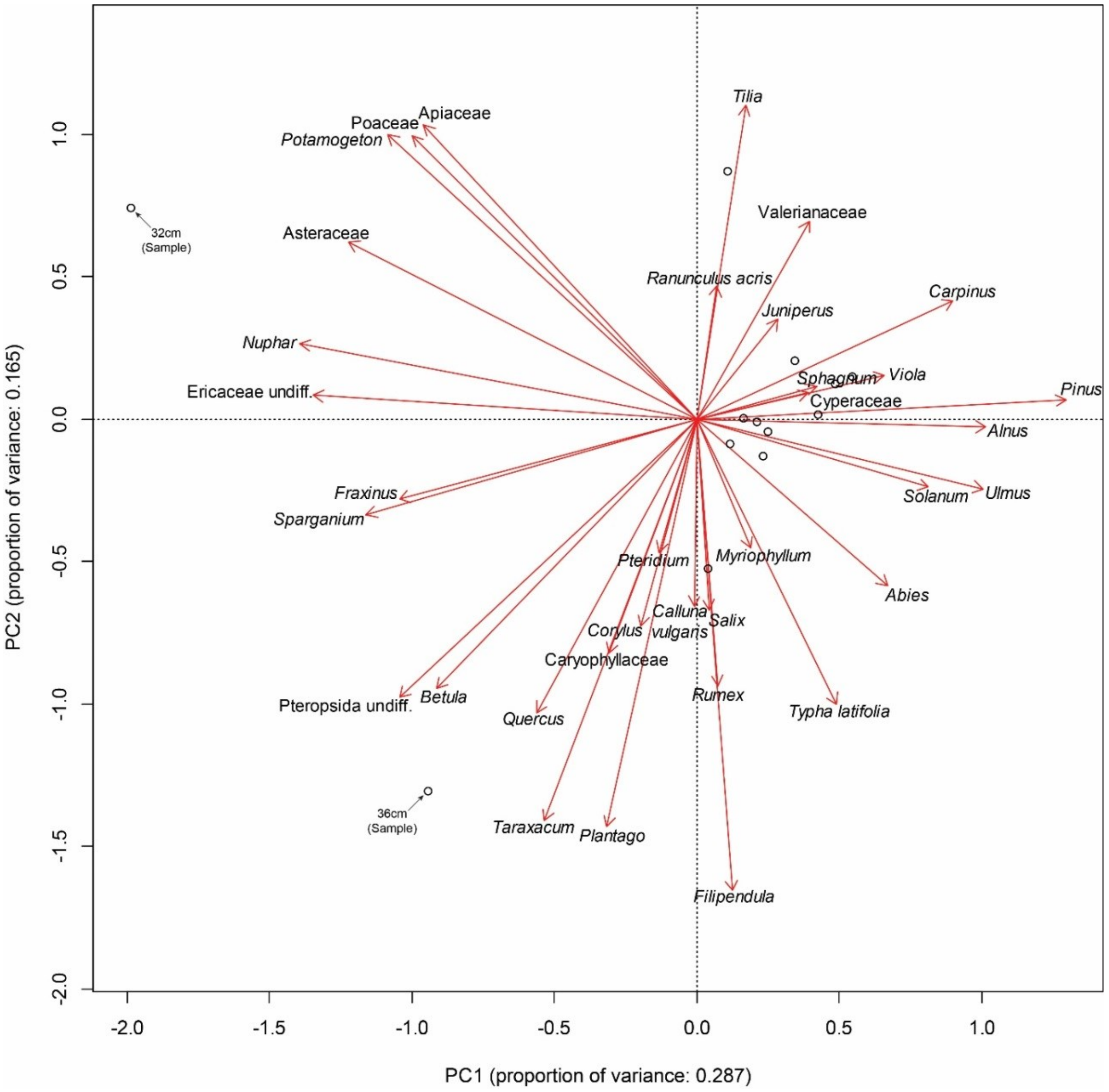


Figure 5.8 – PCA of major pollen and spore taxa from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (Circles represent samples)

In Figure 5.9, the covariance of pollen and spore taxa, relative to coprophilous fungal spore taxa, concentrations of microcharcoal shards and sedimentological variables, is presented. The first axis (CCA1) represents 35.2% of variance, and the second (CCA1) represents 13.6%, and so 51.2% of variance is not accounted for in this plot. The first axis is closely associated with charcoal concentrations, as well as organic content, $CaCO_3$ content and *Sordaria*-type spores to a lesser extent. *Pinus* and *Alnus* abundances appear to co-vary with charcoal, albeit on a short gradient, and *Juniperus* abundances also appear to be related to charcoal to some extent. The rarity of *Juniperus* in the record (Fig. 5.4) means that its absence from pollen samples may not indicate absence in the palaeolandscape, and this should be interpreted with caution. Variance in the second axis is primarily driven by sand and clay content, relative to silt content. Taxa such as Valerianaceae, *Tilia* and *Pteridium* in particular appear to be associated with this gradient, though the vertical clustering of samples indicates that this is also a short gradient. It should be noted that this is not suggestive of the substrate in which these plants were growing, but rather suggests an association with a particular alluvial regime resulting in the deposition of characteristic sediments. Similarly to the PCA (Fig. 5.8), the first axis in Figure 5.8 divides samples from the uppermost 6 cm of the sequence (32 cm and 36 cm) from the remaining samples. The distinctively low pollen concentrations of these samples (see Figure 5.4) mean that disentangling potential ecological differences from apparent differences in the taphonomic environment is difficult, but it is clear that some extent of landscape change is represented in the upper 6 cm.

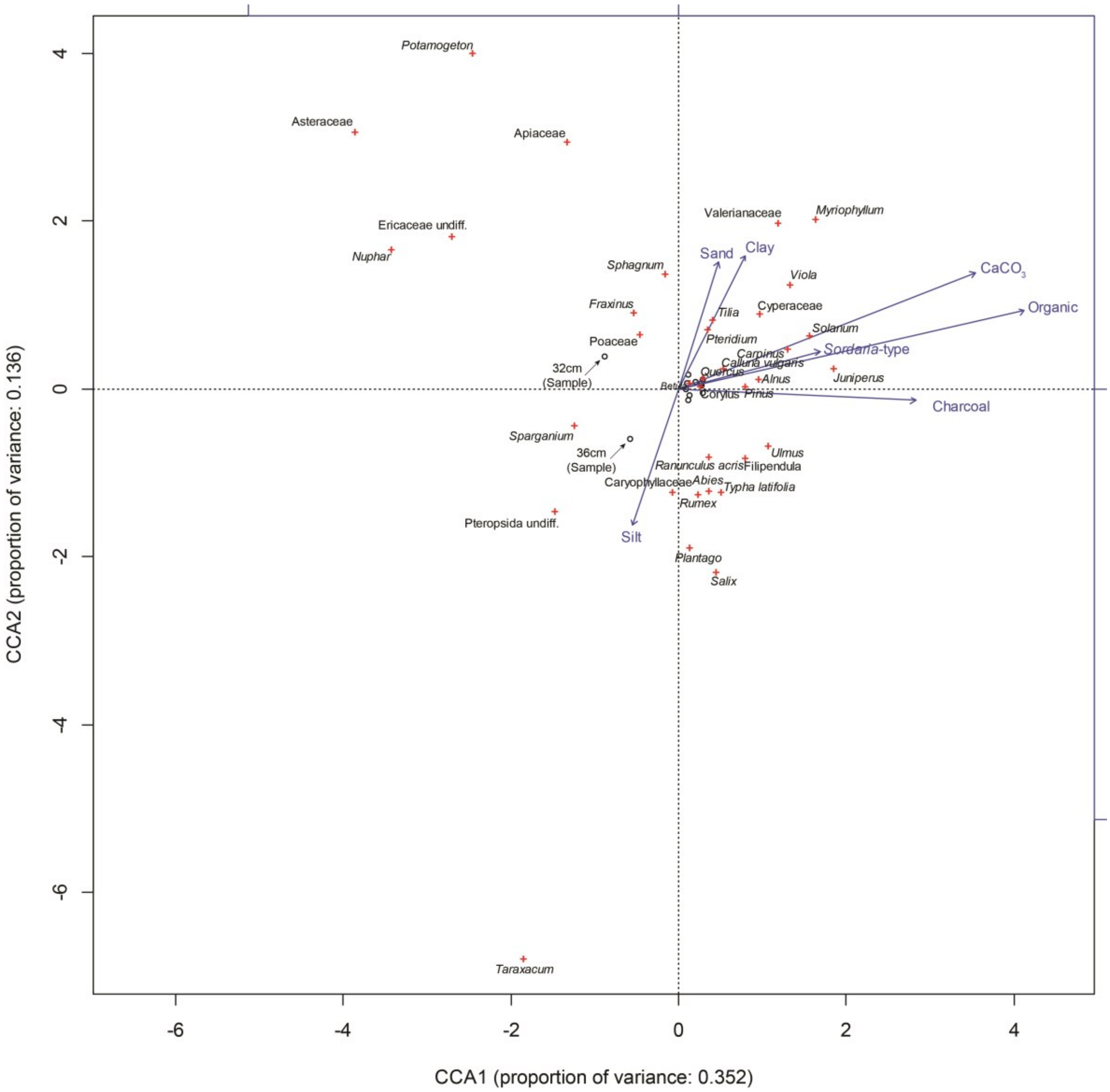


Figure 5.9 – CCA of major pollen and spore taxa, with environmental proxies, from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (Circles represent samples)

5.4.5.3. Ordinations of coleopteran assemblages

As with pollen assemblages, multivariate analyses of Coleopteran functional groups provides insights into numerical relationships, which are complimentary to qualitative stratigraphic analyses. However, as noted in Chapter 3 (Section *3.3.4.*), the low MNI values (<50, *cf.* Hill 2015) for the coleopteran samples mean that any conclusions drawn from these analyses (PCA and CCA) cannot be more than tentative. This is particularly true of the PK14 samples, for which sub-fossil abundances are notably low (see Table 5.4). Principal components analysis (PCA) of the coleopteran assemblages is presented in Figure 5.10. The first axis of this ordination (PC1) explains 26.8% of variance in the sequence, and the second (PC2) explains 22.0%, leaving 41.2% unaccounted for. None of the beetle functional groups are closely related to PC1, though those associated with coniferous woodland and trees (WTC), decaying, foul and rotten environments (DE) and lotic aquatic habitats (AF) are loosely related to this axis. The latter of these is primarily comprised of *Oulimnius* species, and 'WTC' is represented by a single occurrence of *Hylastes attenuatus*. The second axis appears to be driven by a gradient of relative abundances of aquatic generalists (AG) and riparian and waterside taxa (RW), versus open/disturbed habitat taxa (O) and hygrophilous taxa (H). Aquatic generalist taxa are comprised of *Hydraena* sp., *Ochthebius* sp. and Dytiscidae indet. Open/disturbed habitat taxa are represented by several occurrences of *Melanotus punctolineatus*: the most frequently occurring taxon in this sequence. This may suggest variation in the relative influence of terrestrial and aquatic habitats on the sub-fossil beetle fauna, potentially reflecting samples with more allochthonous or autochthonous deposition, respectively. The distribution of samples in Figure 5.10 is also noteworthy: the scattering exhibited indicates a lack of similarity amongst samples. This is likely a product of low coleopteran MNI per sample (see Table 5.4), resulting in stochasticity in the representation of different groups due to unavoidably low effective 'sampling effort'.

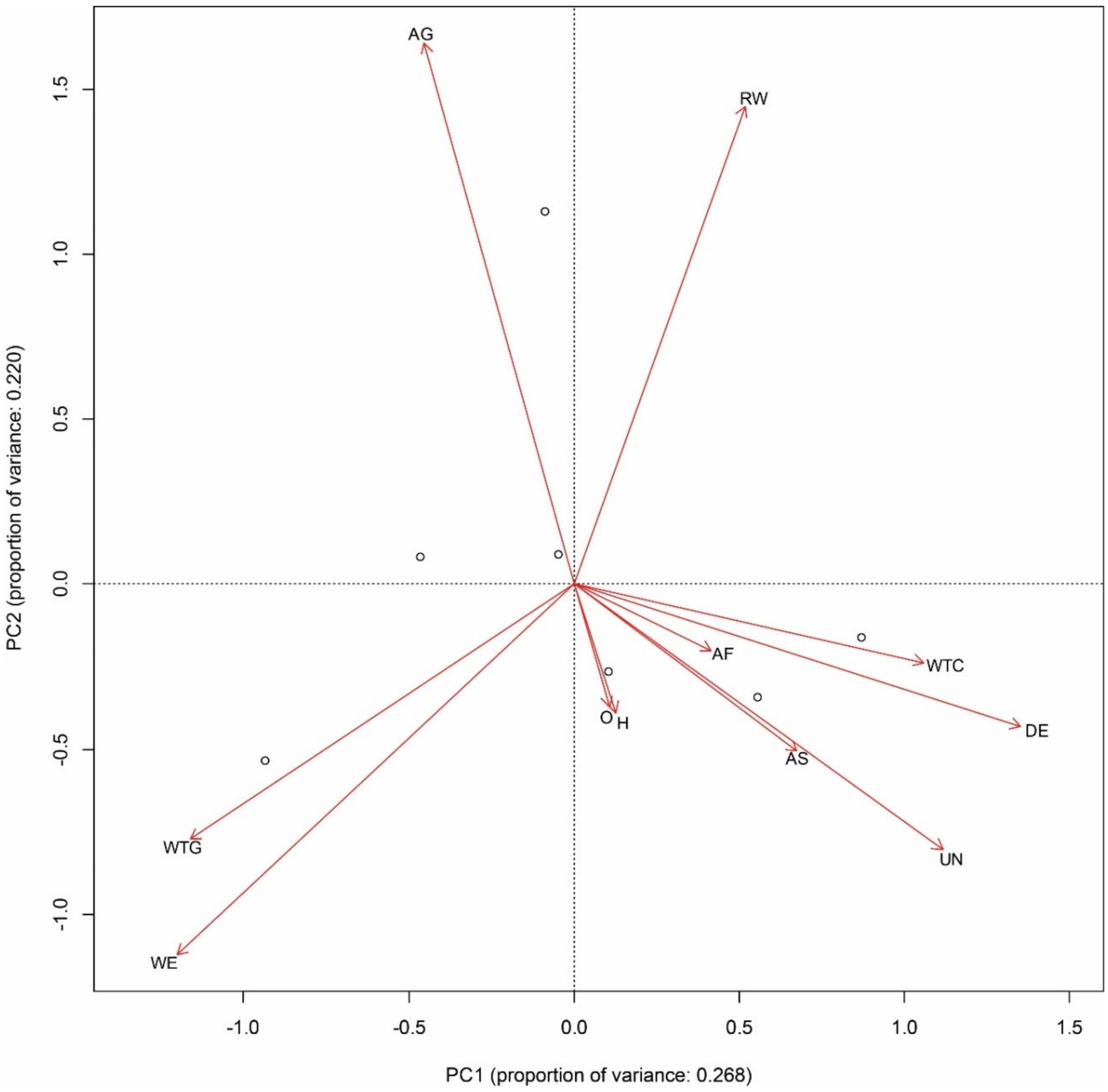


Figure 5.10 – PCA of coleopteran habitat groups from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

The extent of covariance between relative abundances of coleopteran functional groups and environmental proxies (concentrations of *Sordaria*-type spores, concentrations of microcharcoal shards and sedimentological variables) is demonstrated in Figure 5.11. 32.3% of variance is explained by the first axis (CCA1) and 21.8% is explained by the second (CCA2), and 45.9% of variability is unaccounted for. Wetland edge beetles (WE), primarily represented here by *Plateumaris*, are closely associated with the first axis, though do not exhibit covariance with any environmental proxies. This perhaps reflects the importance of reedbed-type habitats in the local environment, and their variable representation in the record. Both charcoal and sand content positively co-vary and are closely aligned to the second axis. There is also some separation of samples on this axis: those with a higher proportion of flowing water indicators (AF) and open/disturbed habitat beetles (O) are apparently associated with higher charcoal and sand content. This may be a product of greater in-washing of material from dry terrestrial habitats during periods of high flow, including associated sediments and insect fauna, though it may also reflect a relationship between wildfire and the open, heath-type habitats favoured by *Melanotus punctolineatus* (Koch 1989b).

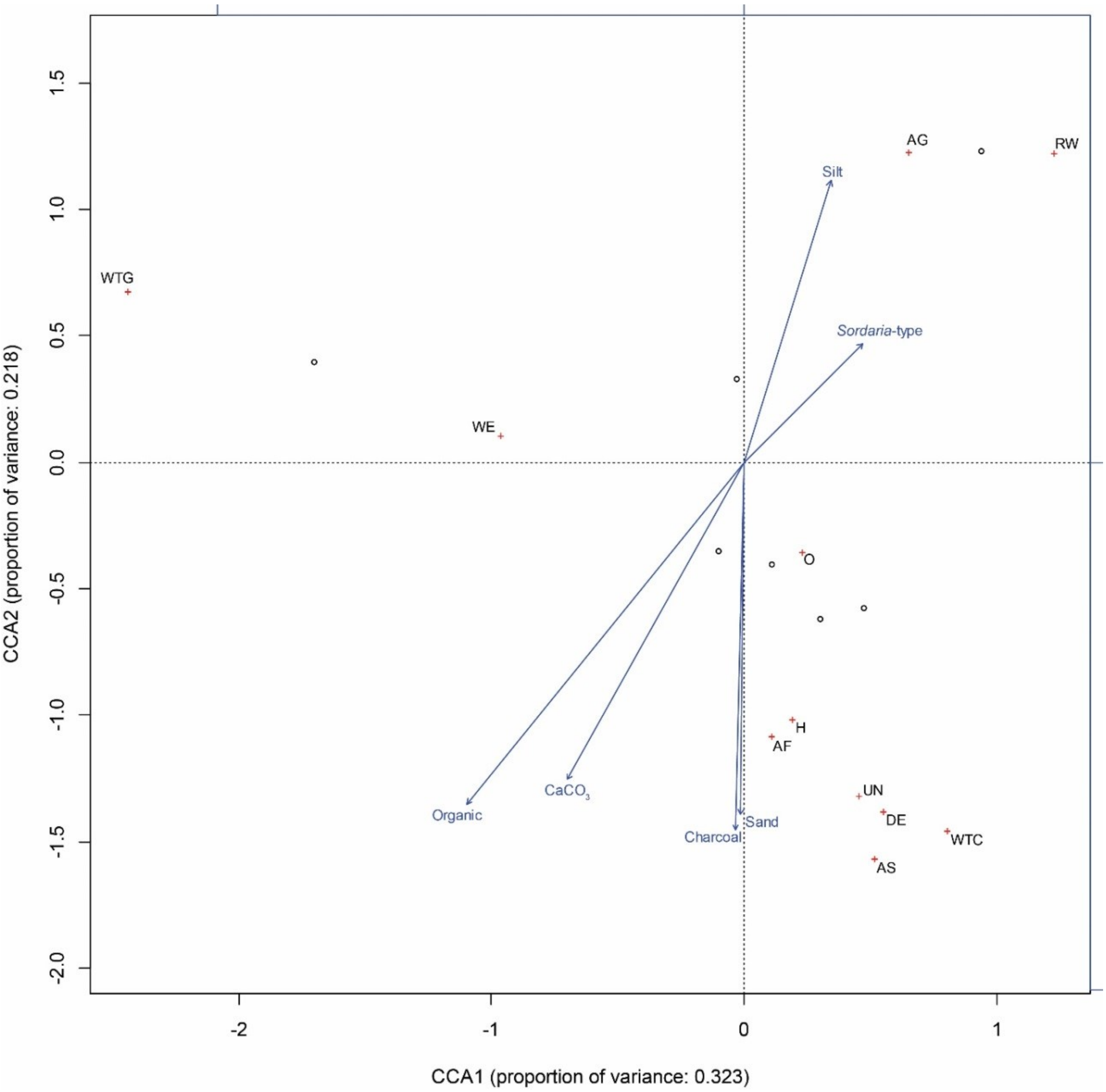


Figure 5.11 – CCA of coleopteran habitat groups and environmental proxies from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

5.4.5.4. Ordinations of combined palynological and coleopteran assemblages

PCA applied to palynological and coleopteran assemblages simultaneously (Fig. 5.12) allows relationships between the datasets to be explored, elucidating potential links between vegetation and beetle assemblages. As in the previous section, the low MNI values (<50, *cf.* Hill 2015) for the coleopteran samples render interpretations drawn from these analyses tentative. The first axis (PC1) accounts for 28.3% of variance and the second (PC2) accounts for 20.8%. 50.9% is therefore unaccounted for in Figure 5.11. Pollen taxa and beetle functional groups plotting to the left of the first axis are primarily those which are more prevalent in the upper 5-10 cm of the sequence (pollen zone PK-P2, Fig. 5.4; coleopteran zone PK-C2, Fig. 5.5): *Potamogeton*, *Ranunculus acris*, Ericaceae undiff., *Nuphar*, Pteropsida undiff., Asteraceae, *Taraxacum, Sparganium*, riparian and waterside beetles (RW) and aquatic generalist beetles (AG). This covariance between taxa and functional groups prevalent in the upper zones reflects broadly synchronous change in beetle and pollen sequences (Figs 5.4 & 5.5). Given that sub-fossil pollen and beetles are typically drawn from differently-sized catchments in the local landscape (*cf.* Smith *et al.* 2010; Hill 2015), this strongly suggests simultaneous influence on both groups as a result of a broader landscape change. Given the decreasing concentration of both pollen and beetles in zones PK-P2 and PK-C2, and increasing prevalence of aquatic pollen types (*Potamogeton*, *Nuphar, Sparganium*), this may partly reflect a taphonomic change: a shrinking of catchments, possibly as a result of local hydrological changes, promoting greater autochthonous deposition of fossil material. This covariance may also be indicative of a concurrent opening of the local landscape, given the lack of arboreal taxa (either insect or pollen) and inclusion in this group of pollen taxa associated with open and disturbed habitats (Ericaceae undiff., Asteraceae, *Taraxacum*), though in this context it is difficult to disentangle taphonomic and ecological changes.

Several taxa indicative of drier conditions are associated with the second axis (PC2) (*Betula*, *Fraxinus*, *Calluna vulgaris*, *Plantago*, *Quercus*). These exhibit negative covariance with several taxa indicative of wetter conditions, including Cyperaceae, *Typha latifolia*, *Sphagnum* and beetles associated with decaying, rotten and foul habitats (DE). This group of beetles includes hygrophilous taxa, such as *Cercyon* sp. and *Anotylus rugosus*. This is not a straightforward wetness gradient, as these taxa are also accompanied by *Abies*, *Carpinus Rumex*, *Tilia* and open/disturbed habitat beetles (O: *Melanotus punctolineatus*), but it does suggest that moisture is a potentially influential factor in determining the characteristics of local vegetation assemblages. It remains difficult to separate taphonomic and ecological signals, but given that both proxies (pollen and beetles) are in agreement, producing ecologically meaningful patterns, assemblage variability cannot be solely attributed to taphonomic changes.

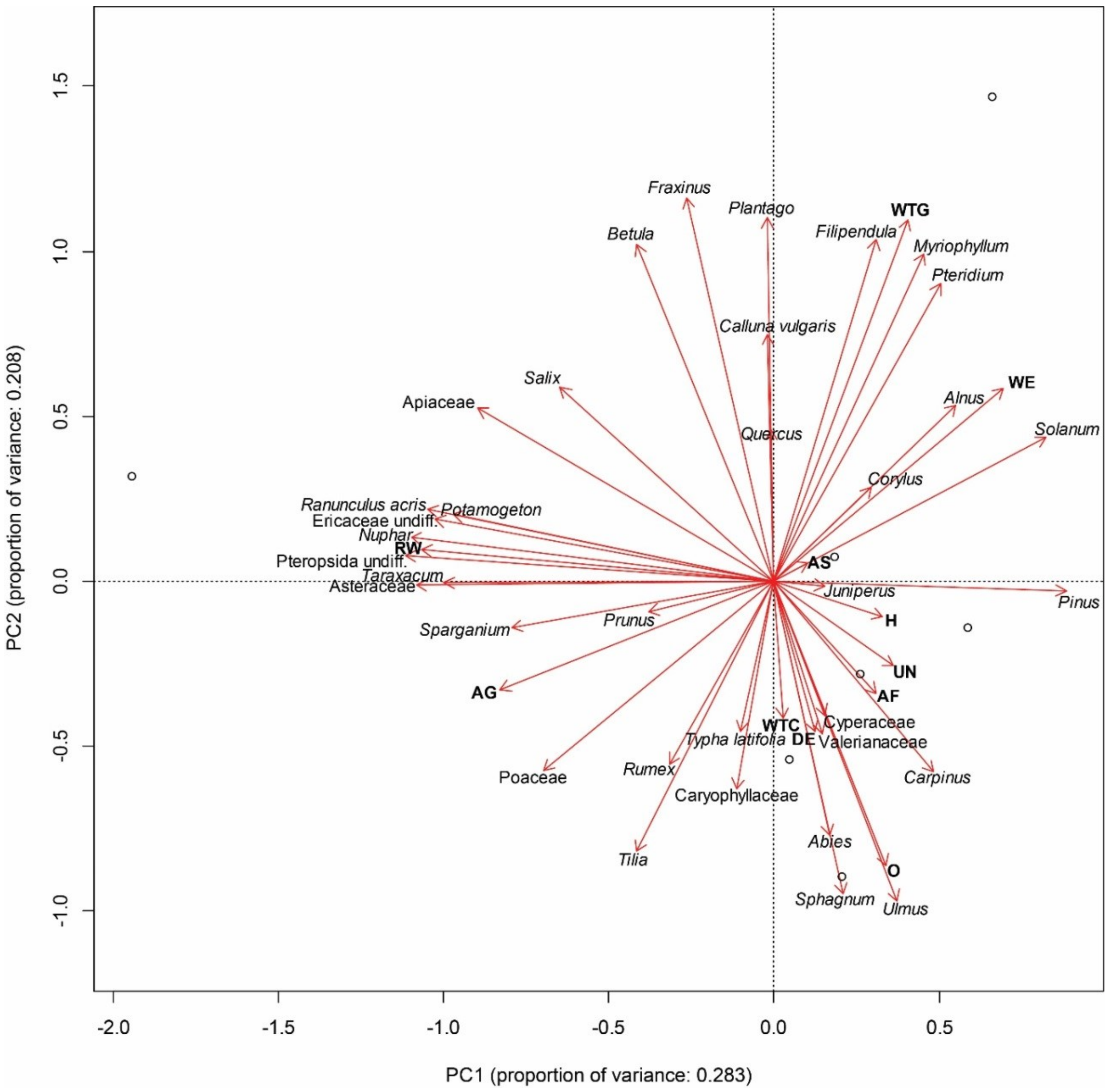


Figure 5.12 – PCA of coleopteran habitat groups and major pollen and spore taxa from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

Applying CCA to palynological and coleopteran assemblages simultaneously allows relationships between these proxies to be explored alongside their relationships with environmental proxies (concentrations of *Sordaria*-type spores, concentrations of microcharcoal shards and sedimentological variables) (Fig. 5.13). The first axis (CCA1) explains 32.1% of variance and the second (PC2) explains 22.3%. Therefore, 45.6% is unaccounted for in Figure 5.12. Similarly to CCA applied to the coleopteran dataset individually (Fig. 5.10), none of the environmental proxies are closely associated with the first axis and relative abundances of wetland edge beetles (WE: *Plateumaris*) are the most prominent feature of this axis. This group exhibits positive covariance with *Filipendula*, and weak negative covariance with Poaceae and Caryophyllaceae. *Filipendula* pollen is often representative of *F. ulmaria*, which is typically associated with wetland edge, riparian and marshland habitats (Rose & O'Reilly 2006). *Filipendula ulmaria* has a preference for basic soils, whereas *F. vulgaris* prefers acid soils (Rose & O'Reilly 2006), and so *F. ulmaria* is more likely in a region with chalk bedrock, though local conditions may have favoured *F. vulgaris*. The covariance of *Filipendula* with wetland edge beetles therefore further emphasises the importance of aquatic-terrestrial ecotonal habitats in the local environment, as well as their variable representation in the record (though the low counts of *Filipendula* pollen render this somewhat tentative).

Sand content and charcoal concentrations are closely associated with the second axis of Figure 5.13 (CCA2), in parallel with the first axis of Figure 5.9 (CCA of pollen assemblages) and the second axis of Figure 5.11 (CCA of beetle assemblages). As in Figure 5.11, sand and charcoal co-vary with lotic beetle taxa (AF) and open/disturbed habitat beetles (O), as well as hygrophilous beetles (H), *Juniperus*, Cyperaceae, Valerianaceae, *Carpinus*, *Ulmus* and *Sphagnum*. Sand and charcoal content also exhibit broad negative covariance with Apiaceae, *Potamogeton*, Pteropsida undiff. and aquatic generalist beetles (AG). As previously discussed, the relationship between sand, charcoal, lotic beetles and open/disturbed habitat beetles may be partly taphonomic (i.e. reflecting enhanced fluvial/alluvial energy, and hence greater in-washing of material from fluvial and sandy habitats), and partly a reflection of a relationship between wildfire and open, heath-type habitats. The additional association with *Juniperus* supports the latter, though the relationship between *Juniperus* and fire is not straightforward (Thomas *et al.* 2007) and *Juniperus* counts are too low to draw any firm conclusions. Associations with taxa less obviously favoured by fire regimes, such as Cyperaceae and *Sphagnum*, may be more a reflection of the taphonomic signal. Regardless of the precise scenario, it is clear that fire was a feature of the palaeolandscape, due to the presence of microcharcoal, and that it exerted some influence on the taxonomic and structural characteristics of local vegetation assemblages. Several taxa also appear to co-vary with *Sordaria*-type spores, including *Taraxacum*, riparian and waterside beetles (RW), Ericaceae undiff., *Sparganium*, *Prunus*, *Salix*, Pteropsida undiff. and Poaceae. However, given the low frequency of occurrence of these spores (two isolated occurrences, see Figure 5.4) and lack of association with either major axis, these associations are more likely to represent a statistical artefact than a 'real' ecological signal.

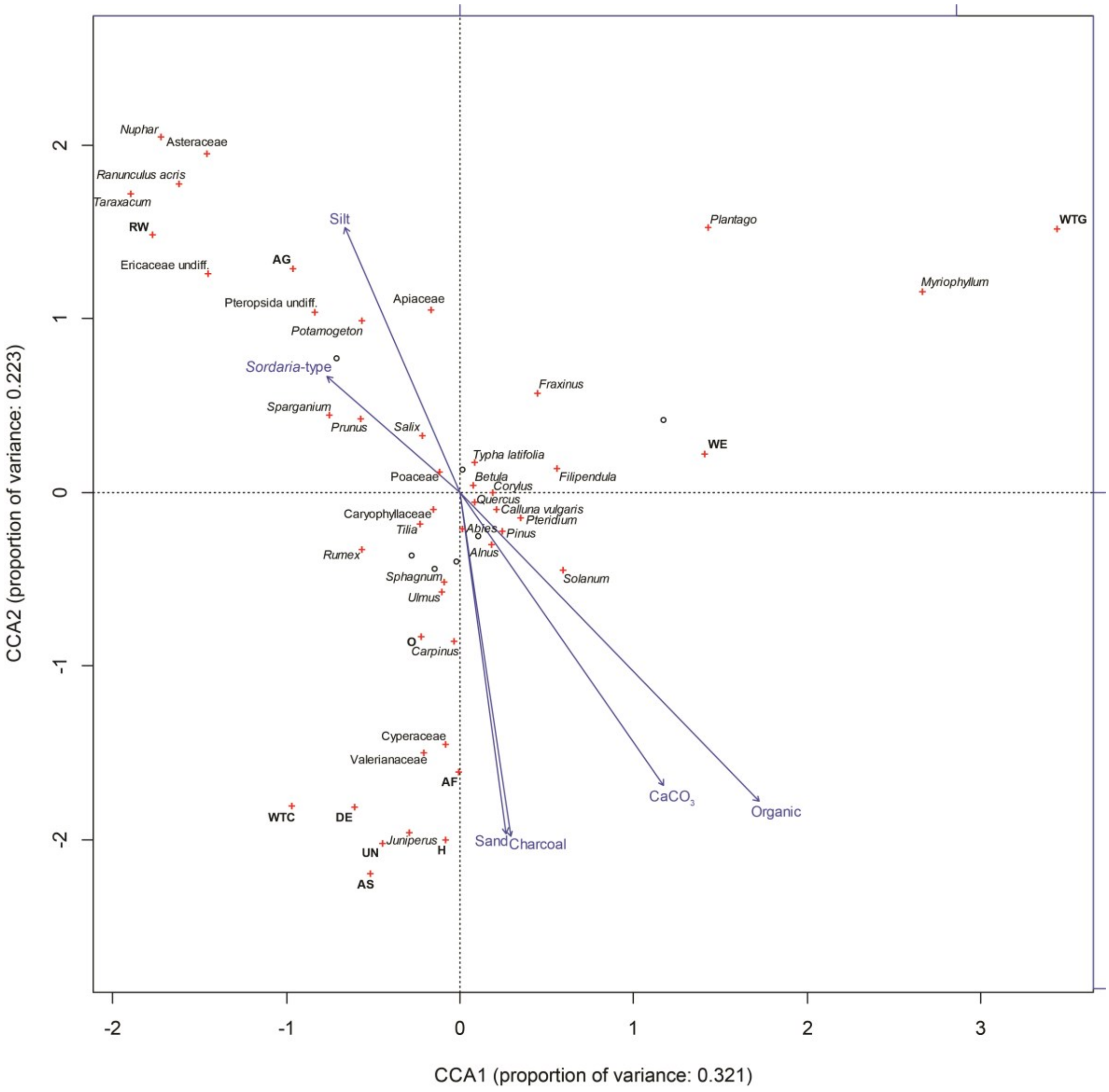


Figure 5.13 – CCA of coleopteran habitat groups, major pollen and spore taxa and environmental proxies from the Cromer Forest-bed at Pakefield (PK14, Fig. 5.2) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

5.4.5.5. Ordination of new (PK14) and Coope (2006) coleopteran assemblages

Figure 5.14 presents the results of PCA used to compare new coleopteran assemblages from Pakefield (PK14, presented in this chapter) with those of Coope (2006). This is performed on a functional group basis, in order to compare the ecological characteristics of each sequence. It should be noted that whilst the new record is higher resolution, with a greater number of samples, Coope's (2006) record has a greater concentration of coleopteran material, and higher 'per sample' MNI (*cf.* Tables 5.4 & 5.5).

The first axis of Figure 5.14 (PC1) represents 27.6% of total variance, and the second represents 18.0%, and 54.4% of variance is not represented. Samples are clearly separated on the first axis, according to sequence, with those from Coope (2006) plotting to the right, and those from the PK14 sequence plotting to the left. Beetle ecological groups are also evenly separated on this basis: seven groups plot to the right, and seven plot to the left. The former includes beetles associated with herbaceous plants (HP), deciduous woodland and trees (WTD), dung (DU), damp conditions (H), lotic conditions (AF), lentic conditions (AS) and decaying/rotten/foul conditions (DE). The latter includes beetles associated with general woodland and tree habitats (WTG), wetland edge habitats (WE), general aquatic habitats (AG), open/disturbed habitats (O), riparian/waterside habitats (RW) and coniferous woodlands and trees (WTC), as well as uncategorised/eurytopic taxa (UN). The most important of these groups, those most closely associated with the first axis, are lotic habitat beetles (AF) and open/disturbed habitat beetles (O). Samples from Coope's (2006) record are characterised by a greater prevalence of Elmidae, particularly *Esolus parallelepipedus* (Table 5.5), whereas PK14 samples are characterised by a greater proportional abundance of Elateridae, particularly *Melanotus punctolineatus* (Table 5.4). This perhaps reflects a greater proportion of dry, open and semi-open habitats in the PK14 record, though taxa such as *Amara infima* and *Bradycellus ruficollis*, which also favour heathland environments (Lindroth 1974), are present in Coope's (2006) record. Similarly, Elmidae (*Oulimnius*) are also present in the PK14 record. Though the differences in total MNI between records (*cf.* Tables 5.4 & 5.5) means that direct comparisons should be undertaken with caution, as certain groups may be either under- or overrepresented, respectively, this analysis highlights potential subtle distinctions in local ecology. On this basis, it seems likely that either the records represent different locations within the palaeolandscape, different periods of time (albeit within the same temperate stage), or both.

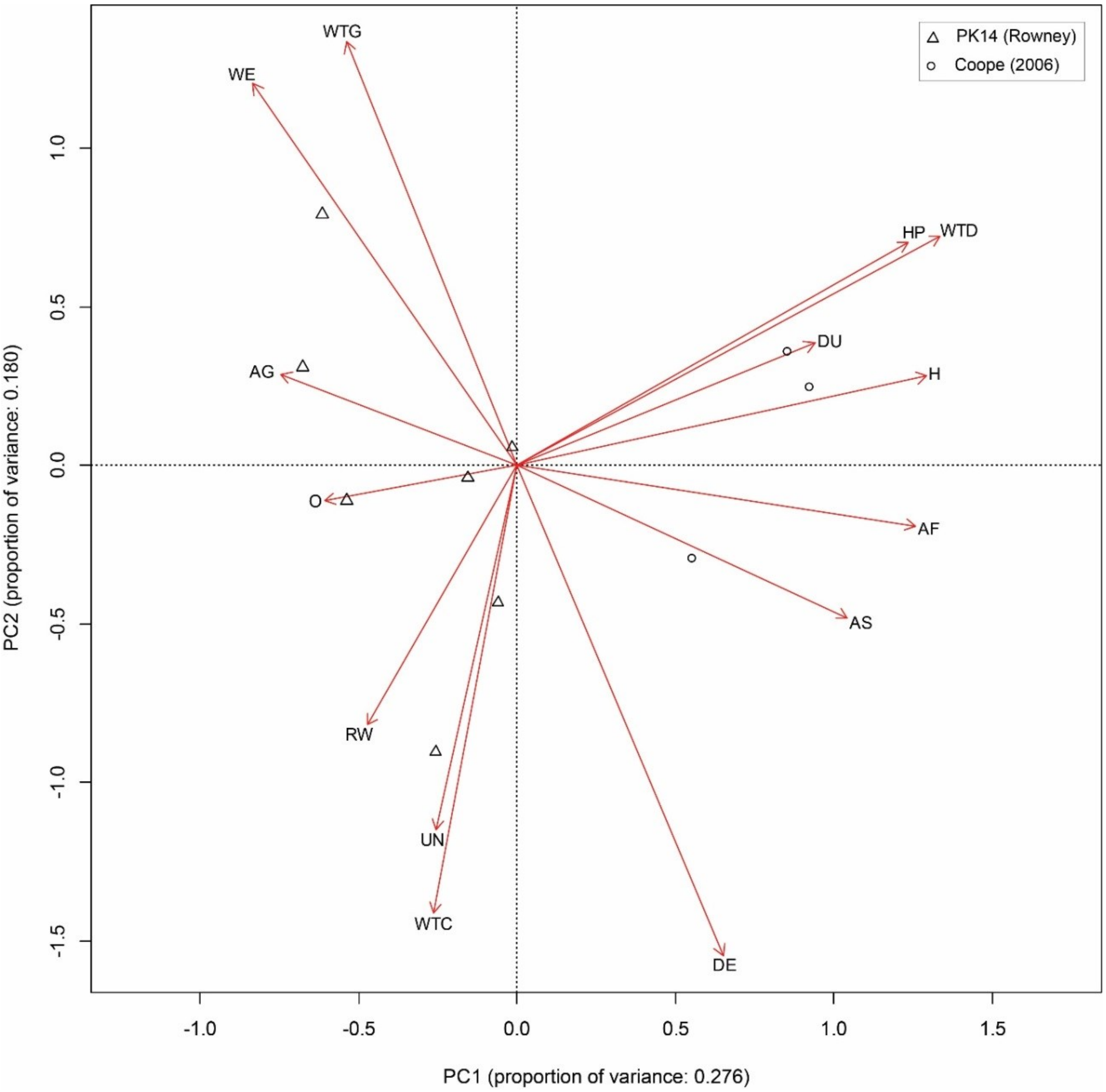


Figure 5.14 – PCA of coleopteran habitat groups from PK14 (this chapter, Fig. 5.2) and Coope (2006) records from the Cromer Forest-bed at Pakefield (See Table 3.1 for habitat group abbreviations) (Circles and triangles represent samples) (See Figure 5.1 for relative locations)

5.5. Local Palaeoenvironmental Summary

This section summarises the key features of local palaeoenvironments, and notable changes, inferred from pollen and beetle assemblages, and sedimentological properties. A brief comparison of the new records with the published records is also given. Disturbance regimes and vegetation dynamics are discussed in detail in Chapter 8, alongside records from West Runton (Chapter 4) and Brooksby (Chapter 6).

5.5.1. Depositional environment

Sedimentological analyses (Fig. 5.3), supplemented with palaeoentomological data (Table, 5.4, Fig. 5.5) provide a reconstruction of the depositional environment of the Cromer Forest-bed at Pakefield, which is broadly consistent with previous interpretations (West 1980a; Candy *et al.* 2006; Coope 2006; Lee *et al.* 2008b). In the basal 2-3 cm of the sequence, sediments are dominated by fine sands, but following this are predominantly composed of fine silts for the remainder of the sequence (Fig. 5.3), though a shift in modal grain size at 52 cm indicates a slight coarsening. Loss-on-ignition data indicate that sedimentary organic content is low throughout the sequence (max. 12.5%), but this slight coarsening is accompanied by a further decrease. Whilst the fine sediments clearly indicate deposition in a low-energy environment, the presence of riffle beetles (Elmidae, Dryopidae) and low organic content suggest predominantly allochthonous deposition from a high-energy environment. In broad agreement with previous interpretations, it is likely that these sediments accumulated in a floodplain wetland, such as a cut-off channel or riparian marshland, or possibly a backwater, which received inputs of sediment during high-flow periods.

5.5.2. Local palaeoenvironment: Vegetation, landscape and climate

Overall, the preceding analyses indicate the presence of an alluvial wetland, set within a landscape of low-density woodland, in the vicinity of a significant fluvial system. The presence of beetle taxa which exist in Britain at present, and deciduous tree pollen, indicates that the climate was broadly temperate, but more precise palaeoclimatic reconstructions were not possible. This is due to an absence of 'MCR species' in new assemblages, with the exception of *Anotylus rugosus*, which is widely eurytopic. No major palaeoenvironmental changes occur in this sequence, but more subtle change is noted.

The lower assemblage zones (PK-P1, 80-36 cm, Fig. 5.4; PK-C1, 75-47 cm, Fig. 5.5) represent the most substantial part of the sequence. A combination of aquatic plants (e.g. *Nuphar*, *Potamogeton*, *Sparganium*) and insects (e.g. *Hydraena* spp., *Ochthebius* sp.), and silt-dominated sediments, indicate a wetland environment. Low sedimentary organic content suggests that this was not strongly eutrophic, though an array of submerged (e.g. *Potamogeton*, *Myriophyllum*), floating-leaved (e.g. *Nuphar*) and emergent (e.g. *Sparganium*, *Typha latifolia*) aquatic macrophytes were present, further evidenced by the presence of *Tanysphyrus lemnae* and *Plateumaris* species. The presence of riffle beetles (Elmidae, Dryopidae; max. relative abundance: 50%) indicates a distinct fluvial influence on this environment, emphasising the alluvial context (as discussed in Section *5.5.1.*). As well as being fringed with emergent vegetation, *Bledius* sp. indicates that the wetland was also bordered by exposed sediments in places, and decaying organic matter in the riparian zone is indicated by *Cercyon* sp. and *Anotylus rugosus*. High arboreal pollen values in this zone (68.87% mean) demonstrate that the wetland was set within a broader wooded landscape, incorporating a diverse range of tree taxa. Wetter areas close to the wetland were likely to have been dominated by *Alnus*, whereas drier areas of woodland appear to have been occupied by a mixture of predominantly, but not exclusively, deciduous taxa (e.g. *Betlua*, *Carpinus*, *Corylus*, *Quercus*, *Tilia*, *Ulmus*). The local source areas of beetle records are well documented (Smith *et al.* 2010; Hill 2015), and so the presence of the bark beetle, *Hylastes attenuatus*, provides confirmation that *Pinus* was locally present, and likely a component of this mixture of trees. *Carpinus* and *Abies* are typically considered 'late immigrants' in British interglacial sequences (Turner & West 1968), and may be used to suggest a late successional stage for this woodland. This is further suggested by the presence of *Hallomenus binotatus*, which is primarily found on fungal fruiting bodies on dead and decaying deciduous and coniferous wood (Koch 1989b) and is indicative of the maturity of these woodland habitats.

Heathland shrubs (e.g. *Calluna vulgaris*, *Juniperus*) and insects (*Melanotus punctolineatus*) imply that woodland habitats were not homogeneously closed-canopy, but rather contained substantial areas of light canopy and clearings, perhaps facilitating regeneration of light-demanding trees such as *Betula* and *Quercus*. The presence of ruderal plants, such as *Plantago* and *Rumex*, suggests that more open areas were maintained through disturbance regimes. In spite of fossil evidence for an array of large herbivores at Pakefield (see Table 5.2), there is little evidence for substantial herbivory-induced impacts on vegetation communities in the present record; *Sordaria*-type spores are present, but rare, and although *Aphodius* are also present, species within this genus are not exclusively coprophilous. However, herbivory cannot be excluded as a potentially influential factor. Conversely, there is some evidence for wildfire-induced disturbance. This provides a more convenient explanation for local vegetation openness: microcharcoal shards are present throughout the sequence, multivariate analyses suggest some quantitative relationship with vegetation assemblages, and indicators of openness include plants such as *Calluna vulgaris*. This species is not an obligate pyrophile, but it is fire-adapted and its growth may be favoured by wildfire (Måren & Vandvik 2009; Davies *et al.* 2010).

The upper assemblage zones (PK-P2, 36-31 cm, Fig. 5.4; PK-C2, 47-28 cm, Fig. 5.5) are most notable for their low concentrations of microfossils. They contain an average of 3601.6 pollen grains cm^{-3} (PK-P2) and 0.22 coleopteran MNI litre^{-1} (PK-C2), as well as low sedimentary organic content (3-7%). This represents a distinct change in the taphonomic environment. Pollen assemblage changes could be tentatively interpreted as indicating an opening of the landscape: relative abundances of Poaceae, Ericaceae and *Pteropsida* increase, whilst arboreal pollen values decrease. Insect assemblages largely confirm the continuation of habitats present in the previous zone, including wetland and open terrestrial habitats, though riffle beetles are notable by their absence. This perhaps reflects diminished fluvial inputs, which may have given rise to decreased microfossil concentrations. Beetles associated with woodlands and trees are also absent, though this could be a reflection of their infrequency in the record, coupled with lower concentrations of coleopteran material. As discussed, it is difficult to disentangle ecological and taphonomic causes of assemblage change here, but multivariate analyses do suggest an ecological component to this, which may be related to changes in local moisture and/or openness. Indeed, wetland terrestrialisation provides a convenient explanation for lower microfossil concentrations, increased local abundances of Poaceae, Ericaceae and *Pteropsida*, and the absence of riffle beetles. However, given the aforementioned poor concentrations, and therefore likely under- and overrepresentation of different taxa, this interpretation must remain tentative.

5.5.3. Broader landscape context: Comparison with previous records

The new multi-proxy record presented here (PK14) is in broad agreement with preceding pollen (West 1980a) and coleopteran (Coope 2006) records. In terms of coleopteran records, the most notable distinction between these records is in their differential concentrations of coleopteran fossil material. This implies distinct taphonomic and sedimentary environments, despite being ostensibly derived from the same sub-unit of the Cromer Forest-bed at Pakefield (West's (1980a) bed 'g'). However, the uppermost sample from Coope's (2006) record (Sample 3) does have a comparable total MNI (Table 5.5) to much of the PK14 record (Table 5.4), perhaps suggesting temporal overlap, with the PK14 record immediately post-dating Coope's (2006) record. Multivariate analyses demonstrate that the PK14 and Coope (2006) records are also distinct in the relative representation of different functional groups (see Section *5.4.5.4.*), though this is almost certainly influenced by differential concentrations of fossil material, at least in part. Given this context, drawing inferences from absences in the more fossil-poor PK14 record (Table 5.4) would not be appropriate, though the absence of southern thermophiles (e.g. *Cybister lateralimarginalis*, *Oxytelus opacus*, *Valgus hemipterus*) in the PK14 record is noted, as these are characteristic of Coope's (2006) record (Coope 2010a). Lack of representation in Coope's (2006) more fossil-rich record (Table 5.5), however, may be more significant. Of particular note is the lack of conifer-obligate woodland and tree taxa in this record, despite the occurrence of *Hylastes attenuatus* in the PK14 record. In the context of the potentially later occurrence of the PK14 record, this may interpreted as indicating a change in local woodland characteristics, with a greater representation of *Pinus* in the vicinity of the wetland during the period represented by PK14. However, this conclusion should be approached with caution, given the low coleopteran abundances in the PK14 record (Table 5.4).

Discerning differences between PK14 and Coope (2006) coleopteran records in climatic terms is more difficult. This is due, in part, to the general absence of 'MCR species' in the former, with the exception of the eurytopic *Anotylus rugosus*. Thus, whilst Coope's (2006) assemblages provide quantitative estimates of a temperate climate, with warm summers and mild winters (Table 5.6), quantitative climate estimates from the PK14 record are unavoidably (and uninformatively) broad. However, as noted, *Cybister lateralimarginalis*, *Oxytelus opacus* and *Valgus hemipterus* are considered to be characteristic of Coope's (2006) Pakefield record (Coope 2010a), but are absent from the PK14 record. These species are present in Central and Southern Europe, but absent from Britain at present, and are considered indicators of warm temperate conditions. The absence of these species, or any other similarly thermophilous taxa, in the PK14 record may suggest a cooler climate. However, given the low abundances of the PK14 record, it cannot be reasonably assumed that these absences are significant, as the possibility remains that they are due to lack of detection, rather than genuine absence.

West's (1980a) pollen records drawn from Pakefield bed 'g' are broadly comparable to the PK14 record in terms of arboreal, shrub and herbaceous assemblages. Arboreal assemblages in both contain a similar array of taxa, at similar abundances, including *Carpinus*, which is a non-ubiquitous component of interglacial pollen assemblages. Ericaceae taxa are similarly comparable, but herbaceous assemblages exhibit minor differences between records, such as a lack of *Armeria* in the PK14 record, and a lack of *Solanum* in West's (1980a) record. Interestingly, both records also exhibit a spike in fern spore abundances, accompanied by lower pollen concentrations, towards the top of the sequences. Collectively, this suggests that these records are broadly contemporary, but represent different locations within the palaeolandscape. The differences between records are not pronounced, however, which suggests relatively low habitat heterogeneity in the palaeolandscape. In terms of woodland structure, this implies that more open habitats, the presence of which is indicated by heathland plants and insects, were relatively evenly distributed, perhaps forming a 'patchwork' of forest and open to semi-open habitats. The presence of large browsing (e.g. *Megaloceros* spp.), grazing (e.g. *Mammuthus trogontherii*, *Hippopotamus antiquus*) and 'mixed feeder' (e.g. *Palaeoloxodon antiquus*, *Stephanorhinus hundsheimensis*) herbivores, and occasional *Sordaria*-type spores (Fig. 5.4), at Pakefield means that herbivory cannot be wholly discounted as a potentially influential factor. The presence of *Castor fiber* (Eurasian beaver) and *Trogontherium cuiveri* (giant beaver) may also have contributed to local canopy openness through the establishment of 'beaver pastures' (areas of coppiced *Salix* and other shrubs) and 'beaver meadows' (terrestrialised beaver ponds) (Coles 2006). However, wildfire provides the most reliably demonstrable mechanism for driving such a pattern, given the apparent relationship between charcoal concentrations and pollen assemblages (see Section *5.4.5.*), and lack of evidence for substantial herbivory (i.e. rarity of *Sordaria*-type spores, Fig. 5.4). However, it should be noted that microcharcoal also exhibits covariance with sand content (Figs. 5.10 & 5.12), suggesting that it is partly derived from in-washing of bank or floodplain sediments. Quantitative reconstructions of climate presented here (Table 5.6) provide neither confirmatory nor contradictory evidence for conditions conducive to wildfire. However, on the basis of palaeopedological evidence, Candy *et al.* (2006) demonstrate a strongly seasonal precipitation regime associated with the Cromer Forest-bed at Pakefield, with low summer precipitation. Unsurprisingly, increased incidence of forest fires in Europe has been linked to low precipitation and low atmospheric moisture in long-term records, and these factors are more influential than temperature (Drobyshev *et al.* 2014, 2016). Furthermore, enhanced storminess in the North Atlantic during early Middle Pleistocene interglacials has been suggested (Candy & McClymont 2013), which would provide a higher frequency of potential ignition events (i.e. lightning strikes).

5.6. Archaeological Postscript

The remains of Palaeolithic industries have been recovered from all sub-units of the Cromer Forest-bed at Pakefield, providing some of the earliest evidence of hominins in Northern Europe (Parfitt *et al.* 2005; Ashton & Lewis 2012). The new analyses presented here provide a more complex view of the local ecology and landscape than in previous studies, indicating the presence of a mosaic landscape, in part maintained through disturbance regimes (e.g. wildfire), incorporating diverse wetland, woodland, semi-open and open habitats. Such landscapes are typical of Palaeolithic *Homo* sites across Eurasia (Finlayson *et al.* 2011), providing a diversity of floral and faunal resources, and the potential for ambushing large mammals. The implication of new analyses presented in this chapter is that intermediate levels of disturbance, capable of producing and maintaining such ‘mosaic’ landscapes, may be a hitherto unrecognised, but important, component of the ecological niche of Palaeolithic *Homo*.

Chapter 6

The Brooksby Sand and Gravel

6.1. Introduction

A new palaeoecological record from the Brooksby Sand and Gravel, an early Middle Pleistocene deposit in northern Leicestershire (Fig. 6.1), is presented. This is primarily based on a sequence of sub-fossil Coleoptera obtained during the author's Master's studies at Royal Holloway University of London (Rowney 2012, unpublished), re-appraised using more sophisticated analytical approaches and supplemented with additional pollen, fungal spore and charcoal analyses. On this basis, inferences are made regarding vegetation structure, interactions between taxa, landscape openness and climatic setting. This work provides evidence for non-analogue eco-climatic conditions previously unrecognised in early Middle Pleistocene contexts.

6.2. Site Background

Brooksby Quarry, northern Leicestershire (52°43'N, 1°00'W, Fig 6.1) is a site which has yielded sedimentary sequences attributed to the early Middle Pleistocene (Cromerian Complex) (Stephens *et al.* 2008), but has received limited attention from a palaeoenvironmental perspective. It has also yielded a large number of Lower Palaeolithic stone tools (Coope 2006; D. Schreve 2012, pers. comm.), for which in-depth climatological and ecological analyses will provide important context.

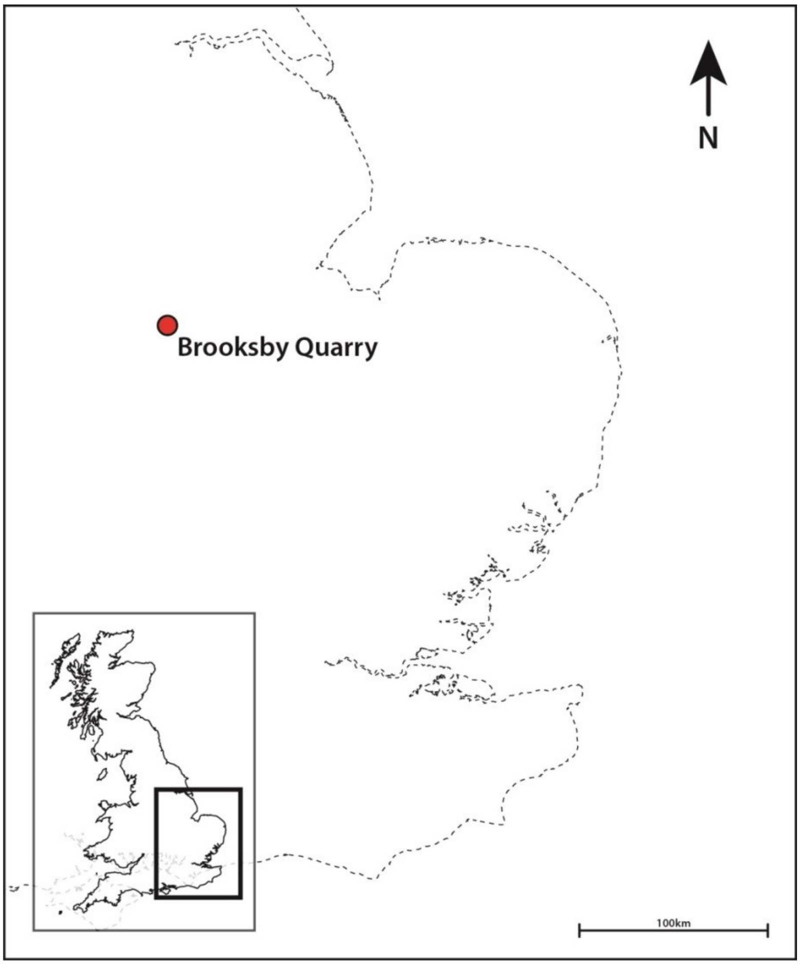


Figure 6.1 – Brooksby Location Map

6.2.1. Chronostratigraphy

The Pleistocene sequence at Brooksby Quarry consists of four primary stratigraphic units (*cf.* Stephens *et al.* 2008). The lowermost unit, the Brooksby Sand and Gravel, is comprised of basal gravels succeeded by medium to fine sands, with occasional pebble-rich and organic horizons (Rice 1991), and deposited in an incised bedrock channel (Challis & Howard 1999). This is overlain by the sands and gravels of the Thurmaston Member, and the sands of the Brandon Member, both generally attributed to the pre-Anglian Bytham river system (Bridgland *et al.* 2015). Finally, the sequence is capped by the Thrussington Till, typically interpreted as being of Anglian (MIS 12) age. This sequence, overlying the Brooksby Sand and Gravel, is equivalent to that overlying a similar deposit at Waverley Wood, Warwickshire (Shotton *et al.* 1993; Keen *et al.*

2006), which is also attributed to the Bytham River system, for which three terraces (*c.* MIS 18, 16 and 12) have been identified (Westaway 2009; Bridgland *et al.* 2015; Candy *et al.*2015, *contra* Gibbard *et al.* 2013). Both Brooksby and Waverley Wood are associated with the youngest Bytham terrace (*c.* MIS 13-12), and are thought to be of comparable age (Stephens *et al.* 2008; Candy *et al.* 2015). Pools Farm Pit, Warwickshire (Maddy *et al.* 1994) is also stratigraphically correlated on a similar basis (Preece *et al.* 2009; Coope 2010a; Bridgland *et al.* 2015). The presence of *Arvicola cantiana* (the evolutionary successor to *Mimomys savini*, see Chapters 5 & 6) in the Waverley Wood sequence (Shotton *et al.* 1993), as well as aminostratigraphic context (Penkman *et al.* 2011, 2013) and position underlying a major till deposit widely attributed to the Anglian glaciation, suggests that Waverley Wood should be placed late in the Cromerian Complex (*c.* MIS 13). Thus, a late Cromerian (*c.* MIS 13) age may be tentatively attributed to the Brooksby Sand and Gravel. The proposed association of the Brooksby Sand and Gravel with the youngest Bytham terrace (Westaway 2009; Bridgland *et al.* 2015; Candy *et al.*2015) supports this.

Table 6.1 Summary of primary stratigraphic units at Brooksby quarry (based on Rice 1991; Stephens *et al.* 2008; Shotton *et al.* 1993 and this chapter)

Unit/Bed	Formation	Climate/Environment	Age
Thrussington Till	Wolston Formation	Glacial	MIS 12
Brandon Member	Baginton Formation	Fluvial. Cool temperate and cold phases represented.	MIS 13-12
Thurmaston Member	Baginton Formation	Fluvial. Cool temperate and cold phases represented.	MIS 13-12
Brooksby Sand and Gravel	N/A	Fluvial. Cool temperate.	*c.* MIS 13

There has been recent debate regarding the origins of deposits attributed to the Bytham River (*cf.* Rose 2009, 2015; Gibbard *et al.* 2013; Belshaw *et al.* 2014; Bridgland *et al.* 2015), including those at Brooksby. For example, Gibbard *et al.* (2013) and Belshaw *et al.* (2014) refute the existence of a pre-Anglian Bytham system, and dispute the fluvial provenance of some of these deposits, attributing them instead to late Middle Pleistocene glaciogenic deposits. This debate has implications regarding the age of the Brooksby Sand and Gravel, but is beyond the scope of the present thesis, and there remains sufficient independent evidence (e.g. Shotton *et al.* 1993; Penkman *et al.* 2011, 2013; Bridgland *et al.* 2015) to suggest an early Middle Pleistocene age for the Brooksby Sand and Gravel, and related deposits. However, it is acknowledged that this chronological determination may be subject to change in light of future research.

6.2.2. Palaeoenvironmental and archaeological context

The palaeoenvironments associated with the Brooksby Sand and Gravel are considerably less well-known that either those of the West Runton Freshwater Bed (Chapter 4) or the Cromer Forest-bed at Pakefield (Chapter 5), though Rice (1991) and Coope (2006) provide some context. Plant macrofossils and pollen from a bulk borehole sample (Rice 1991) indicate the presence of plant taxa associated with marsh (*Carex*, *Menyanthes trifoliata*), heath (*Empetrum nigrum*, *Calluna vulgaris*) and open disturbed (*Plantago*, *Rumex*) habitats, with some deciduous (*Alnus*, *Betula*, *Populus*, *Salix*) and coniferous (*Abies*, *Picea*, *Pinus*) trees. The plant taxa are all present in lowland Britain at the present time, with the exception of *Oxyria digyna* (mountain sorrel), which is an upland species within Britain (Rose & O'Reilly 2006), with a circumpolar arctic-alpine distribution (Wang *et al.* 2016), suggesting a cooler climate than the present. Previously published coleopteran faunas from Brooksby are also limited (Coope 2006) but provide palaeoenvironmental evidence consistent with that of Rice (1991). Sub-fossil beetles indicate the presence of a river (e.g. *Oulimnius troglodytes* Gyll.), with slow reaches or floodplain pools (e.g. *Enochrus* sp.), bordered by marshy habitats with low vegetation (e.g. *Trechus rivularis* Gyll., *Simplocaria semistriata* Fab.), with *Salix* growing locally (e.g. *Isochnus foliorum* Müll.) (Coope 2006). On the basis of the Mutual Climatic Range (MCR) method, Coope (2006) estimated that mean warmest month temperatures were between 15°C and 16°C, and that mean coldest month temperatures were between -10°C and 2°C, which is consistent with the cool temperate affinities of the flora. These coleopteran assemblages are discussed in more detail in Section *6.4.4.*

A large number of Lower Palaeolithic tools have been recovered from Brooksby Quarry, which are thought to be derived from the Brooksby Sand and Gravel, though none have been recovered *in situ* (Coope 2006, D. Schreve 2012, pers. comm.). As with other Lower Palaeolithic tools from the region, they are predominantly formed from quartzite and andesite, as flint is not locally available (Graf 2002). These tools represent a population which was potentially unusual in the context of the Lower Palaeolithic, as they may have inhabited the region under notably cool climatic conditions. Palaeoenvironmental analyses presented here shed light on the (potential) ecology and tolerances of this population (or populations).

6.3. Site-specific Methodology

6.3.1 Sampling, sub-sampling and laboratory procedures

The Brooksby Sand and Gravel palaeochannel fill was sampled by University of Leicester Archaeological Services during gravel extraction by Lafarge Aggregates Ltd.

In February 2012 a series of bulk sediment samples (*c.* 25-30 kg) were extracted at regular intervals through the sequence (*n.b.* more precise information unavailable), alongside a monolith sequence.

Sub-fossil insect specimens were subsequently extracted during June and July 2012 from the bulk samples and identified at Royal Holloway University of London, during the author's MSc studies (Rowney 2012, unpublished). The extraction method broadly followed that presented in Chapter 3, and identification was led by Professor Scott Elias (RHUL, University of London), with active involvement from the author. Professor Robert Angus (RHUL, University of London) assisted in the identification of *Helophorus* specimens.

In June 2015, sub-samples were taken for pollen, spores and charcoal from the 2012 monolith sequence at 8 cm intervals between 4 cm and 142 cm depth. However, the sediments had dried out, and had become mouldy in parts. Pollen preservation was poor throughout and pollen concentrations were correspondingly very low (mean: 3226.4 pollen grains cm^{-3}) (see Section *6.4.2*), and so finer resolution sub-sampling was not carried out. Details of laboratory processes are given in Chapter 3.

Sedimentological analyses (particle size analysis, loss-on ignition) were not carried out on this sequence. This is partly due to limited sediments available for analyses, and also the paucity of accompanying pollen data.

6.3.2. Assemblage zonations

Faunal (coleopteran) assemblage zones were constructed on the basis of a constrained cluster analysis (CONISS, Grimm 1987), with a broken-stick model (Bennett 1996) used as a guide to determine a significant number of zones. These analyses were performed using the R package 'rioja' (Juggins 2015). Pollen assemblages were not divided into assemblage zones, as these data are largely discussed in the context of presences, rather than abundances, given the low concentrations (see Section *6.4.2.*).

6.3.3. Multivariate analyses

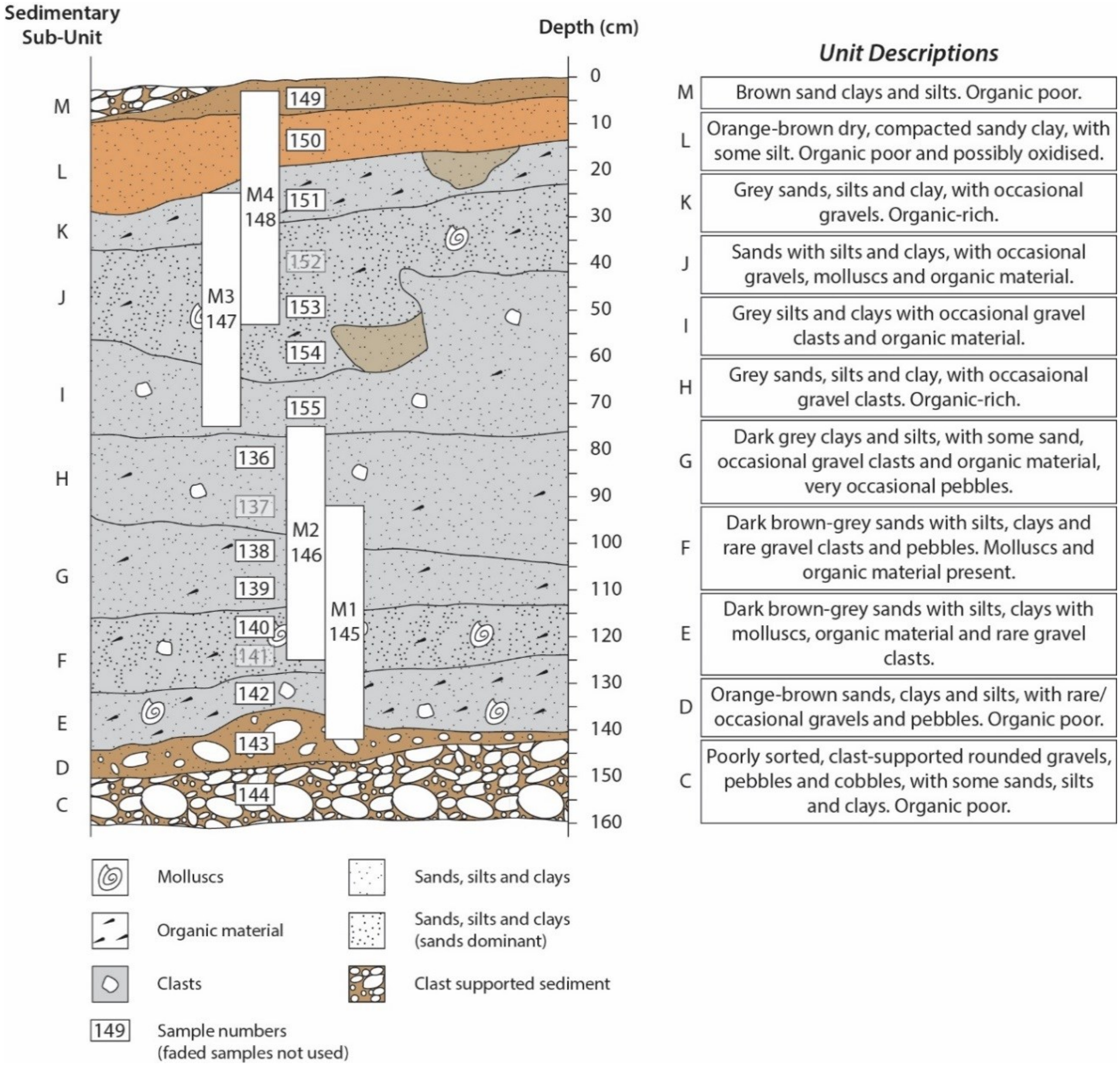
A preliminary detrended correspondence analysis (DCA) applied to the new coleopteran data (functional group relative abundances) produced gradient lengths of <2 (DCA1: 0.74. DCA2: 1.46) and therefore principal components analysis (PCA) was selected as the most appropriate ordination technique. Ordination was also used to compare the new coleopteran sequence presented here with Coope's (2006) Brooksby assemblages. A preliminary DCA of these combined datasets produced gradient lengths of 0.49 (DCA1) and 1.64 (DCA2), and so a PCA was selected as an appropriate ordination technique to apply. It should be noted that the upper- and lowermost samples yielding sub-fossil Coleoptera in the new sequence (samples 150 (10 cm) and 143 (142.5 cm), respectively) were excluded from these analyses. They contained only one or two individuals, giving relative abundance values of 100% for 'hygrophilous' and 'wetland edge' taxa, respectively (see Section *6.4.3.*), skewing ordination axes towards these groups.

Multivariate analyses are more limited in this chapter, largely due to the limitations of the pollen data. The relative abundances of pollen and spore taxa in the present chapter are unlikely to be reliable indicators of relative plant abundances, due to the low pollen concentrations (and hence low pollen counts) (see Section *6.4.2.*), and so were not included in multivariate analyses. Proxies quantified alongside pollen (coprophilous fungal spores, microcharcoal shards) were also not incorporated into such analyses.

6.4. Results

6.4.1. Sedimentology and stratigraphy

Sediments were composed of sands, silts and clays, with some gravels and larger clasts, mollusc remains and organic material. A summary of field-recorded sedimentological properties (recorded by University of Leicester Archaeological Services, D. Schreve 2012, pers. comm.) is given in Figure 6.2.



Unit Descriptions

M	Brown sand clays and silts. Organic poor.
L	Orange-brown dry, compacted sandy clay, with some silt. Organic poor and possibly oxidised.
K	Grey sands, silts and clay, with occasional gravels. Organic-rich.
J	Sands with silts and clays, with occasional gravels, molluscs and organic material.
I	Grey silts and clays with occasional gravel clasts and organic material.
H	Grey sands, silts and clay, with occasaional gravel clasts. Organic-rich.
G	Dark grey clays and silts, with some sand, occasional gravel clasts and organic material, very occasional pebbles.
F	Dark brown-grey sands with silts, clays and rare gravel clasts and pebbles. Molluscs and organic material present.
E	Dark brown-grey sands with silts, clays with molluscs, organic material and rare gravel clasts.
D	Orange-brown sands, clays and silts, with rare/ occasional gravels and pebbles. Organic poor.
C	Poorly sorted, clast-supported rounded gravels, pebbles and cobbles, with some sands, silts and clays. Organic poor.

Figure 6.2 – Sampling log and sub-unit descriptions (XA57) (recorded by University of Leicester Archaeological Services, D. Schreve 2012, pers. comm.) (Figure by the author)

6.4.2. Palynological assemblages

Pollen assemblages are discussed here primarily on the basis of taxon presences in the sequence as a whole, with abundances only accounted for in the broadest terms. This is due to low concentrations of pollen (989.9 to 9109.8 pollen grains cm^{-3}, mean: 3226.4 pollen grains cm^{-3}) (Fig. 6.3), and correspondingly low total land pollen counts (<100 throughout), which mean that observed differences in abundances between pollen taxa and samples cannot be reliably used to infer differences between plant taxon abundances, or temporal changes in these abundances.

Herbaceous pollen taxa are more numerous than arboreal taxa throughout the sequence (Fig. 6.3), and are primarily comprised of an array of marshland and open-ground taxa. The former include the pollen of taxa such as Caryophyllaceae, *Drosera intermedia*, *Lythrum*, *Pinguicula* and *Sphagnum*, indicating the presence of marsh or fen-type habitats. The latter includes generalist open-ground taxa such as *Artemisia* and *Ranunculus acris*, as well as ruderal disturbance indicators (*Plantago* and *Rumex acetosa*). Herbaceous assemblages also include a single occurrence of *Alchemilla alpine* pollen. This species has a predominantly montane distribution in Britain, growing in rocky habitats in upland areas (Rose & O'Reilly 2006).

A range of both deciduous and coniferous tree pollen is present throughout the sequence (Fig. 6.3), generally at low abundances. Deciduous taxa include those typical of temperate conditions (e.g. *Corylus*, *Quercus*, *Ulmus*), as well as those of light (*Betula*) and wet (*Alnus*) woodland. Coniferous taxa include *Pinus* (the most abundant arboreal taxon), *Abies* and a single occurrence of *Tsuga* pollen.

Aquatic pollen assemblages indicate the presence of emergent macrophytes such as *Elodea* and *Stratiotes*, alongside floating-leaved (e.g. *Nuphar*) and submerged (e.g.

Potamogeton) macrophytes, suggesting the presence of a structurally diverse wetland habitat.

Both *Sordaria*-type and *Sporormiella*-type spores are present, indicating herbivore presence, though *Sordaria*-type occurs more frequently (Fig. 6.3). *Podospora*-type spores are absent. Microcharoal shards are also present, with concentrations ranging from 273.3 shards cm^{-3} to 18584 shards cm^{-3}, suggesting low-intensity wildfire, though variations in charcoal concentration should be treated with caution, due to the low pollen counts.

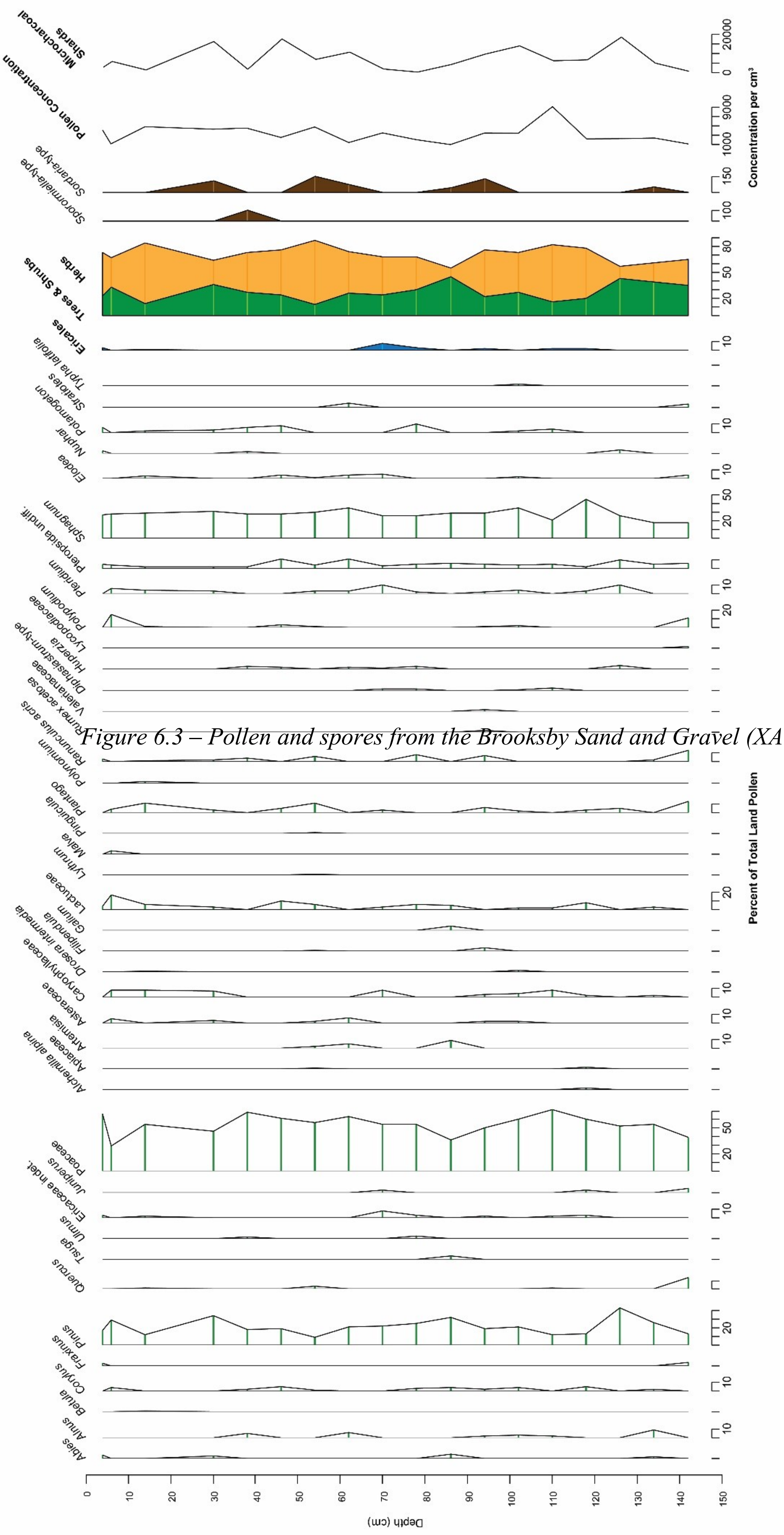


Figure 6.3 – Pollen and spores from the Brooksby Sand and Gravel (XA57, Fig. 6.2) (n.b. Total land

These assemblages suggest the presence of a landscape incorporating fully aquatic habitats, significant open areas, and some woodland. Open areas include both marsh- or fen-type biotopes (likely in the immediate vicinity of fully aquatic areas), and drier, disturbed habitats. Woodlands are evidently also present, though are unlikely to have been dense. These are represented by both deciduous (e.g. *Alnus*, *Corylus*, *Ulmus*) and coniferous (*Abies*, *Pinus*) trees. The presence of *Alchemilla alpina* may tentatively suggest a cool climate, relative to the present. This species is present in Britain and mainland Europe, with a predominantly arctic-montane distribution, and is also present throughout Iceland and Greenland (Rose & O'Reilly 2006; GBIF 2016). However, the simultaneous presence of arboreal taxa typical of temperate climates (e.g. *Quercus*, *Ulmus*) is interesting, perhaps suggesting transitional, non-analogue or continental climatic conditions. The presence of coprophilous fungal spores (*Sordaria*- and *Sporormiella*-type) and microcharcoal shards indicates that herbivory and fire were active processes in the palaeolandscape, though their relative importance cannot be determined.

6.4.3. Coleoptera

The following section presents the results of the extraction and re-analysis of coleopteran remains from the sedimentary sequence, and preliminary ecological interpretations. Thirteen samples were analysed over a depth of 160 cm, with mean weight of 29.08 kg (Table 6.2), but sample volumes were not recorded. In total, 119 MNI (minimum number of individuals) were extracted and identified from this sequence, with individuals from 12 families and 38 genera, 34 of which were identified to species-level.

Table 6.2 Summary of Brooksby (XA57, Fig. 6.2) Coleopteran Samples

Sample Number	Depth (cm)	Weight (kg)	Total MNI	Number of Taxa
149	0-5	24.432	0	0
150	5-15	26.565	1	1
151	15-25	26.522	17	14
153	40-55	29.201	10	8
154	55-65	33.113	12	12
155	65-75	33.869	9	9
136	75-90	34.832	24	18
138	100-105	27.967	14	14
139	105-115	24.344	13	10
140	115-120	29.467	7	7
142	125-140	27.925	10	9
143	140-145	26.061	2	2
144	145-160	30.191	0	0

6.4.3.1. Coleoptera: Limitations and caveats

The coleopteran record presented here provides valuable palaeoenvironmental information, but certain caveats should be borne in mind. Firstly, in the upper and lower *c.* 20 cm of this sequence (Table 6.2) sub-fossil insect material is of low abundance: the uppermost (149) and lowermost samples (144) were devoid of identifiable insect remains, and only 1-2 MNI were identifiable in adjacent samples (samples 150 and 143, respectively). Relative abundances in these samples should be treated with particular caution, and absences cannot be considered significant.

Secondly, only genus-level identification was possible for some specimens. This limits the specificity of the ecological information which can be derived, as the habitat preferences of individual species are often not consistent within a genus. Few in the present sequence were classified as 'uncategorised or eurytopic' (UN), though several were necessarily assigned to relatively broad categories (e.g. *Helophorus* sp. is assigned to AG: aquatic generalists).

6.4.3.2. Coleoptera: Landscape and ecology

The coleopteran sequence has been divided into five faunal assemblage zones (Tables 6.3, Figure 6.4, see also Table 6.4). It is noted that the lowermost and uppermost zones (Br-C1: 160-140 cm and Br-C5: 15-0 cm, respectively) each contain just a single sample, though the sub-fossil assemblages are largely distinct on the basis of low MNI values.

Coleopteran Zone Br-C1 (160-140 cm)

The lowermost zone (Br-C1: 160-140 cm) contains just two species: *Trechus rivularis* and *Arpedium quadrum*. The first of these inhabits fen, mire and peatbog habitats, and the latter is a eurytopic hygrophile (Koch 1989a). *A. quadrum*, whilst not currently present in Britain (Duff 2012), has been recorded in Holocene sequences from Britain (e.g. Elias 2009). Little can be inferred regarding the local landscape on this basis, other than the presence of damp, possibly semi-aquatic, habitats.

Coleopteran Zone Br-C2 (140-115 cm)

Faunal zone Br-C2 (140-115 cm) is marked by an increase in the total MNI and diversity of taxa represented (Tables 6.3 & 6.4, Figure 6.4). Fully aquatic (14.3-20%) and wetland edge (0-10%) beetles provide evidence for some diversity in local wetland habitats. *Helophorus orientalis*, a colonist of temporary ponds, is distributed broadly in

Siberia and North America at present (Angus 1973), though it has previously been recorded in Britain as a Lateglacial sub-fossil (e.g. Coope *et al.* 1997). *Hydraena testacea* is a typical inhabitant of well-vegetated, and therefore relatively permanent, ponds (Foster 2000), which together with *H. orientalis* suggests the presence of both permanent and ephemeral aquatic habitats (e.g. a periodically flooding river, which creates temporary alluvial ponds, or a periodically expanding and contracting wetland). The weevil, *Bagous tubulus*, is oligophagous on *Glyceria* spp. (Koch 1992), indicating that the aquatic-terrestrial ecotone was at least partly colonised by wetland grasses. Hygrophilous taxa (20-28.6%), and those associated with rotten and foul conditions (20-42.9%), are the most numerous groups in this zone. These are generally relatively eurytopic taxa, such as *Arpedium quadrum* (Koch 1989a), and so allow few specific inferences may be made. The rove beetle, *Anotylus sculptus*, is an exception: it is generally associated with rotting plant debris, but with a preference for open habitats (Koch 1989a). Collectively, these taxa suggest that damp habitats, with abundant plant debris, were an important component in the local landscape. Tree-associated and woodland Coleoptera are present in similar relative abundances to aquatic taxa in this zone (14.3-20%), comprising three species. *Polydrusus marginatus* is polyphagous on deciduous trees and 'weakly thermophilous' (*cf.* Koch 1992), whilst *Tachinus caelatus* is known only from Mongolian birch woodlands in a modern context (Ulrich 1975). *Notiophilus biguttatus*, whilst not an obligate woodland species (e.g. Anderson 1996), has a noted preference for clearings and open habitats within wooded areas (Ernsting *et al.* 1992; Duff 1993). These three species suggest the presence of light woodland habitats, potentially in an early successional stage. Collectively, the beetles in this zone indicate the presence of a wetland environment, with significant aquatic-terrestrial ecotonal habitats and light woodland.

Table 6.3 Sub-fossil Coleoptera from the Brooksby Sand and Gravel (XA57, Fig. 6.2)

(AG: Aquatic (general); AS: Aquatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG: Woodland/Trees (general); WTD: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed; DE: Decaying/Foul/Rotten (general); DU: Dung; UN: Uncategorised or Eurytopic; * : Currently absent from Britain according to Duff (2012))

			Median Sample Depth (cm) (upper), Sample Number (lower) and Faunal Zone												
			153	**143**	**133**	**118**	**110**	**103**	**82.5**	**70**	**60**	**47.5**	**20**	**10**	**2.5**
		Habitat	144	143	142	140	139	138	136	155	154	153	151	150	149
Family	**Species**	**Code**	**Br-C1**		**Br-C2**		**Br-C3**					**Br-C4**		**Br-C5**	
Carabidae															
	Trechus rivularius (Gyll.)	H		1											
	Bembidion dauricum (Mots.) *	O											1		
	Bembidion sp.	RW							1	1					
	Notiophilus biguttatus (Fab.)	WTG			1										
	Pterostichus spp.	UN			1		2								
Helophoridae															
	Helophorus cf. *sibiricus* (Mots.) *	AG						1	1						
	Helophorus cf. *orientalis* (Mots.) *	AS			1			1	1	1	1				
	Helophorus sp.	AG			1		3					3	3		
Hydrophilidae															
	Hydrobius fuscipes (L.)	AS									1				
Hydraenidae															
	Hydraena testacea (Curtis)	AS				1			1						
	Enicocerus exsculptus (Germar)	AF					1								
	Ochthebius minimus (Fab.)	AG							1		1	1	1		
	Ochthebius sp.	AG								1					
Staphylinidae															
	Acidota crenata (Fab.)	H							1				1		
	Arpedium brachypterum (Grav.)	H						1		1	1				
	Arpedium quadrum (Grav.) *	H		1	1	1	1								
	Arpedium brunnescens (Sahl.)	H							1						
	Olophrum sp.	H			1					1			1		
	Omalium caesum (Grav.)	DE											1		
	Omalium sp.	DE							1						
	Tachinus pallipes (Grav.)	DE							1						
	Tachinus caelatus (Ullrich) *	WTD				1		1							
	Tachinus sp.	DE				1	1		1			1			
	Atheta sp.	DE				1	1		4	1		1	2		
	Aleocharinae indet.	DE							1						
	Anotylus nitidulus (Grav.)	H						1							
	Anotylus cf. rugosus (Fab.)	DE						1							
	Oxytelus sculptus (Grav.)	DE			2	1	1		3		1	1	1		
	Bledius opacus (Block)	RW									1				
	Bledius cribricollis (Heer)	O						1							
	Bledius nanus (Er.)	O					1								
	Stenus sp.	H				1			1	1			1		
	Quedius sp.	H					1	1							
	Ocypus sp.	UN							1						
	Pycnoglypta lurida (Gyll.) *	H						1							
	Staphylinidae indet.	UN						1							
Scarabaeidae															
	Aphodius cf. *convexus* (Er.) *	DU									1				
	Aphodius sp.	DE									1				
Elmidae															
	Esolus parallelepipedus (Müller)	AF											1		

(Continued overleaf)

Table 6.3 (continued)

			Median Sample Depth (cm) (upper), Sample Number (lower) and Faunal Zone												
			153	**143**	**133**	**118**	**110**	**103**	**82.5**	**70**	**60**	**47.5**	**20**	**10**	**2.5**
			144	143	142	140	139	138	136	155	154	153	151	150	149
Family	**Species**	**Habitat Code**	**Br-C1**		**Br-C2**		**Br-C3**					**Br-C4**		**Br-C5**	
Coccinellidae															
	Scymnus auritus (Thunberg)	WTD									1				
Chrysomelidae															
	Phyllotreta nemorum (L.)	HP					1								
	Phyllotreta nigripes (L.)	HP						1					1		
	Chaetocnema concinna (Marsh)	HP						1							
Apionidae															
	Rhopalapion longirostre (Olivier)	HP										1			
	Oxystoma subulatum (Kirby)	HP							1						
Erirhinidae															
	Grypus brunnirostris (Fab.) *	WE								1		1	1	1	
	Tanysphyrus lemnae (Payk.)	AS								1					
Curculionidae															
	Bagous tubulus (Caldara & O'Brien)	WE			1										
	Ceutorhynchus sp.	HP									1				
	Otiorhynchus cf. *laevigatus* (Fab.)	O									1				
	Otiorhynchus spp.	UN							1		1				
	Polydrusus marginatus (Stephens)	WTD			1				2						
	Sitona sp.	HP						1							
	Trachyphloeus cf. *spinimanus* (Germ.)	O						1				1	1		
	Curculionidae indet.	UN											1		
		Number of Taxa	0	2	9	7	10	14	18	9	12	8	14	1	0
		Total MNI	0	2	10	7	13	14	24	9	12	10	17	1	0

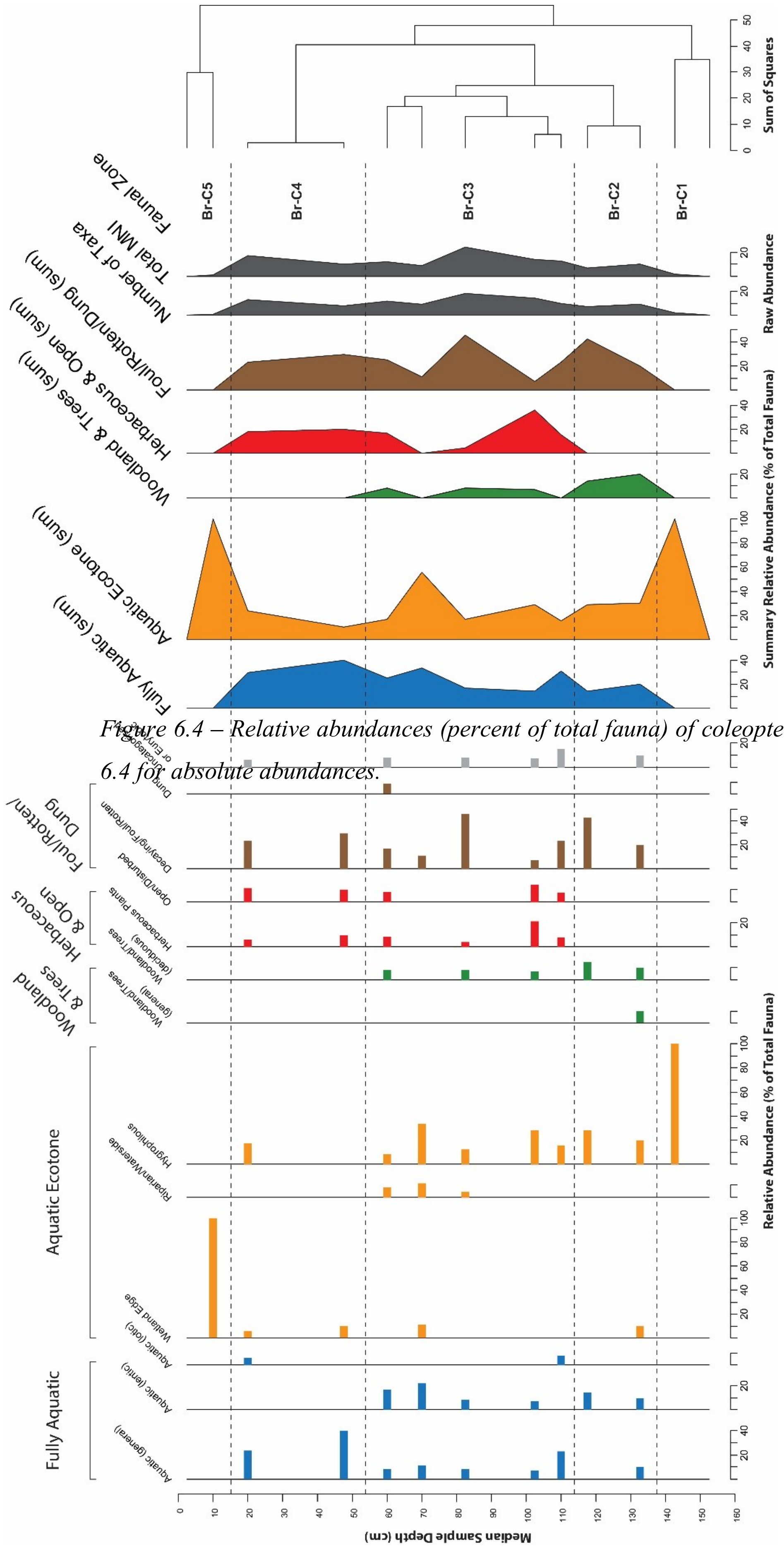


Figure 6.4 – Relative abundances (percent of total fauna) of coleopteran habitat groups from the Brooksby Sa

6.4 for absolute abundances.

Table 6.4 Raw abundances of coleopteran habitat groups from the Brooksby Sand and Gravel (XA57, Fig. 6.2). (Not used in analyses. Included for comparison with relative abundances in Figure 6.4)

Habitat Category	Median Sample Depth (cm) (upper), Sample Number (lower) and Faunal Zone												
	153	**143**	**133**	**118**	**110**	**103**	**82.5**	**70**	**60**	**47.5**	**20**	**10**	**2.5**
	144	143	142	140	139	138	136	155	154	153	151	150	149
	Br-C1		**Br-C2**		**Br-C3**					**Br-C4**		**Br-C5**	
Aquatic (general)	0	0	1	0	3	1	2	1	1	4	4	0	0
Aquatic (lentic)	0	0	1	1	0	1	2	2	2	0	0	0	0
Aquatic (lotic)	0	0	0	0	1	0	0	0	0	0	1	0	0
Wetland Edge	0	0	1	0	0	0	0	1	0	1	1	1	0
Riparian/Waterside	0	0	0	0	0	0	1	1	1	0	0	0	0
Hygrophilous (general)	0	2	2	2	2	4	3	3	1	0	3	0	0
Woodland/Trees (general)	0	0	1	0	0	0	0	0	0	0	0	0	0
Woodland/Trees (deciduous)	0	0	1	1	0	1	2	0	1	0	0	0	0
Woodland/Trees (coniferous)	0	0	0	0	0	0	0	0	0	0	0	0	0
Herbaceous Plants	0	0	0	0	1	3	1	0	1	1	1	0	0
Open/Disturbed	0	0	0	0	1	2	0	0	1	1	2	0	0
Decaying/Foul/Rotten (general)	0	0	2	3	3	1	11	1	2	3	4	0	0
Dung	0	0	0	0	0	0	0	0	1	0	0	0	0
Uncategorised or Eurytopic	0	0	1	0	2	1	2	0	1	0	1	0	0
Fully Aquatic (sum)	0	0	2	1	4	2	4	3	3	4	5	0	0
Aquatic Ecotone (sum)	0	2	3	2	2	4	4	5	2	1	4	1	0
Woodland/Trees (sum)	0	0	2	1	0	1	2	0	1	0	0	0	0
Herbaceous/Open (sum)	0	0	0	0	2	5	1	0	2	2	3	0	0
Foul, Rotten, Dung (sum)	0	0	2	3	3	1	11	1	3	3	4	0	0
Number of Taxa	0	2	9	7	10	14	18	9	12	8	14	1	0
Total MNI	0	2	10	7	13	14	24	9	12	10	17	1	0

Coleopteran Zone Br-C3 (115-55 cm)

In zone Br-C3 (115-55 cm) (Tables 6.3 & 6.4, Figure 6.4), fully aquatic beetles indicate the continuation of a structurally diverse wetland. As in the previous zone, *Helophorus orientalis* indicates the occurrence of temporary waterbodies, an inference which is strengthened by the additional presence of *H. sibiricus*. This species has similar habits, though is also a colonist of snowmelt pools, and has a modern distribution throughout Northern Fennoscandia, Siberia, Northern Mongolia, Hokkaido (Northern Japan), Alaska and Northwest Canada (Angus 1973; Fikáček *et al.* 2011). *Hydrobius fuscipes* is associated with more permanent, low-energy habitats (Hansen 1987), whilst *Enicocerus exsculptus* is an obligate lotic species (Friday 1988). *Grypus brunnirostris*, which feeds on *Equisetum* spp. (Bosmans 2012), is the only direct indicator of aquatic-terrestrial ecotonal vegetation in this zone, suggesting that the wetland margins were perhaps sparsely vegetated. Hygrophilous taxa also give little indication of ecotonal vegetation, as most are rather generalist (e.g. *Arpedium brachypterum*, Harde 1984). However, *Pycnoglypta lurida*, which is distributed from Central and Northeastern Europe to Middle Siberia, often inhabits damp or marshy biotopes in woodland contexts (Shavrin 2016). Beetles associated with foul and rotten habitats in this zone, are also rather eurytopic (e.g. *Omalium caesum*, Koch 1989a), and suggest the presence of decaying plant material, though this may be derived from flood deposition rather than *in situ* vegetation. A single occurrence in this zone of *Aphodius convexus*, a dung-obligate species (Buse *et al.* 2015), provides the only direct evidence in the coleopteran sequence of local herbivore presence.

Amongst woodland and tree taxa, *Tachinus caelatus* and *Polydrusus marginatus* remain present in this zone, indicating low-density deciduous woodland. They are also accompanied by the Coccinellid, *Scymnus auritus*, which is closely associated with *Quercus* spp. (oak) (Atty 1983; Koch 1989b), providing evidence of oak as an additional component of woodland habitats, also indicated by its presence in the pollen record (Fig. 6.3). However, this zone is marked by the appearance of beetles associated with dry open and disturbed habitats, and herbaceous vegetation (max. relative abundance: 35.7%, max. absolute abundance: 5). These include *Bledius cribricollis* and *B. nanus*, which are psammophilous species associated with exposed sediments although, unlike most *Bledius* species, they are not restricted to riparian settings (Koch 1989a). These are accompanied by *Trachyphloeus spinimanus*, which inhabits dry open, disturbed habitats (Hyman 1992), and *Otiorhynchus laevigatus*, which is also found in open habitats (Boháč & Matějka 2016). Chrysomelidae associated with Cruciferae

(*Phyllotreta nemorum*, *P. nigripes*) (Harde 1984) and Polygonaceae, such as *Rumex*, *Persicaria* and *Fallopia* (*Chaetocnema concinna*) (Cox 2007) are also present, as is the weevil *Sitona* sp., which is polyphagous on various legumes (Harde 1984). These beetles suggest some opening of the local landscape, though low-density woodland habitats evidently remained present.

Coleopteran Zone Br-C4 (55-15 cm)

The penultimate zone, Br-C4 (55-15 cm) (Tables 6.3 and 6.4, Figure 6.4), is distinguished by the absence of woodland and tree associated beetles. Fully aquatic taxa are represented by *Ochthebius minimus*, an aquatic generalist (Hansen 1987), and *Helophorus* spp. In the aquatic-terrestrial ecotone, some vegetation remains represented by *Grypus brunnirostris* and *Bagous tubulus*, which are associated with *Equisetum* spp. (Bosmans 2012) and *Glyceria* spp. (Koch 1992), respectively. Hygrophilous species are largely eurytopic (e.g. *Acidota crenata*, Koch 1989a), as are those associated with decaying and foul habitats (e.g. *Omalium caesum*, Koch 1989a). Open ground, disturbed habitat and herbaceous vegetation taxa remain significant. These include *Trachyphloeus spinimanus*, which inhabits dry, disturbed open habitats (Hyman 1992) and *Bembidion dauricum*, which is a circumpolar species often associated with tundra, as well as dry peaty soils with sparse vegetation and birch (*Betula*) (Lindroth 1963, 1985, Ball & Currie 1997). *Phyllotreta nigripes* is a stenophage of Cruciferae, often in open habitats (Koch 1992) and *Rhopalapion longiroste* occurs on various Malvacaeae species (Jones 2006). Whilst relative abundances of each functional group in this zone are generally broadly comparable with the previous zone (Br-C3), the absence of woodland and arboreal species, and continued presence of species associated with sparsely vegetated and disturbed habitats, suggests a more open landscape.

Coleopteran Zone Br-C5 (15-0 cm)

The uppermost zone, Br-C5 (15-0 cm) (Tables 6.3 & 6.4, Figure 6.4), is almost devoid of identifiable insect remains. The only taxon present is *Grypus brunnirostris*, which gives little indication of landscape characteristics, other than the presence of moist habitats with *Equisetum* (Bosmans 2012). However, the virtual absence of sub-fossil insect remains in this zone is coincident with sedimentological change (see Figure 6.2), and is indicative of a distinct shift in taphonomic conditions, possibly associated with channel migration.

In summary, these assemblages are indicative of deposition in a generally low-energy wetland environment, with both permanent and temporary small waterbodies, and occasional fluvial inputs. This appears to have been set within a broader area of marshy ground with low, open vegetation and exposed sediments or soils, with drier open habitats likely further from fully aquatic zones. Light woodland, with *Betula*, *Quercus* and potentially other deciduous trees, was a component of the landscape during part of the sequence, but the gradual replacement of this aspect of the beetle fauna with taxa associated with open habitats and herbaceous vegetation is suggestive of woodland decline and an opening of the landscape.

6.4.3.3. Coleoptera: Climate

The following section presents the results of Mutual Climatic Range (MCR) reconstructions of local palaeoclimates associated with the sedimentary sequence (XA57) (Figure 6.5, Table 6.5). These data are briefly discussed in the context of taxa used in developing the reconstructions, as well as other plant and insect taxa present which provide additional qualitative palaeoclimatic information.

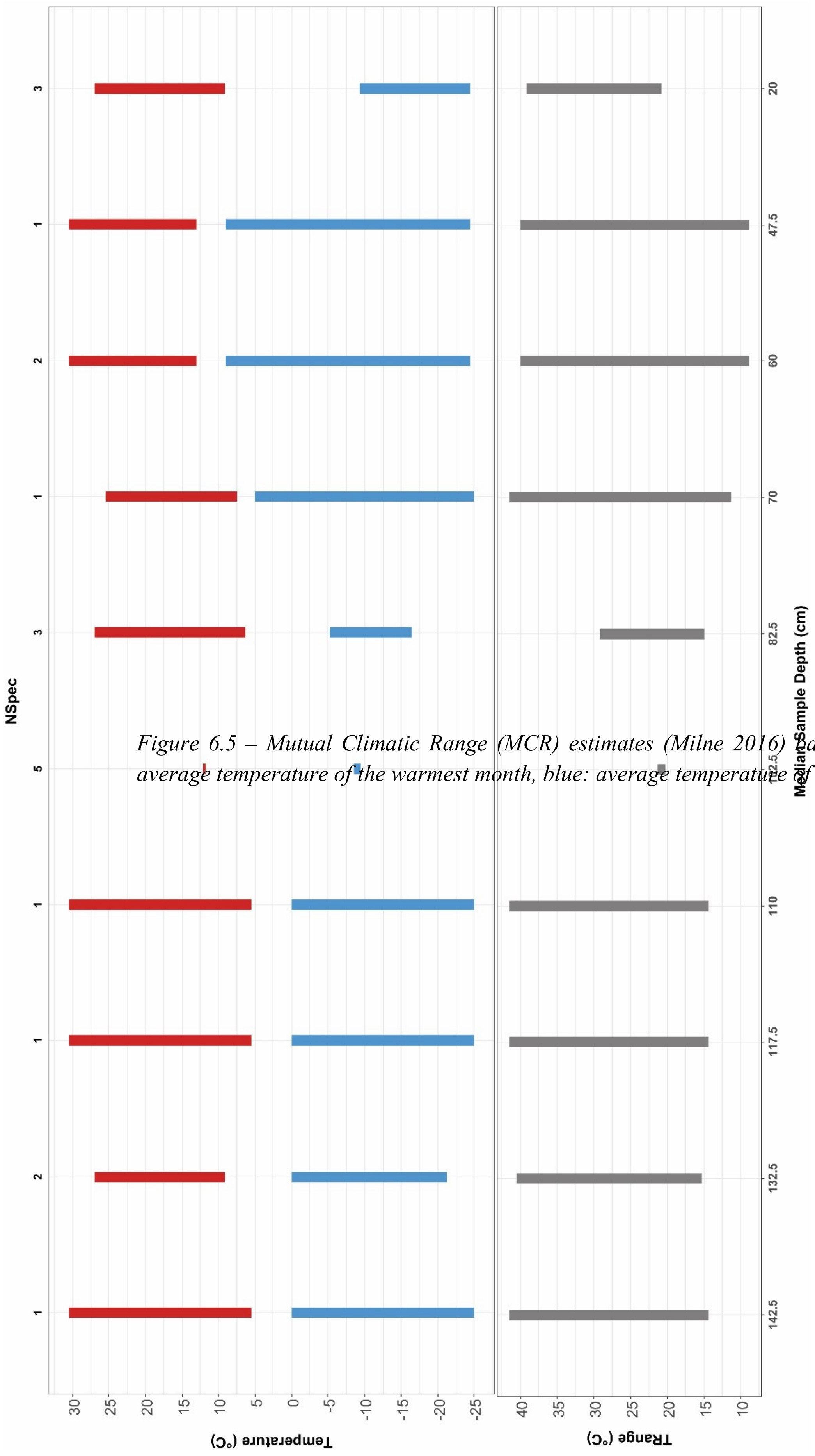


Figure 6.5 – Mutual Climatic Range (MCR) estimates (Milne 2016) based on coleoptera from the Broc
average temperature of the warmest month, blue: average temperature of the coldest month, grey: average

Table 6.5 Mutual Climatic Range (MCR) estimates for the new Brooksby fauna (XA57, Fig. 6.2) presented here, based on new (Milne 2016) MCR methods

Sample Number	**Median Sample Depth (cm)**	**TMax (°C)**	**TMin (°C)**	**TRange (°C)**	**Number of Species**
149	2.5	n/a	n/a	n/a	n/a
150	10	n/a	n/a	n/a	n/a
151	20	9.2 to 27	-24.5 to -9.4	20.8 to 39.1	3*
153	47.5	13 to 30.5	-24.5 to 9	8.8 to 40	1
154	60	13 to 30.5	-24.5 to 9	8.8 to 40	2
155	70	7.5 to 25.5	-25 to 5	11.3 to 41.5	1
136	82.5	6.3 to 27	-16.5 to -5.3	14.95 to 29.1	3*
138	102.5	11.8 to 12.1	-9.5 to -8.5	20.3 to 21.3	5
139	110	5.5 to 30.5	-25 to 0	14.3 to 41.5	1
140	117.5	5.5 to 30.5	-25 to 0	14.3 to 41.5	1
142	132.5	9.1 to 27	-21.25 to 0	15.3 to 40.5	2
143	142.5	5.5 to 30.5	-25 to 0	14.3 to 41.5	1
144	152.5	n/a	n/a	n/a	n/a
Total Fauna	-	11.4 to 25.5	-16.45 to -9.4	20.8 to 29.1	11*

*Climate envelopes not overlapping for all species used (*n.b.* extent of overlap not quantifiable using Milne (2016))

The climatic ranges provided by MCR reconstructions here provide some evidence for cool temperate, and potentially continental, climatic conditions, but give little indication of substantial climate change (Fig. 6.5, Table 6.5). The range estimates are generally rather broad, but sample 138 (median depth 102.5 cm) is more tightly constrained. This sample indicates cool summers (11.8 to 12.1°C), cold winters (-9.5 to -8.5°C) and moderate annual temperature ranges (20.3 to 21.3°C), consistent with modern lowland northern Fennoscandia. It includes cool and cold climate-adapted taxa (*Helophorus sibiricus*, *Arpedium brachypterum*, *Pycnoglypta lurida*), alongside those with more temperate affinities (*Anotylus nitidulus*, *A. rugosus*) (see Table 6.6), with their climate envelopes overlapping at their upper and lower limits, respectively. The cool and cold climate species include two not currently present in Britain: *Helophorus sibiricus*, which is almost circumpolar and is known to colonise snowmelt pools (Angus 1973), and *Pycnoglypta lurida*, which is distributed from Central and Northeastern Europe to Middle Siberia (Shavrin 2016). *Arpedium brachypterum* is present in Britain, but has a broad Holarctic distribution and tends to inhabit upland areas in mid-latitude portions of its range, including Britain (Campbell 1984; Harde 1984; Zanetti 2011). The more temperate-associated species, *Anotylus nitidulus* and *A. rugosus*, are both widespread throughout Britain and Europe (Lott 2009; Schülke 2012). The climate reconstructions with broad ranges are predominantly based on samples in which only eurythermic widespread species (e.g. *Arpedium quadrum*, *Acidota crenata*) were present, thus producing a breadth of values which are relatively uninformative.

The majority of climatic range reconstructions throughout the sequence are overlapping (Figure 6.5, Table 6.5), and so cannot be assumed to represent substantially different climatic regimes, providing little evidence of climatic change. The exceptions to this are samples 153 (median depth: 47.5 cm) and 154 (median depth: 60 cm), which do not overlap with sample 138 (median depth: 102.5 cm) in summer temperatures. This may suggest a slight warming in the upper part of the sequence, but the divergence between these ranges is just 0.9°C. Such minor differences cannot be assumed to be significant, as they are within the errors of the modern climate data from which individual species climate ranges are derived (Hijmans *et al.* 2005), and so are more likely related to limitations in the modelling of individual species thermal tolerance ranges than climatic change.

Table 6.6 Species utilised in Mutual Climatic Range (MCR) reconstructions for Brooksby Sand and Gravel (XA57, Fig. 6.2)

Sample	Median Sample Depth (cm)	Species utilised in MCR
151	20	*Bembidion dauricum* (Mots.) *Acidota crenata* (Fab.) *Ochthebius minimus* (Fab.)
153	47.5	*Ochthebius minimus* (Fab.)
154	60	*Hydrobius fuscipes* (L.) *Ochthebius minimus* (Fab.) *Arpedium brachypterum* (Grav.)
155	70	*Arpedium brachypterum* (Grav.)
136	82.5	*Helophorus sibiricus* (Mots.) *Acidota crenata* (Fab.) *Ochthebius minimus* (Fab.)

(Continued overleaf)

Table 6.6 (continued)

138	102.5	*Helophorus sibiricus* (Mots.) *Arpedium brachypterum* (Grav.) *Anotylus nitidulus* (Grav.) *Anotylus rugosus* (Fab.) *Pycnoglypta lurida* (Gyll.)
139	110	*Arpedium quadrum* (Grav.)
140	117.5	*Arpedium quadrum* (Grav.)
142	132.5	*Notiophilus biguttatus* (Fab.) *Arpedium quadrum* (Grav.)
143	142.5	*Arpedium quadrum* (Grav.)

Table 6.7 Individual species climatic ranges, as determined by Milne (2016) methods

MCR Species	**TMax (°C)**	**TMin (°C)**	**TRange (°C)**	**Sample Presence (Sample Nos.)**
Bembidion dauricum	9.15 to 11.4	-28.4 to -9.4	20.8 to 39.1	151
Notiophilus biguttatus	8.85 to 28.5	-21.5 to 10.2	8.65 to 41	142
Helophorus sibiricus	6.3 to 12.75	-16.45 to -5.3	14.95 to 29.1	138, 136
Hydrobius fuscipes	10.6 to 33.5	-27.55 to 9.95	8.25 to 47.5	154
Ochthebius minimus	13 to 30.5	-24.5 to 9	8.8 to 40	136, 154, 153, 151
Acidota crenata	5.3 to 27	-25 to 7.5	8.65 to 41.5	136, 151
Arpedium brachypterum	7.45 to 25.5	-25 to 5	11.35 to 41.5	138, 155, 154

(Continued overleaf)

Table 6.7 (continued)

Arpedium quadrum	5.5 to 30.5	-25 to 0.05	14.35 to 41.5	143, 142, 140, 139
Anotylus nitidulus	11.35 to 27	-24.5 to 7.5	13.4 to 41.5	138
Anotylus rugosus	9.95 to 27.5	-19.5 to 7	9.05 to 40	138
Pycnoglypta lurida	9.85 to 25.5	-24.5 to -0.4	16.85 to 41.5	138

Samples 151 (median depth: 20 cm) and 136 (median depth 82.5 cm) (Fig. 6.5, Tables 6.5 & 6.6) contained species with envelopes which did not overlap. In sample 151 the climatic envelope for *Bembidion dauricum* does not overlap with that of *Ochthebius minimus*, and in sample 136, the same is true of *Helophorus sibiricus* and *O. minimus*. This was dealt with according to the procedure outlined in Chapter 3 (Section *3.3.3.*) and illustrated in Figure 6.6. This produced rather broad summer temperature range estimates, which whilst likely to be accurate (i.e. containing the ‘true’ value within the range), are imprecise.

The distributional data for *B. dauricum* and *H. sibiricus* in GBIF (GBIF 2016), on which their climatic envelopes are based (Milne 2016), is limited and so their thermal tolerance limits may have been underestimated. In GBIF (GBIF 2016), *B. dauricum* is reported only from Northern and Western Norway, and Northern Canada. However, Lindroth (1963, 1985) reports a circumpolar distribution and Kryzhanovskij *et al.* (1995) suggest presence throughout Siberia and Central Asia, as well as Eastern Europe. For *H. sibiricus*, the GBIF (GBIF 2016) distribution is centred on the Scandinavian Mountains and Northern Mongolia, as well as including isolated occurrences in North Dakota and Western Alaska. However, Angus (1973) and Filáček *et al.* (2011) report a broader distribution, including lowland areas of Norway and

Siberia. On this basis, it seems unlikely that the GBIF (GBIF 2016) distribution for either species (*B. dauricum*, *H. sibiricus*) fully captures the extent of their thermal tolerance limits, as each exists in lower latitude and lower altitude regions (with warmer summers and milder winters) than reported in GBIF (GBIF 2016). Currently, it is not possible to use this information to quantitatively refine the climatic reconstructions which use these species, but it does provide valuable context when interpreting the data.

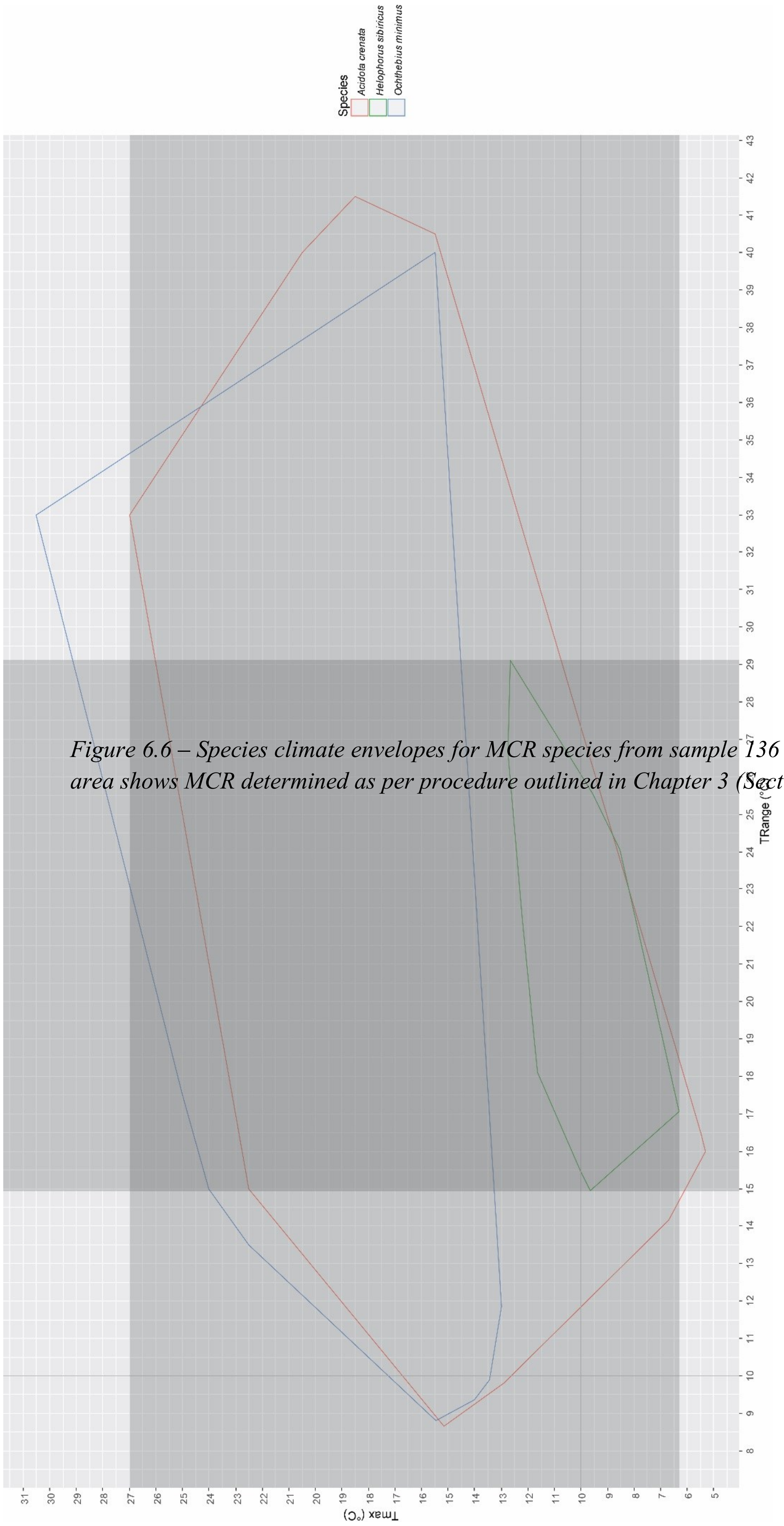


Figure 6.6 – Species climate envelopes for MCR species from sample 136 (XA57, Fig. 6.2*) illustrating*
area shows MCR determined as per procedure outlined in Chapter 3 (Section 3.3.3.).

The interpretation of these MCR reconstructions is complicated by the co-occurrence of temperate plant and insect taxa with cold and cool climate-adapted beetles, as well as a lack of overlap between the climate envelopes certain beetle species. *Ochthebius minimus* occurs alongside both *Helophorus sibiricus* and *Bembidion dauricum* in samples 138 (median depth: 102.5 cm) and 151 (median depth: 20 cm), respectively. However, the climatic envelope of *O. minimus* did not overlap with that of either *H. sibiricus* or *B. dauricum*, primarily as a product of different summer temperature ranges (see Table 6.7) and it is likely that this, at least partly, results from *B. dauricum* and *H. sibiricus* thermal tolerance ranges being underestimated, as discussed. In addition, there are taxonomic issues with *O. minimus*, which may influence the efficacy of its use as a climatic indicator species, particularly in 'cold' faunas. This relates to ongoing debate regarding whether *O. minimus* should be considered distinct from *O. alpinus* and *O. rugulosus* (*c.f.* Jäch 1990, 1998; Cuppen & Nilsson 1991), the former being a high-latitude/altitude species. Therefore, assuming that *O. minimus* is a distinct species, it is likely that its northern limits are either inaccurately or incompletely known due to confusion with *O. alpinus*. This confusion between *O. minimus* and *O. alpinus* in 'cold' faunas has also been highlighted by Buckland & Buckland (2006), who recommend caution in such contexts.

The occurrence of temperate climate-affiliated plants and insects, alongside subarctic, boreal and alpine beetles (e.g. *Bembidion dauricum*, *Helophorus sibiricus*) (Table 6.3) and plants (e.g. *Alchemilla alpina*) (Fig. 6.3), further complicates the interpretation of these assemblages in a climatic context. There is clear pollen evidence for the presence of deciduous tree taxa with temperate affinities, such as *Corylus*, *Quercus* and *Ulmus* throughout the sequence (Fig. 6.3). Furthermore, beetles such as *Polydrusus marginatus*, which is polyphagous on deciduous trees (Koch 1992) and

Scymnus auritus, which is associated with *Quercus* spp. (Atty 1983; Koch 1989b) are also present. The simultaneous presence of cold-adapted species, which have short generation times and are effective dispersers and colonists (e.g. *Bembidion dauricum*, *Helophorus sibiricus*), alongside long-lived and relatively sedentary organisms with temperate affinities (i.e. deciduous trees) may suggest that this sequence represents a transitionary period during, or closely following, a climatic deterioration. Indeed, similar disequilibrium between pollen and insect records has been noted in Lateglacial sequences following climatic deterioration (e.g. Walker *et al.* 1993). Alternatively, stable, continental climatic conditions may also have promoted this combination of seemingly incongruent biota, with different species responding to different aspects of climate. For example, relatively warm spring and summer temperatures may have continued to facilitate deciduous pollen production, whilst cold winter temperatures promoted the establishment of high latitude and montane taxa.

6.4.4. Russell Coope's Brooksby Coleoptera

This section presents beetle assemblages from the Brooksby Sand and Gravel (derived from borehole samples) published in Coope (2006), re-analysed using a functional group approach (Tables 6.8; Fig. 6.7, see also Table 6.9) and Milne (2016) MCR (Fig. 6.8, Table 6.10). This gives emphasis to important aspects of the fauna in an ecological context, provides more accurate climatic reconstructions and facilitates comparison with the new coleopteran record from Brooksby presented in this chapter (XA57: Section *6.4.3.*). Taxonomy has been updated according to Duff (2012), which includes species recorded in Britain as Pleistocene sub-fossils.

Table 6.8 Sub-fossil Coleoptera from the Brooksby Sand and Gravel (Coope 2006)

(AG: Aquatic (general); AS: Aquatic (lentic); AF: Aquatic (lotic); WE: Wetland Edge; RW: Riparian/Waterside; H: Hygrophilous (general); WTG: Woodland/Trees (general); WTD: Woodland/Trees (deciduous); WTC: Woodland/Trees (coniferous); HP: Herbaceous Plants; O: Open/Disturbed; DE: Decaying/Foul/Rotten (general); DU: Dung; UN: Uncategorised or Eurytopic)

			Sample		
		Habitat	Lower		Upper
Family	**Species**	**Code**	6	7	11
Dytiscidae					
	Dytiscidae indet.	AG	1		
Carabidae					
	Trechus rivularius (Gyll.)	H			1
	Trechus secalis (Gyll.)	H		1	1
	Bembidion varium (Olivier)	RW			1
	Bembidion tetracolum (Say)	H			1
	Bembidion gilvipes (Sturm)	H			2
	Bembidion schuppelii (Dejean)	RW		1	
	Patrobus assimilis (Chaudoir)	O			1
	Pterostichus oblongopunctatus (Fab.)	WTD			1
Helophoridae					
	Helophorus grandis (Ill.)	AS		1	
	Helophorus spp.	AG	1	1	1
Hydrophilidae					
	Enochrus sp.	AS			1
	Ceryon tristis (Ill.)	RW			1
Hydraenidae					
	Hydraena sp.	AG		1	1
Staphylinidae					
	Olophrum consimile (Gyll.)	RW		1	
	Arpedium brachypterum (Grav.)	H		2	
	Aleocharinae indet.	DE	1	1	5
	Platystethus nodifrons (Mann.)	H			1
	Bledius sp.	RW			1
	Carpelimus sp.	H		1	2
	Stenus spp.	H		1	1
Byrrhidae					
	Simplocaria semistriata (Fab.)	O		1	
Elmidae					
	Oulimnius troglodytes (Gyll.)	AF		1	
	Oulimnius tuberculatus (Müller)	AF		1	
Apionidae					
	Apion sp.	HP			1
Curculionidae					
	Isochnus foliorum (Müller)	WTD			1
		Number of Taxa	3	13	18
		Total MNI	3	14	24

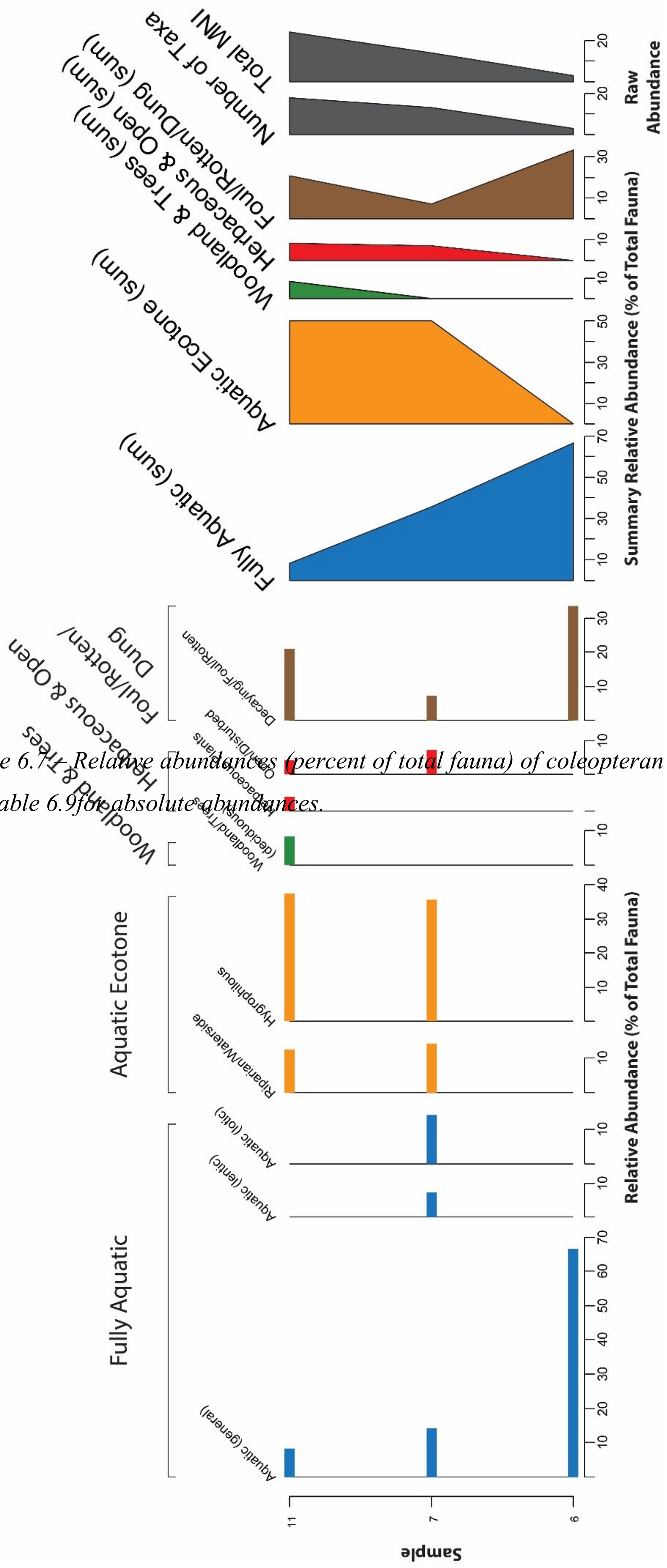


Figure 6.7: Relative abundances (percent of total fauna) of coleopteran habitat groups from the Brooksby Sand a
See Table 6.9for absolute abundances.

Table 6.9 Raw abundances of coleopteran habitat groups from Coope's (2006) Brooksby Fauna.

(Not used in analyses. Included for comparison with relative abundances in Figure 6.7)

Habitat Category	Sample Lower 6	 7	 Upper 11
Aquatic (general)	2	2	2
Aquatic (lentic)	0	1	0
Aquatic (lotic)	0	2	0
Wetland Edge	0	0	0
Riparian/Waterside	0	2	3
Hygrophilous (general)	0	5	9
Woodland/Trees (general)	0	0	0
Woodland/Trees (deciduous)	0	0	2
Woodland/Trees (coniferous)	0	0	0
Herbaceous Plants	0	0	1
Open/Disturbed	0	1	1
Decaying/Foul/Rotten (general)	1	1	5
Dung	0	0	0
Uncategorised or Eurytopic	0	0	0
Fully Aquatic (sum)	2	5	2
Aquatic Ecotone (sum)	0	7	12
Woodland/Trees (sum)	0	0	2
Herbaceous/Open (sum)	0	1	2
Foul, Rotten, Dung (sum)	1	1	5
Number of Taxa	3	13	18
Total MNI	3	14	24

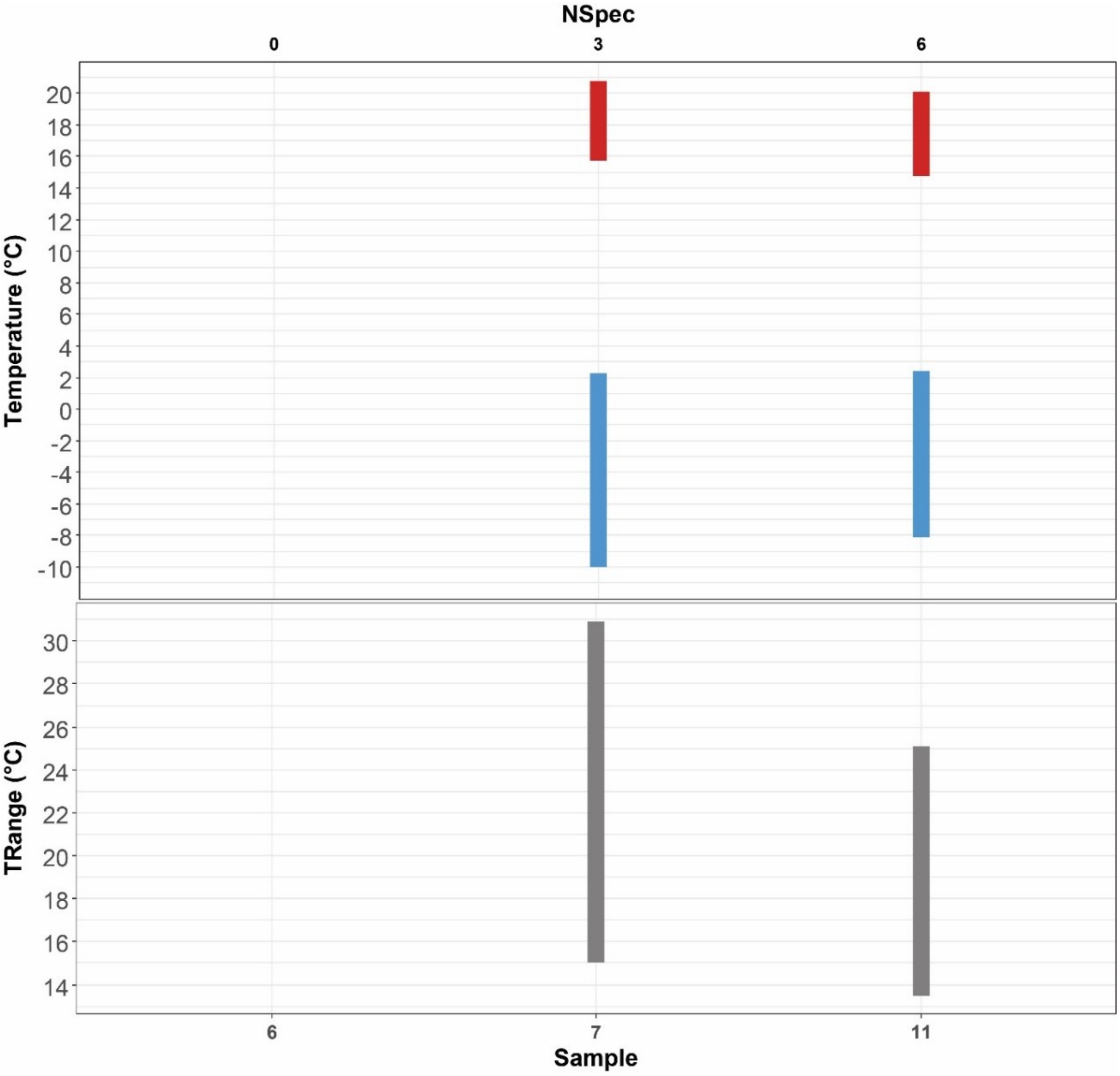


Figure 6.8 – Mutual Climatic Range (MCR) estimates (Milne 2016) based on Coleoptera from Brooksby (red: average temperature of the warmest month, blue: average temperature of the coldest month, grey: average annual temperature range) (original data: Coope 2006) (Horizontal lines highlight overlap between all samples)

Table 6.10 Mutual climatic range (MCR) estimates for Coope's (2006) Brooksby fauna, based on BugsCEP (Buckland & Buckland 2006) and new (Milne 2016) MCR methods

Sample	BugsCEP MCR		New MCR		Number
	TMax (°C)	TMin (°C)	TMax (°C)	TMin (°C)	of Species
6	n/a	n/a	n/a	n/a	0
7	14 to 16	-14 to 2	15.75 to 20.8	-10 to 2.25	4
11	15 to 18	-12 to 4	14.75 to 20.1	-8.1 to 2.4	9
Total Fauna	15 to 16	-12 to 2	15.75 to 19	-6.4 to 2.25	12

A quantitative functional group approach provides a reconstruction of the local palaeolandscape broadly in agreement with that given by Coope (2006), but with additional detail, as well as some differences. Fully aquatic taxa comprise 8.3% to 66.7% (36.9% mean) of the total fauna (Table 6.8, Fig. 6.7), though their relative abundance decreases with increasing effective sample size (i.e. total MNI). Several of these taxa are categorised as generalists due to a lack of taxonomic resolution (Dytiscidae indet., *Helophorus* sp., *Hydraena* sp.), but both lentic and lotic habitats are specifically represented in sample 7 (Tables 6.8 and 6.9, Fig. 6.7). *Helophorus grandis* inhabits small lentic waterbodies, with some preference for temporary and eutrophic pools (Hansen 1987; Koch 1989a), whilst species of *Enochrus* are found in a range of lentic contexts (Friday 1988). The 'riffle beetles' *Oulimnius troglodytes* and *O. tuberculatus* have similar habits and are typically associated with running water, though may also be found at the edges of large lakes (Koch 1989b). The latter is often found amongst algae, moss and other aquatic vegetation (Harde 1984; Koch 1989b). Whilst Coope (2006) noted the presence of a river incorporating both high and low energy mesohabitats, this analysis also indicates a small, possibly ephemeral, lentic waterbody in the vicinity of this river. Deposition of the beetle assemblages likely occurred in this low energy environment, partly via alluvial processes, rather than directly in the fluvial system.

Hygrophilous and riparian beetle abundances (MNI) range from 0-9 and 0-3, respectively, and are broadly indicative of sparsely vegetated marshy habitats, perhaps with some occurrences of *Alnus* or *Salix*. These are partly represented by eurytopic hygrophilous taxa, such as *Bembidion tetracolum*, *B. gilvipes*, *Arpedium brachypterum* (Koch 1989a), *Carpelimus* sp. and *Stenus* spp. (Harde 1984), but several more stenotopic taxa provide additional detail. *Bembidion varium* (Koch 1989a), *B. schueppelii* (Hyman 1992), *Platystethus nodifrons* (Hyman 1994) and *Bledius* sp. (Harde 1984) are all associated with fine, wet sediments at the edges of freshwater. Both *Trechus rivularis* and *T. secalis* inhabit damp habitats, though the former is a stenotopic fen and peatbog species (Luff 1998; Lott 2003), whilst the latter exhibits some preference for shaded habitats (Lindroth 1985). However, beetle species associated with riparian vegetation are scarce in this fauna. *Olophrum consimile* is a riparian species, often associated with *Alnus* and *Salix* litter at the edges of freshwater (Campbell 1983), though it may also be found in mossy habitats (Koch 1989a). *Cercyon tristis* is typically found amongst plant debris at the edges of wetland habitats (Hansen 1987), though this debris may be derived from flood deposition rather than vegetation growing *in situ*.

Coleoptera associated with either herbaceous vegetation or open habitats are relatively scarce in Coope’s (2006) Brooksby fauna (Table 6.8, Fig. 6.7). The former category is represented by a single occurrence of *Apion* sp. in the uppermost sample, species of which may be associated with a range of herbaceous plant taxa (Harde 1984). Beetles associated with open habitats comprise 0% to 7.1% of faunas, and include *Patrobus assimilis*, which inhabits heaths and bogs (Lindroth 1985) and *Simplocaria semistriata*, a moss specialist often found in heaths and sandy areas (Koch 1989b).

Obligate arboreal and woodland beetles are similarly scare, occurring only in the upper sample in which they account for 8.3% of the total fauna (Table 6.8, Fig. 6.7), represented by two species. *Isochnus foliorum* is a leaf-mining weevil which is oligophagous on *Salix* spp. (Koch 1992), confirming the local presence of willow (*Salix*), and *Pterostichus oblongopunctatus* is a eurytopic deciduous (and mixed) woodland species, often associated with relatively light woodland (Lindroth 1986; Luff 1998). As noted by Coope (2006), several other species present, such as *Trechus secalis*, may also inhabit woodland habitats, but are not obligate woodland species (Lindroth 1985).

Foul and rotten habitat beetles represent between 20.8% and 33.3% (20.4% mean) of the total fauna (Table 6.8; Fig. 6.7). However, this group is represented exclusively by Aleocharinae indet., providing little specific information. No dung-obligate beetles were recovered as part of these assemblages.

Mutual Climate Range (MCR) reconstructions on the basis of Coope's (2006) Brooksby fauna (Fig. 6.8, Table 6.10) are broadly consistent between samples and indicate a cool temperate climate, with cool summers (warmest month: 15.75 to 19°C) and cold winters (coldest month: -7.4 to 2.25°C). These estimates suggest slightly milder winters and potentially warmer summers than Coope's (2006) estimates (warmest month: 15 to 16°C, coldest month: -10 to 2°C) and those based on BugsCEP MCR (Buckland & Buckland 2006) (see Table 6.10). However, these results are not contradictory and all suggest a potentially slightly cooler climate than the region at present, which experiences average January temperatures between 1.2 and 7.2°C and average July temperatures between 11.9 and 21.7°C (based on Met Office (2017) Sutton Bonington climate station data).

Collectively, this fauna is indicative of deposition during a cool temperate period, in a floodplain environment with small, temporary alluvial ponds, in the vicinity of an active fluvial system. These aquatic habitats were fringed with open, marshy areas with sparse or low vegetation, and occasional stands of *Salix*. Soils were apparently peaty, and drier areas were likely to have been occupied by heath-type vegetation. Large herbivore presence cannot be inferred. This differs somewhat from Coope's (2006) interpretation, which implied a greater presence of woodland-type habitats, on the basis of the ground beetle (Carabidae) fauna, which includes species such as *Trechus secalis*, *T. rivularis* and *Bembidion gilvipes*, which may inhabit *Alnus* or *Salix* leaf litter, but also a range of other moist habitats. Evidence for peat and heath-type habitats was also largely neglected by Coope (2006).

6.4.5. Multivariate analyses

The results of ordination analyses (principal components analysis) applied to coleopteran datasets are presented in this section. These analyses aim to identify underlying co-variance between coleopteran functional groups, to provide a more nuanced perspective of assemblages than possible with just a stratigraphic diagram. As discussed in Chapter 3, multivariate analyses of coleopteran assemblages use functional groups, rather than taxa, to compensate for the stochastic occurrences of individual species/genera and to facilitate ecologically-based interpretations. The following analyses should approached with due caution; several samples have low absolute abundances (MNI), and many zeroes remain in the datasets (see Tables 6.4 and 6.9). However, they provide some useful insights and facilitate comparison with similar analyses in preceding chapters.

Principal components analysis (PCA) of new (XA57, Fig. 6.2) coleopteran assemblages is presented in Figure 6.9. The first axis (PC1) accounts for 31.4% of variance in the sequence, and the second (PC2) account for 17.7% (50.9% of variance is unaccounted for). The first axis is closely related to relative abundances of hygrophilous taxa (H), which occur primarily in faunal assemblage zones Br-C1, Br-C2 and Br-C3 (Fig. 6.4). They exhibit positive covariance with riparian and waterside taxa (RW), lentic aquatic taxa (AS) and taxa associated with deciduous woodland and trees (WTD), and negative covariance with lotic aquatic taxa (AF). Little can be inferred regarding covariance with either lotic or lentic aquatics; the former occurs only twice at low abundance (Fig. 6.4), and is unlikely to be significant in this context. Lentic aquatics likely become absent in the upper part of the record (zone Br-C4, Fig. 6.4) due to the necessity of classifying *Helophorus* sp. as aquatic generalists (AG), rather than as a result of ‘real’ absence (indeed, aquatic generalists exhibit negative covariance with lentic aquatics here). The covariance of hygrophilous taxa with deciduous woodland and tree taxa, which have a more consistent distribution through the sequence (Fig. 6.4), gives some indication of community and habitat structure. Many of the hygrophilous taxa present are broadly eurytopic and the relationship between these groups suggests that woodland-type habitats occurred in relatively moist areas of the landscape, possibly on the floodplain or in close proximity to aquatic habitats. The second axis is most closely related to low abundance functional groups, with stochastic occurrences: wetland edge (WE) and dung-obligate beetles (DU), the latter of which is represented by a single occurrence of *Aphodius* cf. *convexus* (Fig. 6.4, Table 6.3). This suggests that the second axis does not represent a significant environmental gradient.

Whilst not closely related to either primary axis, the close relationship between open and disturbed habitat taxa (O) and herbaceous plant beetles (HP) provides further insight into community and habitat structure. The close covariance of these groups, also evident in Figure 6.4, is indicative of open habitats with low vegetation. Though no strong negative covariance between these groups and hygrophilous or deciduous woodland beetles is exhibited, their absence in the lower part of the record (Br-C1 & Br-C2, Fig. 6.4), and the general lack of hygrophilous and woodland taxa in the upper parts of the record (Br-C4 & Br-C5, Fig. 6.4) strongly suggest a shift towards more open, drier habitats in the upper zones.

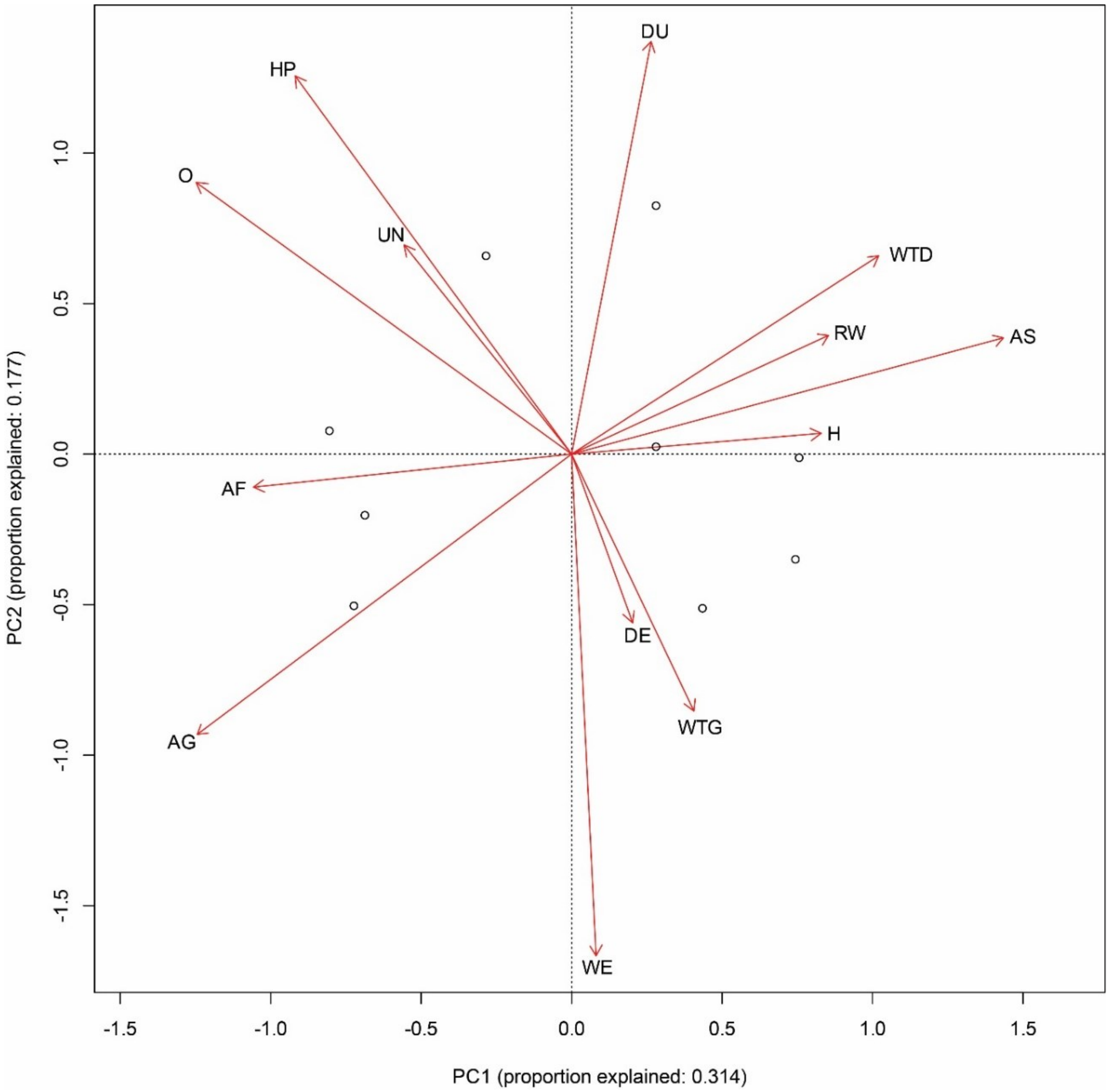


Figure 6.9 – PCA of coleopteran habitat groups from the Brooksby Sand and Gravel (XA57) (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

Figure 6.10 presents the results of PCA used to compare new coleopteran assemblages from Brooksby (XA57, presented in this chapter) with those of Coope (2006). This is performed on a functional group basis, in order to compare the ecological characteristics of each sequence. The first axis (PC1) represents 19.3% of total variance, and the second (PC2) represents 18.9%, leaving 61.8% unrepresented. Samples from Coope's (2006) record are contained within the distribution of samples from the new (XA57) record, suggesting that the assemblages are broadly comparable in functional terms.

Positive covariance between open and disturbed habitat beetles (O) and herbaceous plant beetles (HP) is maintained with the addition of Coope's (2006) assemblages, and both are related to the primary axis (PC1). This emphasises the importance of open habitats with low vegetation in palaeolandscapes associated with the Brooksby Sand and Gravel. These groups exhibit negative covariance with hygrophilous taxa (H), further suggesting a wetness gradient in these assemblages. Interestingly, whilst deciduous woodland and tree taxa evidently remain important with the addition of Coope's (2006) assemblages, given their prominence on the second axis (PC2), their covariance with hygrophilous taxa is not maintained. This suggests that whilst trees are an important component of Brooksby palaeolandscapes, the relative wetness of woodland-type habitats may have varied over time, perhaps related to changing flood regimes or fluvial channel migration.

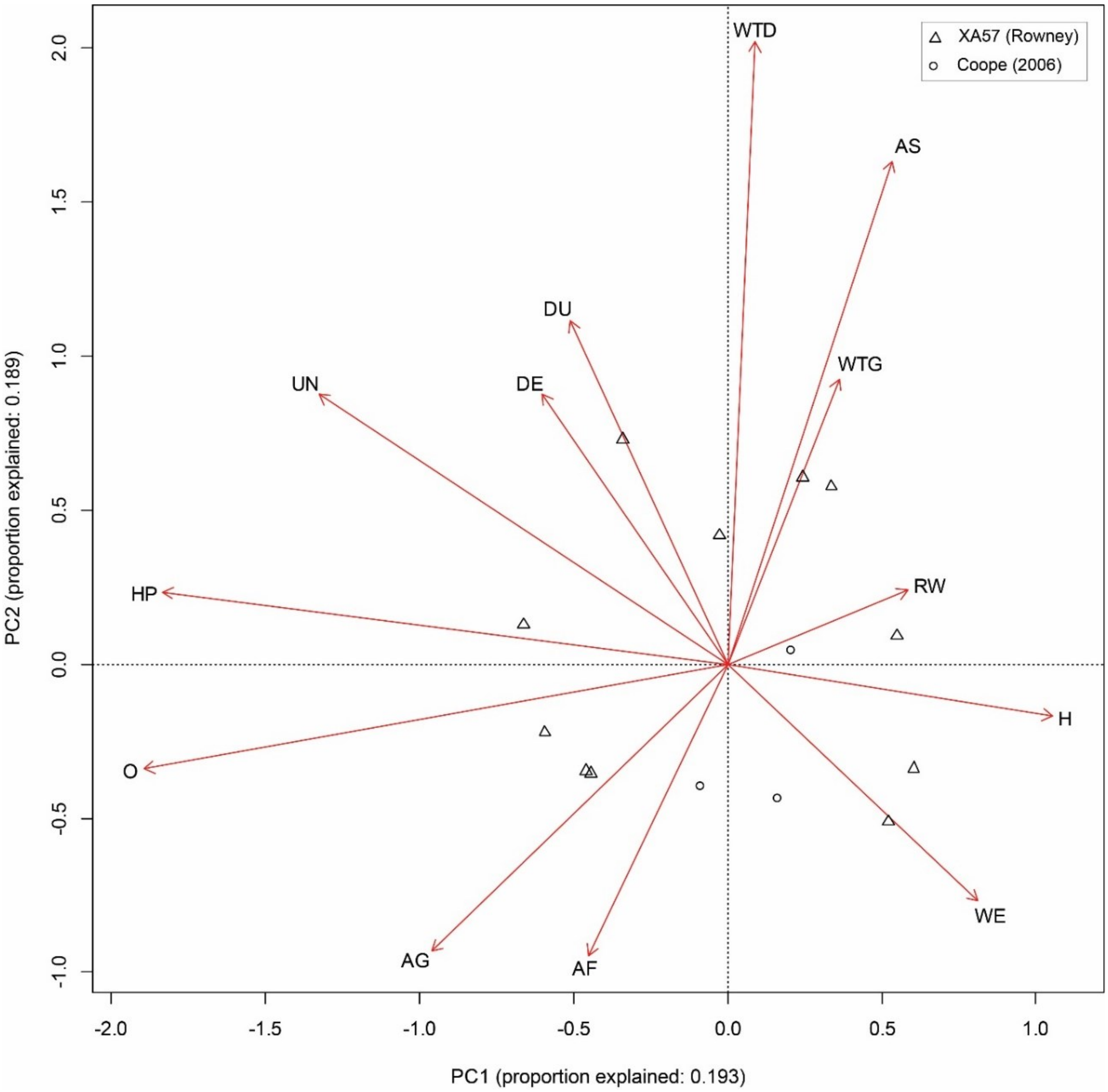


Figure 6.10 – PCA of coleopteran habitat groups from XA57 (this chapter) and Coope (2006) records from the Brooksby Sand and Gravel (See Table 3.1 for habitat group abbreviations) (Circles represent samples)

6.5. Local Palaeoenvironmental Summary

This section summarises the key features of local palaeoenvironments, and notable changes, inferred from pollen and beetle assemblages. A brief comparison of the new records presented here with related records, including Waverley Wood (Shotton *et al.* 1993), is also given. Disturbance regimes and vegetation dynamics are discussed in detail in Chapter 8, alongside records from West Runton (Chapter 5) and Pakefield (Chapter 6).

6.5.1. Depositional environment

Palaeoentomological data (Table 6.3, Fig. 6.4) sedimentological descriptions (Fig. 6.2), and geomorphological setting (Rice 1991; Stephens *et al.* 2008), provide a broad reconstruction of the depositional environment of the Brooksby Sand and Gravel. Sediments are typically dominated by silts, fine sands and clays, with greater sand content below *c.*95 cm (Fig. 6.2), suggesting some upward fining. In combination with beetles associated with lentic habitats (e.g. *Hydraena testacea*, *Tanysphyrus lemnae*), deposition in low energy conditions is indicated. However, these are deposited in an incised bedrock channel (Rice 1991; Stephens *et al.* 2008) and occasional gravel- and pebble-sized clasts also occur throughout the sequence. This provides evidence of a mixed-energy flow regime, with intermittent high energy inputs. During deposition of the Brooksy Sand and Gravel, the bedrock channel was likely cut-off from a primary channel, but received alluvial inputs, and was potentially re-connected to the primary channel during high flow periods. This is further corroborated by the occasional presence of lotic aquatic beetles (*Enicocerus exsculptus*, *Esolus parallelepipedus*). The presence of *Helophorus orientalis* and *H. sibiricus*, colonists of temporary ponds (the latter often associated with snowmelt) (Angus 1973), provides additional important detail, suggesting the presence of ephemeral pools. Collectively, this evidence indicates deposition in a cut-off channel in the floodplain of a river with variable flow regimes.

6.5.2. Local palaeoenvironment: Vegetation, landscape and climate

The analyses presented in this chapter indicate the presence of a floodplain landscape, which was generally rather open, with substantial marshy habitats, some drier areas, and a low density of trees, with some evidence for landscape change. Mutual climatic range (MCR) estimates indicate a cool temperate climate (Fig. 6.5, Table 6.3). The presence of insects and plants with high latitude and montane distributions at present, alongside taxa with temperate affinities, suggest deposition during a period of transitionary or continental climate.

Throughout the sequence, both plants and insects indicate the persistent presence of aquatic habitats, marshy open habitats, dry open habitats and some trees. Whilst aquatic pollen assemblages are largely derived from emergent macrophytes (e.g. *Elodea*, *Stratiotes*), open water taxa are also present (*Nuphar*, *Potamogeton*), and aquatic beetles are drawn from both permanent (e.g. *Hydrobius fuscipes*, *Hydraena testacea*) and temporary (e.g. *Helophorus orientalis*) lentic habitats, as well as fluvial habitats (e.g. *Oulimnius troglodtyes*, *O. tuberculatus*). Together, these suggest a complex and dynamic alluvial wetland, with significant habitat heterogeneity. This likely graded into open, marshy ground, indicated by assemblages of marshland insects (e.g. *Trechus rivularis*, *Grypus brunnirostris*) and herbaceous flora (e.g. Caryophyllaceae, *Drosera intermedia*, *Pinguicula*, *Sphagnum*). Both deciduous (e.g. *Corylus*, *Alnus*, *Quercus*, *Ulmus*) and coniferous (e.g. *Abies*, *Pinus*) arboreal pollen also occur throughout the sequence and trees can be inferred to have remained present in the broader landscape during the period represented.

Whilst the above habitats are broadly consistent throughout the sequence, a gradient towards drier, more open terrestrial habitats is evident in beetle assemblages.

Hygrophilous beetles (e.g. *Trechus rivularis*, *Arpedium quadrum*) positively co-vary with deciduous woodland taxa (e.g. *Scymnus auritus*, *Polydrusus marginatus*) (Fig. 6.8), indicating the local presence of damp woodland-type habitats, which may have been isolated copses or scattered individual trees. These coleopteran groups are present only in lower to middle assemblage zones (Br-C2, 140-115 cm and Br-C3, 115-55 cm) (Table 6.3, Fig. 6.4). They exhibit weak negative covariance with open and disturbed habitat beetles (e.g. *Trachyphloeus spinimanus*, *Otiorhynchus laevigatus*), and those associated with herbaceous taxa (e.g. *Phyllotreta nemorum*, *Chaetocnema concinna*) (Fig. 6.8), which are present only in middle to upper assemblage zones (Br-C3, 115-55 cm and Br-C4, 55-15 cm) (Table 6.3, Fig. 6.4). This suggests that they formed distinct components of the broader community, and that damp woodlands were gradually replaced with drier, open areas with low vegetation. Interestingly, there is no discernible change in arboreal pollen assemblages (Fig. 6.3), potentially indicating that this is only a local signal. Several disturbance processes were evidently functioning in the local landscape, including herbivory (*Sporormiella*- and *Sordaria*-type spores), wildfire (microcharcoal shards) and hydrogeomorphic processes (Elmidae, sedimentology). These provide a convenient explanation for a local-scale openness gradient, though their relative importance is difficult to discern. It should be reiterated that only presences and absences can be inferred on the basis of the present pollen record, due to low concentrations and correspondingly low counts (see Section *6.4.2.*). Thus, the possibility remains that this trend towards increasing openness may be a local expression of landscape-scale change. The driver of this potential change is unclear, but may represent a subtle climatic shift.

The climatic setting of the Brooksby Sand and Gravel is not straightforward, and deposition may have occurred during, or closely following, a climatic deterioration, or under continental climatic conditions. Quantitative MCR reconstructions indicate a cool temperate climate, with potentially cool summers (11.35 to 25.5°C) and cold winters (-16.45 to -9.4°C) (Fig. 6.5, Table 6.5). However, this is complicated by the simultaneous presence of both high latitude/altitude taxa and lowland temperate taxa, forming a non-analogue community. Deciduous trees, such as *Alnus*, *Corylus*, *Quercus* and *Ulmus*, are present throughout the sequence (Fig. 6.3), and their local presence is confirmed by Coleoptera such as *Scymnus auritus* and *Polydrusus marginatus* (Table 6.3). However, these are accompanied by high latitude/altitude insects (e.g. *Bembidion dauricum*, *Helophorus sibiricus*) (which contribute to MCR climate reconstructions) and montane plants (*Alchemilla alpina*), suggesting a distinctly cool temperate climate. The taxa associated with predominantly cool conditions in the present sequence are generally small, highly mobile organisms with short generations (i.e. beetles), whereas those with distinct temperate affinities are large, sedentary organisms with centennial-scale generations (i.e. trees), or are directly associated with these organisms (i.e. arboreal beetles). Thus, the cold-adapted species may have been responding to a climatic downturn, expanding their ranges into lowland England, whilst previously established deciduous trees persisted in the landscape. Similar situations have been noted in Lateglacial sequences (e.g. Walker *et al.* 1993). Alternatively, such a combination of biota may have been facilitated by a continental climate, in which mild spring and summer temperatures stimulated deciduous pollen production, and cold winter temperatures promoted the establishment of high latitude and montane taxa.

6.5.3. Broader landscape context: Comparison with previous records

The data presented in this chapter are in broad agreement with previous palaeoecological records from the Brooksby Sand and Gravel (Rice 1991; Howard 1999; Coope 2006), and inferences regarding regional climate are corroborated by comparison with stratigraphically closely correlated sites (Waverley Wood, Shotton *et al.* 1993; Pool's Farm Pit, Maddy *et al.* 1994). However, it is acknowledged that the potential for multiple channel infills to be represented at Brooksby (as at Waverley Wood: Shotton *et al.* 1993) complicates this. The most notable difference between the XA57 coleopteran record (Section *6.4.3.*) and Coope's (2006) Brooksby record is the absence of arctic-montane taxa in the latter. However, Coope's (2006) record was more limited in both fossil abundances and number, and the physical magnitude (i.e. volume) of sedimentary samples (Coope's (2006) samples were <1 kg), and it was noted that much of the fauna had modern ranges extending to northern Britain, and into Eastern Europe and Siberia. On this basis, 'true' absences of cold-adapted taxa cannot be confirmed, and given the general functional similarity of the beetle faunas, they may be derived from broadly equivalent periods. Indeed, MCR reconstructions based on both faunas provide mutually overlapping ranges estimates. Plant macrofossils and pollen from the Brooksby Sand and Gravel (bulk sample, Rice 1991) also suggest a local environment broadly similar to that of Coope (2006) and the present work: a relatively open landscape, with both marsh and heath communities, and a low density of trees (deciduous and coniferous). Some taxa recorded by Rice (1991) are not represented in the present record (e.g. *Picea*, *Populus*), but absences cannot be assumed to be significant here, given the poor pollen concentrations. The plant taxa all exist in lowland Britain at present, with the exception of *Oxyria dignya*, which is an upland species within Britain (Rose & O'Reilly 2006), with a circumpolar arctic-alpine distribution

(Wang *et al.* 2016). This parallels the simultaneous presence of *Alchemilla alpina* (which has a similar distribution, Rose & O'Reilly 2006), arctic-montane Coleoptera and temperate flora and Coleoptera in the present record (XA57), providing further evidence of non-analogue communities, which may indicate either a transitional or continental climate.

The pre-Anglian sequence at Waverley Wood, Warwickshire (Shotton *et al.* 1993), correlated with the Brooksby Sand and Gravel (see Section *6.2.1.*), corroborates the suggestion of deposition during, or closely following, a climatic deterioration. In functional ecological terms, the communities represented by both deposits appear to be broadly similar, with a combination of floodplain, reedswamp, meadow-type habitats and low-density tree cover also represented at Waverley Wood (Shotton *et al.* 1993). However, the Waverley Wood sediments record a three-part sequence, with a brief climatic deterioration occurring between two more temperate periods. It is notable that the associated pollen record indicates that deciduous trees remained present during this climatic downturn, suggesting this represents a short-lived perturbation, on the scale of the lifetimes of individual trees (centennial-scale) which were able to persist in the landscape. However, it is unlikely that they were able to reproduce, and out-compete arctic-montane plants, during this period. Given the similar combination of seemingly incompatible flora and fauna in the Brooksby Sand and Gravel, and close stratigraphic correlation with Waverley Wood, it seems likely that the Brooksby deposits are associated with the same climatic perturbation. Pre-Anglian sediments at Pools Farm Pit, Warwickshire (Maddy *et al.* 1994), which are likely to be of similar age (Preece *et al.* 2009; Coope 2010a; Bridgland *et al.* 2015), also provide evidence of arctic-alpine and temperate plants and insects co-existing. However, Maddy *et al.* (1994) provide an alternative explanation, suggesting that re-working of older deposits can account for this mixture of cold- and temperate-associated biota. This potential cannot be disregarded, but given the consistency of the signal across several sites (Brooksby, Waverley Wood, Pool's Farm), and evidence for similar biotic disequilibria in Lateglacial records (e.g. Walker *et al.* 1993), a short-lived climatic deterioration provides the most parsimonious explanation for these assemblages.

6.6. Archaeological Postscript

Assemblages of Lower Palaeolithic tools are known from pre-Anglian sediments at both Brooksby (Coope 2006, D. Schreve 2012 pers. comm.) and Waverley Wood (Keen *et al.* 2006). Unfortunately, these have rarely been documented *in situ*, and their provenance is poorly understood (Keen *et al.* 2006). As a result, attribution of hominin presence to the period of climatic deterioration discussed above cannot be more than tentative. However, the possibility of early *Homo* persisting during such a transitional climatic period is at least raised. This would have necessitated behavioural and technological adaptation to potentially harsh winters (if hominin presence could be demonstrated,). Speculatively, this may have included seasonal migration, the control of fire, and the development of complex clothing or shelters. However, there is currently no direct evidence for these behaviours or technologies in Northern Europe during the early Middle Pleistocene (Ashton & Lewis 2012).

Chapter 7

Interglacial Climates in Britain:

Re-evaluating the Mid-Brunhes Transition

7.1. Introduction

The purpose of this chapter is to determine whether there is evidence for the Mid-Brunhes Transition (MBT) in Britain. This will be tested through the application of new approaches to the coleopteran Mutual Climatic Range (MCR) method (Milne 2016) which provide more accurate (and often more precise) palaeoclimatic reconstructions than previous iterations (e.g. Atkinson *et al.* 1987), particularly in the context of winter temperatures (summarised in Chapter 3, Section *3.3.3.*). Increased accuracy and precision will likely elucidate potential climatic distinctions between the interglacial climates of the early Middle Pleistocene (MIS 19-13), and those of the late Middle and Late Pleistocene (MIS 11-5e), in terms of summer temperatures (TMax), winter temperatures (TMin) and/or temperature seasonality (TRange). This represents a significant advancement on previous work on the MBT in Northwest European terrestrial contexts, which was based primarily on summer temperature reconstructions (Candy *et al.* 2010). However, due to the nature of interglacial deposits in Britain (see Section 2.3), the records utilised here typically reflect only short periods of time within interglacials, and this caveat should be borne in mind. Palaeoclimatic reconstructions derived from beetle assemblages provide the basis of this chapter, but are supplemented with reference to other thermally sensitive contemporary biota (e.g. thermophilous plants).

Whilst previously the term ‘Mid-Brunhes Event’ has been used (e.g. EPICA 2004; Jouzel *et al.* 2007; Tzedakis *et al.* 2009; Candy *et al.* 2010; Lang and Wolff 2011), here it is referred to as the ‘Mid-Brunhes Transition’, following the suggestion of Yin (2013). This implies a movement from one state to another without assumptions regarding the temporal or spatial mode of transition, rather than implying rapidity or global synchroneity (as implied by the term ‘event’).

Current knowledge of the Mid-Brunhes Transition and the complexity of its expression, in global terms and in Northwest Europe, have been discussed in detail in Chapter 2 (Section 2.2.).

7.2. Chapter-specific Methods

7.2.1. Choice of sites/records

Based on criteria outlined in Chapter 3 (Section *3.4.1.*), 18 interglacial records from Southern and Eastern Britain have been selected for re-analysis (Fig. 7.1, Table 7.1). These are sites with evidence for ‘fully temperate’ conditions (*sensu lato*), mostly based on pollen records, which are independent of beetle records. These records are drawn from both prior to (i.e. early Middle Pleistocene) and following (i.e. late Middle Pleistocene and Late Pleistocene) the MBT. The new record from the West Runton Freshwater Bed (Chapter 4) has been included on this basis alongside a reconstruction based on Coope’s (2010b) record. The new record from the Brooksby Sand and Gravel (Chapter 6) has been excluded, on the basis of low arboreal pollen values and the presence of arctic-alpine plants. Coope’s (2006) Pakefield assemblage has been utilised, but the new record from Pakefield (Chapter 5) has not been included, as the beetle data are insufficient to derive a useful climatic reconstruction. It is acknowledged that a number of potential additional records (see Table 2.2) have not been included for pragmatic reasons, and preference has been given to notable interglacial records (e.g. Hoxne, West 1956; Trafalgar Square, Franks 1960). Additionally, it should be borne in mind that individual records from within the same marine oxygen isotope stage are unlikely to be directly equivalent in time as most British interglacial records are ‘snapshots’, representing relatively short periods within interglacials (*cf.* Schreve & Candy 2010; Preece & Parfitt 2012). As previously noted (see Section *3.4.1.*), whilst most of these records are derived from fluviatile sedimentary settings, a few are also derived from lacustrine deposits (see Table 2.2). These are likely to differ in relative catchments for beetle remains, and hence the representation of ecological groups (e.g. terrestrial vs. aquatic) and discrepancies have been noted between MCR reconstructions based on terrestrial and aquatic beetles during Lateglacial climatic deteriorations (Elias & Matthews 2014). However, the MCR reconstructions carried out here are unlikely to be affected as only records drawn from fully temperate periods have been selected.

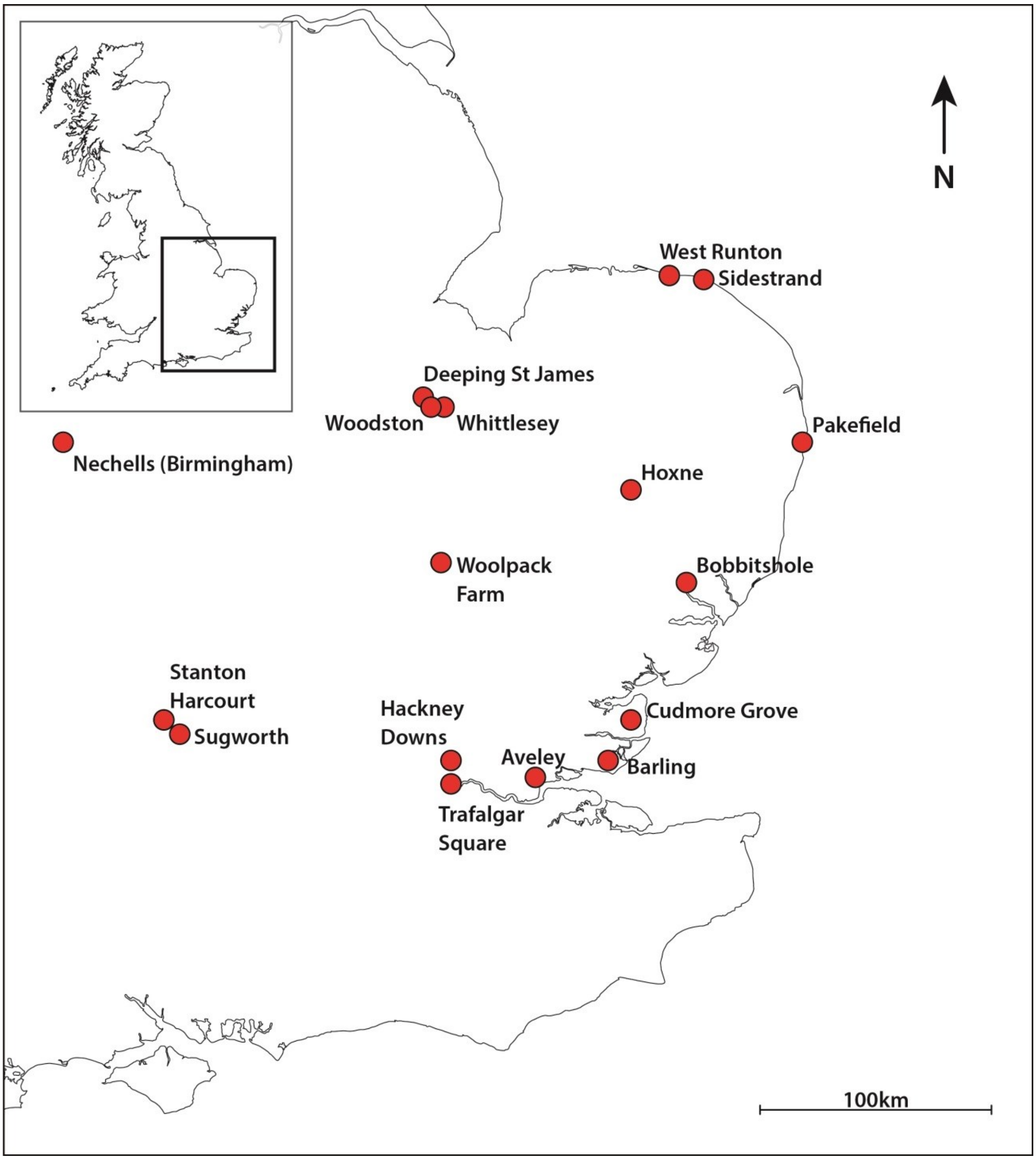


Figure 7.1 – Location of records utilised in the present chapter (also see Tables 2.2 and 7.1 for additional context)

of selected thermophilous organisms noted (also see Figure 7.1) (*Tn*: *Trapa natans* L.; *Sn*:
ginata Michaud; *Uc*: *Unio crassus* Philipsson; *Eo*: *Emys orbicularis* L.; *Ha*: *Hippopotamus*
luding depositional environment, fossil groups analysed and presence/absence of archaeology)

Site/ Deposit Name	**Latitude**	**Longitude**	**Interglacial (MIS)**	**philous Taxa**							**References**
				Tn	***Sn***	***Nm***	***Bm***	***Uc***	***Eo***	***Ha***	
Trafalgar Square	51°30'27"N	0°7'42"W	5e	✓		✓	✓			✓	Franks 1960; Preece 1999; Coope 2001, unpublished
Deeping St James	52°39'28"N	0°14'58"W	5e		✓	✓	✓				Keen *et al.* 1999
Bobbitshole	52°1'46"N	1°7'47"E	5e		✓	✓	✓		✓		Sparks 1957; West 1957; Coope 1974; Stuart 1979
Woolpack Farm	52°17'54"N	0°5'47"W	5e				✓				Gao *et al.* 2000
Aveley (Sandy Lane Quarry)	51°30'1"N	0°14'5"E	7				✓				West 1969; Holyoak 1983; Coope 2001; Schreve 2001b
Stanton Harcourt	51°44'22"N	1°24'17"W	7								Briggs *et al.* 1985; Buckingham *et al.* 1996
Whittlesey	52°33'45"N	0°9'21"W	7				✓	✓			Langford *et al.* 2007, 2014
Barling	51°34'19"N	0°47'2"E	9	✓		✓	✓				Bridgland *et al.* 2001
Cudmore Grove	51°47'24"N	0°59'34"E	9			✓			✓		Roe *et al.* 2009
Hackney Downs	51°32'60"N	0°3'0"W	9	✓	✓	✓	✓	✓			Green *et al.* 2006
Hoxne (Stratum D)	52°21'3"N	1°11'59"E	11			✓					West 1956; Coope 1993; Ashton *et al.* 2008a
Nechells (Birmingham)	52°29'27"N	1°52'24"W	11								Duigan & Godwin 1956; Shotton *et al.* 1965
Woodston	52°32'43"N	0°14'48"W	11			✓					Horton *et al.* 1991, 1992
Sidestrand, (*Unio* -bed)	52°54'21"N	1°22'27"E	*c.* 13	✓		✓	✓	✓		✓	West 1980a; Preece *et al.* 2009
Sugworth	51°42'10"N	1°15'33"W	*c.* 15	✓		✓		✓			Gibbard & Pettit 1978; Osborne 1980; Shotton *et al.* 1980; West 1980a
West Runton	52°56'30"N	1°15'17"E	*c.* 15-17			✓					West 1980a; Coope 2000, 2010b; this thesis
Pakefield	52°25'45"N	1°43'50"E	*c.* 15-17	✓	✓	✓				✓	West 1980a; Parfitt *et al.* 2005; Coope 2006; this thesis

7.2.2. Analtyical considerations

A number of the interglacial records included in this chapter have only one sample (e.g. Bobbitshole, Coope 1974; Sidestrand (*Unio*-bed), Preece *et al.* 2009), for which deriving a single MCR reconstruction is relatively straightforward. However, compromise is necessary when deriving single reconstructions from more detailed, sequential records with multiple samples (e.g. Woolpack Farm, Gao *et al.* 2000; Sugworth, Osborne 1980). This must be undertaken for the purpose of drawing general comparisons between interglacial records, and because a full, in-depth appraisal of the insect faunas from each site is beyond the scope of the present thesis. Rather, a broad overview of what may be quantitatively inferred is intended here, and several approaches may be taken in this context. For example, a single reconstruction may be derived based on the total coleopteran fauna from each site, as standard in previous studies (e.g. Coope 2006; Candy *et al.* 2010). Alternatively, samples may be treated sequentially, with a reconstruction derived for each, and the overlap between these reconstructions used as a single record for the site. Finally, groups of samples may be analysed, in order to determine peak or average temperature within a sequence. However, in reality these approaches are unlikely to result in significantly different reconstructions in the present context. Therefore, in order to facilitate more direct inter-study comparisons, single MCR reconstructions from multi-sample records are derived here based on the total fauna from these records, as this approach has been frequently used in previous studies (e.g. Coope 2006; Candy *et al.* 2010).

It should be noted that the WorldClim data (Hijmans *et al.* 2005), which Milne (2016) species climate envelopes are based on, have typical errors of *c.* 0-1°C. This should be borne in mind when comparing reconstructions in this chapter.

7.3. Results

The following section will present and assess the climate reconstructions in Figure 7.2 and Table 7.2. Firstly, this will be according to individual temperate-climate episodes (correlated with marine oxygen isotopic stages or substages, e.g. MIS 5e), or groups of temperate episodes (e.g. 'Cromerian Complex'), and secondly in the broader context of pre- and post-Anglian interglacials. The purpose of this chapter is not to focus on individual sites, but rather to provide a broad overview of MIS 19-5e interglacial climates in Britain. New reconstructions are presented first, and additional context provided by non-coleopteran thermophilous organisms (see Chapter 3, Section *3.4.2.*) is given at the end of each section. Full species lists for each site are not included, but are freely available through the BugsCEP database (Buckland & Buckland 2006). Rather, information is provided here on selected beetle species, chosen on the basis of their importance in constraining climate estimates for each site (Table 7.3): climatic envelopes from tens of species may be included in MCR reconstructions, but generally around three to four species ('constraining taxa') are more important than the others. In a typical assemblage the climatic envelopes of most other species will be broad and of limited value in providing constraint to climatic reconstructions. This is illustrated in Figure 7.3. In Figure 7.2, the average warmest (16.6°C) and coldest (2.6°C) temperatures, and average annual temperature range (14°C), for 52°N, 0°E (1950-2000, Fick & Hijmans 2017) are also displayed in order to provide a convenient fixed point of comparison for the interglacial records, though it should be noted that these values do not necessarily reflect 'peak' conditions for the present interglacial (the Holocene). For Mid-Holocene (6ka BP) Northwest Europe, Davis *et al.* (2003) estimated temperature anomalies for the warmest month of *c.* +1-2°C, and for the coldest month of *c.* -1°C, relative to a reconstruction of 60 BP (i.e. 1980 CE) temperatures. (*n.b.* Davis *et al.'s* (2003) 60 BP temperatures are not specified in the original publication.)

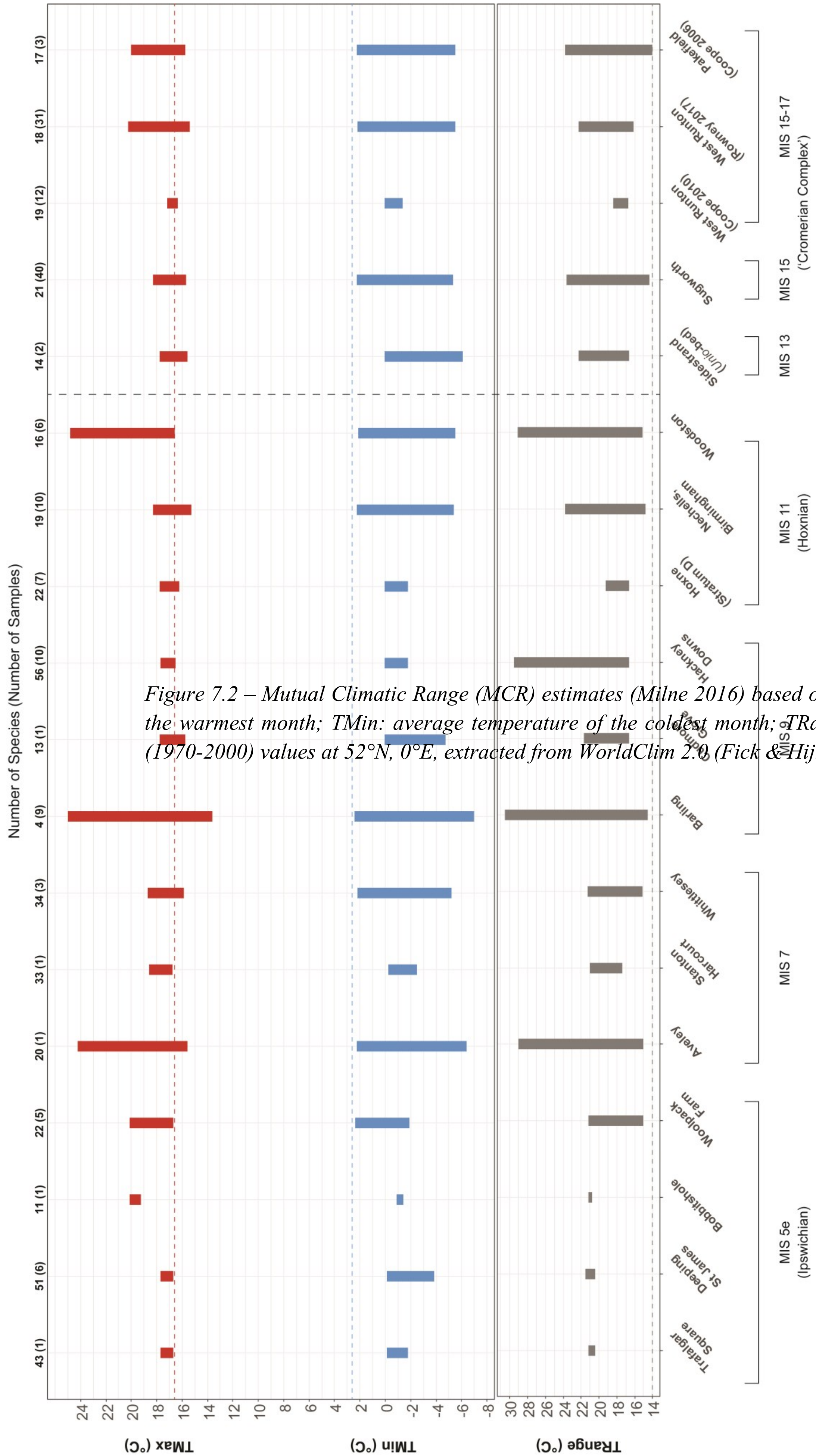


Figure 7.2 – Mutual Climatic Range (MCR) estimates (Milne 2016) based on coleopteran re
the warmest month; TMin: average temperature of the coldest month; TRange: average an
(1970-2000) values at 52°N, 0°E, extracted from WorldClim 2.0 (Fick & Hijmans 2017) (see

Table 7.2 Mutual Climatic Range (MCR) estimates (Milne 2016) based on coleopteran records from sites listed in Table 7.1, rounded to one decimal place. (TMax: average temperature of the warmest month; TMin: average temperature of the coldest month; TRange: average annual temperature range). Modern mean (1970-2000) values at 52°N, 0°E, extracted from WorldClim 2.0 (Fick & Hijmans 2017). Illustrated in Figure 7.2. (See Figure 2.3 for comparison.)

Site/ Deposit Name	**MIS**	**Temperature (°C)**			**No. of Species**	**100% Overlap**
		TMax	**TMin**	**TRange**		
50°N, 0°E (1970-2000)	modern	16.6	2.6	14	n/a	n/a
Trafalgar Square	5e	16.7 to 17.7	-1.8 to -0.1	20.5 to 21.2	43	No
Deeping St James	5e	16.7 to 17.7	-3.9 to -0.1	20.5 to 21.6	51	No
Bobbitshole	5e	19.3 to 20.2	-1.4 to -0.9	20.8 to 21.2	11	Yes
Woolpack Farm	5e	16.7 to 20.2	-1.9 to 2.4	15 to 21.2	22	Yes
Aveley (Sandy Lane Quarry)	7	15.6 to 24.3	-6.4 to 2.3	15 to 29	20	Yes
Stanton Harcourt	7	17.3 to 18.6	-2.5 to -0.3	17.4 to 21	33	Yes
Whittlesey	7	15.9 to 18.7	-5.2 to 2.2	15.1 to 21.3	34	Yes
Barling	9	13.7 to 25	-7 to 2.5	14.5 to 30.6	4	Yes
Cudmore Grove	9	15.8 to 17.8	-4.8 to 0.1	16.7 to 21.7	13	Yes
Hackney Downs	9	16.6 to 17.7	-1.8 to 0.1	16.7 to 29.5	56	No
Hoxne (Stratum D)	11	16.3 to 17.8	-1.8 to 0.1	16.7 to 19.3	22	Yes
Nechells (Birmingham)	11	15.3 to 18.3	-5.4 to 2.3	14.8 to 23.8	19	Yes
Woodston	11	16.6 to 24.8	-5.5 to 2.2	15.1 to 29.1	16	Yes
Sidestrand, (*Unio* -bed)	*c.* 13	15.6 to 17.8	-6.1 to 0.1	16.7 to 22.3	14	Yes
Sugworth	*c.* 15	15.7 to 18.3	-5.3 to 2.3	14.4 to 23.6	21	Yes
West Runton (Coope 2010)	*c.* 15-17	16.4 to 17.2	-1.4 to 0.1	16.7 to 18.4	19	Yes
West Runton (Rowney)	*c.* 15-17	15.4 to 20.3	-5.5 to 2.2	16.1 to 22.3	18	Yes
Pakefield (Coope 2006)	*c.* 15-17	15.8 to 20	-5.5 to 2.3	14 to 23.8	17	Yes

or selected species occurring in interglacial records. Species selected are those most
f. Fig. 7.3) in Figure 7.2 and Table 7.2. Data derived according to Milne (2016)

Family	Species	Temperature (°C)			Site/Record Presence																			Currently absent from Britain
					MIS 5e				MIS 7			MIS 9			MIS 11			MIS 13-17						
		Tmax	TMin	TRange	Trafalgar Square	Deeping St James	Bobbitshole	Woolpack Farm	Aveley (Sandy Lane Quarry)	Stanton Harcourt	Whittlesey	Barling	Cudmore Grove	Hackney Downs	Hoxne (Stratum D)	Nechells (Birmingham)	Woodston	Sidestrand, (*Unio* -bed)	Sugworth	West Runton (Coope 2010)	West Runton (Rowney)	Pakefield (Coope 2006)	
Gyrinidae	*Gyrinus suffriani* (Scriba)	15.1 to 26.5	-8 to 7.5	10.4 to 34.5	✓	✓	✓		✓														
Dytiscidae	*Liopterus haemorrhoidalis* (Fab.)	10.9 to 18.5	-6.2 to -0.1	16.7 to 24.7		✓									✓								
Carabidae	*Trechus obtusus* (Er.)	10.2 to 27	-11.5 to 7.6	8.7 to 29.5		✓					✓						✓			✓	✓		
	Bembidion gilvipes (Sturm)	8.9 to 20.1	-11 to 4.4	12 to 26.4		✓				✓	✓			✓					✓			✓	
	Bembidion assimile (Gyll.)	15.3 to 26	-10 to 7	10.2 to 30.5	✓	✓	✓				✓			✓	✓								
	Bembidion clarkii (Dawson)	16.4 to 17.2	-1.5 to 0.1	16.7 to 18.4																✓			
	Bembidion fumigatum (Duft.)	15.1 to 20.1	-1.8 to 4.4	11.9 to 21.5											✓								
	Bembidion minimum (Fab.)	13.15 to 27	-7 to 5.5	10.8 to 31.5										✓				✓					
	Bembidion quadripustulatum (Serv.)	15.5 to 28.5	-5.5 to 7.5	11.9 to 31		✓																	
	Bembidion octomaculatum (Goeze)	16.3 to 29.5	-5.5 to 3.9	13.3 to 31.5	✓	✓				✓				✓		✓	✓						
	Bembidion biguttatum (Fab.)	12.9 to 19.3	-9.5 to 4.9	10.7 to 21.6		✓					✓			✓									
	Bembidion transparens (Gebler)	11.5 to 25.5	31.4 to 3.7	11.3 to 46.5					✓														*
	Pterostichus gracilis (Dejean)	15.5 to 17.8	-7.8 to 0.1	16.7 to 23.3	✓	✓							✓	✓	✓			✓		✓			
	Pterostichus minor (Gyll.)	13.6 to 25.5	-11.9 to 2.2	15.1 to 32		✓					✓			✓	✓		✓						
	Pterostichus diligens (Sturm)	9.3 to 25.5	-24.5 to 2.4	12.2 to 40.5							✓				✓				✓	✓		✓	
	Pterostichus vernalis (Panz.)	12.3 to 25	-14 to 2.5	14.2 to 34.5	✓	✓	✓					✓		✓		✓	✓	✓					
	Pterostichus strenuus (Panz.)	9.7 to 25.5	-14.5 to 7	12.2 to 38.5	✓	✓				✓	✓		✓	✓		✓			✓			✓	

(Continued overleaf)

Family	Species	Temperature (°C)			Site/Record Presence																		Currently absent from Britain
					MIS 5e				MIS 7			MIS 9			MIS 11			MIS 13-17					
		Tmax	TMin	TRange	Trafalgar Square	Deeping St James	Bobbitshole	Woolpack Farm	Aveley (Sandy Lane Quarry)	Stanton Harcourt	Whittlesey	Barling	Cudmore Grove	Hackney Downs	Hoxne (Stratum D)	Nechells (Birmingham)	Woodston	Sidestrand, (*Unio*-bed)	Sugworth	West Runton (Coope 2010)	West Runton (Rowney)	Pakefield (Coope 2006)	
	Zabrus tenebrioides (Goeze)	16.6 to 20.6	-1.9 to 3.9	13 to 21.2	✓		✓	✓						✓									
	Chlaenius sulcicollis (Payk.)	10.9 to 18.5	-6.2 to -0.1	16.7 to 24.7	✓									✓									*
	Oodes gracilis (Villa & Villa)	16.7 to 30.7	-6.5 to 0.7	20.5 to 33	✓	✓	✓																*
	Syntomus foveatus (Geoff.)	14 to 27	-5.5 to 7.5	10.3 to 30.5	✓																	✓	
	Odacantha melanura (L.)	15.6 to 29.5	-10.8 to 5	12.5 to 31.5	✓		✓		✓				✓		✓				✓			✓	
Helophoridae	*Helophorus grandis* (Ill.)	15.8 to 20.9	-10.1 to 2.3	15 to 30.9						✓	✓												
Hydrophilidae	*Megasternum concinnum* (Marsh.)	13.9 to 25	-25 to 2.4	15 to 40.5		✓		✓	✓					✓									
Hydraenidae	*Ochthebius bicolon* (Germ.)	12.7 to 25	-7 to 7.5	9.5 to 31.5										✓		✓			✓	✓			
Staphylinidae	*Platystethus nitens* (Sahl.)	14.6 to 30.5	-6.5 to 7.5	12.3 to 33		✓			✓	✓	✓			✓	✓				✓				
	Ochthephilum fracticorne (Payk.)	14.7 to 18.5	-6.2 to 3.1	14.2 to 24.7												✓			✓				
Scarabaeidae	*Aegialia sabuleti* (Panz.)	8.9 to 22.5	-24.5 to 1	14.7 to 41.5						✓													*
	Aphodius subeterraneus (L.)	13.3 to 30.5	-10 to 8	15.5 to 33																	✓		
	Aphodius plagiatus (L.)	14 to 20.3	-5.5 to 5	10.5 to 22.4																	✓		
	Valgus hemipterus (L.)	13.7 to 30.5	-7 to 12.5	11.3 to 33	✓	✓	✓					✓	✓	✓					✓			✓	*

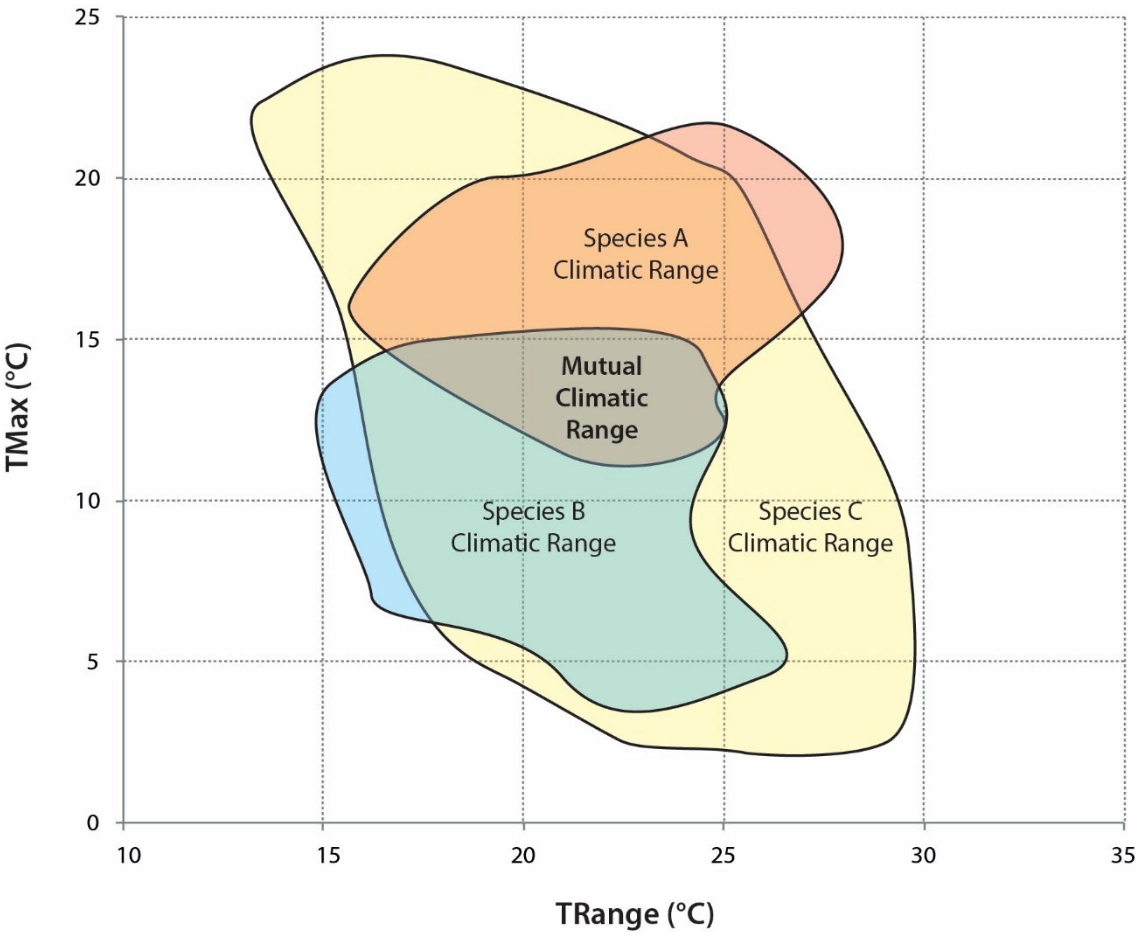


Figure 7.3 – Hypothetical MCR illustrating the importance of 'constraining taxa'. In this case, the MCR estimate would not change if Species C were removed, but would change if Species A or Species B were removed. Species A and Species B are therefore the 'constraining taxa', and are more important than Species C in this context

7.3.1. MIS 5e: The Ipswichian

The Ipswichian Interglacial (correlated with Marine Oxygen Isotope Substage 5e, and the Eemian of continental Europe) has been widely recognised as an especially 'warm' interglacial (Coope 2010a; Masson-Delmotte 2010; Turney & Jones 2010), though Candy *et al.* (2016) suggest that this is only true of specific sites. In a British context this is generally demonstrated by evidence for enhanced summer warmth, and whilst it has been suggested that this may have been associated with cooler winters, (e.g. Candy *et al.* 2016), it has not previously been conclusively demonstrated. (See also Zagwijn 1996b, which suggests that parts of the Eemian were characterised by enhanced climatic continentaliy.) Here, the Last Interglacial is represented by four sites: Trafalgar Square, Deeping St James, Bobbitshole and Woolpack Farm (see Figure. 7.2 & Table 7.2).

Reconstructions of average warmest month (TMax) temperatures for MIS 5e are generally well constrained, and demonstrate conditions similar to or warmer than the present day (Fig. 7.2, Table 7.2). Records from Trafalgar Square, Deeping St James and Bobbitshole each provide TMax estimates with approximately 1°C ranges, though Woolpack Farm gives a range of approximately 3.5°C.

Both Trafalgar Square (16.7 to 17.7°C) and Deeping St James (16.7 to 17.7°C) indicate average July temperatures either broadly consistent with or slightly warmer than modern average July temperatures (16.6°C) (Fig. 7.2, Table 7.2). These reconstructions are at the lower end of (or cooler than) previous range estimates for these sites (Candy *et al.* 2010, 2016). However, the new reconstructions for two of the sites presented here are based on less than 100% overlap between individual species climate envelopes (SCRs) (Trafalgar Square and Deeping St James). As demonstrated using selected taxa in Figure 7.4, there are points at which two to three SCRs overlap, but there is no point at which all four selected SCRs overlap. However, when species TMax ranges are considered independently of TRange (see Chapter 3, Section *3.3.3.*, and illustrated in Figure 7.4), an average July temperature estimate of 16.7 to 17.7°C is derived for both sites.

The Bobbitshole TMax range presented here (19.3 to 20.2°C) is notably higher than TMax values for Trafalgar Square and Deeping St James, as well as modern values (Fig. 7.2, Table 7.2). This is consistent with previous reconstructions for other Ipswichian sites (though not those for Bobbitshole) (Coope 2010a, Candy *et al.* 2016) and notably warmer than present day July temperatures. Unlike Trafalgar Square and Deeping St James, this is based on 100% overlap between SCRs, with *Zabrus* *tenebrioides* and *Oodes gracilis* being the most important species in constraining this range (Table 7.3). The former is currently present in Britain (Duff 2012), but has a range that extends across much of continental Europe, (including Mediterranean regions), the Middle East and Central Asia (Lindroth 1986; Luff 1998). The latter is widespread across Central and Southern Europe and extends into Central Asia, and occurs locally in Scandinavia (Lindroth 1986), but is not currently present in Britain (Duff 2012). These species were also present at Trafalgar Square but, unlike Bobbitshole, were accompanied by species such as *Pterostichus gracilis* and *Chlaenius sulcicollis*, which appear to favour cooler, more oceanic climatic conditions, particularly compared to *Oodes gracilis*.

The Woolpack Farm TMax estimates are broader (16.7 to 20.2°C), encompassing values from Trafalgar Square, Deeping St James and Bobbitshole (Fig. 7.2, Table 7.2). This is less informative, but indicates summers at least as warm as the present, and are consistent with both lower (Trafalgar Square, Deeping St James) and higher (Bobbitshole) estimates, due to the range breadth.

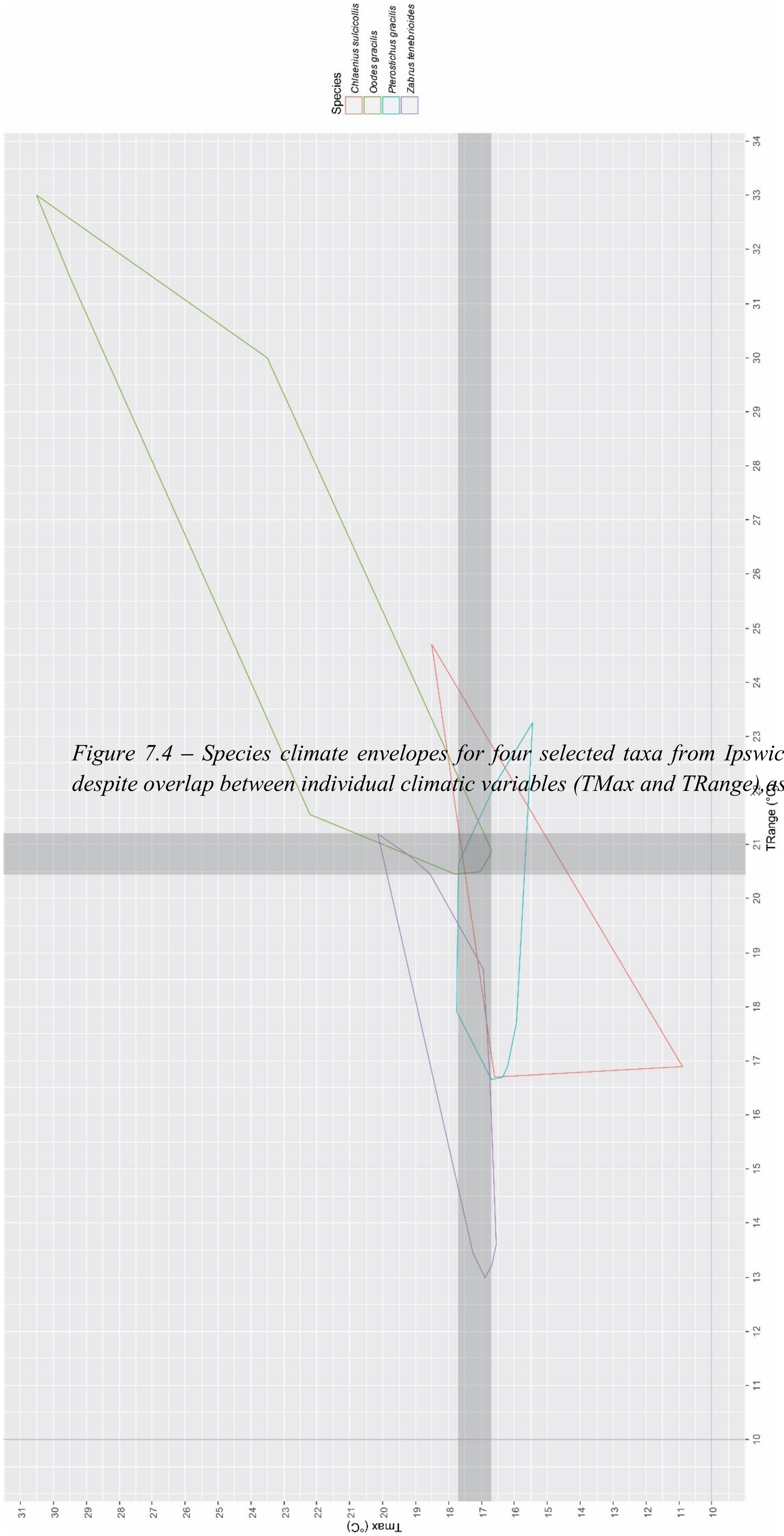


Figure 7.4 – Species climate envelopes for four selected taxa from Ipswichian deposits at Trafalgar Square il despite overlap between individual climatic variables (TMax and TRange) as shown by shaded areas.

Reconstructions of average coldest month (TMin) temperatures for MIS 5e sites vary in extent of constraint, but generally indicate winter temperatures notably cooler than the present (2.6°C) (Fig. 7.2, Table 7.2). Bobbitshole provides the most precise estimate (-1.4 to -0.9°C), and indicates January temperatures around 2.5°C cooler than the present. As discussed above, reconstructions from Trafalgar Square and Deeping St James are based on less than 100% overlap between SCRs, but each suggests an upper limit of -0.1°C, around 1.5°C lower than the present. Woolpack Farm provides the broadest estimate (-1.9 to 2.4°C), and the upper limit is also slightly below modern values. These estimates are uniformly indicative of winters cooler than the present day, and result from the presence of continental species, such as *Oodes gracilis* and *Valgus hemipterus*, which inhabit regions with greater temperature seasonality than modern Britain. *Valgus hemipterus* is found throughout Central and Southern Europe, as well as the Middle East (Koch 1989b; GBIF 2016).

TRange estimates for MIS 5e sites are very tightly constrained around 21°C, with the exception of Woolpack Farm (Fig. 7.2, Table 7.2). They indicate temperature seasonality in excess of the region at present (modern TRange: 14°C), and the existence of continental-type climatic conditions. Again, this is due to the presence of species presently characteristic of more continental regions, such as *O. gracilis* and *V. hemipterus*.

All four MIS 5e sites contain non-insect species typically considered indicators of enhanced interglacial warmth (Table 7.1). These include indicators of enhanced summer warmth, including *Emys orbicularis* (Bobbitshole) and *Trapa natans* (Trafalgar Square), which corroborate TMax values indicating July temperatures warmer than the present. *Hippopotamus amphibius* is also present at Trafalgar Square, in spite of the potentially cool winter temperatures indicated by the coleopteran fauna. This species is generally thought to be limited by winter temperatures (see Chapter 3, Section *3.4.2.*), but its climatic niche may be more complex than previously realised. Rather, European hippopotamus populations of may have been more tolerant of cool winter temperatures than previously realised.

These reconstructions confirm the suggestion of Candy *et al.* (2016) that MIS 5e climates in Britain were not necessarily ‘warmer’, and that the reality is more complex. Rather, it appears they were characterised by continental climatic characteristics: enhanced summer warmth and somewhat diminished winter temperatures, relative to the region at present, at least for the periods of the Ipswichian represented by the records analysed here.

7.3.2. MIS 7

The penultimate interglacial (correlated with Marine Oxygen Isotope Stage 7) is widely recognised as being climatically complex at both regional (Schreve 2001b; Candy & Schreve 2007) and global scales (Lang & Wolff 2011; Berger *et al.* 2015), and has been suggested to include more than one full interglacial stage (Berger *et al.* 2015). In Britain, it is also widely recognised as incorporating an extended grassland phase under fully temperate conditions during the later part of the interglacial (Schreve 2001b; Candy & Schreve 2007). Here, MIS 7 is represented by three sites: Aveley (Sandy Lane Quarry), Stanton Harcourt and Whittlesey (see Figure. 7.2 and Table 7.2).

July temperature (TMax) estimates from Aveley are too broad to be particularly informative (15.6 to 24.25°C), though there is no suggestion of summers dramatically cooler than the present (Fig. 7.2, Table 7.2). This lack of constraint is due to the absence of stenothermic species from MCR estimates (see Table 7.3). Stanton Harcourt and

Whittlesey, on the other hand, provide relatively well constrained TMax estimates (17.3 to 18.6°C and 15.9 to 18.7°C, respectively), indicating summers similar to, or slightly warmer than, the present. The constraint of the Stanton Harcourt estimate is due to the co-occurrence of *Bembidion octomaculatum*, *Helophorus grandis*, and *Aegialia sabuleti* (Table 7.3). *Bembidion octomaculatum* and *H. grandis* are currently present in Britain (Duff 2012), as well as in continental Europe. Both are widely distributed across Europe (Hansen 1987; Koch 1989a; Luff 1998), though *H. grandis* is possibly concentrated in more Northern and Western (oceanic) regions (GBIF 2016). *Aegialia sabuleti* is currently considered to be absent from Britain (Duff 2012), but present in Central Europe and Fennoscandia (Landin 1961; Koch 1989b; GBIF 2016). However, this is due to a taxonomic revision which identified British populations of *A. sabuleti* as a separate species: *A. insularis* (Pittino 2006), subsequent to the original Stanton Harcourt publication (Briggs *et al.* 1985). Therefore, it is unclear whether specimens in this record represent *A. sabuleti* or *A. insularis*. Here, it has been considered as *A. sabuleti*, but its climatic envelope should be approached with some caution. The Whittlesey MCR is also partly constrained by *H. grandis*, as well as *Pterostichus minor*, *B. assimile* and *B. biguttatum* (Table 7.3). The latter three species all have broad distributions across much of Europe, extending into Western Siberia (Lindroth 1985, 1986; Luff 1998).

TMin estimates for MIS 7 sites are also contrasting in terms of relative constraint (Fig. 7.2, Table 7.2). The Aveley and Whittlesey faunas give broader estimates (-6.4 to 2.3°C and -5.2 to 2.2°C, respectively) than that from Stanton Harcourt (-2.5 to -0.3°C). The former two suggest winters temperatures similar to, or cooler than, the region at present, and the latter indicates cooler winters. However, the Stanton Harcourt assemblage is partially constrained by *A. sabuleti* (Table 7.3), which as discussed above, may actually be *A. insularis*. This is considered endemic to Britain

(Pittino 2006), including Southern Britain (GBIF 2016), and would therefore not suggest cooler winters, and so this result should be treated with caution.

TRange estimates for all MIS 7 sites suggest temperature seasonality either similar to or greater than the region at present (Fig. 7.2, Table 7.2). Stanton Harcourt seasonality appears somewhat greater than the present (17.4 to 21°C), but as with the TMin values, this should be approached with caution.

Though Stanton Harcourt MCR estimates give a clearer indication of climates distinct from the present, Whittlesey and Aveley are associated with additional thermophilous organisms (Table 7.1). For Whittlesey these are *Belgrandia marginata* and *Unio crassus*, and *B. marginata* for Aveley. *Emys orbicularis* has also been recorded from Stoke Tunnel (Suffolk) (Stuart 1979), which is correlated with Aveley (Sand Lane Quarry) by mammal assemblage zonation (Schreve 2001a). This is of particular note, as *E. orbicularis* is a reliable indicator of summer temperatures warmer than present day Britain (see Section *3.4.2.*).

7.3.3. MIS 9

Marine Oxygen Isotope Stage 9 is represented here by three sites: Barling, Cudmore Grove and Hackney Downs (see Figure. 7.2 & Table 7.2).

TMax reconstructions from Cudmore Grove and Hackney Downs are relatively well-constrained (15.8 to 17.8°C and 16.6 to 17.7°C, respectively), whilst Barling beetle faunas provide a broader TMax range (13.7 to 25°C) (Fig. 7.2, Table 7.2). These ranges are consistent with modern TMax values for the region (16.6°C), though slightly warmer (or cooler, in the case of Barling and Cudmore Grove) July temperatures are also possible.

TMin reconstructions provide some suggestion of conditions distinct from the region at present (Fig. 7.2, Table 7.2). The Barling TMin range is broad (-7 to 2.5°C), but indicates that winters were not warmer than the present, while both Cudmore Grove (-4.8 to 0.1°C) and Hackney Downs (-1.8 to 0.1°C) suggest winter temperatures >2.5°C cooler than the region at present. However, the upper limits of these reconstructions (0.1°C) are constrained by the presence of *Pterostichus gracilis* (see Table 7.3), which is present throughout Europe (except the far north) (Lindroth 1986; Luff 1998; GBIF 2016). This includes East Anglia and Southern England, which suggests that the winter temperature range for this species has been underestimated (modern average January temperatures in this region are around 2.6°C, Fick & Hijmans 2017). Though the reason for this underestimation is unclear, it demonstrates that whilst cooler winters than the present are feasible, they should not be assumed on this basis of this species.

With regards to TRange reconstructions, both Barling and Hackney Downs estimates are very broad (14.5 to 30.6°C and 16.7 to 29.5°C), though for Cudmore Grove they are more constrained (16.7 to 21.7°C) (Fig. 7.2, Table 7.2). They suggest temperature seasonality either similar to, or greater than, the region at present.

Non-insect thermophilous organisms, currently absent from Britain, are also present at all three sites (Table 7.1). These are particularly diverse at Hackney Downs, and include *Trapa natans*, *Salvinia natans*, *Najas minor*, *Belgrandia marginata* and *Unio crassus*. Notably, *Emys orbicularis* is also recorded from Cudmore Grove (Roe *et al.* 2009). The presence of these species, alongside quantitative coleopteran MCR reconstructions (Fig. 7.2, Table 7.2), adds additional weight to the suggestion of climatic conditions distinct from the present during MIS 9, perhaps indicating warmer spring and summer temperatures in all three records.

7.3.4. MIS 11: The Hoxnian

The Hoxnian Interglacial (correlated with Marine Oxygen Isotope Stage 11), is widely recognised as having a remarkably long interglacial peak (Lisiecki & Raymo 2005; Candy *et al.* 2014 and references therein), and is often suggested as a potential analogue for the Holocene, due to comparable orbital parameters (Loutre & Berger 2003; Tzedakis 2010; Candy *et al.* 2014). Here, it is represented by three records: Hoxne (Stratum D), Nechells (Birmingham) and Woodston (Fig. 7.2, Table 7.2).

July temperature reconstructions for Hoxnian records indicate summer temperatures similar to the region at present (Fig. 7.2, Table 7.2). Hoxne (Stratum D) and Nechells (Birmingham) TMax reconstructions (16.3 to 17.8°C and 15.3 to 18.3°C, respectively) are both within *c.* 1-2°C of the present. Woodston TMax is broader (16.6 to 24.8°C), but indicates temperatures at least as warm as the present. The most constrained estimate is from Hoxne (Stratum D), the type site for the Hoxnian. This estimate is primarily constrained by *Pterostichus gracilis* and *Bembidion fumigatum*, both of which have distributions which include (but are not limited to) southern Britain (Luff 1998; GBIF 2016).

For TMin reconstructions for MIS 11 records, only Hoxne (Stratum D) provides a well constrained estimate: -1.8 to 0.1°C (Fig. 7.2, Table 7.2). This suggests winter temperatures slightly cooler than those of the present, however given that the upper limit is constrained at 0.1°C by *P. gracilis*, a similar issue to Cudmore Grove and Hackney Downs (MIS 9) is encountered, and it is noted that this species currently inhabits southern Britain. Therefore, it is possible that winter temperatures were comparable to the present, but may have been slightly cooler. Indeed, this is also suggested by broader TMin reconstructions from Nechells (Birmingham) and Woodston (-5.4 to 2.3°C and -5.5 to 2.2°C, respectively).

Similarly to TMin estimates, only Hoxne (Stratum D) provides a well constrained estimate of Hoxnian temperature seasonality (TRange): 16.65 to 19.25°C (Fig. 7.2, Table 7.2). This indicates an annual thermal range either relatively similar to, or potentially slightly greater than, the present. The TRange estimates from Nechells (Birmingham) and Woodston are broader (14.8 to 23.8°C and 15.1 to 29.1°C, respectively), but do not contradict this interpretation.

The Hoxnian records analysed here all contain limited evidence for 'exotic' thermophilous non-insect organisms (Table 7.1). The record from Nechells (Birmingham) contains none of the selected taxa (Section *3.4.2.*), and *Najas minor* is the only species amongst these known from Hoxne (Stratum D) and Woodston. This species is known to exhibit niche plasticity (Wang *et al.* 2017), and so palaeoclimatic inferences based on its presence, particularly in the absence of other similar taxa must be undertaken cautiously. However, in spite of this it is currently absent from Britain, either as an invasive or native species (Wang *et al.* 2017), and its presence in these records is at least suggestive of climatic conditions not directly equivalent to those of the present, though differences may have been be slight. Though this cannot be used to constrain reconstructions provided by beetle assemblages, its presence at least corroborates the suggestion of climates distinct from the present. This is broadly consistent with other recent reconstructions of Hoxnian climates (e.g. Candy *et al.* 2014).

7.3.5. MIS 17-13: 'Cromerian Complex' interglacials

There are fewer available palaeoentomological datasets relating to pre-Anglian (pre-MIS 12) interglacials, but those analysed here provide invaluable comparison to post-Anglian interglacials, and context for the MBT. Evidence from several temperate-climate deposits spanning the early Middle Pleistocene (MIS 17-13) is represented in this section, based on five records from four sites: Sidestrand (*Unio*-bed), Sugworth, West Runton (Coope 2010b and data from Chapter 4) and Pakefield (Fig. 7.2, Table 7.2). Despite likely being derived from multiple interglacials, MCR estimates are broadly consistent between records.

Reconstructions of warmest month temperatures (TMax) for 'Cromerian Complex' interglacials are all broadly consistent with summer temperatures for the region at present (Fig. 7.2, Table 7.2). The most constrained estimate is from Coope's (2010b) West Runton record: 16.4 to 17.2°C, which is <1°C different from the present (16.6°C, Fick & Hijmans 2017), indicating comparable summer temperatures. This is primarily constrained by the presence of *Bembidion clarkii*, which is largely restricted to oceanic and coastal areas of Northwest Europe (Lindroth 1985; GBIF 2016) with relatively low seasonality, cool summers and mild winters. TMax estimates based on records from Sidestrand (*Unio*-bed) and Sugworth Coleoptera are slightly broader, but also indicate climates roughly similar to the present (15.6 to 17.8°C and 15.7 to 18.3°C, respectively). Interestingly, this is in spite of the presence of *Valgus hemipterus* at Sugworth. This species is often considered an indicator of enhanced warmth, due to its current absence from Britain and presence in Southern and Central Europe (e.g. Coope 2010a; Candy *et al.* 2010). However, this species is also present in northwest Belgium and the western Netherlands (GBIF 2016), which experience milder, more oceanic-type summers than Central and Southern Europe. Therefore, *V. hemipterus* perhaps requires only marginally-elevated summer temperatures relative to southern Britain at present. However, as its larvae develop in the rotten or dead wood of deciduous trees (Harde 1984; Koch 1989b), its current absence from Britain may also be explained by the loss of suitable habitats during the Holocene (Robinson 2013). Furthermore, the northern limits of its distribution may be additionally limited by a climatic factor other than average July temperatures (e.g. numbers of days exceeding a particular temperature, precipitation seasonality). Regardless of the precise scenario, its presence is at least suggestive of climatic conditions slightly different from those experienced in southern Britain at present.

TMax estimates based on new West Runton coleopteran assemblages (WR14, Chapter 4) and Coope's (2006) Pakefield assemblages are very similar, but broader than those of other pre-Anglian records presented here (Fig. 7.2, Table 7.2). They are 15.4 to 20.3°C and 15.8 to 20°C, respectively, indicating July temperatures either broadly similar to the region at present, or potentially warmer. With the exception of *Valgus hemipterus* from Pakefield, these reconstructions are entirely based on species currently present in Britain, further suggesting a general similarity to present day climates. However, as discussed in Chapter 5, there is sufficient palaeoecological and palaeopedological evidence from Pakefield to infer climatic conditions distinct from those represented by the West Runton Freshwater Bed, particularly regarding the seasonality of precipitation (Candy *et al.* 2006).

Range estimates for January temperatures (TMin) from pre-Anglian records are generally broad, but consistent, with the exception of that based on Coope's (2010b) West Runton record (Fig. 7.2, Table 7.2). TMin estimates from Sugworth, the new West Runton record (Chapter 4) and Coope's (2006) Pakefield record are virtually indistinguishable: each has an upper limit close to modern day values, and a lower limit of *c.* -.5.5°C. The upper TMin limits for Sidestrand (*Unio*-bed) and Coope's (2010b) West Runton fauna are both slightly lower at 0.1°C, due to the presence of *Pterostichus gracilis* and *Bembidion clarkii*, respectively, in these records. As discussed above, the significance of this value based on the presence of these species should be approached with due caution as they are both currently present in southern Britain, and as discussed in Chapter 4 (Section *4.4.4.2.*), the presence of *B. clarkii* is indicative of climatic conditions broadly similar to the region at present. Collectively, these records suggest that pre-Anglian interglacial winter temperatures were not warmer than the present, but leave potential for cooler winters in some cases.

TRange reconstructions are similarly broad, and are consistently overlapping between records (Fig. 7.2, Table 7.2). The lower limits of Sugworth and Pakefield TRange estimates are both similar to the present day, and whilst the lower limits for Sidestrand (*Unio*-bed) and both West Runton records are slightly higher (*c.* 16.5°C) they are not vastly different. With the exception of the estimate based on Coope's (2010b) West Runton fauna, TRange upper limits are consistently *c.* 22 to 24°C, indicating the potential for enhanced seasonality, relative to the present. The upper TRange limit from Coope's (2010b) West Runton fauna is 18.4°C, based on the presence of *Bembidion clarkii*, suggesting temperature seasonality broadly similar to the present.

All four 'Cromerian Complex' sites utilised here have evidence for the presence of non-insect thermophilous organisms (Table 7.1). *Najas minor* is present at all sites, though without the presence of other similar taxa, as at West Runton, little can be inferred regarding palaeoclimatic conditions based on this species. However, at Sidestrand (*Unio*-bed), Sugworth and Pakefield, it is accompanied by other 'exotic' thermophiles. *Trapa natans* is present at all three sites, *Unio crassus* is present at Sidestrand (*Unio*-bed) and Sugworth, and *Hippopotamus antiquus* is known from Sidestrand (*Unio*-bed) and Pakefield. Sidestrand (*Unio*-bed) and Pakefield also record the presence of *Belgrandia marginata* and *Salvinia natans*, respectively. For West Runton, the general absence of such species, in spite of extensive palaeontological investigations at the site (e.g. West 1980a; Stuart & Lister 2010), corroborates the suggestion of climatic conditions similar to the region at present. For the other four sites, the presence of various thermally-sensitive 'exotic' taxa suggests that climatic conditions were not directly comparable to the present, and that 'true' TMax values lie towards the upper limits of the range estimates.

These reconstructions are broadly comparable to those of previous authors (e.g. Coope 2006; Candy *et al.* 2010), and significantly they offer no suggestion of 'muted' interglacial intensity during this period. During the temperate stages represented, July temperatures were at least as warm as the present, and winter temperatures may have been cooler, but not warmer.

7.4. The Mid-Brunhes Transition: Preliminary Interpretations

The new analyses presented in this chapter provide a refined view of temperate climates in Britain from *c.* 712-126 ka (MIS 17-5e), particularly regarding winter temperatures and annual temperature seasonality. It is demonstrated that throughout multiple interglacial periods, coldest month temperatures were never milder than those currently experienced in southern Britain, but were potentially cooler at times. Furthermore, temperature seasonality may have been enhanced, relative to the present, during some periods, but was unlikely to have been lessened. There is also no evidence for a distinction between pre- and post-MBT interglacials in Britain (and by extension, Northwest Europe) on the basis of summer temperatures (TMax), winter temperatures (TMin) or temperature seasonality (TRange). Whilst this does not contradict previous conclusions regarding MBT expression in Britain (Candy *et al.* 2010), it represents a significant advancement in the depth of understanding of this phenomenon. This is discussed further, and its implications explored, in Chapter 8.

It is acknowledged that most of the records analysed here are ‘snapshots’, representing only short periods within interglacials, and the analysis of records representative of full interglacial sequences would be necessary for these findings to be truly conclusive. Also, whilst efforts have been made to ensure that the records are representative of fully temperate interglacial substages (see Section *3.4.1.*), the fact remains they are not necessarily drawn from equivalent substages. For example, the Ipswichian records utilised here (see Table 7.1) may be attributed to early temperate substages (Ip I-II) on the basis of pollen biostratigraphy (Stuart 1979; Keen *et al.* 1999; Preece 1999; Gao *et al.* 2000), whereas the MIS 7 records have been attributed to late temperate stages on the basis of mammalian (Schreve 2001a) and pollen (Langford *et al.* 2014) biostratigraphy. However, it should also be borne in mind that any such determinations of interglacial substage in the context of the British Middle Pleistocene should be made with caution, particularly those based on pollen records. Regional interglacial patterns of pollen succession are typically based on records with little (if any) independent chronological control, and are often derived from fragmentary, fluvially-derived pollen records (Thomas 2001; Rose 2009). Therefore, while the likelihood is that the records used here are not drawn from directly equivalent substages, specific assignments to substages have not been undertaken.

7.5. Comparisons to Previous Reconstructions

The purpose of this chapter is not to review previous work, but the MCR reconstructions in this chapter (calculated using Milne (2016) species climate envelopes) are a significant improvement on those in previous studies (e.g. Coope 2006; Candy *et* *al.* 2010) (most are provided in Figure 2.3), and a brief comment is given here. In general, the new reconstructions do not contradict (and often support) those of previous authors, but do offer better constrained temperature estimates, allowing for a more nuanced view of interglacial climates during the Middle and Late Pleistocene (MIS 19-5e) for the periods represented by the analysed records.

Range reconstructions of average July temperatures (TMax) given here are generally overlapping with other earlier reconstructions based on the same assemblage data (e.g. Coope 2006; Candy 2010). However, they are usually closer to modern values for the region (average July temperature at 50°N, 0°E, 1970-2000: 16.6°C; Fick & Hijmans 2017). For example, TMax values of 16 to 24°C have previously been reported for Sidestrand (*c.* MIS 13) (Preece *et al.* 2009; Candy *et al.* 2010), whereas here they are 15.6 to 17.8°C. Similarly, Coope (2006) gave TMax values of 17 to 23°C for Pakefield (*c.* MIS 15-17), but here they are 15.8 to 20°C. This also highlights the tendency towards the overestimation of TMax values in previous MCR reconstructions, which has often been noted (e.g. Atkinson *et al.* 1987; Elias & Matthews 2014).

Average January temperature ranges (TMin) here are often twice as well constrained as those from previous work (e.g. Coope 2006; Candy *et al.* 2010). On average (mean), TMin ranges here have a *c.* 5°C extent, whereas in Candy *et al.* (2010) average TMin ranges span around 10°C. For example, previous TMin values for Woolpack Farm (MIS 5e) have a range of 8°C (-4 to 4°C) (Candy *et al.* 2010, 2016), whereas here they have a range of 4.3°C (-1.9 to 2.4°C). For Sugworth (*c.* MI 15), the improvement was less pronounced: from a 10°C range (-6 to 4°C: Candy *et al.* 2010) to a 7.6°C range (-5.3 to 2.3°C: this chapter). However, reconstructions based on Barling (MIS 9) assemblages were dramatically improved, from a 23°C range (-11 to 13°C: Bridgland *et al.* 2001; Candy *et al.* 2010), to a 9.5°C range (-7 to 2.5°C: this chapter). Crucially, this improvement has allowed the comparison of pre- and post-MBT winter temperatures, leading to the conclusions that interglacials both prior to and following the MBT cannot be distinguished on the basis of winter temperatures in Britain. However, the possibility remains that study of longer records, or records representing different parts of interglacial periods, may change this conclusion in the future.

Reconstructions of annual temperature range (TRange) have previously received little, if any, mention in studies of interglacial palaeoclimates based on beetle assemblages. However, in the present study Milne's (2016) improvements to TMin estimates have also led to improved TRange estimates, allowing comment on temperature seasonality. This has allowed the suggestion that there is no general pattern in temperature seasonality amongst interglacials either preceding or following the MBT in Britain. Rather, they are remarkably consistent in this regard.

Chapter 8

General Discussion and Synthesis

8.1. Introduction

This chapter summarises the findings of Chapters 4 to 7, and contextualises them according to their broader significance. The first section deals with insights gained from Chapters 4 to 6 regarding the ecology of early Middle Pleistocene interglacial environments, with a particular focus on disturbance processes. Herbivore activity, wildfire and hydrogeomorphic processes are each considered in turn. Evidence for each of these disturbance agents, and their influence on vegetation characteristics, is compared between case study sites (West Runton, Pakefield and Brooksby) and wider research, and generalities are inferred. The second section is concerned with the palaeoclimatic reconstructions presented in Chapter 7. These reconstructions are discussed in terms of their implications for interglacial climates in Britain, as well as in the global context of early Middle Pleistocene interglacial climates. Finally, the implications for contemporary Lower Palaeolithic populations in Northwest Europe, in terms of both ecological and climatological inferences, are briefly explored.

8.2. Ecological Insights from Interglacial Records

The complexity and dynamism of local ecology during early Middle Pleistocene interglacials has been demonstrated at site level in Chapters 4 to 6. In this section, the generalities and contrasts between these records are explored, and set within the wider context of the ecology of temperate-climate episodes in Northwest Europe, with a particular focus on disturbance processes, and their relationships with vegetation, habitat heterogeneity, biodiversity and ecosystem function. The nuances and perspectives developed are of significance to palaeoecologists interested in the function, dynamics and structure of past ecosystems. They also hold additional value for archaeologists and conservation ecologists. Early Middle Pleistocene interglacial sequences provide some of the earliest evidence for the presence of *Homo* in Northern Europe (e.g. Parfitt *et al.* 2005; Hosfield 2011; Candy *et al*. 2015), and the present work thus provides further insights into the ecological dynamics of early hominin landscapes. These are likely to have been small, sparse populations (Ashton & Lewis 2012), and though they undoubtedly exerted some influence (e.g. via hunting), they are discussed here as largely passive components of the landscape, rather than as major drivers of ecological change. Additionally, such studies are also of interest for neo-ecologists interested in conservation strategies which seek to restore ecosystem processes and biotic interactions that are diminished (or absent) in modern landscapes (e.g. 'rewilding'-type approaches, *sensu* Pereira & Navarro 2015). In this context, these records represent idealised 'laboratory experiments' in this context: they provide insights into vegetation dynamics, relative to herbivory and other disturbance processes, with absent or minimal human influence, and with diverse suites of competitive, facultative and trophic interactions, in a temperate Northwest European context.

Palaeoecological datasets from Chapters 4 (West Runton), 5 (Pakefield) and 6 (Brooksby) are summarised in Figure 8.1, highlighting the dissimilarities between each site in terms of ecological characteristics. The West Runton record (WR14, Fig. 4.2) is characterised by pollen assemblages with herbaceous pollen abundances (53.8%) greater than those of arboreal pollen (46.2%) (Fig. 8.1 A), and coleopteran assemblages dominated by aquatic ecotone taxa (mostly Donaciinae) (50.7%), with high levels of fully aquatic Coleoptera (30.5%) and relatively few terrestrial Coleoptera (woodland and trees: 0.9%; herbaceous and open/disturbed: 1.9%; foul/rotten/dung: 8.3%) (Fig. 8.1 B). The Pakefield record (PK14, Fig. 5.2) has a much greater arboreal pollen component (68.9%), relatively low herbaceous pollen abundances (26.7%) and a small proportion of ericale pollen (4.5%) (Fig. 8.1 A). This is strongly indicative of greater woodland cover represented by the PK14 record, relative to the WR14 record. The Coleoptera from Pakefield are similarly wetland-dominated (fully aquatic: 32.2%; aquatic ecotone: 33.6%), but with a greater proportion of both woodland and tree Coleoptera (10.0%) and Coleoptera associated with herbaceous plants and open/disturbed habitats (10.61%) (Fig. 8.1 B). However, these should be interpreted with caution, given the particularly low MNI values associated with the PK14 coleopteran record (Table 5.4). In the Brooksby record (XA57, Fig 6.2) a more open landscape than those represented at West Runton and Pakefield is indicated by comparatively low arboreal pollen values (27.7%) and high herbaceous pollen values (71.1%) (Fig. 8.1 A). However, as discussed in Section *6.4.2.*, abundances in this pollen record should be approached with caution, due to the low pollen concentrations (mean: 3226.4 pollen grains cm^{-3}), and correspondingly low counts (<100 grains per sample). Assemblages of sub-fossil Coleoptera from Brooksby have a lower fully aquatic component (20.3%) than either West Runton or Pakefield, though relative abundances of aquatic ecotone Coleoptera are similarly substantial (38.6%) (Fig. 8.1 B). Relative abundances of foul/rotten/dung Coleoptera are notably higher in the Brooksby record (20.8%) than in either the West Runton or Pakefield records, suggesting more abundant rotting organic material and/or dung in the local area.

Concentrations of coprophilous fungal spores and charcoal, and mean grain size, also vary between the records (Fig. 8.1 C, D & E). Concentrations of coprophilous fungal spores are relatively low in the Pakefield (52.8 cm^{-3}) and Brooksby records (37.0 cm^{-3}), and substantially higher in the West Runton record (884.7 cm^{-3}) (Fig. 8.1 C). Given the highly localised catchments for sub-fossil coprophilous fungal spores (Baker *et al.* 2016), this is not evidence for an absence of large herbivores at Pakefield or Brooksby, but is firm evidence for their presence, and potentially abundance, at West Runton. Charcoal concentrations from West Runton and Pakefield are relatively similar (24336.2 shards cm^{-3} and 22779 shards cm^{-3}, respectively), but much lower at Brooksby (7263.3 shards cm^{-3}) (Fig. 8.1 D), perhaps indicating less burning in the landscape at Brooksby (though as with the Brooksby pollen record, this should be approached with caution, *cf.* Section *6.4.2.*). Grain size in the West Runton sequence is generally slightly coarser (4.4 phi: coarse silt) than that from Pakefield (5.4 phi: medium silt), suggesting a marginally more energetic hydrogeomorphic regime (Fig. 8.1 E) (*n.b.* data not available for Brooksby).

The detail within these datasets, and its ecological implications, are discussed further in the following sections.

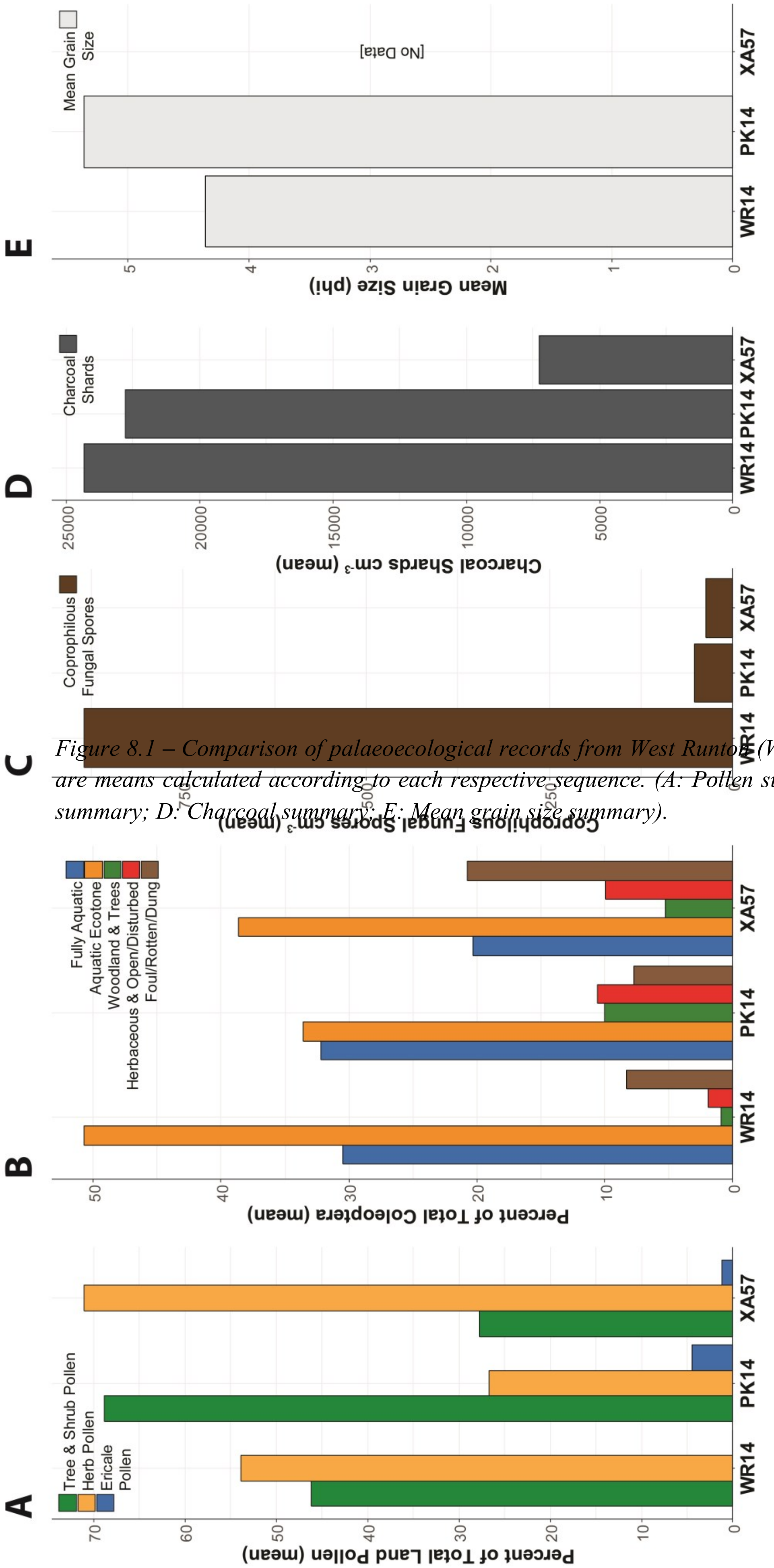


Figure 8.1 – Comparison of palaeoecological records from West Runton (WR14, Fig. 4.2), Pakefield (
are means calculated according to each respective sequence. (A: Pollen summary; B: Coleopteran ha
summary; D: Charcoal summary; E: Mean grain size summary).

8.2.1. Herbivore activity and vegetation communities

Diverse suites of large herbivores are well known from interglacial contexts in Northwest Europe (e.g. Schreve 2001; Bradshaw *et al.* 2003; Kahlke *et al.* 2011), and it follows that herbivory is an enduring component of interglacial environments. Large herbivores may interact with vegetation communities via numerous mechanisms, including direct consumption of plant tissues (grazing and browsing), trampling, uprooting, seed dispersal and nutrient recycling (Doughty *et al.* 2016; Malhi *et al.* 2016; Smith *et al.* 2016). These activities may have complex ecological consequences, altering various aspects of local ecology. These include vegetation density, floral and faunal community composition and diversity, faunal behaviour, rates of nutrient cycling, nutrient spatial distribution, and the functioning of other disturbance processes, such as burning and flooding (reviewed in detail elsewhere, e.g. Schmitz 2008; Johnson 2009; Marquis 2010; Foster *et al.* 2014a). Consequently, the presence (or absence) of large herbivores is often implicated as a major factor in determining the characteristics of Late Pleistocene and Early Holocene vegetation communities (e.g. Svenning 2002; Bradshaw & Hannon 2004; Gill *et al.* 2009; Johnson 2009; Gill 2014; Sandom *et al.* 2014; Bakker *et al.* 2016). Additionally, beavers (*Castor fiber*) and giant beavers (*Trogontherium cuvieri*), the activities of which may increase local vegetation diversity and alter hydrological regimes (Coles 2006), have also been recorded from Middle Pleistocene sites (Stuart 1975; Stuart & Lister 2001; Maul & Parfitt 2010). However, in spite of its likely broad significance as a disturbance factor during past interglacials, herbivore-associated disturbance is often only briefly referred to at the site-specific level in pre-Holocene contexts (e.g. Keen *et al.* 1999; Green *et al.* 2006; Field & Peglar 2010), and rarely discussed in more detail, with rare exceptions (e.g. Gibbard & Stuart 1975; Sandom *et al.* 2014).

In this thesis, the analysis of coprophilous fungal spores, alongside pollen and coleopteran assemblages, has allowed for more detailed exploration of herbivore-vegetation interactions at the site-specific level. Interactions between herbivores and vegetation communities are most clearly recognisable in the record from the West Runton Freshwater Bed (Chapter 4). Here, the consistent presence of both dung fungi (e.g. *Sporormiella*-type spores) and *Aphodius* sp. (and other dung beetles, *sensu lato*) indicates continuous herbivore presence. Coprophilous fungal spore concentrations are also notably higher at West Runton than at either Pakefield or Brooksby (Fig. 8.1 C). Unfortunately, the low taxonomic resolution of *Aphodius* sp. (see Chapter 4, Section *4.4.3.1.*) and low sample sizes (<50 MNI per sample, *cf.* Hill 2015) hampers estimations of local herbivore abundance on the basis of coleopteran dung faunas (as in Smith *et al.* 2010, 2014; Hill 2015). However, there is notable shift in the prevalence of different fungal spore types (e.g. decreased prevalence of *Sordaria*-type spores), coincident with a shift in the vegetation community towards greater deciduous tree abundance. There is some evidence to suggest that different species of coprophilous fungi have preferences for the dung of different herbivore types (Richardson 2001). Therefore, as the change is in spore types, rather than spore abundances, a change in local herbivore assemblage composition or behaviour, as opposed to herbivore abundance, is implied. This may be indicative of locally increased grazing intensity (as opposed to browsing, or more indiscriminate mixed feeding), reducing predation of young trees and competition for light, thereby facilitating the growth of light-demanding taxa such as *Quercus* and *Corylus*. Indeed, a similar situation has been directly observed in a modern context at Oostvardersplassen nature reserve (Netherlands). Cornelissen (2017) found that cattle (*Bos taurus*) grazing on a floodplain area prevented the establishment of young trees and shrubs, but facilitated grazing by geese (*Anser anser* and *Branta leucopsis*). In turn, the cattle were locally outcompeted by the geese, and then grazed preferentially in woodland areas instead, particularly during winter months. This allowed trees and shrubs to begin growing on the floodplain. Whilst it would be presumptive to use this as direct analogue for West Runton, it serves as a valuable example of the potential complexity in herbivore-vegetation relationships, and the types of competitive interactions that may have driven past ecological changes. It demonstrates the potential complexity within herbivore-vegetation interactions, and highlights the potential for local biotic interactions to drive changes in herbivore behaviour and distribution, which in turn provide potential explanations for changes in pollen and coprophilous fungal spore assemblages, such as those at West Runton.

In contrast to West Runton, the prominence of herbivore activity at Pakefield (Chapter 5) and Brooksby (Chapter 6) is less obvious. In the Pakefield record, coprophilous fungal spores were rare, and no dung-obligate Coleoptera were identified. Whilst there is direct evidence of the presence of a diverse range of herbivores at Pakefield in the form of sub-fossil remains (Stuart & Lister 2001), the scarcity of evidence for dung-obligate biota (either fungal or faunal) suggests that local herbivore densities were lower than at West Runton. In the Brooksby record, there is no associated vertebrate fossil record, but there is more evidence of dung-obligate biota (coprophilous fungal spores and *Aphodius convexus*) than at Pakefield (see also Figure 8.1 B & C), which is suggestive of moderate local herbivore density. (As with West Runton, more precise estimations of herbivore presence were not possible.) Pakefield therefore appears to be distinctive from both West Runton and Brooksby in this regard, and the most convenient explanation for this lies in the relative lack of openness indicated at Pakefield. Whilst Coleoptera (e.g. *Melanotus punctolineatus*) and certain plants (e.g. *Calluna vulgaris*) indicate the presence of some open habitats at Pakefield, the overall picture from pollen evidence is of a more wooded landscape, with lower grass abundances, than at either West Runton or Brooksby. Low herbivore densities may have been a simultaneous cause and consequence of this, as tree and shrub taxa were likely under less pressure from herbivory, while low grass abundances and physically limited space for megafauna may have made the established woodland less attractive to some larger herbivores, such as *Mammuthus trogontherii* and *Megaloceros* spp., which may have been more confined to open floodplain areas. It may even be speculated that the lower Poaceae pollen abundances in the Pakefield record are a result of a more spatially limited floodplain, leading to lower abundances of aquatic, semi-aquatic and hygrophilous grasses. However, the records from West Runton, Pakefield and Brooksby are likely to be representative of only short periods of time and not representative of entire interglacials, (though more precise estimates are not possible). This is particularly true of Pakefield, which registers little vegetation change, and as such any temporal relationships are difficult to discern.

General assessments of the relationship between herbivores and vegetation in pre-Holocene contexts (Svenning 2002; Bradhsaw *et al.* 2003; Sandom *et al.* 2014) have emphasised the importance of herbivores in maintaining local openness in European interglacial landscapes. The analyses presented here are broadly supportive of this pattern, but highlight the potential complexity of such relationships. However, a greater number of records are required to draw general conclusions regarding early Middle Pleistocene palaeoenvironments in this context. Svenning (2002) and Bradshaw *et al.* (2003) also draw attention to the inherent complexity in these relationships, pointing out that the activities of herbivores likely benefitted various light-demanding tree species, which cannot regenerate under closed canopy conditions, but are typical of interglacial environments in Northwest Europe (e.g. *Quercus* spp., *Corylus avellana*). For example, forest windthrow events create openings on the canopy, and the feeding and trampling activities of herbivores may subsequently have maintained this openness for sufficient time to allow regeneration of these tree taxa. Additionally, the tree felling activites of modern proboscideans (*Loxodonta africana*) are well-documented (Chafota & Owen-Smith 2009; Asner & Levick 2012; Asner *et al.* 2016), and it is reasonable to consider that European interglacial Proboscidea (e.g. *Mammuthus trogontherii*, *Palaeoloxodon antiquus*) are likely to have directly contributed to gap creation processes through equivalent behaviours. Similarly, the feeding and dam-building activities of beavers (*Castor fiber*) and giant beavers (*Trogontherium cuvieri*) at West Runton (Stuart 1975; Maul & Parfitt 2010) and Pakefield (Stuart & Lister 2001) are also likely to have exerted additional pressure on riparian trees. They may also have contributed to local canopy openness through the establishment of 'beaver pastures' (areas of coppiced *Salix* and other shrubs) and 'beaver meadows' (terrestrialised beaver ponds) (Coles 2006). At the scale of a single site, the effect of large herbivores was previously posited by Gibbard & Stuart (1975), who suggested that the local abundance and diversity of herbaceous assemblages, associated with Last Interglacial (Ipswichian) deposits at Barrington (Cambridgeshire), were likely facilitated by the presence of large herbivores such as *Hippopotamus*. Coope (1974) also suggested that local openness at another Ipswichian site (Bobbitshole) may have been driven by the trampling and feeding activities of large herbivores, on the basis of several dung beetle (Scarabaeidae) species. Indeed, Bakker *et al.* (2016) have hypothesised a similar relationship between local herbivore density, and relative openness and habitat diversity for Northwest European interglacial environments more generally (see Figure 8.2). Such a relationship is strongly suggested by the case studies presented here, which provide important empirical corroboration for Bakker *et al.*'s (2016) hypothetical model. However, differences in herbivore behaviour between sites should not be ignored. Tooth wear analyses reveal that at Pakefield herbivore diets were more graze-dominated, whereas at West Runton they included more browse, even amongst typical 'grazing' taxa such as

Equus (Rivals & Lister 2016). Herbivores at West Runton may therefore have had a disproportionate impact on woody vegetation, contributing to the lower canopy cover indicated by the pollen record. The reasons for these differences in feeding patterns are unclear, but it may be speculated that they are due to differences in the availability, accessibility and edibility of woody vegetation at each site. Pakefield appears to represent a more spatially consistent woodland, whereas landscapes at West Runton were more heterogeneous, and less densely wooded. Due to less competition for light amongst trees in this context, there may have been a greater proportion of young trees close to the sampling site at West Runton, with foliage which was more easily accessible and digestible.

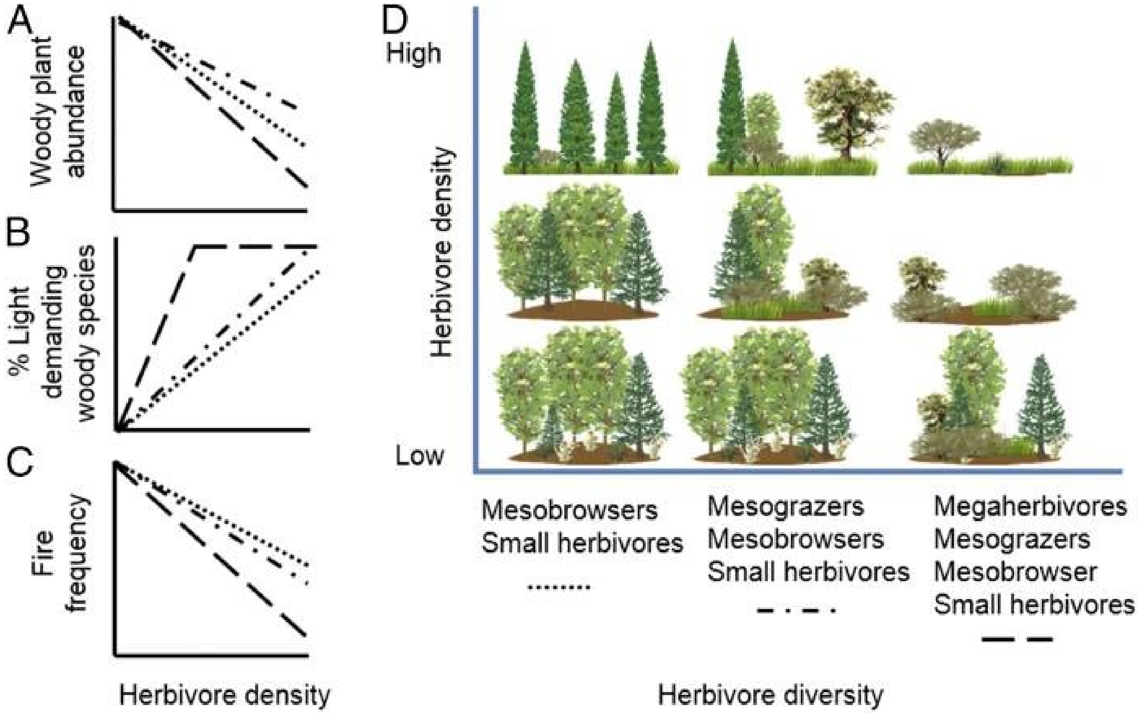


Figure 8.2 – Hypothesised impact of large herbivore abundance and functional diversity on: (A) woody plant abundance, (B) percentage of light-demanding woody species, (C) fire frequency, and (D) overall vegetation structure (from Bakker et al. 2016)

8.2.2. Wildfire and vegetation communities

Wildfire regimes are widely recognised as an important disturbance factor in vegetation communities (e.g. Svenning 2002; Lindbladh *et al.* 2013; Drobyshev *et al.* 2014;

Bakker *et al.* 2016), functionally comparable to herbivory in certain respects (Bond & Keeley 2005). In Holocene palaeoecology, pyrogenic influences on vegetation are given considerable attention (e.g. Whitehouse 2000; Power *et al.* 2008; Olsson *et al.* 2010; Marlon *et al.* 2013; Grant *et al.* 2014), whereas in the early Middle Pleistocene of Northern Europe, the influence of wildfire on vegetation characteristics is much less frequently identified and discussed (e.g. Coxon *et al.* 1994; Coxon 1996; Kuneš *et al.* 2013). Though this lack of attention is undoubtedly due in part to the improbability of anthropogenic burning during this period (Roebroeks & Villa 2011), some level of wildfire activity is evident, due to the presence of charcoal in early Middle Pleistocene sediments, warranting the consideration of fire as a potential agent of vegetation change.

Microcharcoal shards are recorded in sediments from all three case study sites (West Runton, Pakefield and Brooksby) (Fig. 8.1 D), and it follows that burning of some level must have occurred in the landscapes surrounding each site. This may have a local component but, as with arboreal pollen, this is likely to be a predominantly regional signal (Clark 1988; Clark *et al.* 1998; Carcaillet *et al.* 2001). Wildfire is most prominently implicated as a determinant of vegetation structure in the record from Pakefield (Chapter 5), in which a ‘patchwork’ of mixed deciduous-coniferous forest and open to semi-open habitats is inferred on the basis of both pollen and beetle records. In combination with this landscape structure, a seasonally-dry climate (Candy *et al.* 2006) conducive to wildfire (Drobyshev *et al.* 2014, 2016), and the relative prominence of fire-advantaged plants such as *Calluna vulgaris*, other Ericales and *Pinus* (Agee 1998; Måren & Vandvik 2009; Davies *et al.* 2010), are strongly suggestive of an important role for fire in determining vegetation characteristics. At West Runton (see Chapter 4), fire appears to have been more significant in one part of the sequence: the lowest section of the record which is *Pinus*-dominated, and in which, charcoal abundances and sand content are greatest. *Pinus* is known to be associated with, and favoured by, fire regimes (Agee 1998; Whitehouse 2000; Fernandes *et al.* 2008; Olsson *et al.* 2010), as well as sandy, disturbed habitats (Hille & den Ouden 2004) (though neither is a requirement of *Pinus*). This may have been the case at West Runton, though there is no firm evidence of widespread sandy habitats. Though not a mutually exclusive consideration, the simultaneously heightened microcharcoal and sand content may also suggest greater in-washing of bank or floodplain sediments. The relative importance of wildfire at Brooksby is difficult to assess (see Chapter 6), but its occurrence is evident, due to the presence of microcharcoal shards. Interestingly, in spite of other parallels with modern and Holocene fire regimes in Northwest Europe (e.g. association with *Pinus* and *Calluna vulgaris*), there is no evidence for pyrophilous beetles at any of the three sites. Such species are extremely rare in pre-Holocene interglacial records from Britain (according to occurrences noted in the BugsCEP database, Buckland & Buckland 2006), but pyrophilous assemblages have been recorded alongside other evidence of burning in Holocene records from Britain (Whitehouse 1997, 2000) and Scandinavia (Olsson & Lemdahl 2009, 2010; Olsson *et al.* 2010). Speculatively, this may suggest that the frequency and/or intensity of wildfires in Britain were too low to support significant populations of pyrophilous insects, though there are major caveats associated with this suggestion. Firstly, in Middle Pleistocene records evidence for wildfire is predominantly regional in scale (i.e. microcharcoal, Clark 1988), whereas subfossil beetle records are generally local in scale (Hill 2015). Conversely, Holocene records for pyrophilous insects are associated with local-scale evidence of burning (i.e. macrocharcoal) (Whitehouse 1997, 2000; Olsson & Lemdahl 2009, 2010; Olsson *et al.* 2010). Therefore, the absence of pyrophilous insects in the present study may be a function of the spatial representation of subfossil beetle records, rather than an absence in the broader landscape. They may also have been present locally, but as rare species, and therefore difficult to detect as fossils. It has also been suggested that megaherbivore populations may have diminished fire frequency, relative to the Holocene, through the consumption of potential fuel sources (Gill 2009). This may have been an additional supressing factor in Middle Pleistocene interglacials.

Relationships between fire regimes and vegetation in pre-Holocene interglacials have received limited attention (*cf.* Kuneš *et al.* 2013), but the new case studies presented here develop this knowledge base and provide a picture consistent with previous studies. At Marks Tey (Essex) and Hoxne (Suffolk) wildfire has been implicated in driving an expansion of grassland, herbaceous vegetation and *Pinus* during the Hoxnian (MIS 11) (Turner 1970), and wildfire has also been found to be associated with *Pinus* and increased openness (indicated by non-arboreal pollen) during the Gortian interglacial in Ireland (MIS 11) (Coxon *et al.* 1994; Coxon 1996). Similarly, Kuneš *et al.* (2013) found that the occurrence of wildfire was associated with increased *Pinus-Calluna* vegetation (and openness) in a deposit attributed to MIS 11 from Trelde Klint in Denmark. New findings regarding relationships between fire regimes and vegetation presented in this thesis are consistent with previous studies, suggesting a long-term association between openness, *Pinus* and fire regimes in Northwest European landscapes during temperate periods. Hominin agency in initiating fires during the early Middle Pleistocene in Britain is not beyond possibility, but there is currently no firm evidence for the controlled use of fire in Britain (or elsewhere in Europe) prior to MIS 11 (Preece *et al.* 2006; Roebroeks & Villa 2011), though firm evidence has been found at individual sites in Isreal (*c.* ≤790 ka BP: Goren-Inbar *et al.* 2004) and South Africa (*c.* 1 Ma BP: Berna *et al.* 2012).

8.2.3. Hydrogeomorphic processes and vegetation communities

Hydrogeomorphic processes and vegetation are inextricably linked and mutually influential in riparian zones (Brown *et al.* 1997; Steiger *et al.* 2005; Gurnell 2014). Alluvial processes can both prevent and facilitate plant colonisation and growth (through periodic flooding and sediment deposition, respectively), whilst vegetation growth may stabilise banks and enhance sedimentation, and also instigate flooding and alter channel forms via the deposition of large woody debris (Viles *et al.* 2008). At all three case study sites, both lentic (e.g. *Nuphar*, *Tanysphyrus lemnae*) and lotic (e.g. various Elmidae) biota are recorded simultaneously, indicating variable energy regimes at the sites of deposition and proximity to active channel systems. On this basis, it is clear that hydrogeomorphic processes were occurring in the landscape (and were likely mutually influential with vegetation communities to some extent) in all cases. Indeed, given the prominence of fluviatile deposits amongst Middle Pleistocene temperate stage records in Britain (see Table 2.2), complex interactions between hydrogeomorphic processes and vegetation are likely to have been common feature of the environments represented (Gibbard and Lewin 2002). However, amongst the case studies presented here, only the record from West Runton provides a clear suggestion of the nature of this relationship, or at least part of it. Here, simultaneous upward-fining of the sedimentary record is associated with increasing proportions of deciduous arboreal pollen, illustrated both stratigraphically and through multivariate analyses. As discussed in Chapter 4, this is unlikely to reflect a simple model of one environmental process or variable driving another directly, but possibly a combination of reciprocal processes. For example, periodic flooding may have created and maintained open areas directly adjacent to the channel, whilst the growth of *Alnus* and *Salix* may have been favoured in wet areas subject to occasional lower-energy alluvial deposition, at the expense of taxa preferring drier soils, such as *Quercus* and *Abies*. *Alnus* and *Salix* may have subsequently contributed to the stabilisation of alluvial sediments and soil formation in these areas *Alnus* pollen often dominates pollen assemblages from sites where *Alnus* trees are locally abundant (>60%: Waller *et al.* 2005). Therefore, the moderate *Alnus* pollen values from West Runton (WR14 maximum: 30.82%, Fig. 4.4), and evidence for the simultaneous presence of dry woodland taxa (e.g. *Abies*), suggests that such alluvial processes were spatially complex, leading to the local presence of both wetter and drier areas. The potential for the damming effects of beavers (*Castor fiber*) and giant beavers (*Trogontherium cuiveri*) at West Runton (Stuart 1975; Maul & Parfitt 2010) (and Pakefield, Stuart & Lister 2001) further complicates this picture, as this may also have contributed towards sediment stabilisation (Coles 2006). This is an isolated example but provides an illustration of the potential complexity of interactions between hydrogeomorphic and biotic processes in pre-Holocene temperate settings.

8.2.4. Further potential sources of disturbance

Disturbance agents other than herbivores, wildfire and hydrogeomorphic processes, such as wind and pathogens, are less easily observed in 'palaeo-records'. However, they are of no lesser potential importance and require consideration. Wind-related disturbance is important in European forest ecosystems (Dale *et al.* 2001; Schelhaas *et al.* 2003), particularly as a major driver of 'gap' creation via tree felling and mortality. This facilitates the regeneration of light-demanding plants, and increases local habitat heterogeneity, leading to increased faunal and floral diversity (Muscolo *et al.* 2014), particularly amongst insects (Bouget & Duelli 2004). Wind disturbances may also weaken trees, without causing mortality (e.g. leaf damage) (Gardiner *et al.* 2016), which may make them more susceptible to other disturbance agents. On the basis of enhanced temperature gradients in the North Atlantic during the early Middle Pleistocene, it has been suggested that Britain and Northwest Europe experienced enhanced storminess during this period (Candy & McClymont 2013). This would certainly have led to increased wind-related disturbance, influencing forest structure, successional turnover rates and landscape-scale biodiversity (γ-diversity). However, proxy evidence for the ecological effects of this (e.g. storminess records correlated with pollen records) in Northwest Europe is not (yet) apparent.

Fungal (e.g. Dutch elm disease) and faunal (e.g. Scolytinae) parasites of living trees are a notable source of disturbance in modern and Holocene forests (Waller 2013; Morris *et al.* 2015). The effects of such parasitic organisms, and their interactions with other stresses, have been observed in modern contexts (e.g. Thomas *et al.* 2002; Raffa *et al.* 2008; Pautasso *et al.* 2013), and implicated in declines of particular tree species during the Holocene (see Waller 2013 for a review). Often, this is in the context of large-scale 'outbreaks', but these organisms also persist at low levels, inducing less severe disturbances, with attacks on individual trees often facilitated by damage or weakening by other disturbance agents or climatic factors (Waller 2013). However, there is potential for such disturbances to be detected using palaeoecological methods, particularly in the context of large-scale 'outbreaks' (Waller 2013; Seddon *et al.* 2014). For example, declines in particular tree taxa, or changes in forest structure, may be detected using pollen records, which may theoretically be correlated with proxy evidence for increased abundances of associated pathogenic organisms (e.g. fungal spores, Scolytinae remains) (Waller 2013; Morris *et al.* 2015). In the context of this thesis, though the remains of several Scolytinae species have been recorded (e.g. *Scolytus multistriatus* Marsh., *Hylastes attenuatus* Er.), their abundances are by no means unusual, and certainly do not indicate 'outbreak' events. Whilst the habits of Scolytinae are often parasitic on living trees (Duffy 1953), and they likely induced some level of stress on their hosts, the available evidence does not suggest that they were a major source of disturbance in the present study. Rather, the presence of Scolytinae is primarily indicative of the availability of their preferred hosts in this context. However, it remains possible that parasitic fungi and insects may have induced greater disturbance during the early Middle Pleistocene than recorded in this work, particularly at times of enhanced climatic stress for deciduous trees, such as during interglacial-glacial transitions.

8.2.5. Summary and future research

Disturbance regimes are clearly important in the ecology of early Middle Pleistocene interglacial environments, and the evidence presented here suggests the roles of herbivore activity, wildfire and hydrogeomorphic processes in determining local vegetation structure. Additionally, it is shown that the relative influence of different disturbance agents varies between sites, emphasising the importance of local (e.g. herbivore density, hydrogeomorphic processes) and climatic (e.g. precipitation seasonality) factors particular to each record. This suggests that such spatially and temporally local factors are of greater importance in determining the influence of disturbance regimes than characteristics shared between records, such as the presence of large herbivores and atmospheric CO_2 ≤260ppmv (Lüthi *et al.* 2008) (see Section 2.4). However, in order to fully substantiate this in the present context, it would be necessary to study several temporally synchronous, but spatially distinct, records. Furthermore, though each disturbance agent has been discussed largely in isolation, in reality all would have acted together in concert, operating in complex systems of mutually influential interactions. Given knowledge of disturbance regimes in modern and Holocene contexts (e.g. Bradshaw *et al.* 2003; Viles *et al.* 2008; Turner 2010; Seidl *et al.* 2014), these are not necessarily surprising results. However, whilst the influence of disturbance regimes in pre-Holocene interglacial settings has previously been suggested (e.g. Gibbard & Stuart 1975; Keen *et al.* 1999; Green *et al.* 2006; Field & Peglar 2010), the nuance of such relationships has not often been explored in detail in these contexts, particularly for early Middle Pleistocene interglacial settings (*cf.* Kuneš *et al.* 2013).

Further study must be carried out in order to achieve a greater understanding of the ecological effects of disturbance regimes in pre-Holocene settings, which can be achieved through a combination of neo- and palaeoecology. Towards this end, more studies explicitly addressing multiple disturbance processes in interglacial records must be undertaken. Of particular value, in the context of modern climate change, would be to use these records to determine the influence of different climatic regimes on the functioning and impacts of disturbance processes. The development of a disturbance 'indicator package' (*sensu* Kenward & Hall 1997), incorporating faunal, floral, fungal and sedimentological indicators of different disturbance agents, would be of great value in determining long-term trends in disturbance regimes. Additionally, studies of disturbance-vegetation interactions in modern settings will continue to be informative in the study of past and present ecosystems.

These conclusions are of interest beyond palaeoecology, for conservation practitioners interested in the restoration of ecosystem processes and biotic interactions (e.g. 'rewilding'-type approaches, *sensu* Pereira & Navarro 2015). In particular, evidence is given indicating that it is possible for large herbivores to exist at densities sufficient to exert noticeable influence on vegetation communities in Northwest Europe, but without preventing woodland regeneration. However, large predators are also ubiquitous alongside large herbivores in such early Middle Pleistocene contexts (Lewis *et al.* 2010; Kahlke *et al.* 2011). These include large Felidae (e.g. *Panthera leo*, *Homotherium latidens*), Canidae (e.g. *Canis lupus*, *Xenocyon lycaonoides*), Ursidae (*Ursus* spp.) and Hyaenidae (e.g. *Crocuta crocuta*), as well as *Homo* spp. Their importance in providing a 'top-down' control on herbivore abundances should not be underestimated. The presence of such predators may also affect herbivore behaviour indirectly through fear, altering their local distribution and feeding habits, with cascading effects on tree regeneration (e.g. Kuijper *et al.* 2013). The absence (or rarity) of large carnivores, typical of early Middle Pleistocene interglacials, in modern European contexts prevents direct comparison.

The potential complexity of interacting disturbance regimes, and importance of local factors in determining their relative influences, in the absence of human intervention, emphasises the need for caution in such endeavours. This complexity and variability mean that the precise effects of reinstating, or instigating, independently operating disturbance processes (e.g. re-introducing herbivory by unmanaged large herbivores) are likely to be difficult to predict. Depending on the context, this may not be problematic, but it should be borne in mind that such projects may have ecological consequences beyond those intended.

8.3. Interglacial Climates and the Mid-Brunhes Transition

The new analyses presented in Chapter 7 offer a refined view of interglacial climates in Britain during the Middle and Late Pleistocene (*c.* 780-125 ka, MIS 19-5e), particularly regarding winter temperatures and annual temperature seasonality. These reconstructions are remarkable for their consistency, between and within marine oxygen isotope stages, and prior to and following the Mid-Brunhes Transition (MBT). This strongly supports the view that the MBT does not have a recognisable temperature signal in British terrestrial contexts. This is in broad agreement with previous research in the region (Candy *et al.* 2010; Candy & McClymont 2013), though it does give a contradictory perspective to previous suggestions that the MBT may have been marked by a shift in winter temperatures or temperature seasonality in these contexts (*cf.* Candy

& McClymont 2013). However, the presently unexplored possibility is that it may be registered in another aspect of climate in this region (e.g. precipitation, storminess), and this possibility is discussed below (Section *8.3.2.*). It is also suggested that whilst coldest month temperatures were potentially cooler than those currently experienced in southern Britain during certain periods at the sites investigated, they were never milder (see Figure 7.2 & Table 7.2). Furthermore, temperature seasonality may have been enhanced, relative to the present, during some periods, but appears unlikely to have been reduced.

8.3.1. Implications for Middle Pleistocene interglacial climates in the British Isles

Studies of interglacial climates in Britain and Northwest Europe have previously been focussed on the reconstruction of summer temperatures (e.g. Coope 2006; Candy *et al.* 2010), largely owing to methodological limitations when reconstructing other climatic variables (e.g. low precision of winter temperature reconstructions). However, in the present thesis, interglacial winter temperatures and temperature seasonality have been estimated with sufficient precision to explore these variables during the periods of time represented at the sites included in this investigation.

The new reconstructions presented in Chapter 7 are broadly consistent throughout the Middle Pleistocene. This provides strong indication that thermoclimatic conditions in Britain (and by extension, Northwest Europe) were largely unaffected by the MBT, according to records from the sites investigated. This is shown by reconstructions of July temperatures (TMax), January temperatures (TMin) and temperature seasonality (TRange), none of which vary according to whether they precede or follow the MBT. Additionally, it is shown that the occurrence of ‘exotic’ thermophilous taxa, which may indicate enhanced warmth (during various seasons), is also consistent both prior and subsequent to the MBT (as previously highlighted by Candy *et al.* 2010). The new reconstructions are based on several aspects of climate (TMax, TMin and TRange), and so expand significantly on previous analyses, which were based only on summer temperatures as an indicator of interglacial ‘warmth’ (Candy *et al.* 2010). This is an unexpected result, as there is good evidence that global climatic and atmospheric conditions during early Middle Pleistocene interglacials were distinct from those of the late Middle Pleistocene (see Chapter 2, Section *2.2.4.*). In particular, an enhanced temperature gradient in the North Atlantic, a more southerly Polar Front (Candy & McClymont 2013), and atmospheric CO_2 concentrations 20-30ppmv lower than late Middle Pleistocene interglacials (Lüthi *et al.* 2008) mark this period. Given this context, it is highly unlikely that interglacial climates in Britain during the early Middle Pleistocene were directly analogous to those of the late Middle and Late Pleistocene, but it seems this difference is likely to be reflected in variables other than temperature (e.g. precipitation variables). Indeed, a more southerly polar front during this period has been suggested (*cf.* Candy & McClymont 2013), which may have driven enhanced precipitation in Western Europe. This concurs with evidence from Atapuerca, northwest Spain, for a wetter climate during early Middle Pleistocene interglacials, based on changes in herpetofaunal assemblages (Blain *et al.* 2009, 2012). Therefore, given the significant lack of evidence for a temperature signal, a change in precipitation regimes or storm frequency may mark the MBT in Northwest Europe. This theory is explored further in Section *8.3.2.* A further point of consideration is that during the early Middle Pleistocene, Britain was a permanent peninsula of Europe during both glacial and interglacial periods (Gupta *et al.* 2007; Rose 2009). The dispersal of terrestrial flora and fauna from southern refugial areas into Britain was therefore not restricted by interglacial sea level rise during this period, which may have led to enhanced diversity in biological assemblages, as well as potentially altered timing of arrival in Britain for terrestrial biota. However, the testing of these theories is beyond the scope of the present thesis. Additionally, as discussed in Section *2.4.2.*, notably lower atmospheric CO_2 during early Middle Pleistocene interglacials (≤260ppmv: Lüthi *et al.* 2008) is likely to have impacted on plant growth and reproduction, with complex ecological consequences, though the precise nature of such impacts are not presently discernible.

The reconstructions in Chapter 7 (Fig. 7.2, Table 7.2) have also given new insights into the nuance of interglacial climates in Britain. In particular, they reveal that enhanced summer warmth may sometimes have been accompanied by cooler winters, though this is not a general pattern. This has been previously posited (e.g. Candy *et al.* 2016), but not demonstrated. The new coleopteran MCR reconstruction from Chapter 7 for Bobbitshole (MIS 5e), the Ipswichian type site, provides the most striking illustration of this finding. It indicates average January temperatures *c.* 3-4°C cooler than the region at present, and July temperatures *c.* 3-4°C warmer (Fig. 7.2, Table 7.2) at this site. Though reconstructions from other sites in Chapter 7 deviate less notably from modern values, the Bobbitshole reconstruction serves to demonstrate effectively that discussing mid-latitude interglacial climates in terms of overall 'warmth' or 'intensity' is perhaps too simplistic. Rather, the inherent intra-annual complexity and nuance should be recognised, as far as preservation of the evidence allows.

As discussed in Section 7.4, there are two notable caveats associated with these findings which should be borne in mind. Firstly, most of the records analysed here are 'snapshots', representing only short periods within interglacials, and the analysis of records representative of full interglacial sequences would be necessary for these findings to be truly conclusive. Secondly, the records used in Chapter 7 are unlikely to be drawn from directly equivalent interglacial substages. Therefore, comparisons between records are not necessarily made on a ‘like-for-like’ basis.

8.3.2. Broader implications for interglacial climates and the Mid-Brunhes Transition

The analyses and discussion presented here represent significant progress towards solving the question of MBT expression in Northwest Europe, and open new lines of enquiry into this phenomenon. On the basis of reconstructions of summer and winter temperatures, as well as temperature seasonality, it has been demonstrated that this transition is unlikely to have a temperature component in this region. Following from this, an alternative theory is explored in this section: MBT expression in Northwest Europe may be more closely related to precipitation or storm regimes, controlled by orbitally-mediated hemispheric temperature gradients. It is acknowledged that other complex factors (e.g. the North Atlantic Oscillation) are also potentially important in this context, or that there may be an absence of MBT expression in Northwest Europe, but evidence for such scenarios is not forthcoming at present.

Enhanced precipitation during the early Middle Pleistocene in Northwest Europe may be inferred on the basis of several lines of evidence. Firstly, reconstructions of sea surface temperatures from the North Atlantic suggest a more southerly polar front during this period (Candy & McClymont 2013), and this may have driven enhanced precipitation in Western Europe. This is corroborated by reconstructions of mean annual precipitation from Atapuerca in northwest Spain (based on herpetofaunal assemblages), which suggest a wetter climate during early Middle Pleistocene interglacials (Blain *et al.* 2009, 2012). (However, the conclusions of Blain *et al.* (2009, 2012) should be approached with caution, as palaeoclimatic inferences are based on species climatic envelopes which do not account for non-Iberian portions of species ranges.) Further east, in the western Balkans, there is also some suggestion of a shift from more to less humid interglacials during the Middle Pleistocene. This is registered in Serbian loess sequences as a shift towards more steppic environments (Fitzsimmons *et al.* 2012), and a shift from cooler and wetter to drier and warmer climates is registered by a range of proxies at Lake Ohrid, FYROM/Albania (Wagner *et al.* 2017). These proxy signals are less conclusively associated with the MBT, due to chronological uncertainties. The Serbian loess sequences currently lack chronological control (Fitzsimmons *et al.* 2012), and the precise timing of transition in Lake Ohrid is unclear, but suggested to be *c.*300 ka (Wagner *et al.* 2017). However, this does not rule out MBT influence. As suggested in Chapter 2 (Section *2.2.3.*), on the basis of a lack of evidence from continental Siberia (e.g. Prokopenko *et al.* 2002, 2006; Melles *et al.* 2012), the MBT may be an ocean-propagated signal. This would account for a weaker, or less distinct, influence in the Balkans (Serbian loess, Lake Ohrid) compared to Iberia (Atapuerca). This may also account for the lack of influence on arboreal pollen values at Tenaghi Philippon in Greece (Tzedakis *et al.* 2006), which lies slightly further east than both the Serbian loess deposits and Lake Ohrid (see Figure 2.2 for a map).

The global characteristics (e.g. orbital configuration) of early Middle Pleistocene interglacials provide a mechanism for driving potentially wetter interglacials in Western Europe, and also offer an explanation for the clearer signal in high-latitude and oceanic records. The amplitude of variation in orbital obliquity is generally greater in the late Middle and Late Pleistocene, than in the early Middle Pleistocene (Berger *et al.* 2015). Consequently, a link between the MBT and orbital parameters has been suggested, and variations in obliquity are often cited as potentially significant (EPICA 2004; Jouzel *et al.* 2007; Yin & Berger 2010; Lang & Wolff 2011; Yin 2013; Berger *et al.* 2015). In particular, obliquity is a noted control on high-latitude summer insolation (Yin &

Berger 2012). Modelling experiments (Yin & Berger 2010; Yin 2013) have shown that variations in high-latitude insolation, primarily driven by these variations in obliquity, are the dominant control on interglacial 'intensity' (*sensu* Yin 2013) during the last 800 ka. Additionally, Berger *et al.* (2015) noted that interglacial 'peaks' (as defined by LR04 benthic δ^{18}O: Liseicki & Raymo 2005) tend to be preceded by *c.* 10 ka (obliquity-driven) high-latitude summer insolation positive anomalies, which are greater following the MBT. This indicates cooler high latitudes, relative to mid- and low latitudes, prior to the MBT, and therefore enhanced latitudinal temperature gradients during the early Middle Pleistocene (illustrated in Figure 8.3).

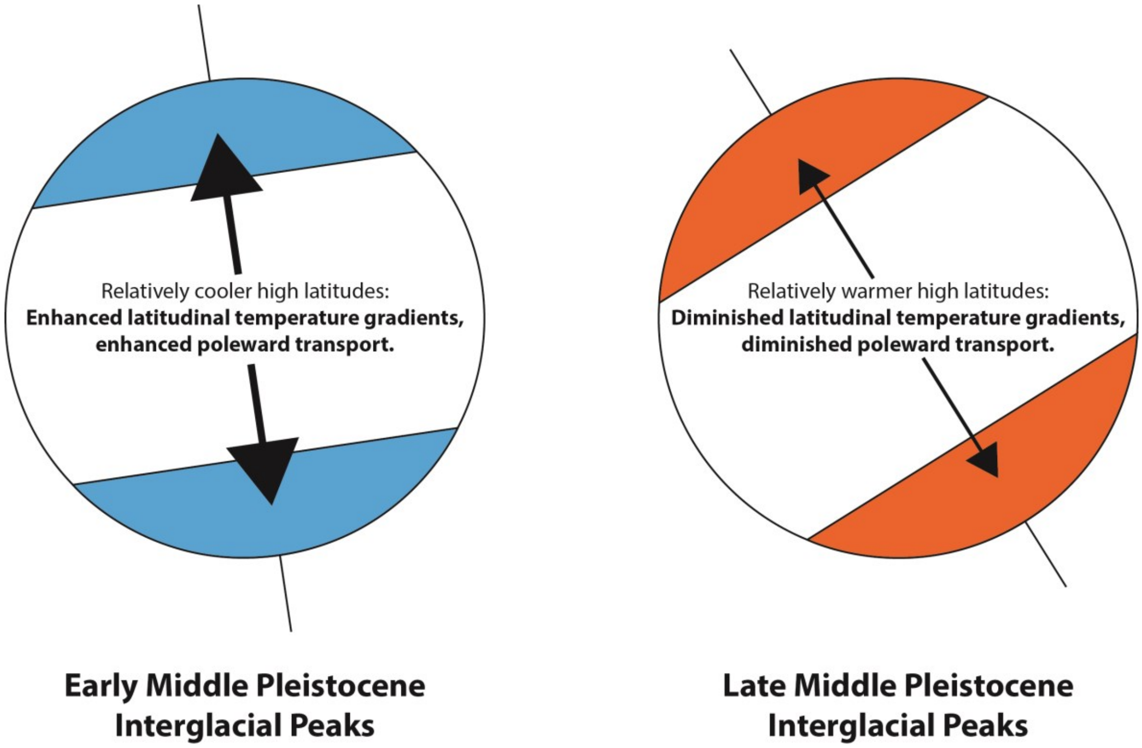


Figure 8.3 – Schematic illustrating the postulated effects of lower obliquity during early Middle Pleistocene interglacial peaks, relative to late Middle Pleistocene interglacial peaks

This general pattern of lower high-latitude summer insolation preceding the MBT (inferred from lower obliquity), provides a coherent explanation for its clearer signal in high-latitude (e.g. EPICA 2004; Jouzel 2007) and cryospherically-influenced deep ocean (e.g. Jansen *et al.* 1986; Lisiecki & Raymo 2005) temperature records, than those from mid-latitudes (e.g. Candy *et al.* 2010; this thesis, Chapter 7). It also provides a convenient explanation for the enhanced temperature gradients between high and mid-latitudes in the North Atlantic during early Middle Pleistocene interglacials, observed by Candy & McClymont (2013). Furthermore, an enhanced temperature gradient between high and low latitudes is known to drive increased poleward moisture transport (Loutre *et al.* 2004). This accords with observations of generally wetter interglacial climates in Europe prior to the MBT (Blain *et al.* 2012; Fitzsimmons *et al.* 2012; Wagner *et al.* 2017) discussed earlier, as well as the suggestion that this is an ocean-propagated signal (and therefore clearer in Western Europe than in Eastern Europe). This further suggests that MBT influence in Britain and Northwest Europe is more likely to be evident in hydroclimatic variables than in thermoclimatic variables. However, this is unlikely to have been straightforward, as there are some indications of more seasonal precipitation regimes in Britain during early Middle Pleistocene interglacials, relative to the present. This has been suggested on the basis of palaeopedological and stable isotopic evidence from Pakefield (*c.* MIS 15-17, Candy *et al.* 2006), and Ostracoda δ^{18}O from Boxgrove (*c.* MIS 13, Holmes *et al.* 2010). Enhanced annual precipitation has also been suggested for West Runton (*c.* MIS 15-17) on the basis of herpetofaunal assemblages (Böhme 2010: sampled close to Coope's (2010b) beetle sequence (see Figure 4.1)), which may have even occurred simultaneously with altered precipitation seasonality. Finally, the general pattern corresponds to ideas proposed by Ruddiman *et al.* (1989) and Song *et al.* (2014), in the context of the Mid-Pleistocene Revolution (MPR). This is a shift from 41 ka obliquity-dominated climatic cycles during the Early Pleistocene, to 100 ka eccentricity/precession-dominated climatic cycles from *c.* 900 ka BP (Middle and Late Pleistocene) (Pisias & Moore 1981; Ruddiman *et al.* 1989; Maslin & Ridgwell 2005). Their work suggests that the MBT is not a separate phenomenon from the MPR, but rather that it represents the ‘final throes’ of the MPR. The early Middle Pleistocene may therefore be viewed as a transitionary period between obliquity-dominated cycles and eccentricity-dominated cycles, in which obliquity and eccentricity/precession were co-dominant in their effects on global climate. This is supported by the apparent influence of obliquity on early Middle Pleistocene interglacial climates explored here.

8.3.3. Summary and future research

This section has shown that interglacial thermoclimatic conditions in Britain are unlikely to have been significantly affected by the MBT. Rather, it seems that the signature of this transition in Northwest Europe is more likely to lie in interglacial hydroclimatic conditions, due to enhanced poleward moisture transport as a result of generally diminished high-latitude summer insolation during the early Middle Pleistocene. This work has illustrated the complexity of interglacial climates in Northwest Europe, and suggests caution in applying the concept of ‘interglacial intensity’ (*cf.* Tzedakis *et al.* 2009; Berger *et al.* 2015) at regional spatial scales. At a global scale, ‘interglacial intensity’ is generally demonstrated by proxies of total ice volume, sea level or atmospheric greenhouse gas concentrations (e.g. Lisiecki & Raymo 2005; Lüthi *et al.* 2008; Tzedakis *et al.* 2009 and others), but as highlighted by the present work, the propagation of ‘global’ climatic conditions at regional scales is not straightforward. The potential consequences of a wetter climate in Northwest Europe during the early Middle Pleistocene in terms of ecology and landscape are not yet clear, though would likely have led to the formation of more extensive fluvial and wetland systems. This may have favoured certain organisms, and indeed the timing of *Alnus* expansion in Britain appears to have varied amongst Middle Pleistocene temperate stages, potentially occurring earlier in the Cromerian than in the Hoxnian or Ipswichian stages (*sensu* West 1980b). However, though it is tempting to interpret this as a response to (potentially) wetter conditions during early Middle Pleistocene interglacials (the Cromerian, *sensu* West 1980b), this is complicated by a lack of independent chronological controls on Middle Pleistocene pollen records from Britain. This is a particular problem for early Middle Pleistocene records, for which pollen biostratigraphy is based on a series of fragmentary sequences from fluvial and alluvial settings (West 1980a). Therefore, without independent chronological controls, it is difficult to verify whether Cromerian expansions of *Alnus* are indeed broadly simultaneous and 'early', or if they are simply representative of local ecological changes.

Future research into the MBT in Northwest Europe should focus on reconstructing hydroclimatic variables (e.g. mean annual precipitation, precipitation seasonality, storminess). Whilst reconstructions of such variables have occasionally been undertaken for individual Middle Pleistocene sites in Britain (e.g. Candy *et al.* 2006; Böhme 2010; Holmes *et al.* 2010), this has never been carried out for a suite of sites spanning the Middle Pleistocene. Such investigations may be undertaken by re-sampling for proxies already employed in such contexts (e.g. Ostracoda δ^{18}O: Holmes *et al.* 2010). Alternatively, pre-existing Middle Pleistocene plant macrofossil records in Britain (e.g. West 1980a) are similar in temporal coverage to coleopteran records, and have been effectively utilised in pre-Holocene contexts to reconstruct hydroclimatic variables elsewhere in Europe (e.g. Kühl *et al.* 2007). This represents a potentially promising avenue of enquiry into the representation of the MBT in mid-latitude Northwest Europe, particularly given the potential for applying modern niche modelling techniques to such datasets for the purposes of palaeoclimate reconstructions (e.g. Polly & Eronen 2011; Svenning *et al.* 2011). This could potentially be used to develop functional categories of plants according to hydroclimatic variables, the relative abundances of which may then provide insights into interglacial hydroclimatic conditions. However, the prominence of wetland deposits amongst interglacial records (see Table 2.2.) in Britain may complicate this.

8.4. Archaeological Relevance

The early Middle Pleistocene in Britain is associated with evidence for some of the earliest range expansions of *Homo* into Northern Europe (Parfitt *et al.* 2005; Hosfield *et al.* 2011; Ashton & Lewis 2012; Preece & Parfitt 2012). As with any other large mammal, the environmental context of hominin occurrence is fundamental to understanding these early hominin populations (Candy *et al.* 2011), and a preference for mosaic landscapes, incorporating wetland, woodland, semi-open and open habitats, is noted amongst Eurasian Palaeolithic *Homo* (Finlayson *et al.* 2011). Ecological analyses presented here suggest the importance of disturbance regimes in driving and maintaining such habitat heterogeneity in Northwest Europe during the early Middle Pleistocene. The most significant disturbance agents are likely to vary with time and space, but it is implicit that levels of disturbance capable of producing and maintaining such 'mosaic' landscapes may be a hitherto unrecognised, but important, component of the ecological niche of Palaeolithic *Homo* in Eurasia. Furthermore, this suggests a dual importance for large herbivores at sites such as Pakefield and Brooksby (both noted for hominin presence: Parfitt *et al.* 2005; D. Schreve 2012, pers. comm.). As a source of food and raw materials, the value of large herbivores to *Homo* spp. is self-evident, but they may also have played an important facultative role as 'ecosystem engineers', acting to maintain mosaic landscapes with high local habitat diversity. Such landscapes would likely have provided a diversity of resources for *Homo* spp. (food, raw materials), as well as facilitating hunting through ambush strategies, due to the combination of open, semi-open and woodland habitats (Finlayson *et al.* 2011). The hunting and resource gathering activities of these hominins also undoubtedly exerted some level of disturbance on the ecosystems in which they were present. However, given that these are likely to have been small, sparse populations (Ashton & Lewis 2012), their ecological influence is unlikely to have been extensive.

The suggestion that climates in Britain during the early Middle Pleistocene may have been wetter is also of potential archaeological significance. Such climatic conditions would have led to more extensive wetlands and floodplain landscapes. These areas provided notable advantages to Lower Palaeolithic populations, particularly in terms of the quality and diversity of food resources available (Brown *et al.* 2013). These include a broad range of food sources available year round, including foods with high fat content (e.g. fish, waterfowl, *Castor fiber* tails), high carbohydrate content (e.g. underground storage organs of plants such as *Typha latifolia*, *Trapa natans* and *Nuphar lutea*) and important vitamins (e.g. *Nasturium officinale*) (Brown *et al.* 2013). The availability of nutrition during winter months may have been a notable barrier to early hominin range expansions into Northern Europe (Roebroeks 2001), and an enhanced availability of wetland resources may have alleviated this. Wetter climates during early Middle Pleistocene interglacials may therefore have partly facilitated such early incursions of hominins into Northern Europe, though other factors including technological (e.g. clothing) and behavioural (e.g. seasonal migration) adaptations may have also been important. However, there is currently no direct evidence for such behaviours or technologies in Northern Europe during the early Middle Pleistocene (Ashton & Lewis 2012).

Chapter 9

Conclusions

This thesis provides new insights into the complexity, dynamism and nuance of local ecology and regional climate during early Middle Pleistocene (*c.* 780-430 ka, MIS 19-13) interglacials in Britain, and the main findings and implications are summarised here.

Disturbance regimes (herbivore activity, wildfire and hydrogeomorphic processes) are shown to be important determinants of local vegetation structure and habitat heterogeneity at three early Middle Pleistocene sites (West Runton, Pakefield, Brooksby). The available evidence suggests that the relative influence of different disturbance agents varies between sites, emphasising the importance of factors which are spatially (e.g. herbivore density, hydrogeomorphic processes) and temporally (e.g. climate) particular to each record. This suggests that site-specific factors are more significant in this context than those shared between records (e.g. large herbivore presence, atmospheric CO_2 ≤260ppmv: Lüthi *et al.* 2008). Further study of additional early Middle Pleistocene records explicitly addressing multiple disturbance processes is necessary to fully substantiate this, particularly given that a range of caveats are associated with determining the local significance of different disturbance agents (discussed in Chapters 4-6).

Based on the records analysed, there is no forthcoming evidence for the Mid-Brunhes Transition (MBT) in Britain (and by extension, Northwest Europe) on the basis of thermoclimatic variables (summer temperatures, winter temperatures, temperature seasonality), reconstructed using the coleopteran Mutual Climatic Range (MCR) method. In this region, MBT expression is more likely to be reflected in hydroclimatic variables (e.g. enhanced mean annual precipitation, precipitation seasonality or storminess) due to enhanced poleward moisture transport during the early Middle Pleistocene. This would likely have led to the formation of more extensive fluvial and wetland systems than in late Middle Pleistocene interglacials. Future palaeoclimatic research focussed on the reconstruction of hydroclimatic variables in Northwest Europe will be valuable in this context. It has also shown that high summer temperatures may be accompanied by low winter temperatures (relative to the present day) in some individual cases (e.g. Bobbitshole), suggesting caution in applying the concept of ‘interglacial intensity’ at regional spatial scales.

Both ecological and climatic components of this thesis also have implications for contemporary Lower Palaeolithic populations in Northwest Europe. Firstly, the importance of disturbance regimes in driving and maintaining habitat heterogeneity suggests that they are a significant, but hithero unrecognised, factor in the ecological niche of Palaeolithic *Homo* in Eurasia, due to a preference for mosaic landscapes. Secondly, potentially wetter climates during this period may have partly facilitated early incursions of hominins into the region, due to the enhanced availability of important wetland resources, though other factors (e.g. technological and behavioural adaptations) are also likely to have been important.

References

Aalbersberg G., Litt T. (1998). Multiproxy climate reconstructions for the Eemian and Early Weichselian. *Journal of Quaternary Science* **13**: 367–390.

Agee J.K. (1998). Fire and pine ecosystems. In: *Ecology and Bioegeography of Pinus*. (Ed. D.M. Richardson), pp. 193–218. Cambridge University Press, Cambridge.

Akhmetova L.A., Frolov A.V. (2014). A review of the scarab beetle tribe Aphodiini (Coleoptera, Scarabaeidae) of the fauna of Russia. *Entomological Review* **94**: 846–879.

Alexander K. (2002). *The invertebrates of living and decaying timber in Britain and Ireland - a provisional annotated checklist*. English Nature Research Report 467, Peterborough.

Allen D.J. (2011). *Salvinia natans*. http://www.iucnredlist.org/details/163996/1. Accessed July 2006.

Anderson R. (1996). *Species inventory for Northern Ireland. Carabid beetles.* Belfast.

Anderson R. (1997). *Northern Ireland species inventories: Rove beetles (Coleoptera: Staphylinidae)*. Environment and Heritage Service Publications, Belfast.

Angus R.B. (1973). Pleistocene *Helophorus* (Coleoptera, Hydrophilidae) from Borislav and Starunia in the Western Ukraine, with a Reinterpretation of M. Lomnicki's Species, Description of a New Siberian Species, and Comparison with British Weichselian Faunas. *Philosophical Transactions of the Royal Society B: Biological*

Sciences **265**: 299–326.

Ashton N.M., Lewis S.G. (2012). The environmental contexts of early human occupation of northwest Europe: The British Lower Palaeolithic record. *Quaternary International* **271**: 50–64.

Ashton N.M., Lewis S.G., Parfitt S.A., Penkman K.E.H., Russell Coope G. (2008a). New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. *Quaternary Science Reviews* **27**: 652–668.

Ashton N.M., Parfitt S.A., Lewis S.G., Coope G.R., Larkin N.R. (2008b). Happisburgh Site 1 (TG388307). In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 151–156. Quaternary Research Association.

Ashton N.M., Lewis S.G., Stringer C.B. (2011). *The Ancient Human Occupation of Britain (Developments in Quaternary Science 14)*. Elsevier, Amsterdam.

Asner G.P., Levick S.R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters* **15**: 1211–1217.

Asner G.P., Vaughn N., Smit I.P.J., Levick S.R. (2016). Ecosystem-scale effects of megafauna in African savannas. *Ecography* **39**: 240–252.

van Asperen E.N., Kirby J.R., Hunt C.O. (2016). The effect of preparation methods on dung fungal spores: Implications for recognition of megafaunal populations. *Review of Palaeobotany and Palynology* **229**: 1–8.

Atkinson T., Briffa K., Coope G.R. (1987). Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*: 587–592.

Atty D.B. (1983). *Coleoptera of Gloucestershire*. D.B. Atty, Cheltenham.

Baker A.G., Bhagwat S.A., Willis K.J. (2013). Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews* **62**: 21–31.

Baker A.G., Cornelissen P., Bhagwat S.A., Vera F.W.., Willis K.J. (2016). Quantification of population sizes of large herbivores and their long-term functional role in ecosystems using dung fungal spores. *Methods in Ecology and Evolution* **7**: 1273–1281.

Bakker E.S., Gill J.L., Johnson C.N., Vera F.W., Sandom C.J., Asner G.P., Svenning J.-C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences* **113**: 847–855.

Ball G., Currie D. (1997). Ground beetles of the Yukon Ground Beetles (Coleoptera: Trachypachidae and Carabidae) of the Yukon: Geographical Distribution , Ecological Aspects, and Origin of the Extant Fauna. In: *Insects of the Yukon*. (Eds H. Danks & J. Downes), pp. 445–489. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.

Bates M.R., Parfitt S.A., Roberts M.B. (1997). The chronology, palaeogeography and archaeological significance of the marine quaternary record of the West Sussex Coastal Plain, Southern England, U.K. *Quaternary Science Reviews* **16**: 1227–1252.

Beal L.M., De Ruijter W.P.M., Biastoch A., Zahn R. (2011). On the role of the Agulhas system in ocean circulation and climate. *Nature* **472**: 429–36.

Beesley A. (1988). *The Climate and Environmental Significance of an Interglacial Fauna from Itteringham, Norfolk.* Unpublished MSc. University of Birmingham.

Belshaw R.K., Gibbard P.L., Murton J.B., Murton D.K. (2014). Early Middle Pleistocene drainage in southern central England. *Netherlands Journal of Geosciences - Geologie en Mijnbouw* **93**: 135–145.

Bennett K. (1996). Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* **132**: 155–170.

Berger A., Crucifix M., Hodell D., Mangili C., McManus J., Otto-Bliesner B., Pol K., Raynaud D., Skinner L., Tzedakis P.C., Wolff E.W., Yin Q., Abe-Ouchi A., Barbante C., Brovkin V., Cacho I., Capron E., … Honisch N. (2015). Interglacials of the last 800,000 years. *Reviews of Geophysics* **54**: 162–219.

Berna F., Goldberg P., Horwitz L.K., Brink J., Holt S., Bamford M., Chazan M. (2012). Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. *Proceedings of the National Academy of Sciences* **109**: E1215–E1220.

Beug H. (2004). *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Dr Friedrich Pfeil, Germany.

Binney H.A., Waller M.P., Bunting M.J., Armitage R.A. (2005). The interpretation of fen carr pollen diagrams: The representation of the dry land vegetation. *Review of Palaeobotany and Palynology* **134**: 197–218.

Bintanja R., van de Wal R.S.W., Oerlemans J. (2005). Modelled atmospheric temperatures and global sea levels over the past million years. *Nature* **437**: 125–8.

Bishop M. (1982). The mammal fauna of the early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset. *Special Papers in Palaeontology* **28**: 1–108.

Blaauw M. (2012). Out of tune: the dangers of aligning proxy archives. *Quaternary Science Reviews* **36**: 38–49.

Blackford J.J., Innes J.B. (2006). Linking current environments and processes to fungal spore assemblages: Surface NPM data from woodland environments. *Review of Palaeobotany and Palynology* **141**: 179–187.

Blackford J.J., Innes J.B., Hatton J.J., Caseldine C.J. (2006). Mid-Holocene environmental change at Black Ridge Brook , Dartmoor , SW England : A new appraisal based on fungal spore analysis. **141**: 189–201.

Blain H.-A., Bailon S., Cuenca-Bescós G., Arsuaga J.L., Bermúdez de Castro J.M., Carbonell E. (2009). Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. *Journal of human evolution* **56**: 55–65.

Blain H.-A., Cuenca-Bescos G., Lozano-Fernandez I., Lopez-Garcia J.M., Olle a., Rosell J., Rodriguez J. (2012). Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence. *Geology* **40**: 1051–1054.

Blake J. (1890). The geology of the country near Yarmouth and Lowestoft. *Memoirs of the Geological Survey of England and Wales*.

Bloemendal J., Liu X., Sun Y., Li N. (2008). An assessment of magnetic and geochemical indicators of weathering and pedogenesis at two contrasting sites on the Chinese Loess plateau. *Palaeogeography, Palaeoclimatology, Palaeoecology* **257**: 152–168.

Boháč J., Matějka K. (2016). Communities of Epigeic Beetles in Tree Line from Montaine Spruce Forest to Secondary Meadow in the Different Stage of the Forest Decline in the Area of Modrava (Bohemian Forest, Czech Republic). *Ekológia (Bratislava)* **35**: 340–349.

Böhme M. (2010). Ectothermic vertebrates, climate and environment of the West Runton Freshwater Bed (early Middle Pleistocene, Cromerian). *Quaternary International* **228**: 63–71.

Bonan G.B. (2008). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**: 1444–1449.

Bond W.J., Keeley J.E. (2005). Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**: 387–394.

Bond W.J., Midgley J.J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution* **16**: 45–51.

Boreham S., White T.S., Bridgland D.R., Howard A.J., White M.J. (2010). The Quaternary history of the Wash fluvial network, UK. *Proceedings of the Geologists' Association* **121**: 393–409.

Bosmans B. (2012). Recent finds of notable Curculionoidea (Coleoptera) for the province of Limburg. *Phegea* **40**: 82–85.

Bouget C., Duelli P. (2004). The effects of windthrow on forest insect communities: a literature review. *Biological Conservation* **118**: 281–299.

Bowen D.Q., Rose J., McCabe A.M., Sutherland D.G. (1986). Correlation of quaternary glaciations in England, Ireland, Scotland and Wales. *Quaternary Science Reviews*

5: 299–340.

Bowestead S. (1999). *A revision of the Corylophidae (Coleoptera) of the West Palaearctic region*. Muséum d'histoire naturelle Genève, Geneva.

Bradshaw R.H.W., Hannon G.E. (2004). The Holocene Structure of North-west European Temperate Forest Induced from Palaeoecological Data. In: *Forest Biodiversity: Lessons from History for Conservation*. (Eds O. Honnay, K. Verheyen, B. Bossuyt & M. Hermy), pp. 11–25. CABI Publishing, Cambridge, USA.

Bradshaw R.H.W., Hannon G.E., Lister A.M. (2003). A long-term perspective on ungulate–vegetation interactions. *Forest Ecology and Management* **181**: 267–280.

Bray P.J., Blockley S.P.E., Coope G.R., Dadswell L.F., Elias S.A., Lowe J.J., Pollard A.M. (2006). Refining mutual climatic range (MCR) quantitative estimates of palaeotemperature using ubiquity analysis. *Quaternary Science Reviews* **25**: 1865–1876.

Breda M., Collinge S.E., Parfitt S.A., Lister A.M. (2010). Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy I: Rhinocerotidae and Bovidae. *Quaternary International* **228**: 136–156.

Bridgland D.R., Antoine P., Limondin-Lozouet N., Santisteban J.I., Westaway R., White M.J. (2006). The Palaeolithic occupation of Europe as revealed by evidence from the rivers: Data from IGCP 449. *Journal of Quaternary Science* **21**: 437–455.

Bridgland D.R., Howard A.J., White M.J., White T.S., Westaway R. (2015). New insight into the Quaternary evolution of the River Trent, UK. *Proceedings of the*

Geologists' Association **126**: 466–479.

Bridgland D.R., Preece R.C., Roe H.M., Tipping R.M., Coope G.R., Field M.H., Robinson J.E., Schreve D.C., Crowe K. (2001). Middle Pleistocene interglacial deposits at Barling, Essex, England: Evidence for a longer chronology for the Thames terrace sequence. *Journal of Quaternary Science* **16**: 813–840.

Bridgland D.R., Schreve D.C. (2004). Quaternary lithostratigraphy and mammalian biostratigraphy of the Lower Thames terrace system, South-East England. *Quaternaire* **15**: 29–40.

Briggs D.J., Gilbertson D.D. (1980). Quaternary Processes and Environments in the upper Thames Valley. *Transactions of the Institute of British Geographers* **5**: 53–65.

Briggs D.J., Coope G.R., Gilbertson D.D. (1985). *The Chronology and Environmental Framework of Early Man in the Upper Thames Valley*. British Archaeological Reports.

Broecker W.S. (1998). Paleocean circulation during the lst deglaciation: A bipolar seasaw? *Paleoceanography* **13**: 119–121.

Brough S., Barclay J., Andrews J., Bescoby D. (2010). Micro-tephra in the West Runton Freshwater Bed : Preliminary results. *Quaternary International* **228**: 21–24.

Brown A.G., Basell L.S., Robinson S., Burdge G.C. (2013). Site distribution at the edge of the Palaeolithic world: A nutritional niche approach. *PLoS ONE* **8**: 1–14.

Brown A.G., Carpenter R.G., Walling D.E. (2008). Monitoring the fluvial palynomorph load in a lowland temperate catchment and its relationship to suspended sediment and discharge. *Hydrobiologia* **607**: 27–40.

Brown A.G., Harper D., Peterken G. (1997). European Floodplain Forests: Structure, Functioning and Management. *Global Ecology and Biogeography* **6**: 169–178.

Buckingham C.M., Roe D.A., Scott K. (1996). A preliminary report on the Stanton Harcourt Channel Deposits (Oxfordshire, England): geological context, vertebrate remains and palaeolithic stone artefacts. *Journal of Quaternary Science* **11**: 397–415.

Buckland P.C., Buckland P.I., Panagiotakopulu E. (2016). Caught in a trap: landscape and climate implications of the insect fauna from a Roman well in Sherwood Forest. *Archaeological and Anthropological Sciences*: DOI 10.1007/s12520-016-0338-8.

Buckland P.I., Buckland P.C. (2006). Bugs Coleopteran Ecology Package. www.bugscep.com.

Bullock J. (1993). Host Plants of British Beetles: A List of Recorded Associations. *Amateur Entomologist* **11a**: 1–24.

Bunimovitz S., Barkai R. (1996). Ancient bones and modern myths: Ninth millennium BC hippopotamus hunters at Akrotiri Aetokremnos, Cyprus? *Journal of Mediterranean Archaeology* **9**: 83–94.

Bunting M.J. (2008). Pollen in wetlands: Using simulations of pollen dispersal and deposition to better interpret the pollen signal - A PolLandCal contribution. *Biodiversity and Conservation* **17**: 2079–2096.

Buse J., Šlachta M., Sladecek F.X.J., Pung M., Wagner T., Entling M.H. (2015).

Relative importance of pasture size and grazing continuity for the long-term conservation of European dung beetles. *Biological Conservation* **187**: 112–119.

Caley T., Giraudeau J., Malaizé B., Rossignol L., Pierre C. (2012). Agulhas leakage as a key process in the modes of Quaternary climate changes. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 6835–9.

Campbell J. (1983). A revision of the North American Omaliinae (Coleoptera: Staphylinidae). The genus Olophrum Erichson. *Canadian Entomologist* **115**: 577–622.

Campbell J. (1984). A revision of the North American omaliinae (coleoptera: staphylinidae): the genera Arpedium Erichson and Eucnecosum Reitter. *The Canadian Entomologist* **116**: 487–527.

Campbell J.F., Fletcher W.J., Hughes P.D., Shuttleworth E.L. (2016). A comparison of pollen extraction methods confirms dense-media separation as a reliable method of pollen preparation. *Journal of Quaternary Science* **31**: 631–640.

Candy I., Coope G.R., Lee J.R., Parfitt S.A., Preece R.C., Rose J., Schreve D.C. (2010). Pronounced warmth during early Middle Pleistocene interglacials: Investigating the Mid-Brunhes Event in the British terrestrial sequence. *Earth-Science Reviews* **103**: 183–196.

Candy I., Mcclymont E.L. (2013). Interglacial intensity in the North Atlantic over the last 800000 years: Investigating the complexity of the mid-Brunhes Event. *Journal of Quaternary Science* **28**: 343–348.

Candy I., Rose J., Lee J.R. (2006). A seasonally “dry” interglacial climate in eastern England during the early Middle Pleistocene: Palaeopedological and stable isotopic evidence from Pakefield, UK. *Boreas* **35**: 255–265.

Candy I., Schreve D.C. (2007). Land-sea correlation of Middle Pleistocene temperate sub-stages using high-precision uranium-series dating of tufa deposits from southern England. *Quaternary Science Reviews* **26**: 1223–1235.

Candy I., Schreve D.C., Sherriff J., Tye G.J. (2014). Marine Isotope Stage 11: Palaeoclimates, palaeoenvironments and its role as an analogue for the current interglacial. *Earth-Science Reviews* **128**: 18–51.

Candy I., Schreve D.C., White T.S. (2015). MIS 13-12 in Britain and the North Atlantic: Understanding the palaeoclimatic context of the earliest Acheulean. *Journal of Quaternary Science* **30**: 593–609.

Candy I., Silva B., Lee J.R. (2011). Climates of the early Middle Pleistocene in Britain: Environments of the Earliest Humans in Northern Europe. In: *The Ancient Human Occupation of Britain (Developments in Quaternary Science 14)*. (Eds N.M. Ashton, S.G. Lewis & C.B. Stringer), pp. 11–22. Elsevier, Amsterdam.

Candy I., White T.S., Elias S.A. (2016). How warm was Britain during the Last Interglacial? A critical review of Ipswichian (MIS 5e) palaeotemperature reconstructions. *Journal of Quaternary Science* **31**: 857–868.

Carcaillet C., Bouvier M., Fréchette B., Larouche A.C. a. C., Richard P.J.H.P.J.H. (2001). Comparison of pollen-slide and sieving methods in lacustrine charcoal analyses for local and regional fire history. *The Holocene* **11**: 467–476.

Carrión J.S., Rose J., Stringer C. (2011). Early Human Evolution in the Western Palaearctic: Ecological Scenarios. *Quaternary Science Reviews* **30**: 1281–1295.

Chafota J., Owen-Smith N. (2009). Episodic severe damage to canopy trees by elephants: interactions with fire, frost and rain. *Journal of Tropical Ecology* **25**: 341.

Challis K., Howard A.J. (1999). *Brooksby Agricultural College: archaeological evaluation of a potential quarry for Lafarge Redland Ltd.* Lafarge Redland Ltd, Trent & Peak Archaeological Unit, Nottingham.

Channell J.E.T., Hodell D.A., Singer B.S., Xuan C. (2010). Reconciling astrochronological and 40Ar/39Ar ages for the Matuyama-Brunhes boundary and late Matuyama Chron. *Geochemistry, Geophysics, Geosystems* **11**: 1–21.

Clark J.S. (1988). Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research* **30**: 67–80.

Clark J.S., Lynch J., Stocks B.J., Goldammer J.G. (1998). Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene* **8**: 19–29.

Cohen K.M., MacDonald K., Joordens J.C.A., Roebroeks W., Gibbard P.L. (2012). The earliest occupation of north-west Europe: a coastal perspective. *Quaternary International* **271**: 70–83.

Coles B. (2006). *Beavers In Britain's Past*. Oxbow Books, Oxford.

Coltorti M., Feraud G., Marzoli A., Peretto C., Ton-That T., Voinchet P., Bahain J.J., Minelli A., Thun Hohenstein U. (2005). New ^{40}Ar/^{39}Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quaternary International* **131**: 11–22.

Conedera M., Tinner W., Neff C., Meurer M., Dickens A.F., Krebs P. (2009). Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews* **28**: 555–576.

Coope G.R. (1974). Interglacial coleoptera from Bobbitshole, Ipswich, Suffolk. *Journal of the Geological Society* **130**: 333–340.

Coope G.R. (1986). Coleopteran Analysis. In: *Handbook of Holocene Palaeoecology and Palaeohydrology*. (Ed. B. Berglund), pp. 703–713. Wiley, Chichester.

Coope G.R. (1989). Coleoptera from the Lower Channel, Brandon. In: *West Midland Field Guide*. (Ed. D.H. Keen), pp. 27–28. Quaternary Research Association.

Coope G.R. (1992). The High Lodge insect fauna. In: *High Lodge. Excavations by G. de G. Sieveking, 1962-8, and J. Cook, 1988*. (Eds N.M. Ashton, J. Cook, S.G. Lewis & J. Rose), pp. 117–119. British Museum, London.

Coope G.R. (1993). Late-Glacial (Anglian) and Late-Temperate (Hoxnian) Coleoptera. In: *The Lower Palaeolithic Site at Hoxne, England*. (Eds R. Singer, B. Gladfelter & J. Wymer), pp. 156–162. University of Chicago Press.

Coope G.R. (1995). The Effects of Quaternary Climatic Changes on Insect Populations: Lessons from the Past. In: *Insects in a changing environment*. (Eds R. Harrington & N. Stork), pp. 29–48. Academic Press, London.

Coope G.R. (2000). Coleoptera from Beeston and West Runton, Norfolk. In: *The Quaternary of Norfolk & Suffolk Field Guide*. (Eds S.G. Lewis, C. Whiteman & R.C. Preece), pp. 73–76. Quaternary Research Association.

Coope G.R. (2001). Biostratigraphical distinction of interglacial coleopteran assemblages from southern Britain attributed to Oxygen Isotope Stages 5e and 7. *Quaternary Science Reviews* **20**: 1717–1722.

Coope G.R. (2006). Insect faunas associated with palaeolithic industries from five sites of pre-Anglian age in central England. *Quaternary Science Reviews* **25**: 1738–1754.

Coope G.R. (2010a). Coleopteran faunas as indicators of interglacial climates in central and southern England. *Quaternary Science Reviews* **29**: 1507–1514.

Coope G.R. (2010b). Coleoptera from the Cromerian Type Site at West Runton, Norfolk, England. *Quaternary International* **228**: 46–52.

Coope G.R., Field M.H., Gibbard P.L., Greenwood M., Richards A.E. (2002). Palaeontology and biostratigraphy of Middle Pleistocene river sediment in the Mathon Member, at Mathon, Herefordshire, England. *Proceedings of the Geologists' Association* **113**: 237–258.

Coope G.R., Gibbard P.L., Hall A.R., Preece R.C., Robinson J.E., Sutcliffe A.J. (1997). Climatic and environmental reconstructions based on fossil assemblages from Middle Devensian (Weichselian) deposits of the river thames at South Kensington, Central London, UK. *Quaternary Science Reviews* **16**: 1163–1195.

Coope G.R., Kenward H.K. (2007). Evidence from coleopteran assemblages for a short but intense cold interlude during the latter part of the MIS11 Interglacial from Quinton, West Midlands, UK. *Quaternary Science Reviews* **26**: 3276–3285.

Cornelissen P. (2017). *Large herbivores as a driving force of woodland-grassland cycles: The mutual interactions between the population dynamics of large herbivores and vegetation development in a eutrophic wetland*. Wageningen University.

Cowling S.A., Sage R.F. (1998). Interactive Effects of Low Atmospheric CO_2 and Elevated Temperature on Growth, Photosynthesis and Respiration in *Phaseolus vulgaris*. *Plant, Cell and Environment* **21**: 427–435.

Cowling S.A., Sykes M.T. (1999). Physiological Significance of Low Atmospheric CO_2 for Plant–Climate Interactions. *Quaternary Research* **52**: 237–242.

Cox M. (2007). *Atlas of the seed and leaf beetles of Britain and Ireland*. Pisces Publications, Newbury.

Coxon P. (1996). The Gortian temperate stage. *Quaternary Science Reviews* **15**: 425–436.

Coxon P., Hannon G.E., Foss P. (1994). Climatic deterioration and the end of the Gortian Interglacial in sediments from Derrynadivva and Burren Townland, near Castlebar, County Mayo, Ireland. *Journal of Quaternary Science* **9**: 33–46.

Cozza R., Galanti G., Bitonti M.B., Innocenti A.M. (1994). Effect of Storage at low Temperature on the Germination of the Waterchestnut (Trapa natans L.). *Phyton (Horn, Austria)* **34**: 315–320.

Crucifix M., Hewitt C.D. (2005). Impact of vegetation changes on the dynamics of the atmosphere at the Last Glacial Maximum. *Climate Dynamics* **25**: 447–459.

Cuppen J.G.M., Nilsson A.N. (1991). *Ochthebius rugulosus* Wollaston in Fennoscandia (Coleoptera, Hydraenidae). *Entomologisk Tidskrift* **112**: 39–42.

Dale V.H., Joyce L. a, McNulty S., Neilson R.P., Ayres M.P., Flannigan M.D., Hanson P.J., Irland L.C., Lugo A.E., Peterson C.J., Simberloff D., Swanson F.J., Stocks B.J., Wotton B.M. (2001). Climate Change and Forest Disturbances. *Bioscience* **51**:

723–734.

Davey N., Bridgland D.R., Keen D.H., Coope G.R., Seddon M., Holyoak D.T. (1991). Maxey gravel pit, near Peterborough TF1307. In: *Central East Anglia and the Fen Basin: Field Guide*. (Eds S.G. Lewis, C. Whiteman & D.R. Bridgland), pp. 185–208. Quaternary Research Association.

Davies G.M., Smith A.A., MacDonald A.J., Bakker J.D., Legg C.J. (2010). Fire intensity, fire severity and ecosystem response in heathlands: Factors affecting the regeneration of Calluna vulgaris. *Journal of Applied Ecology* **47**: 356–365.

Davis B.A.S., Brewer S., Stevenson A.C., Guiot J., Allen J., Almqvist-Jacobson H., Ammann B., Andreev A.A., Argant J., Atanassova J., Balwierz Z., Barnosky C.D., Bartley D.D., De Beaulieu J.L., Beckett S.C., Behre K.E., Bennett K.D., … Zernitskaya V.P. (2003). The temperature of Europe during the Holocene reconstructed from pollen data. *Quaternary Science Reviews* **22**: 1701–1716.

Davis O.K. (1987). Spores of the dung fungus *Sporormiella*: Increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* **28**: 290–294.

Davis O.K., Shafer D.S. (2006). *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology* **237**: 40–50.

Davis S.R., Brown A.G., Dinnin M.H. (2007). Floodplain connectivity, disturbance and change: A palaeoentomological investigation of floodplain ecology from south-west England. *Journal of Animal Ecology* **76**: 276–288.

deMenocal P.B. (2004). African climate change and faunal evolution during the

Pliocene-Pleistocene. *Earth and Planetary Science Letters* **220**: 3–24.

Denic M., Stoeckl K., Gum B., Geist J. (2014). Physicochemical assessment of *Unio crassus* habitat quality in a small upland stream and implications for conservation. *Hydrobiologia* **735**: 111–122.

Dennell R.W., Martinón-Torres M., Bermúdez de Castro J.M. (2011). Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews* **30**: 1511–1524.

Doughty C.E., Roman J., Faurby S., Wolf A., Haque A., Bakker E.S., Malhi Y., Dunning J.B., Svenning J.-C. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences* **113**: 868–873.

Dreyfus G.B., Raisbeck G.M., Parrenin F., Jouzel J., Guyodo Y., Nomade S., Mazaud A. (2008). An ice core perspective on the age of the Matuyama-Brunhes boundary. *Earth and Planetary Science Letters* **274**: 151–156.

Drobyshev I., Bergeron Y., Vernal A. de, Moberg A., Ali A.A., Niklasson M. (2016). Atlantic SSTs control regime shifts in forest fire activity of Northern Scandinavia. *Scientific Reports* **6**: 22532.

Drobyshev I., Granström A., Linderholm H.W., Hellberg E., Bergeron Y., Niklasson M. (2014). Multi-century reconstruction of fire activity in northern European boreal forest suggests differences in regional fire regimes and their sensitivity to climate. *Journal of Ecology* **102**: 738–748.

Duff A.G. (1993). *Beetles of Somerset: their status and distribution*. Somerset Archaeological & Natural History Society, Taunton.

Duff A.G. (2012). *Checklist of Beetles of the British Isles*, Second Edi. Pemberley Books (Publishing), UK.

Duffy E.A.J. (1953). *Coleoptera Scolytidae and Platypodidae. Handbooks for the Identification of British Insects. Vol. V Part 15.* Royal Entomological Society, St. Albans.

Duigan S.L. (1963). Pollen Analyses of the Cromer Forest Bed Series in East Anglia. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* **246**: 149–203.

Duigan S.L., Godwin H. (1956). Pollen analysis of the Nechells interglacial deposits, Birmingham. *Quarterly Journal of the Geological Society* **112**: 373–391.

Eaton E., Caudullo G., de Rigo D. (2016). *Tilia cordata*, *Tilia platyphyllos* and other limes in Europe: distribution, habitat, usage and threats. In: *European Atlas of Forest Tree Species*. (Eds J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant & A. Mauri), pp. 184–185. Publ. Off. EU, Luxembourg.

Elderfield H., Ferretti P., Greaves M., Crowhurst S.J., McCave I.N., Hodell D.A., Piotrowski A.M. (2012). Evolution of Ocean Temperature and Ice Volume Through the Mid-Pleistocene Climate Transition. *Science* **337**: 704–709.

Elias S.A. (2010). *Advances in Quaternary Entomology (Developments in Quaternary Science 12)*. Elsevier, Amsterdam.

Elias S.A., Anderson K.H., Andrews J.T. (1996). Late Wisconsin climate in northeastern USA and southeastern Canada, reconstructed from fossil beetle assemblages. *Journal of Quaternary Science* **11**: 417–421.

Elias S.A., Matthews I.P. (2014). A comparison of reconstructions based on aquatic and terrestrial beetle assemblages: Late glacial-Early Holocene temperature reconstructions for the British Isles. *Quaternary International* **341**: 69–79.

Elias S.A., Webster L., Amer M. (2009). A beetle's eye view of London from the Mesolithic to Late Bronze Age. *Geological Journal* **44**: 537–567.

Elliott J.M. (2008). The ecology of riffle beetles (Coleoptera: Elmidae). *Freshwater Reviews* **1**: 189–203.

Epica C.M. (2006). One-to-one coupling of glacial climate variability in Greenland and Antarctica. *Nature* **444**: 195–198.

EPICA Community Members (2004). Eight glacial cycles from an Antarctic ice core. *Nature* **429**: 623–8.

Ernsting G., Isaaks J.A., Berg M.P. (1992). Life cycle and food availability indicies in *Notiophilus biguttatus* (Coleoptera, Carabidae. *Ecological Entomology* **17**: 33–42.

Fernandes P.M., Vega J.A., Jiménez E., Rigolot E. (2008). Fire resistance of European pines. *Forest Ecology and Management* **256**: 246–255.

Fick S.E., Hijmans R.J. (2017). Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*: DOI 10.1002/joc.5086.

Field M.H., Peglar S.M. (2010). A palaeobotanical investigation of the sediments from the West Runton Mammoth site. *Quaternary International* **228**: 38–45.

Fikáček M., Prokin A., Angus R.B. (2011). A long-living species of the hydrophiloid beetles: *Helophorus sibiricus* from the early Miocene deposits of Kartashevo

(Siberia, Russia). *ZooKeys* **254**: 239–54.

Finlayson C., Carrión J., Brown K., Finlayson G., Sánchez-Marco A., Fa D., Rodríguez-Vidal J., Fernández S., Fierro E., Bernal-Gómez M., Giles-Pacheco F. (2011). The Homo habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quaternary Science Reviews* **30**: 1525–1532.

Fischer A., Marshall P., Camp A. (2013). Disturbances in deciduous temperate forest ecosystems of the northern hemisphere: Their effects on both recent and future forest development. *Biodiversity and Conservation* **22**: 1863–1893.

Fitzsimmons K.E., Marković S.B., Hambach U. (2012). Pleistocene environmental dynamics recorded in the loess of the middle and lower Danube basin. *Quaternary Science Reviews* **41**: 104–118.

Foster C.N., Barton P.S., Lindenmayer D.B. (2014a). Effects of large native herbivores on other animals. *Journal of Applied Ecology* **51**: 929–938.

Foster G.N. (2000). *A review of the scarce and threatened Coleoptera of Great Britain. Part 3: Water Beetles*. UK Joint Nature Conservation Committee, Peterborough.

Foster G.N., Bilton D., Friday L.E. (2014b). *Keys to the adults of the water beetles of Britain and Ireland (part 2). Handbooks for the identification of British Insects, 4(5b)*. Royal Entomological Society, St. Albans.

Foster G.N., Friday L.E. (2011). *Keys to the adults of the water beetles of Britain and Ireland (Part 1). Handbooks for the Identification of British Insects, 4, 5*. Field Studies Council for the Royal Entomological Society.

Franks J. (1960). Interglacial Deposits at Trafalgar Square, London. *New Phytologist* **59**: 145–152.

Friday L.E. (1988). A key to the adults of British water beetles. *Field Studies* **7**: 1–151.

Gałka A., Szmeja J. (2013). Phenology of the aquatic fern *Salvinia natans* (L.) All. in the Vistula Delta in the context of climate warming. *Limnologica* **43**: 100–105.

Gao C., Keen D.H., Boreham S., Coope G.R., Pettit M.E., Stuart A.J., Gibbard P.L. (2000). Last Interglacial and Devensian deposits of the River Great Ouse at Woolpack Farm, Fenstanton, Cambridgeshire, UK. *Quaternary Science Reviews* **19**: 787–810.

Gaudio N., Balandier P., Dumas Y., Ginisty C. (2011). Growth and morphology of three forest understorey species (*Calluna vulgaris*, *Molinia caerulea* and *Pteridium aquilinum*) according to light availability. *Forest Ecology and Management* **261**: 489–498.

Gardiner B., Berry P., Moulia B. (2016). Review: Wind impacts on plant growth, mechanics and damage. *Plant Science* **245**: 94–118.

GBIF (2016). *Global Biodiversity Information Facility*. http://www.gbif.org/. Accessed November 2016.

van Geel B. (2001). Non-Pollen Palynomorphs. In: *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous indicators*. (Eds J.P. Smol, H.J. Birks & W.M. Last), pp. 99–119. Kluwer Academic Publishers.

Gerhart L.M., Ward J.K. (2010). Plant responses to low CO_2 of the past. *New Phytologist* **188**: 674–695.

Gibbard P.L., Aalto M., Coope G.R., Currant A.P., McGlade J.M., Peglar S.M., Preece R.C., Turner C., Whiteman C., Wrayton R. (1996). Early Middle Pleistocene fossiliferous sediments in the Kesgrave Formation at Broomfield Essex. In: *The early Middle Pleistocene in Europe1*. (Ed. C. Turner), pp. 83–119. Balkema, Rotterdam.

Gibbard P.L., Boreham S., Andrews J.E., Maher B. a. (2010). Sedimentation, geochemistry and palaeomagnetism of the West Runton Freshwater Bed, Norfolk, England. *Quaternary International* **228**: 8–20.

Gibbard P.L., Lewin J. (2002). Climate and related controls on interglacial fluvial sedimentation in lowland Britain. *Sedimentary Geology* **151**: 187–210.

Gibbard P.L., Moscariello A., Bailey H., Boreham S., Koch C., Lord A., Whittaker J.E., Whiteman C. (2008). Comment: Middle Pleistocene sedimentation at Pakefield, Suffolk, England. *Journal of Quaternary Science* **23**: 85–92.

Gibbard P.L., Pettit M. (1978). The Palaeobotany of Interglacial Deposits at Sugworth, Berkshire. *New Phytologist* **81**: 465–477.

Gibbard P.L., Stuart A.J. (1975). Flora and vertebrate fauna of the Barrington Beds. *Geological Magazine* **112**: 493–501.

Gibbard P.L., Turner C., West R.G. (2013). The Bytham river reconsidered. *Quaternary International* **292**: 15–32.

Gill J.L. (2014). Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytologist* **201**: 1163–1169.

Gill J.L., Mclauchlan K.K., Skibbe A.M., Goring S., Zirbel C.R., Williams J.W. (2013).

Linking abundances of the dung fungus *Sporormiella* to the density of bison: Implications for assessing grazing by megaherbivores in palaeorecords. *Journal of Ecology* **101**: 1125–1136.

Gill J.L., Williams J.W., Jackson S.T., Lininger K.B., Robinson G.S. (2009). Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**: 1100–1103.

Girling M. (1980). *Two Late Pleistocene insect faunas from Lincolnshire*. Unpublished PhD thesis. University of Birmingham.

Goren-Inbar N., Alperson N., Kislev M.E., Simchoni O., Melamed Y., Ben-Nun A., Werker E. (2004). Evidence of Hominin Control of Fire at Gesher Benot Ya'aqov, Israel. *Science* **304**: 725–727.

Graf A. (2002). Lower and Middle Palaeolithic Leicestershire and Rutland: progress and potential. *Transactions of the Leicestershire Archaeological and Historical Society* **76**: 1–46.

Grant M.J., Hughes P.D.M., Barber K.E. (2014). Climatic influence upon early to mid-Holocene fire regimes within temperate woodlands: A multi-proxy reconstruction from the New Forest, southern England. *Journal of Quaternary Science* **29**: 175–188.

Green C.P., Branch N.P., Russell Coope G., Field M.H., Keen D.H., Wells J.M., Schwenninger J.L., Preece R.C., Schreve D.C., Canti M.G., Gleed-Owen C.P. (2006). Marine Isotope Stage 9 environments of fluvial deposits at Hackney, north London, UK. *Quaternary Science Reviews* **25**: 89–113.

Green C.P., Coope G.R., Jones R.L., Keen D.H., Bowen D.Q., Currant A.P., Holyoak

D.T., Ivanovich M., Robinson J.E., Rogerson R.J., Young R.C. (1996). Pleistocene deposits at Stoke Goldington, in the valley of the Great Ouse, UK. *Journal of Quaternary Science* **11**: 59–87.

Grimm E.C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* **13**: 13–35.

Guo Z., Biscaye P., Wei L., Chen X., Peng S., Liu T. (2000). Summer monsoon variations over the last 1.2 Ma from the weathering of loess-soil sequences in China. *Geophysical Research Letters* **27**: 1751–1754.

Gupta A.K., Sarkar S., De S., Clemens S.C., Velu A. (2010). Mid-Brunhes strengthening of the Indian Ocean Dipole caused increased equatorial East African and decreased Australasian rainfall. **37**: 6–11.

Gupta S., Collier J.S., Palmer-Felgate A., Potter G. (2007). Catastrophic flooding origin of shelf valley systems in the English Channel. *Nature* **448**: 342–345.

Gurnell A. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms* **39**: 4–25.

Hamblin R.J.O., Moorlock B.S.P., Rose J., Lee J.R., Riding J.B., Booth S.J., Pawley S.M. (2005). Revised Pre-Devensian glacial stratigraphy in Norfolk, England, based on mapping and till provenance. *Geologie en Mijnbouw/Netherlands Journal of Geosciences* **84**: 77–85.

Hansen M. (1987). *The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica, 18*. Scandinavian Science Press, Leiden.

Harde K. (1984). *A Field Guide in Colour to Beetles*. Octopus, London.

Harris S., Mix A. (1999). Pleistocene Precipitation Balance in the Amazon Basin Recorded in Deep Sea Sediments. *Quaternary Research* **26**: 14–26.

Hayashi T. (2011). Monospecific planktonic diatom assemblages in the Paleo-Kathmandu Lake during the middle Brunhes Chron: Implications for the paradox of the plankton. *Palaeogeography, Palaeoclimatology, Palaeoecology* **300**: 46–58.

Heil C.W., King J.W., Zárate M.A., Schultz P.H. (2010). Climatic interpretation of a 1.9 Ma environmental magnetic record of loess deposition and soil formation in the central eastern Pampas of Buenos Aires, Argentina. *Quaternary Science Reviews* **29**: 2705–2718.

Heiri O., Lotter A.F., Lemcke G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* **25**: 101–110.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.

Hill G.E. (2015). *Reconstructing Holocene Landscape Cover Using Sub-fossil Coleoptera*. Unpublished PhD thesis. Queen's University Belfast.

Hille M., den Ouden J. (2004). Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire and soil scarification. *European Journal of Forest Research* **123**: 213–218.

Hocknull S.A., Zhao J., Feng Y., Webb G.E. (2007). Responses of Quaternary rainforest vertebrates to climate change in Australia. *Earth and Planetary Science Letters* **264**: 317–331.

Holland D. (1972). A key to the larvae, pupae and adults of the British species of Elminthidae. *Freshwater Biological Association Scientific Publications* **26**: 1–58.

Holmes J.A., Atkinson T., Fiona Darbyshire D.P., Horne D.J., Joordens J., Roberts M.B., Sinka K.J., Whittaker J.E. (2010). Middle Pleistocene climate and hydrological environment at the Boxgrove hominin site (West Sussex, UK) from ostracod records. *Quaternary Science Reviews* **29**: 1515–1527.

Holyoak D.T. (1983). A Late Pleistocene interglacial flora and molluscan fauna from Thatcham, Berkshire, with notes on Mollusca from the interglacial deposits at Aveley, Essex. *Geological Magazine* **120**: 623–629.

Holyoak D.T., Preece R.C. (1985). Late Pleistocene Interglacial Deposits at Tattershall, Lincolnshire. *Philosophical Transactions of the Royal Society B: Biological Sciences* **311**: 193–236.

Hönisch B., Hemming N.G., Archer D., Siddall M., McManus J.F. (2009). Atmospheric carbon dioxide concentration across the mid-Pleistocene transition. *Science* **324**: 1551–4.

Hoogakker B.A.A., Smith R.S., Singarayer J.S., Marchant R., Prentice I.C., Allen J.R.M., Anderson R.S., Bhagwat S.A., Behling H., Borisova O., Bush M., Correa-Metrio A., De Vernal A., Finch J.M., Fréchette B., Lozano-Garcia S., Gosling W.D., … Tzedakis P.C. (2016). Terrestrial biosphere changes over the last 120 kyr. *Climate of the Past* **12**: 51–73.

Horton A., Keen D.H., Davey N. (1991). Hicks No. 1 Brickyard, Fletton, Peterborough

(TL 190956). In: *Central East Anglia and the Fen Basin: Field Guide1*. (Eds S.G. Lewis, C. Whiteman & D.R. Bridgland), pp. 131–164. Quaternary Research Association.

Horton A., Keen D.H., Field M.H., Robinson J.E., Coope G.R., Currant A.P., Graham D.K., Green C.P., Phillips L.M. (1992). The Hoxnian Interglacial Deposits at Woodston, Peterborough. *Philosophical Transactions of the Royal Society B: Biological Sciences* **338**: 131–164.

Horwitz L.K., Tchernov E. (1990). Cultural and Environmental Implications of Hippopotamus Bone Remains in Archaeological Contexts in the Levant. *Bulletin of the American Schools of Oriental Research* **280**: 67–76.

Hosfield R. (2011). The British Lower Palaeolithic of the early Middle Pleistocene. *Quaternary Science Reviews* **30**: 1486–1510.

Houston Durrant T., de Rigo D., Caudullo G. (2016). *Alnus glutinosa* in Europe: distribution, habitat, usage and threats. In: *European Atlas of Forest Tree Species*. (Eds J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant & A. Mauri), pp. 64–65. Publ. Off. EU, Luxembourg.

Howard A.J. (1999). *Brooksby Agricultural College, Report on Palaeobiological Assessment*. Trent and Peak Archaeological Unit.

Howard A.J., Mighall T.M., Field M.H., Griffiths H.I., Macklin M.G. (2000). Early Holocene environments of the River Ure near Ripon, North Yorkshire, UK. *Proceedings of the Yorkshire Geological Society* **53**: 31–41.

Huntley B. (2012). Reconstructing palaeoclimates from biological proxies: Some often overlooked sources of uncertainty. *Quaternary Science Reviews* **31**: 1–16.

Hyman P. (1992). *A review of the scarce and threatened Coleoptera of Great Britain, Part 1 (Revised & updated by M.S.Parsons)*. UK Joint Nature Conservation Committee, Peterborough.

Hyman P. (1994). *A review of the scarce and threatened Coleoptera of Great Britain. Part 2. (Revised and updated by M.S. Parsons*. UK Joint Nature Conservation Committee, Peterborough.

Jäch M.A. (1990). Revision of the Palaearctic species of the genus Ochthebius Leach. V. The subgenus *Asiobates* (Coleoptera: Hydraenidae). *Koleopterischen Rundschau* **60**: 37–105.

Jäch M.A. (1998). Revision of the Palearctic species of the genus Ochthebius Leach XX. The *O. (Asiobates) rugulosus* Wollaston species complex (Coleoptera: Hydraenidae). *Koleopterologische Rundschau* **68**: 175–187.

Jackson S.T., Blois J.L. (2015). Community ecology in a changing environment: Perspectives from the Quaternary. *Proceedings of the National Academy of Sciences* **112**: 4915–4921.

Jansen J., Kuijpers A., Troelstra S. (1986). A Mid-Brunhes Climatic Event: Long-Term Changes in Global Atmosphere and Ocean Circulation. *Science* **232**: 619–622.

Jeffers E.S., Bonsall M.B., Froyd C.A., Brooks S.J., Willis K.J. (2015). The relative importance of biotic and abiotic processes for structuring plant communities through time. *Journal of Ecology* **103**: 459–472.

Johnson C.N. (2009). Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings. Biological sciences / The Royal Society* **276**: 2509–19.

Johnson C.N., Rule S., Haberle S.G., Turney C.S.M., Kershaw A.P., Brook B.W. (2015). Using dung fungi to interpret decline and extinction of megaherbivores: Problems and solutions. *Quaternary Science Reviews* **110**: 107–113.

Jones R.A. (2006). Rhopalapion longirostre (Olivier, 1807) (Apionidae) finally discovered in Britain. *The Coleopterist* **15**: 93–97.

Jones R.L., Keen D.H. (1993). *Pleistocene Environments in the British Isles*. Chapman & Hall, London.

Jouzel J., Masson-Delmotte V., Cattani O., Dreyfus G., Falourd S., Hoffmann G., Minster B., Nouet J., Barnola J.M., Chappellaz J., Fischer H., Gallet J.C., Johnsen S., Leuenberger M., Loulergue L., Luethi D., Oerter H., … Wolff E.W. (2007). Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science* **317**: 793–6.

Juggins S. (2015). rioja: Analysis of Quaternary Science Data. R Package version 0.9-3. https://cran.r-project.org/web/packages/rioja.

Kahlke R.-D., García N., Kostopoulos D.S., Lacombat F., Lister A.M., Mazza P.P.A., Spassov N., Titov V. V. (2011). Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* **30**: 1368–1395.

Kahlke R.-D., Kaiser T.M. (2011). Generalism as a subsistence strategy: Advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). *Quaternary Science Reviews* **30**: 2250–2261.

Keen D.H., Bateman M.D., Coope G.R., Field M.H., Langford H.E., Merry J.S., Mighall T.M. (1999). Sedimentology, palaeoecology and geochronology of Last Interglacial deposits from Deeping St James, Lincolnshire, England. *Journal of Quaternary Science* **14**: 411–436.

Keen D.H., Coope G.R., Jones R.L., Field M.H., Griffiths H.I., Lewis S.G., Bowen D.Q. (1997). Middle Pleistocene deposits at Frog Hall Pit, Stretton-on-Dunsmore, Warwickshire, English Midlands, and their implications for the age of the type Wolstonian. *Journal of Quaternary Science* **12**: 183–208.

Keen D.H., Hardaker T., Lang A.T.O. (2006). A Lower Palaeolithic industry from the Cromerian (MIS 13) Baginton Formation of Waverley Wood and Wood Farm Pits, Bubbenhall, Warwickshire, UK. *Journal of Quaternary Science* **21**: 457–470.

Kenward H.K. (2006). The visibility of past trees and woodland: testing the value of insect remains. *Journal of Archaeological Science* **33**: 1368–1380.

Kenward H.K., Hall A. (1997). Enhancing Bioarchaeological Interpretation Using Indicator Groups: Stable Manure as a Paradigm. *Journal of Archaeological Science* **24**: 663–673.

Kerney M.P. (1977). British Quaternary non-marine Mollusc: a brief review. In: *British Quaternary Studies: Recent Advances*. (Ed. F.W. Shotton), pp. 31–42. Clarendon Press, Oxford.

Koch K. (1989a). *Die Käfer Mitteleuropas. Ökologie, 1*. Goecke & Evers, Krefeld.

Koch K. (1989b). *Die Käfer Mitteleuropas, Ökologie 2*. Goecke & Evers, Krefeld.

Koch K. (1992). *Die Käfer Mitteleuropas. Ökologie 3*. Goecke & Evers, Krefeld.

Korhola A.A., Tikkanen M.J. (1997). Evidence for a more recent occurrence of water chestnut (*Trapa natans* L.) in Finland and its palaeoenvironmental implications. *The Holocene* **7**: 39–44.

Kryzhanovskij O., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K. V., Shilenkov V.G. (1995). *A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae)*. Pensoft, Moscow.

Kühl N., Litt T., Schölzel C., Hense A. (2007). Eemian and Early Weichselian temperature and precipitation variability in northern Germany. *Quaternary Science Reviews* **26**: 3311–3317.

Kuijper D.P.J., de Kleine C., Churski M., van Hooft P., Bubnicki J., Jedrzejewska B. (2013). Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieża Primeval Forest, Poland. *Ecography* **36**: 1263–1275.

Kuneš P., Kjærsgaard Sørensen M., Buylaert J.P., Murray A.S., Houmark-Nielsen M., Odgaard B.V. (2013). A new Middle Pleistocene interglacial record from Denmark: Chronostratigraphic correlation, palaeovegetation and fire dynamics. *Boreas* **42**: 596–612.

Kuneš P., Odgaard B.V., Gaillard M.J. (2011). Soil phosphorus as a control of productivity and openness in temperate interglacial forest ecosystems. *Journal of Biogeography* **38**: 2150–2164.

Landin B.O. (1961). Ecological Studies on Dung-Beetles. *Opuscula Entomologica* **Suppl. 19**.

Lane S., Mann D.J. (2016). *A review of the status of the beetles of Great Britain. The stag beetles, dor beetles, dung beetles, chafers and their allies - Lucanidae,* *Geotrupidae, Trogidae and Scarabaeidae*. Natural England, Peterborough.

Lang N., Wolff E.W. (2011). Interglacial and glacial variability from the last 800 ka in marine, ice and terrestrial archives. *Climate of the Past* **7**: 361–380.

Langford H.E., Bateman M.D., Penkman K.E.H., Boreham S., Briant R.M., Coope G.R., Keen D.H. (2007). Age-estimate evidence for Middle-Late Pleistocene aggradation of River Nene 1st Terrace deposits at Whittlesey, eastern England. *Proceedings of the Geologists' Association* **118**: 283–300.

Langford H.E., Boreham S., Coope G.R., Fletcher W., Horne D.J., Keen D.H., Mighall T., Penkman K.E.H., Schreve D.C., Whittaker J.E. (2014). Palaeoecology of a late MIS 7 interglacial deposit from eastern England. *Quaternary International* **341**: 27–45.

Lansdown R.V. (2014). *Najas minor*. http://www.iucnredlist.org/details/164446/0. Accessed June 2017.

Lee J.R., Rose J., Candy I., Barendregt R.W. (2006). Sea-level changes, river activity, soil development and glaciation around the western margins of the southern North Sea Basin during the Early and early Middle Pleistocene: Evidence from Pakefield, Suffolk, UK. *Journal of Quaternary Science* **21**: 155–179.

Lee J.R., Pawley S.M., Rose J., Moorlock B.S.P., Riding J.B., Hamblin R.J.O., Candy I., Barendregt R.W., Booth S.J., Harrison A.M. (2008a). Pre-Devensian lithostratigraphy of shallow marine, fluvial and glacial sediments in northern East Anglia. In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 42–59. Quaternary Research Association.

Lee J.R., Candy I., Rose J., Barendregt R.W. (2008b). Pakefield Cliffs (TM 537 888):

Complex patterns of sea-level change, river activity, soil development and glaciation during the Early and early Middle Pleistocene. In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 114–129. Quaternary Research Association.

Lee J.R., Rose J., Candy I., Barendregt R.W., Moorlock B.S.P., Riding J.B., Hamblin R.J.O. (2008c). Reply: Middle Pleistocene sedimentation at Pakefield, Suffolk, England. *Journal of Quaternary Science* **23**: 93–98.

Lee J.R., Rose J., Hamblin R.J.., Moorlock B.S.P. (2004). Dating the earliest lowland glaciation of eastern England: a pre-MIS 12 early Middle Pleistocene Happisburgh glaciation. *Quaternary Science Reviews* **23**: 1551–1566.

Legendre P., Birks H.J.B. (2012). From Classical to Canonical Ordination. In: *Tracking Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques*. (Eds H.J.B. Birks, A.F. Lotter, S. Juggins & J.P. Smol), pp. 201–248. Springer, London.

Lewis M., Pacher M., Turner A. (2010). The larger Carnivora of the West Runton Freshwater Bed. *Quaternary International* **228**: 116–135.

Lewis S.G., Maddy D., Buckingham C., Coope G.R., Field M.H., Keen D.H., Pike A.W.G., Roe D.A., Scaife R.G., Scott K. (2006). Pleistocene fluvial sediments, palaeontology and archaeology of the upper River Thames at Latton, Wiltshire, England. *Journal of Quaternary Science* **21**: 181–205.

Lewis S.G., Parfitt S.A., Preece R.C., Sinclair J., Coope G.R., Field M.H., Maher B.A., Scaife R., Whittaker J.E. (2004). Age and palaeoenvironmental setting of the Pleistocene vertebrate fauna at Norton Subcourse, Norfolk. In: *The Quaternary*

Mammals of Southern and Eastern England. (Ed. D.C. Schreve), pp. 5–17. Quaternary Research Association.

Lindbladh M., Fraver S., Edvardsson J., Felton A. (2013). Past forest composition, structures and processes – How paleoecology can contribute to forest conservation. *Biological Conservation* **168**: 116–127.

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Lexer M.J., Marchetti M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* **259**: 698–709.

Lindroth C.H. (1945). Die fennoskandischen Carabiden, 1. *Göteborg kgl. Vetensk. Handl.* **B4**: 1–709.

Lindroth C.H. (1963). The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 3. *Opuscula Entomologica* **Suppl. 24**: 201–408.

Lindroth C.H. (1974). *Coleoptera: Carabidae. Handbooks for the Identification of British Insects IV,2*. Royal Entomological Society, St. Albans.

Lindroth C.H. (1985). *The Carabidae (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 15, 1*. E.J.Brill, Leiden.

Lindroth C.H. (1986). *The Carabidae (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 15, 2*. E.J.Brill, Leiden.

Lisiecki L.E., Raymo M.E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records. *Paleoceanography* **20**: 1–17.

Lister A.M., Parfitt S.A., Owen F.J., Collinge S.E., Breda M. (2010). Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy II: Cervidae, Equidae and Suidae. *Quaternary International* **228**: 157–179.

Lister A.M., Stuart A.J. (2010). The West Runton mammoth (*Mammuthus trogontherii*) and its evolutionary significance. *Quaternary International* **228**: 180–209.

Lopes-Lima M., Kebapçı U., Van Damme D. (2014). *Unio crassus*. http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T22736A42465628.en. Accessed July 2006.

Lott D. (2003a). *An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) found in the British Isles including a literature review of their ecology*. English Nature Report No. 488. Peterborough.

Lott D. (2009). *The Staphylinidae (rove beetles) of Britain and Ireland. Part 5: Scaphidiinae, Piestinae, Oxytelinae. Handbooks for the identification of British insects, 12, 5*. Field Studies Council for the Royal Entomological Society.

Lott D.A. (2003b). An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) found in the British Isles including a literature review of their ecology. *English Nature Research Reports* **488**: 1–85.

Lott D., Anderson R. (2011). *The Staphylinidae (rove beetles) of Britain and Ireland Parts 7 & 8: Oxyporinae, Steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae. Handbooks for the Identification of British Insects, 12, Part 7.* Royal Entomological Society, St. Albans.

Loulergue L., Schilt A., Spahni R., Masson-Delmotte V., Blunier T., Lemieux B., Barnola J.-M., Raynaud D., Stocker T.F., Chappellaz J. (2008). Orbital and millennial-scale features of atmospheric CH_4 over the past 800,000 years. *Nature* **453**: 383–386.

Loutre M.F., Berger A. (2003). Marine Isotope Stage 11 as an analogue for the present interglacial. *Global and Planetary Change* **36**: 209–217.

Loutre M.F., Paillard D., Vimeux F., Cortijo E. (2004). Does mean annual insolation have the potential to change the climate? *Earth and Planetary Science Letters* **221**: 1–14.

Luff M. (1998). *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain*. Centre for Ecology & Hydrology, Biological Records Centre, Abbots Ripton.

Luff M. (2007). *The Carabidae (ground beetles) of Britain and Ireland. Handbooks for the Identification of British Insects, 4, 2*, 2nd edn. Royal Entomological Society, St. Albans.

Lüthi D., Le Floch M., Bereiter B., Blunier T., Barnola J.-M., Siegenthaler U., Raynaud D., Jouzel J., Fischer H., Kawamura K., Stocker T.F. (2008). High-resolution carbon dioxide concentration record 650,000-800,000 years before present. *Nature* **453**: 379–82.

Maddy D., Coope G.R., Gibbard P.L., Green C.P., Lewis S.G. (1994). Reappraisal of Middle Pleistocene fluvial deposits near Brandon, Warwickshire and their significance for the Wolston glacial sequence. *Journal of the Geological Society* **151**: 221–233.

Maddy D., Lewis S.G., Scaife R.G., Bowen D.Q., Coope G.R., Green C.P., Hardaker T., Keen D.H., Rees-Jones J., Parfitt S.A., Scott K. (1998). The Upper Pleistocene deposits at Cassington, near Oxford, England. *Journal of Quaternary Science* **13**: 205–231.

Majerus M. (1991). Habitat and Host Plant Preferences of British Ladybirds (Col., Coccinellidae). *Entomologist's Monthly Magazine* **127**: 167–175.

Malhi Y., Doughty C.E., Galetti M., Smith F.A., Svenning J.-C., Terborgh J.W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences* **113**: 838–846.

Mann D.J., Garvey L. (2014). *Aphodius (Liothorax) niger* (Illiger) (Scarabaeidae: Aphodiinae) inside and outside the New Forest. *The Coleopterist* **23**: 138–142.

Mansell L.J., Whitehouse N.J., Gearey B.R., Barratt P., Roe H.M. (2014). Holocene floodplain palaeoecology of the Humberhead Levels; implications for regional wetland development. *Quaternary International* **341**: 91–109.

Måren I.E., Vandvik V. (2009). Fire and regeneration: The role of seed banks in the dynamics of northern heathlands. *Journal of Vegetation Science* **20**: 871–888.

Marlon J.R., Bartlein P.J., Daniau A.L., Harrison S.P., Maezumi S.Y., Power M.J., Tinner W., Vanniére B. (2013). Global biomass burning: A synthesis and review of Holocene paleofire records and their controls. *Quaternary Science Reviews* **65**: 5–25.

Marquis R.J. (2010). The role of herbivores in terrestrial trophic cascades. In: *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*. (Eds J.W. Terborgh & J.A. Estes), pp. 109–123. Island Press, Washington DC.

Maslin M.A., Ridgwell A.J. (2005). Mid-Pleistocene revolution and the "eccentricity myth." *Geological Society, London, Special Publications* **247**: 19–34.

Masson-Delmotte V., Stenni B., Pol K., Braconnot P., Cattani O., Falourd S., Kageyama M., Jouzel J., Landais A., Minster B., Barnola J.M., Chappellaz J., Krinner G., Johnsen S., Röthlisberger R., Hansen J., Mikolajewicz U., Otto-Bliesner B. (2010). EPICA Dome C record of glacial and interglacial intensities. *Quaternary Science Reviews* **29**: 113–128.

Maul L.C., Markova A.K. (2007). Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe. *Quaternary International* **160**: 81–99.

Maul L.C., Parfitt S.A. (2010). Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. *Quaternary International* **228**: 91–115.

Mauri A., de Rigo D., Caudullo G. (2016). *Abies alba* in Europe: distribution, habitat, usage and threats. In: *European Atlas of Forest Tree Species*. (Eds J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant & A. Mauri), pp. 48–49. Publ. Off. EU, Luxembourg.

Meckler A.N., Clarkson M.O., Cobb K.M., Sodemann H., Adkins J.F. (2012). Interglacial Hydroclimate in the Tropical West Pacific Through the Late Pleistocene. *Science* **336**: 1301–1304.

Melles M., Brigham-Grette J., Minyuk P.S., Nowaczyk N.R., Wennrich V., Deconto R.M., Anderson P.M., Andreev A. a, Coletti A., Cook T.L., Haltia-Hovi E., Kukkonen M., Lozhkin A. V, Rosén P., Tarasov P., Vogel H., Wagner B. (2012). 2.8 Million Years of Arctic Climate Change from Lake El'gygytgyn, NE Russia.

Science **337**: 315–320.

Met Office (2017). *Met Office - UK Climate*. http://www.metoffice.gov.uk/climate/. Accessed July 2017.

Meusel H., Jäger E., Rauschert S., Weinert E. (1978). *Vergleichende Chorologie der zentraleuropaischen Flora 1*. Fischer, Jena.

Milne M.G. (2016). *Environmental niche evolution and ancestral niche reconstruction*. Unpublished PhD thesis. Queen’s University Belfast.

Mitchell T.D., Jones P.D. (2005). An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology* **25**: 693–712.

Mooney S.D., Tinner W. (2011). The analysis of charcoal in peat and organic sediments. *Mires and Peat* **7**: 1–18.

Moore P., Webb J., Collinson M.E. (1991). *Pollen Analysis*. Blackwell, Oxford.

Morris J.L., Courtney Mustaphi C.J., Carter V.A., Watt J., Derr K., Pisaric M.F.J., Anderson R.S., Brunelle A.R. (2015). Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. *Quaternary International* **387**: 72–86.

Morris M. (1997). *Broad-Nosed Weevils. Coleoptera : Curculionidae (Entiminae) Handbooks for the Identification of British Insects, 5, part 17a*. Royal Entomological Society, St. Albans.

Murton J.B., Baker A.G., Bowen D.Q., Caseldine C.J., Coope G.R., Currant A.P., Evans J.G., Field M.H., Green C.P., Hatton J., Ito M., Jones R.L., Keen D.H., Kerney M.P., McEwan R., McGregor D.F.M., Parish D., … Smart P.L. (2001). A late Middle Pleistocene temperate-periglacial-temperate sequence (Oxygen Isotope Stages 7-5e) near Marsworth, Buckinghamshire, UK. *Quaternary Science Reviews* **20**: 1787–1825.

Muscolo A., Bagnato S., Sidari M., Mercurio R. (2014). A review of the roles of forest canopy gaps. *Journal of Forestry Research* **25**: 725–736.

NBN (2016). *National Biodiversity Network Gateway*. https://data.nbn.org.uk/. Accessed June 2006.

Newcombe G., Campbell J., Griffith D., Baynes M., Launchbaugh K., Pendleton R. (2016). Revisiting the Life Cycle of Dung Fungi, Including *Sordaria fimicola*. *Plos One* **11**: e0147425.

Nuñez M.R., Bravo F., Calvo L. (2003). Predicting the probability of seed germination in *Pinus sylvestris* L. and four competitor shrub species after fire. *Annals of Forest Science* **60**: 75–81.

Okansen J., Blanchet F., Kindt R., Legendre P., Minchin P., O'Hara R., Simpson G., Solymos P., Henry M., Stevens H., Wagner H. (2015). Vegan: Community Ecology Package. R package version 2.2-1. http://cran.r-project.org/package=vegan.

Olsson F., Gaillard M.-J., Lemdahl G., Greisman A., Lanos P., Marguerie D., Marcoux N., Skoglund P., Wäglind J. (2010). A continuous record of fire covering the last 10,500 calendar years from southern Sweden — The role of climate and human activities. *Palaeogeography, Palaeoclimatology, Palaeoecology* **291**: 128–141.

Olsson F., Lemdahl G. (2009). A continuous Holocene beetle record from the Stavsåkra, southern Sweden: implications for site Stavsa the last 10 600 years of forest and land use history. **24**: 612–626.

Olsson F., Lemdahl G. (2010). A forest history for the last 10 900 years at the site Storasjö, southern Sweden: implications from beetle assemblages. *Journal of Quaternary Science* **25**: 1211–1221.

Osborne P.J. (1980). The Insect Fauna of the Organic Deposits at Sugworth and Its Environmental and Stratigraphic Implications. *Philosophical Transactions of the Royal Society B: Biological Sciences* **289**: 119–133.

Osborne P.J., Shotton F.W. (1968). The Fauna of the Channel Deposit of Early Saalian Age at Brandon, Warwickshire. *Philosophical Transactions of the Royal Society B: Biological Sciences* **B254**: 417–424.

Parfitt S.A. (2005). A butchered bone from Norfolk: evidence for very early human presence in Britain. *Archaeology International* **8**: 14–17.

Parfitt S.A. (2008). Pakefield Cliffs: Archaeology and Palaeoenvironment of the Cromer Forest-bed Formation. In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 130–136. Quaternary Research Association.

Parfitt S.A., Barendregt R.W., Breda M., Candy I., Collins M.J., Coope G.R., Durbidge P., Field M.H., Lee J.R., Lister A.M., Mutch R., Penkman K.E.H., Preece R.C., Rose J., Stringer C.B., Symmons R., Whittaker J.E., … Stuart A.J. (2005). The earliest record of human activity in northern Europe. *Nature* **438**: 1008–1012.

Parfitt S.A., Ashton N.M., Lewis S.G., Abel R.L., Coope G.R., Field M.H., Gale R., Hoare P.G., Larkin N.R., Lewis M.D., Karloukovski V., Maher B. a, Peglar S.M., Preece R.C., Whittaker J.E., Stringer C.B. (2010). Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* **466**: 229–233.

Parfitt S.A., Roberts M.B. (1999). Human modification of faunal remains. In: *Boxgrove: a Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex*. (Eds M.B. Roberts & S.A. Parfitt), pp. 395–415. English Heritage, London.

Patterson W.A., Edwards K.J., Maguire D.J. (1987). Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews* **6**: 3–23.

Pautasso M., Aas G., Queloz V., Holdenrieder O. (2013). European ash (*Fraxinus excelsior*) dieback - A conservation biology challenge. *Biological Conservation* **158**: 37–49.

Pawley S.M., Bailey R.M., Rose J., Moorlock B.S.P., Hamblin R.J.O., Booth S.J., Lee J.R. (2008). Age limits on Middle Pleistocene glacial sediments from OSL dating, north Norfolk, UK. *Quaternary Science Reviews* **27**: 1363–1377.

Pedro J.B., Van Ommen T.D., Rasmussen S.O., Morgan V.I., Chappellaz J., Moy A.D., Masson-Delmotte V., Delmotte M. (2011). The last deglaciation: Timing the bipolar seesaw. *Climate of the Past* **7**: 671–683.

Penkman K.E.H., Preece R.C., Bridgland D.R., Keen D.H., Meijer T., Parfitt S.A., White T.S., Collins M.J. (2011). A chronological framework for the British Quaternary based on *Bithynia* opercula. *Nature* **476**: 446–449.

Penkman K.E.H., Preece R.C., Bridgland D.R., Keen D.H., Meijer T., Parfitt S.A., White T.S., Collins M.J. (2013). An aminostratigraphy for the British Quaternary based on *Bithynia* opercula. *Quaternary Science Reviews* **61**: 111–134.

Penkman K.E.H., Preece R.C., Keen D.H., Collins M.J. (2010). Amino acid geochronology of the type Cromerian of West Runton, Norfolk, UK. *Quaternary International* **228**: 25–37.

Pepin L., Raynaud D., Barnola J.-M., Loutre M.F. (2001). Hemispheric roles of climate forcings during glacial- interglacial transitions as deduced from the Vostok record and LLN-2D model experiments. *Journal of Geophysical Research* **106**: 31,885-31,892.

Pereira H.M., Navarro L.M. (2015). *Rewilding European Landscapes*. Springer, London.

Perry D.W. (1986). *The analysis of sub-fossil insect assemblages: a numerical approach*. Unpublished PhD thesis. University of Birmingham.

Petit J.-R., Raynaud D., Basile I., Chappellaz J., Ritz C., Delmotte M., Legrand M., Lorius C., Pe L. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429–413.

Pieau C., Dorizzi M. (1981). Determination of temperature sensitive stages for sexual differentiation of the gonads in embryos of the turtle, *Emys orbicularis*. *Journal of Morphology* **170**: 373–382.

Pigott C.D., Huntley J.P. (1978). Factors Controlling the Distribution of Tilia Cordata At the Northern Limits of Its Geographical Range: I. Distribution in North-West England. *New Phytologist* **81**: 429–441.

Pigott C.D., Huntley J.P. (1980). Factors Controlling the Distribution of Tilia Cordata At the Northern Limits of Its Geographical Range: II. History in North-West England. *New Phytologist* **84**: 145–164.

Pillans B., Bourman R. (2001). Mid pleistocene arid shift in southern Australia, dated by magnetostratigraphy. *Australian Journal of Soil Research* **39**: 89–98.

Pillans B., Gibbard P.L. (2012). The Quaternary Period. In: *The Geologic Time Scale 2012*. pp. 979–1010.

Pisias N.G., Moore T.C. (1981). The evolution of Pleistocene climate: A time series approach. *Earth and Planetary Science Letters* **52**: 450–458.

Pittino R. (2006). A revision of the genus *Psammoporus* Thompson 1859 in Europe, with description of two new species (Coleoptera, Scarabaeoidea: Aegialiidae). *Geomale Italiana d'Entomologia* **11**: 325–342.

Pivotti I., Agoglitta R., Zunino M., Piattella E., Dellacasa M., Corallini C., Mifsud D. (2011). The Scarabaeoidea of the Maltese Islands (Central Mediterranean) (Coleoptera). *Bulletin of the Entomological Society of Malta* **4**: 85–124.

Polly P.D., Eronen J.T. (2011). Mammal associations in the Pleistocene of Britain: Implications of Ecological Niche Modelling and a Method for Reconstrucing Palaeoclimate. In: *The Ancient Human Occupation of Britain. Develompents in Quaternary Science*. (Eds N.M. Ashton, S.G. Lewis & C.B. Stringer), pp. 279–304. Elsevier, Amsterdam.

Poska A., Pidek I.A. (2010). Pollen dispersal and deposition characteristics of Abies alba, Fagus sylvatica and Pinus sylvestris, Roztocze region (SE Poland). *Vegetation History and Archaeobotany* **19**: 91–101.

Power M.J., Marlon J., Ortiz N., Bartlein P.J., Harrison S.P., Mayle F.E., Ballouche A., Bradshaw R.H.W., Carcaillet C., Cordova C., Mooney S.D., Moreno P.I., Prentice I.C., Thonicke K., Tinner W., Whitlock C., Zhang Y., … Zhang J.H. (2008).

Changes in fire regimes since the last glacial maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* **30**: 887–907.

Preece R.C. (1990). The Molluscan Fauna of the Middle Pleistocene Interglacial Deposits at Little Oakley, Essex, and Its Environmental and Stratigraphical Implications. *Philosophical Transactions of the Royal Society B: Biological Sciences* **328**: 387–407.

Preece R.C. (1999). Mollusca from Last Interglacial fluvial deposits of the River Thames at Trafalgar Square, London. *Journal of Quaternary Science* **14**: 77–89.

Preece R.C. (2001). Molluscan evidence for differentiation of interglacials within the “Cromerian Complex.” *Quaternary Science Reviews* **20**: 1643–1656.

Preece R.C. (2010). The molluscan fauna of the Cromerian type site at West Runton, Norfolk. *Quaternary International* **228**: 53–62.

Preece R.C., Parfitt S.A. (2000). The Cromer Forest-bed Formation: new thoughts on an old problem. In: *The Quaternary of Norfolk & Suffolk Field Guide*. (Eds S.G. Lewis, C. Whiteman & R.C. Preece), pp. 1–27. Quaternary Research Association.

Preece R.C., Parfitt S.A. (2008). The Cromer Forest-bed Formation: some recent developments relating to early human occupation and lowland glaciation. In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 60–83. Quaternary Research Association.

Preece R.C., Parfitt S.A. (2012). The Early and early Middle Pleistocene context of human occupation and lowland glaciation in Britain and northern Europe. *Quaternary International* **271**: 6–28.

Preece R.C., Gowlett J.A.J., Parfitt S.A., Bridgland D.R., Lewis S.G. (2006). Humans in the Hoxnian: Habitat, context and fire use at Beeches Pit, West Stow, Suffolk, UK. *Journal of Quaternary Science* **21**: 485–496.

Preece R.C., Parfitt S.A., Russell Coope G., Penkman K.E.H., Ponel P., Whittaker J.E. (2009). Biostratigraphic and aminostratigraphic constraints on the age of the Middle Pleistocene glacial succession in north Norfolk, UK. *Journal of Quaternary Science* **24**: 557–580.

Prokopenko A.A., Hinnov L.A., Williams D.F., Kuzmin M.I. (2006). Orbital forcing of continental climate during the Pleistocene: a complete astronomically tuned climatic record from Lake Baikal, SE Siberia. *Quaternary Science Reviews* **25**: 3431–3457.

Prokopenko A.A., Williams D.F., Kuzmin M.I. (2002). Muted climate variations in continental Siberia during the mid-Pleistocene epoch. 65–68.

Pushkina D., Bocherens H., Ziegler R. (2014). Unexpected palaeoecological features of the Middle and Late Pleistocene large herbivores in southwestern Germany revealed by stable isotopic abundances in tooth enamel. *Quaternary International* **339–340**: 164–178.

Raffa K.F., Aukema B.H., Bentz B.J., Carroll A.L., Hicke J. a., Turner M.G., Romme W.H. (2008). Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *BioScience* **58**: 501.

Rahmstorf S. (2007). GLACIAL CLIMATES | Thermohaline Circulation. In: *Encyclopedia of Quaternary Science*. (Ed. S.A. Elias), pp. 739–750. Elsevier Ltd.

Raper D., Bush M. (2009). A test of *Sporormiella* representation as a predictor of megaherbivore presence and abundance. *Quaternary Research* **71**: 490–496.

Raynaud D., Barnola J.-M., Souchez R., Lorrain R., Petit J.-R., Duval P., Lipenkov V. (2005). The record for marine isotopic stage 11. *Nature* **436**: 39–40.

Reid C. (1882). The geology of the country around Cromer. *Memoirs of the Geological Survey of England and Wales*.

Reid C. (1893). A Fossiliferous Pleistocene Deposit at Stone on the Hampshire Coast. *Quarterly Journal of the Geological Society* **49**: 325–329.

Rice J. (1991). Distribution and provenance of the Baginton Sand and Gravel in the Wreake Valley, northern Leicestershire, England: Implications for inter-regional correlation. *Journal of Quaternary Science* **6**: 39–54.

Richardson M.J. (2001). Diversity and occurrence of coprophilous fungi. *Mycological Research* **105**: 387–402.

Rivals F., Lister A.M. (2016). Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain. *Quaternary Science Reviews* **146**: 116–133.

Roberts M.B., Stringer C.B., Parfitt S.A. (1994). A hominid tibia from Middle Pleistocene sediments at Boxgrove, UK. *Nature* **369**: 311–313.

Robinson M. (1981). The Iron Age to early Saxon environment of the upper Thames terraces. In: *The Environment of Man: the Iron Age to the Anglo-Saxon Period*. (Eds M. Jones & G. Dimbleby), pp. 251–286. B.A.R. British Series 87, Oxford.

Robinson M. (1983). Arable/Pastoral Ratios From Insects. In: *Integrating the Subsistence Economy (British Archaeological Reports, International Series 181)*.

(Ed. M. Jones), pp. 19–47. British Archaeological Reports, Oxford.

Robinson M. (1991). The Neolithic and later Bronze Age insect assemblages. In: *Excavation and salvage at Runnymede Bridge,1978: The Bronze Age Waterfront site*. (Ed. S. Needham), pp. 277–325. British Museum, London.

Robinson M. (2013). Holocene archaeological evidence of extinct and very rare British Scarabaeoidea. *Environmental Archaeology* **18**: 143–153.

Roe H.M., Coope G.R., Devoy R.J.N., Harrison C.J.O., Penkman K.E.H., Preece R.C., Schreve D.C. (2009). Differentiation of MIS 9 and MIS 11 in the continental record: vegetational, faunal, aminostratigraphic and sea-level evidence from coastal sites in Essex, UK. *Quaternary Science Reviews* **28**: 2342–2373.

Roebroeks W. (2001). Hominid behaviour and the earliest occupation of Europe: an exploration. *Journal of human evolution* **41**: 437–61.

Roebroeks W. (2006). The human colonisation of Europe: where are we? *Journal of Quaternary Science* **21**: 425–435.

Roebroeks W., Villa P. (2011). On the earliest evidence for habitual use of fire in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 5209–14.

Rose F., O'Reilly C. (2006). *The Wild Flower Key: How to identify wild flowers, trees and shrubs in Britain and Ireland*, 2nd edn. Penguin Books Ltd, London.

Rose J. (2009). Early and Middle Pleistocene landscapes of eastern England. *Proceedings of the Geologists' Association* **120**: 3–33.

Rose J. (2015). The Quaternary of the River Trent: Critical evidence for glaciation, river development and land uplift within and close to the limits of lowland glaciation in north Midland England. *Proceedings of the Geologists' Association* **126**: 449–452.

Rose J., Juby C., Bullen M., Davies S., Branch N., Gammage Z., Candy I., Palmer A. (2008). The stratigraphy, sedimentology, palaeoenvironments and duration of the early Middle Pleistocene sediments at West Runton, north Norfolk. In: *The Quaternary of Northern East Anglia Field Guide*. (Eds I. Candy, J.R. Lee & A.M. Harrison), pp. 157–181. Quaternary Research Association.

Rose J., Moorlock B.S.P., Hamblin R.J.O. (2001). Pre-Anglian fluvial and coastal deposits in Eastern England: Lithostratigraphy and palaeoenvironments. *Quaternary International* **79**: 5–22.

Rossignol-Strick M., Paterne M., Bassinot F.C., Emeis K.-C., De Lange G.J. (1998). An unusual mid-Pleistocene monsoon period over Africa and Asia. *Nature* **392**: 269–272.

Rousseau M. (2009). *Understanding the (in)efficiency of paraffin floatation for archaeoentomological work : methodological test, reasons, and implications*. Unpublished MA thesis.University of York.

Rowney F.M. (2012). *Early Middle Pleistocene insects from Brooksby, Leicestershire: The palaeoenvironments of an ancient hominin occupation site*. Unpublished MSc dissertation. Royal Holloway, University of London.

Ruddiman W.F., Raymo M., Martinson D.G., Clement B., Backman J. (1989). Pleistocene evolution: northern hemisphere ice sheets and North Atlantic Ocean. *Paleoceanography* **4**: 353–412.

Rule S., Brook B.W., Haberle S.G., Turney C.S.M., Kershaw a. P., Johnson C.N.

(2012). The Aftermath of Megafaunal Extinction: Ecosystem Transformation in Pleistocene Australia. *Science* **335**: 1483–1486.

Sandom C.J., Ejrnæs R., Hansen M.D.D., Svenning J.-C. (2014). High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **111**: 4162–7.

Schelhaas M.-J.M.-J.M.-J.J.M.-J., Nabuurs G.-J.J.G.-J., Schuck A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology* **9**: 1620–1633.

Schmitz O.J. (2008). Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution and Systematics* **39**: 133–152.

Schneeweiss N. (2004). Climatic impact on reproductive success of *Emys orbicularis* at the northwestern border of the species' range (Germany). *Biologia* **59**: 131–137.

Schofield J.E., Bunting M.J. (2005). Mid-Holocene presence of water chestnut (*Trapa natans* L.) in the meres of Holderness, East Yorkshire, UK. *The Holocene* **15**: 687–697.

Schreve D.C. (2001a). Differentiation of the British late Middle Pleistocene interglacials: The evidence from mammalian biostratigraphy. *Quaternary Science Reviews* **20**: 1693–1705.

Schreve D.C. (2001b). Mammalian evidence from Middle Pleistocene fluvial sequences for complex environmental change at the oxygen isotope substage level. *Quaternary International* **79**: 65–74.

Schreve D.C. (2009). A new record of Pleistocene hippopotamus from River Severn terrace deposits, Gloucester, UK-palaeoenvironmental setting and stratigraphical significance. *Proceedings of the Geologists' Association* **120**: 58–64.

Schreve D.C., Candy I. (2010). Interglacial climates: Advances in our understanding of warm climate episodes. *Progress in Physical Geography* **34**: 845–856.

Schülke M. (2012). Oxytelinae (exklusive *Ochthephilus* und *Thinobius*). In: *Die Käfer Mitteleuropas. 4. Staphylinidae (exklusive Aleocharinae, Pselaphinae und Scydmaenidae)*. (Eds V. Assing & M. Schülke), pp. 207–266, 283–286. Spektrum Akademischer, Heidelberg.

Seddon A.W.R., Mackay A.W., Baker A.G., Birks H.J.B., Breman E., Buck C.E., Ellis E.C., Froyd C. a., Gill J.L., Gillson L., Johnson E. a., Jones V.J., Juggins S., Macias-Fauria M., Mills K., Morris J.L., Nogués-Bravo D., … Witkowski A. (2014). Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology* **102**: 256–267.

Seidl R., Fernandes P.M., Fonseca T.F., Gillet F., Jönsson A.M., Merganičová K., Netherer S., Arpaci A., Bontemps J.-D., Bugmann H., González-Olabarria J.R., Lasch P., Meredieu C., Moreira F., Schelhaas M.-J., Mohren F. (2011). Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling* **222**: 903–924.

Seidl R., Rammer W., Spies T.A. (2014). Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications* **24**: 2063–2077.

Seppä H., Bjune A.E., Telford R.J.J., Birks H.J.B., Veski S. (2009). Last nine-thousand years of temperature variability in Northern Europe. *Climate of the Past* **5**: 523–

535.

Shakun J.D., Lea D.W., Lisiecki L.E., Raymo M.E. (2015). An 800-kyr record of global surface ocean δ18O and implications for ice volume-temperature coupling. *Earth and Planetary Science Letters* **426**: 58–68.

Shavrin A. V. (2016). *A review of the genus Pycnoglypta Thomson, 1858 (Staphylinidae, Omaliinae, Omaliini) with notes on related taxa*. Magnolia Press, New Zealand.

Shotton F.W., Goudie A.S., Briggs D.J., Osmaston H.A. (1980). Cromerian Interglacial Deposits at Sugworth, Near Oxford, England, and Their Relation to the Plateau Drift of the Cotswolds and the Terrace Sequence of the Upper and Middle Thames. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **289**: 55–86.

Shotton F.W., Keen D.H., Coope G.R., Currant A.P., Gibbard P.L., Aalto M., Peglar S.M., Robinson J.E. (1993). The Middle Pleistocene deposits of Waverley Wood Pit, Warwickshire, England. *Journal of Quaternary Science* **8**: 293–325.

Shotton F.W., Osborne P.J., Sylvester-Bradley P.C. (1965). The Fauna of the Hoxnian Interglacial Deposits of Nechells, Birmingham. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **248**: 353–378.

Siegenthaler U., Stocker T.F., Monnin E., Lüthi D., Schwander J., Staufer B., Raynaud D., Barnola J.-M., Fischer H., Masson-Delmotte V., Jouzel J. (2005). Stable Carbon Cycle – Climate Relationship During the Late Pleistocene. *Science* **2**: 1313–1317.

Smith D., Howard A.J. (2004). Identifying changing fluvial conditions in low gradient alluvial archaeological landscapes: can coleoptera provide insights into changing discharge rates and floodplain evolution? *Journal of Archaeological Science* **31**: 109–120.

Smith D., Nayyar K., Schreve D.C., Thomas R., Whitehouse N.J. (2014). Can dung beetles from the palaeoecological and archaeological record indicate herd concentration and the identity of herbivores? *Quaternary International* **341**: 119–130.

Smith D., Whitehouse N.J., Bunting M.J., Chapman H. (2010). Can we characterise "openness" in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Forest, England. *The Holocene* **20**: 215–229.

Smith F.A., Doughty C.E., Malhi Y., Svenning J.-C., Terborgh J. (2016). Megafauna in the Earth system. *Ecography* **39**: 99–108.

Sommer R.S., Persson A., Wieseke N., Fritz U. (2007). Holocene recolonization and extinction of the pond turtle, *Emys orbicularis* (L., 1758), in Europe. *Quaternary Science Reviews* **26**: 3099–3107.

Song Y., Fang X., King J.W., Li J., Naoto I., An Z. (2014). Magnetic parameter variations in the Chaona loess/paleosol sequences in the central Chinese Loess Plateau, and their significance for the middle Pleistocene climate transition. *Quaternary Research (United States)* **81**: 433–444.

Sparks B.W. (1957). The Non-Marine Mollusca of the Interglacial Deposits at Bobbitshole, Ipswich. *Philosophical Transactions of the Royal Society B: Biological Sciences* **241**: 33–44.

Spiller D.A., Agrawal A.A. (2003). Intense Disturbance Enhances Plant Susceptibility to Herbivory: Natural and Experimental Evidence. *Ecology* **84**: 890–897.

Steiger J., Tabacchi E., Dufour S., Corenblit D., Peiry J.L. (2005). Hydrogeomorphic processes affecting riparian habitat within alluvial channel-floodplain river systems: A review for the temperate zone. *River Research and Applications* **21**: 719–737.

Stephens M., Challis K., Graf A., Howard A.J., Rose J., Schreve D.C. (2008). New Exposures of Bytham River Desposits at Brooksby, Leicestershire, UK: Context and Importance. *Quaternary Newsletter* **115**: 14–27.

Stewart J.R. (2010). The bird remains from the West Runton Freshwater Bed, Norfolk, England. *Quaternary International* **228**: 72–90.

Stockmar J. (1971). Tablets with spores used in absolute pollen analysis. *Pollen et Spores* **13**: 615–621.

Stringer C., Trinkaus E., Roberts M.B., Parfitt S.A., Macphail R.I. (1998). The Middle Pleistocene tibia from Boxgrove. *Journal of Human Evolution* **34**: 509–547.

Stuart-Haëntjens E.J., Curtis P.S., Fahey R.T., Vogel C.S., Gough C.M. (2015). Net primary production exhibits a threshold response to increasing disturbance severity in a temperate deciduous forest. *Ecology* **96**: 2478–2487.

Stuart A.J. (1975). The vertebrate fauna of the type Cromerian. *Boreas* **4**: 63–76.

Stuart A.J. (1979). Pleistocene occurrences of the European pond tortoise (*Emys orbicularis* L.) in Britain. *Boreas* **8**: 359–371.

Stuart A.J. (1996). Vertebrate faunas from the early Middle Pleistocene of East Anglia. In: *The early Middle Pleistocene in Europe*. (Ed. C. Turner), pp. 9–24. Balkema, Rotterdam.

Stuart A.J., Larkin N.R. (2010). Taphonomy of the West Runton Mammoth. *Quaternary International* **228**: 217–232.

Stuart A.J., Lister A.M. (2001). The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: Evidence for a new temperate episode in the British early Middle Pleistocene. *Quaternary Science Reviews* **20**: 1677–1692.

Stuart A.J., Lister A.M. (2010). The West Runton Freshwater Bed and the West Runton Mammoth: Summary and conclusions. *Quaternary International* **228**: 241–248.

Suganuma Y., Yokoyama Y., Yamazaki T., Kawamura K., Horng C.S., Matsuzaki H. (2010). ^{10}Be evidence for delayed acquisition of remanent magnetization in marine sediments: Implication for a new age for the Matuyama-Brunhes boundary. *Earth and Planetary Science Letters* **296**: 443–450.

Sun J., Lü T., Zhang Z., Wang X., Liu W. (2012). Stepwise expansions of C_4 biomass and enhanced seasonal precipitation and regional aridity during the Quaternary on the southern Chinese Loess Plateau. *Quaternary Science Reviews* **34**: 57–65.

Sun X., Luo Y., Huang F., Tian J., Wang P. (2003). Deep-sea pollen from the South China Sea: Pleistocene indicators of East Asian monsoon. *Marine Geology* **201**: 97–118.

Sun Y., Chen J., Clemens S.C., Liu Q., Ji J., Tada R. (2006). East Asian monsoon variability over the last seven glacial cycles recorded by a loess sequence from the northwestern Chinese Loess Plateau. *Geochemistry, Geophysics, Geosystems* **7**: 1–16.

Svenning J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation* **104**: 133–148.

Svenning J.-C., Fløjgaard C., Marske K.A., Nógues-Bravo D., Normand S. (2011). Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**: 2930–2947.

Taeubert J.E., El-Nobi G., Geist J. (2014). Effects of water temperature on the larval parasitic stage of the thick-shelled river mussel (*Unio crassus*). *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 231–237.

Tanskanen H., Venäläinen A., Puttonen P., Granström A. (2005). Impact of stand structure on surface fire ignition potential in *Picea abies* and *Pinus sylvestris* forests in southern Finland. *Canadian Journal of Forest Research* **420**: 410–420.

Temme A.A., Cornwell W.K., Cornelissen J.H.C., Aerts R. (2013). Meta-analysis reveals profound responses of plant traits to glacial CO_2 levels. *Ecology and Evolution* **3**: 4525–4535.

Temme A.A., Liu J.C., Cornwell W.K., Cornelissen J.H.C., Aerts R. (2015). Winners always win: Growth of a wide range of plant species from low to future high CO_2. *Ecology and Evolution* **5**: 4949–4961.

Thomas F.M., Blank R., Hartmann G. (2002). Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology* **32**: 277–307.

Thomas G.N. (2001). Late Middle Pleistocene pollen biostratigraphy in Britain: Pitfalls and possibilities in the separation of interglacial sequences. *Quaternary Science Reviews* **20**: 1621–1630.

Thomas P.A., El-Barghathi M., Polwart A. (2007). Biological Flora of the British Isles: *Juniperus communis* L. *Journal of Ecology* **95**: 1404–1440.

Torres V., Hooghiemstra H., Lourens L., Tzedakis P.C. (2013). Astronomical tuning of long pollen records reveals the dynamic history of montane biomes and lake levels in the tropical high Andes during the Quaternary. *Quaternary Science Reviews* **63**: 59–72.

Troels-Smith J. (1955). Karakterisering af løse jordarter (Characterization of unconsolidated sediments). *Danmarks Geologiske Underøgelse Series IV* **3**: 73.

Turner C. (1970). The Middle Pleistocene Deposits at Marks Tey, Essex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **257**: 373–437.

Turner C. (1996). A brief survey of the early Middle Pleistocene in Europe. In: *The early Middle Pleistocene in Europe*. (Ed. C. Turner), pp. 295–317. Balkema, Rotterdam.

Turner C., West R.G. (1968). The subdivision and zonation of interglacial periods. *Eiszeitalter und Gegenwart* **19**: 93–101.

Turner M.G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology* **91**: 2833–2849.

Turney C.S.M., Jones R.T. (2010). Does the Agulhas Current amplify global temperatures during super-interglacials? *Journal of Quaternary Science* **25**: 839–843.

Tye G.J., Sherriff J., Palmer A.P., Candy I., Schreve D.C. (2012). The expression of MIS 11 palaeoclimate in a lacustrine record: An annually resolved archive from Marks Tey, eastern England. *Geophysical Research Abstracts* **14**: 12280.

Tzedakis P.C. (2010). The MIS 11-MIS 1 analogy, southern European vegetation, atmospheric methane and the "early anthropogenic hypothesis." *Climate of The Past* **6**: 131–144.

Tzedakis P.C., Hooghiemstra H., Pälike H. (2006). The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quaternary Science Reviews* **25**: 3416–3430.

Tzedakis P.C., Raynaud D., McManus J.F., Berger A., Brovkin V., Kiefer T. (2009). Interglacial diversity. *Nature Geoscience* **2**: 751–755.

Ulrich W.H. (1975). *Monographie der Gattung Tachinus Gravenhorst (Coleoptera Staphylinidae) mit Bermerkungen zur Phylogenie und Verbreitung der Arten*. Christian-Albrechts Universitat, Keil.

Vera F.W.M. (2000). *Grazing Ecology and Forest History*. CABI Publishing, Oxford.

Viles H., Naylor L., Carter N., Chaput D. (2008). Biogeomorphological disturbance regimes: progress in linking ecological and geomorphological systems. *Earth Surface Processes and Landforms* **33**: 1419–1435.

Wagner B., Wilke T., Francke A., Albrecht C., Baumgarten H., Bertini A., Combourieu-Nebout N., Cvetkoska A., D'Addabbo M., Donders T.H., Föller K., Giaccio B., Grazhdani A., Hauffe T., Holtvoeth J., Joannin S., Jovanovska E., … Zhang X.S. (2017). The environmental and evolutionary history of Lake Ohrid (FYROM/Albania): Interim results from the SCOPSCO deep drilling project. *Biogeosciences* **14**: 2033–2054.

Wagner G.A., Krbetschek M., Degering D., Bahain J., Shao Q., Falguères C., Voinchet P., Dolo J.-M., Garcia T., Rightmire P. (2010). Radiometric dating of the type-site for *Homo heidelbergensis* at Mauer, Germany. *Proceedings of the National Academy of Sciences* **107**: 19726–19730.

Walker M.J.C., Coope G.R., Lowe J.J. (1993). The Devensian (Weichselian) Lateglacial palaeoenvironmental record from Gransmoor, East Yorkshire, England. A contribution to the "North Atlantic seaboard programme" of IGCP-253, "Termination of the Pleistocene." *Quaternary Science Reviews* **12**: 659–680.

Walkling A. (1996). *Coleopteran records from the last interglacial-glacial transition*. Unpublished PhD thesis. University of London.

Waller M.P. (2013). Drought, disease, defoliation and death: Forest pathogens as agents of past vegetation change. *Journal of Quaternary Science* **28**: 336–342.

Waller M.P., Binney H.A., Bunting M.J., Armitage R.. (2005). The interpretation of fen carr pollen diagrams: pollen-vegetation relationships within the fen carr. *Review of Palaeobotany and Palynology* **133**: 179–202.

Wang C.-J., Wan J.-Z., Qu H., Zhang Z.-X. (2017). Climatic niche shift of aquatic plant invaders between native and invasive ranges: a test using 10 species across different biomes on a global scale. *Knowledge & Management of Aquatic Ecosystems* **418**.

Wang Q., Liu J., Allen G.A., Ma Y., Yue W., Marr K.L., Abbott R.J. (2016). Arctic plant origins and early formation of circumarctic distributions: a case study of the mountain sorrel, *Oxyria digyna*. *New Phytologist* **209**: 343–353.

Ward J.K. (2005). Evolution and Growth of Plants in a Low CO2 World. In: *A history of atmospheric CO_2 and its effects on plants, animals, and ecosystems*. (Eds J.R. Ehleringer, T.E. Cerling & M.D. Dearing), pp. 232–257. Springer, New York.

Webster J.M., Davies P.J. (2003). Coral variation in two deep drill cores: Significance for the Pleistocene development of the Great Barrier Reef. *Sedimentary Geology* **159**: 61–80.

Weng C. (2005). An improved method for quantifying sedimentary charcoal via a volume proxy. *Holocene* **15**: 298–301.

West R.G. (1956). The Quaternary Deposits at Hoxne, Suffolk. *Philosophical Transactions of the Royal Society B: Biological Sciences* **239**.

West R.G. (1957). Interglacial Deposits at Bobbitshole, Ipswich. *Philosophical Transactions of the Royal Society B: Biological Sciences* **241**: 1–31.

West R.G. (1969). Pollen analyses from interglacial deposits at Aveley and Grays, Essex. *Proceedings of the Geologists' Association* **80**: 271–IN1.

West R.G. (1980a). *The pre-glacial Pleistocene of the Norfolk and Suffolk coasts*. Cambridge University Press, Cambridge.

West R.G. (1980b). Pleistocene Forest History in East Anglia. *New Phytologist* **85**: 571–622.

West R.G., Sparks B.W., Sutcliffe A.T. (1960). Coastal Interglacial Deposits of the English Channel. *Philosophical Transactions of the Royal Society B: Biological Sciences* **243**.

Westaway R. (2009). Quaternary vertical crustal motion and drainage evolution in East Anglia and adjoining parts of southern England:Chronology of the Ingham River terrace deposits. *Boreas* **38**: 261–284.

Westaway R., Bridgland D.R., White M. (2006). The Quaternary uplift history of central southern England: evidence from the terraces of the Solent River system and nearby raised beaches. *Quaternary Science Reviews* **25**: 2212–2250.

Whitehouse N.J. (1997). Insect faunas associated with *Pinus sylvestris* L. from the mid-Holocene of the Humberhead Levels, Yorkshire, U.K. In: *Studies in Quaternary Entomology - An Inordinate Fondness for Insects*. (Eds A.C. Ashworth, P.C. Buckland & J.P. Sadler), pp. 293–303. John Wiley & Sons Ltd.

Whitehouse N.J. (2000). Forest fires and insects: palaeoentomological research from a subfossil burnt forest. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164**: 231–246.

Whitehouse N.J. (2004). Mire ontogeny, environmental and climatic change inferred from fossil beetle successions from Hatfield Moors, eastern England. *The Holocene* **14**: 79–93.

Whitehouse N.J. (2006). The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. *Quaternary Science Reviews* **25**: 1755–1789.

Whitehouse N.J., Smith D. (2010). How fragmented was the British Holocene wildwood? Perspectives on the “Vera” grazing debate from the fossil beetle record. *Quaternary Science Reviews* **29**: 539–553.

Whiteman C. (2002). Implications of a middle pleistocene ice-wedge cast at Trimingham, Norfolk, eastern England. *Permafrost and Periglacial Processes* **13**: 163–170.

Willis K.J., Birks H.J.B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science* **314**: 1261–1265.

Wood J.R., Wilmshurst J.M. (2012). Wetland soil moisture complicates the use of *Sporormiella* to trace past herbivore populations. *Journal of Quaternary Science* **27**: 254–259.

Wood J.R., Wilmshurst J.M. (2013). Accumulation rates or percentages? How to quantify *Sporormiella* and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. *Quaternary Science Reviews* **77**: 1–3.

Wood J.R., Wilmshurst J.M., Turney C.S.M., Fogwill C.J. (2016). Palaeoecological signatures of vegetation change induced by herbivory regime shifts on subantarctic Enderby Island. *Quaternary Science Reviews* **134**: 51–58.

Wood J.R., Wilmshurst J.M., Worthy T.H., Cooper A. (2011). *Sporormiella* as a proxy for non-mammalian herbivores in island ecosystems. *Quaternary Science Reviews* **30**: 915–920.

Yin Q. (2013). Insolation-induced mid-Brunhes transition in Southern Ocean ventilation and deep-ocean temperature. *Nature* **494**: 222–5.

Yin Q., Berger A. (2010). Insolation and CO_2 contribution to the interglacial climate before and after the Mid-Brunhes Event. *Nature Geoscience* **3**: 243–246.

Yin Q., Berger A. (2012). Individual contribution of insolation and CO_2 to the interglacial climates of the past 800,000 years. *Climate Dynamics* **38**: 709–724.

Zagwijn W. (1996a). The Cromerian Complex Stage of the Netherlands and correlation with other areas in Europe. In: *The early Middle Pleistocene in Europe*. (Ed. C. Turner), pp. 145–172. Balkema, Rotterdam.

Zagwijn W. (1996b). An analysis of Eemian climate in Western and Central Europe.

Quaternary Science Reviews **15**: 451–469.

Zanetti A. (2011). Omaliinae. In: *Die Käfer Mitteleuropas. 4. Staphylinidae (exklusive Aleocharinae, Pselaphinae und Scydmaenidae)*. (Eds V. Assing & M. Schülke), pp. 49–117. Spektrum Akademischer, Heidelberg.

Appendices

Appendix 1: The West Runton (WR14) Sequence

Section Location

TG 18851 43079 (± 7 m)

c. 263 m East of datum at 'West Runton Gap' (see Figure 4.1)

Unit Descriptions

Total Depth: 197 cm (Wroxham Crag 27 cm; West Runton Freshwater Bed 175 cm)

Units described from the base of the sequence in Table A.1 (see also Figures A.1 and 4.2).

Table A.1 WR14 Sub-unit descriptions (see also Figure 4.2)

Sub-unit	A
Depth	197 cm to 175 cm
Description	Coarse sand with rounded gravel clasts. Orange-brown. Erosional contact with above unit. Grain size variable in drapes, etc. Wroxham Crag.
Troels-Smith Code	Nig2, Strat1, Sicc4, Elas0, Lime1 (Gmin3, Gmaj1)
Munsell Colour(s)	7.5YR 5/8
Sub-unit	B
Depth	175 cm to 136 cm
Description	Grey silty clay interbedded and deformed. Shells and shell fragments towards the top. Some shells and fine sand.
Troels-Smith Code	Nig3, Strat1, Sicc3, Elas0, Lime1 (As2, Ag2, test+, Ld+, Dl+)
Munsell Colour(s)	2.5Y 2/0 (dark) and 5YR 3/1 (light)

(Continued overleaf)

Table A.1 Continued

Sub-unit	C
Depth	136 cm to 121 cm
Description	Light brown. Shallow lens (superficial) of coarse sand and rounded gravel clasts interbedded with v. dark (darker than above unit) clayey silt.
Troels-Smith Code	Nig2, Strat1, Sicc4, Elas0, Lime1 (Gmin3, Gmaj1 / Ag3, As1)
Munsell Colour(s)	10YR 6/6
Sub-unit	D
Depth	121 cm to *c.* 30 cm
Description	Dark grey/black, fine grained clayey silt with slight upward fining. *c.* 60 cm increasing proportion of shells, and fine sand. Lens of (Gmin3, ptest1, As+, Ag+) *c.* 20x6 cm at *c.* 100 cm. Occasional other small sand lenses (*c.* 2-3 cm). Occasional flame structures towards the base from sandy unit.
Troels-Smith Code	Nig4, Strat1, Sicc3, Elas0, Lime0 (Ag3, As1, Gmin+, test+, Ld+, Dl+)
Munsell Colour(s)	2.5Y 2/0
Sub-unit	E
Depth	*c.* 30 cm to 0 cm
Description	Deformed unit of grey clays. Much mixing with lower unit, creating wispy structures. Reddened in top 3-4 cm (*n.b.* Some reddened, oxidised material was removed from the top during cleaning for sampling).
Troels-Smith Code	Nig2, Strat1, Sicc3, Elas1 (Ag1, As3, Ld+)
Munsell Colour(s)	5YR 3/1 (grey) and 5YR 3/2 (oxidised)

Insect Samples

Table A.2 WR14 Insect Sample Numbers and Depths

Sample Number	Sample Depth (cm)
1	0-5
2	5-10
3	10-15
4	15-20
5	20-25
6	25-30

(Continued overleaf)

Table A.2 Continued

7	30-35
8	35-40
9	40-45
10	45-50
11	50-55
12	55-60
13	60-65
14	65-70
15	70-75
16	75-80
17	80-85
18	85-90
19	90-95
20	95-100
21	100-105
22	105-110
23	110-117
24	117-125
25	125-130
26	130-135
27	135-140
28	140-145
29	145-150
30	150-155
31	155-162

Monoliths

Monolith A (upper, right): 100 cm to 0 cm

Monolith B (lower, left): 175.5 cm to 75.5 cm

(See Figure 4.2)

Photograph

Figure A.1 – WR14 sequence (West Runton Freshwater Bed) after cleaning, prior to sampling (see Figure 4.1 for location)

Appendix 2: The Pakefield (PK14) Sequence

Section Location

TM 53685 88445 (see Figure 5.1)

Unit Descriptions

Total Depth: 92 cm

Units described from the base of the sequence in Table A.2 (see also Figures A.2 and 5.2). Section dipping *c.* 15°.

Table A.3 PK14 Sub-unit descriptions (see also Figure 5.2)

Sub-unit	A
Depth	92 cm to 89 cm
Description	Mostly obscured. Light grey clay with some silt. Appears massive, but poor exposure. Presumed to continue deeper.
Troels-Smith Code	Nig1, Str0, Si3, El1 (As3, Ag1)
Munsell Colour(s)	5Y 5/1
Sub-unit	B
Depth	89 cm to 75 cm
Description	Orange-brown sandy, clayey silts. Some small, subtle compression structures. Relatively sharp boundary with above unit.
Troels-Smith Code	Nig2, Str1, Si2, El1 (Ag2, As2, Gmin1)
Munsell Colour(s)	10 YR 4/6
Sub-unit	C
Depth	75 cm to 41 cm
Description	Dark grey clayey silts, indistinctly stratified. Occasional reddened flame-like structures. Top *c.* 7 cm oxidised (dark red-brown). Graded boundary with above unit.
Troels-Smith Code	Nig3, Str1, Si2, El1 (Ag2, As2, Ld+)
Munsell Colour(s)	10 YR 3/1 and 10YR 3/2 (reddened)

(Continued overleaf)

Table A.3 Continued

Sub-unit	D
Depth	41 cm to 28 cm
Description	Light grey silty clays, slightly reddened in lower half. Indistinctly stratified. Rare flecks of dark (organic) detritus. Relatively sharp boundary with overlying unit.
Troels-Smith Code	Nig1, Str1, Si3, El1 (As3, Ag1, Ld+)
Munsell Colour(s)	10 YR 5/3 and 10YR 5/4 (reddened)
Sub-unit	E
Depth	28 cm to 0 cm
Description	Light reddish-brown silty clays, coarsely stratified, alternating between redder and less-red layers. Slight upward fining.
Troels-Smith Code	Nig2, Strat1, Si3, El1 (As3, Ag1)
Munsell Colour(s)	10YR 5/6 and 2.5Y 5/4

Insect Samples

Table A.4 PK14 Insect Sample Numbers and Depths

Sample Number	Sample Depth (cm)
1	28-41
2	41-47
3	47-52
4	52-57
5	57-62
6	62-67
7	67-75

Monolith

Monolith A: 81 cm to 31 cm

(See Figure 5.2)

Photograph

Figure A.2 – PK14 sequence (Cromer Forest Bed at Pakefield) after cleaning and monolith insertion, prior to removing monolith and bulk samples (see Figure 4.1 for location)