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by

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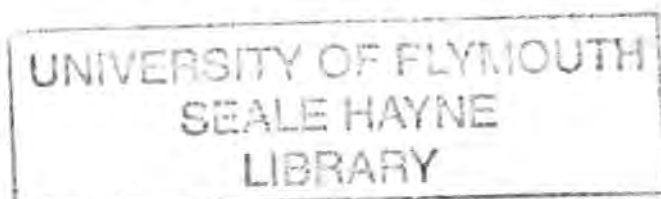
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ABSTRACT

The potential of different field boundary types in lowland farmland to contribute to arthropod biodiversity and sustainable agriculture was investigated. Field boundaries, categorised according to nationally applicable definitions, were found to represent ecologically differing habitats based on their woody abundance and the frequency of young and mature emergent trees. These habitat characteristics were determining factors in the community structure and composition of overwintering epigeal arthropods.

Hedgerows supported the most species rich carabid and staphylinid assemblage. Degraded hedgerow boundaries supported the most equitable carabid community, and provided a refuge for carabid species with poor dispersal power to a greater extent that hedgerows or post and wire fences. The grassy and natural regeneration vegetation associated with post and wire boundaries supported high densities of all taxa particularly overwintering carabid and staphylinid polyphagous predators. A subset of all field boundary types was required for complete species representation, indicating that maximising the heterogeneity of field boundary habitats represented at the farm-scale will enhance arthropod biodiversity in farmland.

Carabidae and Staphylinidae actively selected overwintering sites and the physiological condition of polyphagous predators was generally high. It was concluded that heterogeneous distributions in field boundaries were more likely to be the result of differential microhabitat selection rather than differential survival overwinter. This indicated that favourable overwintering microhabitats occurred in all field boundary types. Generally, overwintering survival did not appear to be a regulating factor in the population dynamics of polyphagous predators. Margins adjacent to pre-existing boundaries may contribute to enhanced densities and physiological condition of some polyphagous predators, both over winter and in early spring.

The results were discussed in relation to field boundary management and agri-environment policy.

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

Relevant scientific seminars, conferences and workshops were regularly attended at which work was often presented, and several papers prepared for publication.

Publications

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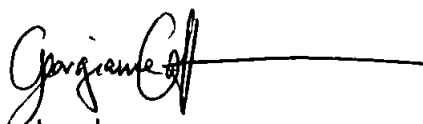
Conserving biodiversity in Farmland, Postgraduate workshop, September 2000, University of Dundee.
'The potential of different field boundary types to support beneficial arthropod populations, and implications for their management.'

Ecology and evolution in a changing world. Graduate Student Workshop, January 2000, Imperial College at Silwood Park, University of London.
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CHAPTER ONE: INTRODUCTION

1.1 FIELD BOUNDARIES IN LOWLAND FARMLAND

'Field boundary' is a generic term used to describe any linear feature that demarcates a field. There is currently an estimated 1.3 million kilometres of field boundary in England and Wales (Haines-Young *et al.*, 2000), and in lowland farmland they comprise the dominant form of semi-natural habitat (Barr *et al.*, 1993).

1.1.1 Classification and stock

Field boundary habitats vary in botanical composition, vegetation structure (woody canopy, emergent trees and herbaceous vegetation), additional features (bank, margin, fence, ditch) and management. Due to the complexity and range of field boundary habitats, a systematic method of classifying linear features is required before their ecology may be fully understood. The most comprehensive survey of field boundaries in the U.K was conducted as part of the Countryside Survey 2000 (CS2000) by the Centre for Ecology and Hydrology (Haines-Young *et al.*, 2000). Within this survey, the difficulty of comparing different habitats was resolved by recording all attributes present in a field boundary separately. Particular features were then prioritised in a hierarchy based on perceived ecological value to produce seven major field boundary types (Table 1.1.1). Field boundaries were classed as decreasing in ecological value in the order: hedge > remnant hedge > wall > line of trees/shrubs/relict hedge with fence > line of trees/shrubs/relict hedge > bank/grass strip/margin > fence.

In England and Wales, hedgerows and post and wire fences form the dominant field boundary types (69.5% in total), with a combination of remnant and relict hedgerows (16.5% in total), walls and banks/grass strips forming the remainder (Table 1.1.2) (Haines-Young *et al.*, 2000).

1.1.2 Origin

In lowland farmland, hedgerows are the traditional field boundary type (Rackham, 1986). Hedgerows may be planted, originate as relicts of former woodland that has since been cleared away or develop accidentally along an existing linear feature where management is restricted (Rackham, 1986). In the past 50 to 60 years, the intensification of UK agriculture has resulted in major changes within the farmed landscape in terms of its scale, structure and component habitat elements. The drive for maximum arable acreage, coupled with modernised farm machinery motivated a trend for field enlargement. This resulted in the large-scale removal of traditional hedgerow field boundaries and various types of grassy field margin to increase field size and minimise management costs (Greaves & Marshall, 1987). Where field boundaries were required, hedgerows have frequently been replaced with post and wire fences (Barr *et al.* 1993; Haines-Young *et al*, 2000). In addition to direct removal, lack of management or mismanagement has resulted in widespread hedgerow deterioration to remnant and relict status (Barr *et al.*, 1991, 1994; Haines-Young *et al.*, 2000). Neglected hedgerows may take over 20 years to deteriorate (DETR, 2001), implying that those which are currently mis-managed or unmanaged may be declining in quality. In addition, lack of net change in hedgerow length since the early 1990s obscures the turnover between hedgerows removed and newly created hedgerows (Barr *et al.*, 1993; Haines-Young *et al.*, 2000). It has been recognised that older hedgerows tend to be more species rich (Hooper, 1970); therefore newly created hedgerows may not have the same ecological value. They will also lack the archaeological value recognised in older hedgerows (Anon., 1997).

Hedgerow	A more or less continuous line of woody vegetation that has been subjected to a regime of cutting in order to maintain a linear shape. When hedge management is abandoned (i.e. not in the past 5 years) and the overall natural shape of the component tree species is regained, or when the bottom 2m (or less) of the feature is not more or less continuous, then the feature can no longer be described as a hedge (and might be considered as, for example, a line of trees or shrubs).
Remnant hedgerow	A line of woody vegetation showing where a hedge has once been. The feature may still be cut or trimmed, but the bottom 2m (or less) of the feature is no longer continuous. If the feature has not been cut, the overall natural shape of the component tree species has not yet been completely regained.
Relict hedgerow	A line of woody vegetation where the bottom 2m or less of the feature is no longer continuous and the overall natural shape of the component tree species has been regained.
Line of trees/shrubs	A single width line of individual trees or scrub which is at least 20m long. The gap between individual features should not exceed the average canopy width of the two individuals on either side.
Fence	A permanent post and wire or rail structure, including wooden, concrete or metal posts. May or may not be associated with an additional feature such as grass/natural regeneration margin or ditch.
Bank/Grass strip	An earth or stone faced bank with or without a fence. A grass/ natural regeneration linear strip without a fence.
Wall	A built structure of natural stone or manufactured blocks, mostly of traditional dry stone wall construction but including mortared walls. Includes walls with fences and lines of trees or shrubs.

Table 1.1.1 Definition of field boundary types identified by the Countryside Survey 2000 (based on Haines-Young *et al.*, 2000).

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	Length ('000km)	S.E. ('000km)	% Stock
Hedgerow	449.3	21.2	35.8
Remnant hedgerow	52.3	4.3	4.2
Line of trees/shrubs/relict hedge and fence	70.0	5.1	5.6
Line of trees/shrubs/relict hedge	83.4	5.1	6.7
Bank/grass strip	70.0	7.4	5.6
Fence	423.2	16.9	33.7
Wall	105.8	12.8	8.4

Table 1.1.2 Estimates of field boundary stock in England and Wales in 1998 with standard error (S.E.) estimates and the percentage of the total field boundary stock represented by each type (Haines-Young *et al.*, 2000).

1.1.3 Function

The primary function of field boundaries was for stock control, but they potentially fulfill a variety of environmental, agronomic, conservation and recreation roles in farmland (Marshall & Moonen, 2002). Field boundary networks influence landscape hydrology (Viaud *et al.*, 2001) and individual features may restrict agro-chemical spray drift (de Snoo, 1999), run-off (Daniels & Gilliam, 1996) and soil erosion (Van Dijk *et al.*, 1996) and thereby act as buffers to protect water courses or semi-natural habitat. The presence of field boundaries may also enhance abiotic conditions for crop or livestock, reduce weed ingress or herbicicide use (Marshall & Moonen, 2002; Smith *et al.*, 1999) and support beneficial arthropod populations such as pollinators (Lagerlof *et al.*, 1992) and natural enemies (Cowgill *et al.*, 1993; Powell, 2000; Landis *et al.*, 2000). Field boundaries play a vital role in supporting floral (Marshall & Moonen, 2002; Wilson, 1994) and faunal (Smith *et al.*, 1993; Barr *et al.*, 1995; Dover & Sparks, 2000; Maudsley, 2000; Meek *et al.*, 2002) biodiversity in agricultural landscapes. This can create recreational and economic benefits for land managers, for example, by supporting game bird populations (Potts, 1986).

1.1.4 Policy

Agricultural objectives in the U.K. are increasingly linked to enhancing biodiversity and the development of sustainable farming (Curry, 2002). The majority of research into the value of field boundaries to support farmland biodiversity and provide beneficial agronomic functions has focused firstly on hedgerows as the traditional field boundary, and secondly on field margins as a versatile means of conservation enhancement. Field margins refer to strips of land between the field and a pre-existing boundary. A number of policy instruments have been implemented to enhance or protect the representation of hedgerows and encourage the creation of field margins in farmland.

Agri-environment schemes such as the Countryside Stewardship Scheme (CSS) and Environmentally Sensitive Areas (ESA) provide financial incentives and best-practice advice for farmers to sympathetically manage existing, restore degraded (through laying, coppicing or planting up) and create new hedgerows (DEFRA, 2003a).

Grants are available for the creation of field margins of wild-flowers or tussocky grasses as overwintering habitat for natural enemies of arable crop pests, amongst other field margin options. Creation of beetle banks sown with tussocky grasses is also recommended in large arable fields to enhance biological control (GCT, 2001). To date, nearly 10,000km of degraded hedgerow have been restored and approximately 13,000km of grass margin established as part of CSS agreements. However, this amounts to only a small proportion of the total field boundary stock in England and Wales.

The introduction of the Hedgerow Regulations in 1997 (Anon., 1997) aimed to protect from removal hedgerows that are classed as important in terms of their ecological, historical or landscape value. Criteria used to identify 'important' hedgerows have recently been reviewed (DEFRA, 2003b). A hedgerow is currently classed as ecologically important or species rich if it supports more than five woody species (not including climbers) in a standard 30 m length (or four woody species in northern England) or supports priority species included in the U.K. Biodiversity Action Plan (Anon., 1995). No criteria on hedgerow connections were included despite widespread recognition of the ecological value of connectivity to other field boundary or woodland habitats (DETR, 2001). The wildlife value of field boundaries has also been recognised by the creation of two Priority Habitats in the U.K. Biodiversity Action Plans designed to conserve Ancient and/or Species Rich Hedgerows and Cereal Field Margins (Anon., 1995).

1.2 FIELD BOUNDARIES AND ARTHROPOD COMMUNITIES

Farmland arthropods use field boundaries as sites for overwintering and aestivation, refuge from detrimental agronomic practices or unsuitable microclimatic conditions, behavioural reference points (e.g. for mating), oviposition, plant and invertebrate food sources and host species. Arthropods are considered accurate and sensitive indicators of the state of the environment due to their representation of a spectrum of life traits, frequently with a high degree of specialisation and short life cycles (Luff *et al.*, 1992;

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Kremen *et al.*, 1993). As a result, they are considered to be more sensitive to changes in habitat, landscape and farming systems than plants and vertebrates (Burel *et al.*, 1998). In addition, physical environmental factors may shape arthropod species assemblages more than biological relationships such as competition (Loreau, 1992). As a result, the community structure and composition of arthropods are likely to reflect differences in field boundary habitat type. Field boundary types differ in botanical composition, habitat structure and management and these factors have been shown to influence arthropod community structure and composition (Burel & Baudry, 1995; Maudsley *et al.*, 1997). In addition, characteristics of the field boundary network and landscape structure may influence arthropod assemblages locally (Den Boer, 1990; Petit, 1994). The influence of historical factors on arthropod communities is difficult to quantify and beyond the limitations of this study but must be recognised as a potentially important factor (Burel, 1993; Petit & Burel, 1998; Conrad *et al.*, 2001).

1.2.1 Arthropod habitat preferences and dispersal ability

Farmland supports a complex, diverse and characteristic arthropod fauna within which Coleoptera, and particularly the beetle families Carabidae and Staphylinidae are both speciose and abundant (Potts & Vickerman, 1974). Arthropods differ according to their habitat preferences in farmland, and their ability to move between different habitat elements (Thiele, 1977; Duelli *et al.*, 1990; Turin *et al.*, 1991). These differences will influence how individuals utilise field boundaries, and are frequently critical to the persistence of species populations in farmland, and consequently the arthropod composition of field boundaries (Den Boer, 1977, 1987, 1990; Maelfait *et al.*, 1994). Habitat preferences generally result from a response to underlying environmental conditions rather than vegetation type, though vegetation will influence microclimatic variables.

Many carabid species have been categorised according to habitat preference and dispersal ability (Thiele, 1977; Duelli *et al.*, 1990; Lindroth, 1992; Ribera *et al.*, 1999; Fournier & Loreau, 2001) and these functional groups reflect patterns observed in other arthropod taxa (Duelli & Obrist, 1995). Species that are active in crop or pasture fields

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during their reproductive period are categorised as field or open habitat species (Thiele, 1977). In annual cropping systems the field represents a cyclically disturbed and ephemeral habitat. Many species that exploit this habitat show seasonal migration between field and field boundary at different stages in their life cycle. Species typical of fields are generally eurytopic, and some have almost ubiquitous distributions between habitat elements (Duelli *et al.*, 1990). To highlight variations in habitat use within farmland, open habitat species can be further categorised into adult and larval overwinterers (Den Boer & Den-Danje, 1990). Adult overwinterers (e.g. *Bembidion lampros* and *Pterostichus cupreus*) show seasonal migration between the crop to reproduce and field boundaries where they overwinter. Larval overwinterers (e.g. *P. melanarius, P.madidus* and *Harpalus rufipes*) generally complete their life cycle in the field where they overwinter as larvae. However, some mature adults of larval overwintering species will overwinter in field boundaries to reproduce for a second year. In addition, the adults of some larval overwintering species may use field boundaries during the summer as sites for refuge from unsuitable microclimatic conditions, oviposition and larval development (Wallin & Ekbom, 1988; Descender & Alderweireldt, 1988). Many species of Staphylinidae also show seasonal dependence on field boundary habitat for overwintering and migrate into crop or pasture fields in spring (Dennis & Fry, 1992). Carabid species that show seasonal migration between field and boundary tend to disperse by walking whilst many of the more abundant and ubiquitous staphylinid species of mixed arable-pastoral farming systems disperse by flight (Coombes & Sotherton, 1986; Hunter *et al.*, 1991; Levesque & Leseque, 1995). Despite the fact that these carabids are generally restricted to ground movement, many open field carabids are categorised as having high or medium powers of dispersal (Lindroth, 1992; Den Boer *et al.*, 1980; Fournier & Loreau, 2001).

Other arthropod species in farmland show a strong preference for semi-natural wooded habitat in farmland and are referred to as woodland origin or closed habitat species (Thiele, 1977). Closed habitat species are described as exhibiting a 'hard edge' response to habitat type, showing no measurable population exchange between neighbouring habitats (Duelli *et al.*, 1990). Typical carabid woodland species are more

stenotopic in the environmental conditions they will tolerate. They generally favour damp and shaded conditions and are characteristically autumn breeders (e.g. *Bembidion lunulatum, Leistus rufescens, Pterostichus strennus* and *Pterostichus vernalis*) (Thiele, 1977; Fournier & Loreau, 2001). Closed habitat species vary in their ability to colonise woody linear features depending on habitat suitability (i.e. woodiness) and on the continuity and connectivity of the field boundary network and adjacent woodlands (Burel, 1989; Petit, 1994). The majority disperse by walking and many are restricted in their dispersal power. Consequently, they are highly vulnerable to the processes of farming intensification and fragmentation of suitable habitat in farmland (Den Boer, 1977, 1987, 1990; Turin & Peters, 1986).

1.2.2 Botanical composition

Field boundaries support a high diversity of plant species in lowland agricultural landscapes (Barr *et al.*, 1993) and have been identified as a key habitat for plant conservation (Bunce *et al.*, 1994; Freemark *et al.*, 2002). More than 40 woody and 270 herbaceous species have been identified in hedgerow plots (Barr *et al.*, 1993) whilst, for example, the hedge check list of the Cornish Biological Records Unit (CBRU) has 872 species and sub-species of plant and ferns, of which 32 are scarce and 13 are listed in the Red Data Books (Menneer, 1994). Poor management of boundary habitats due to intensive farming have been implicated in an overall decline in farmland floral diversity (Marshall & Moonen, 2002).

(i) Woody species

The most frequent hedgerow canopy species are hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*) and hazel (*Corylus avellana*), though many other deciduous woodland tree and shrub species are common. A quarter of hedgerows sampled nationwide for the CS2000 had five or more woody species in a standard 30m length of the hedge and 86% had more than two species (Haines-Young *et al.*, 2000). The hedgerow canopy will also support soft woody climbers and ramblers, particularly bramble (*Rubus fruticosus*) and ivy (*Hedera helix*) (Wilson & Sotherton, 1994). The number of woody species within a hedgerow may be indicative of its origin (Pollard *et*

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al., 1974; Rackham, 1986) and age (Hooper, 1970). For example, planted hedgerows tend to be species poor and dominated by either hawthorn or blackthorn.

(ii) Herbaceous species

The herbaceous composition of linear features is strongly influenced by adjacent land-use and field boundary management (French & Cummins, 2001; Maudsley *et al.*, 2002; Marshall & Moonen, 2002). For example, French & Cummins (2001) identified four herbaceous communities in hedgerows that were described by their strong associations with adjacent land-use: intensive arable, rotational, grassland and woodland. Linear features adjacent to intensively managed pasture and arable crops supported the lowest herbaceous species richness compared to boundaries bordering a range of rural land-use types due to the combined impact of disturbance and increased nutrient status (Hegarty & McAdam, 1994). This results in dominance by a few highly competitive species including common nettle (*Urtica dioica*), creeping thistle (*Cirsium arvense*), cleavers (*Galium aparine*), hedge bindweed (*Calystegia sepium*), field bindweed (*Convolvulus arvensis*), barren brome (*Bromus sterilis*) and wild oat (*Avena* spp.) species (Smith *et al.*, 1993; Boatman *et al.*, 1994). The herbaceous flora may also be indicative of field boundary management. For example, reduced cutting frequency will enable tall herbs and grass species to develop, such as couch *(Agropyron repens)*, cocksfoot (*Dactylis glomerata*), yorkshire fog (*Holcus lanatus*), cow parsley (*Anthriscus sylvestris*), hogweed (*Heracleum sphondylium*) and strongly growing species such as meadow buttercup (*Rannunculus acris*). Frequent cutting, flailing or grazing will encourage fine leaved grasses including common bent (*Agrostis capillaris*) and the fescues (*Festuca* spp.), and rosette forming species such as creeping buttercup (*Ranunculus repens*), greater plantain (*Plantago major*) and dandelion (*Taraxacum* spp.) (Dowdewell, 1987).

Although the presence of a woody canopy will influence the microclimate it remains uncertain to what extent it will influence the species composition of the hedge-base (Bunce *et al.*, 1994; Boatman *et al.*, 1994; McCollins *et al.*, 2000). Certain species, including cow parsley, cleavers, ground ivy (*Glechoma hederacea*) and hogweed are more likely to be present in herbaceous vegetation if a woody boundary is present

(Boatman *et al*, 1994). However woodland type plants such as dogs mercury (*Mercurialis perennis*) and foxglove (*Digitalis purpurea*) are typically poor colonisers and their occurence in a hedge-base would depend on hedgerow origin, age, canopy width, habitat quality (in this case its 'woodiness') and landscape characteristics such as distance to nearest woodland and connectivity of the boundary to wooded habitat (Forman & Baudry, 1984; Baudry & Merriam, 1988; Burel & Baudry, 1990; McCollin *et al.*, 2000). Forman & Baudry (1984) describe the influence of aspect, with twice as many herbaceous species growing on the 'sunny' side of a hedge, while mosses were restricted to the 'shady' side.

As hedgerows deteriorate, associated changes in light, wind and temperature may result in the loss of some woodland type species, and colonisation by open field and forest edge plants (Barr *et al.*, 1993). Ancillary fencing, frequently used to make degraded hedgerows stockproof or to protect the hedge-base and lower canopy from grazing, was considered to increase botanical diversity through bird mediated dispersal (Forman & Baudry, 1984).

(iii) Botanical composition and arthropod diversity

Plant diversity is a strong determinant of arthropod diversity. The diversity of plant species directly influences the diversity of herbivorous invertebrates, that will in turn influence the diversity of predatory, parasitic and symbiotic species (Southwood *et al.*, 1979; Strong *et al.*, 1984). There are also more complex interactions, whereby the maintenance of predator and parasite diversity by local herbivore diversity prevents competitive exclusion thereby allowing a high diversity of herbivores to exist (Seimann *et al.* 1998). Diversity of detritivore species will be influenced by the variety of leaf litter produced (Hovermeyer, 1999). Several studies have shown that the diversity of field boundary invertebrates is strongly related to the diversity of plants within the habitat (Pollard *et al.*, 1974; Bowden & Dean, 1977; Thomas & Marshall, 2000). This relationship is evidenced at the landscape scale where field boundaries support higher diversity of both plants and arthropods than the crop habitat (Forman & Baudry, 1984;

Thomas & Marshall, 2000) and between different field boundary habitats (Maudsley *et al.*, 1997).

An increase in the functional diversity of plants may be as effective in enhancing arthropod diversity as increasing the number of plant species *per se* (Seimann *et al.* 1998). For example, different guilds of herbivores will feed on leaves, stems, bark, buds, flowers, fruits, seeds or galls of plants and they will differentiate between flowering and non-flowering, vegetative and woody, shrubs and trees, annual, biennial and perennial. A plant community offering sequential production of resources will provide a more constant supply of nectar, pollen, leaves, fruits and nuts to support individual species throughout their life-cycle and a greater range of species with differing life-cycles. In mixed hedgerows flowering can occur on blackthorn in March, hawthorn in May, dog rose (*Rosa canina*) and bramble in June onwards and ivy in autumn (Maudsley, 2000). A diversity of flower types will provide nectar resources for long- and short-tongued pollinators (Marshall & Moonen, 2002). The architectural diversity, arising from the age and growth form of individual plants, may also be an important determinant of arthropod diversity (Lawton, 1983). For example, hedge architecture is particularly important for spiders, perhaps due to their web building requirement (Hatley & McMahon, 1980).

Tree and shrub species differ in the arthropod communities they support. For example, hawthorn has 209 associated insect and arachnid species, blackthorn 153, field maple (*Acer campestre*) 51, whilst holly (*Ilex aquifolium*) only has 10 (Kennedy & Southwood, 1984). However, many arthropods are strongly associated with particular host plants, so if these are absent from a field boundary, their dependent arthropods will be also (Clements & Toft, 1992). Joyce (2000) found the abundance of the beetle families Carabidae and Staphylinidae to be associated with the presence of hawthorn and hazel in the hedgerow. The large arthropod community associated with these woody species may provide abundant prey items for these predatory beetle families.

On average, herbaceous plants support fewer arthropod species than the more architecturally complex woody or shrub species (Joyce, 2000). However, Greaves &

Marshall (1987) noted that low herbaceous vegetation, in particular perennials, had the most influence in supporting epigeal arthropod diversity. Entire communities of arthropods may be associated with herbaceous plant groups such as umbellifers, thistles and nettles. For example, 107 insect species are associated with stinging nettles (*U. dioica* and *U. urens*) and of those 31 species (from the orders Coleoptera, Diptera, Heteroptera, Homoptera and Lepidoptera) are thought to be restricted to these plants. A host of secondary insect visitors are subsequently attracted to nettles to predate or parasitise the primary visitors, including Coccinellidae, Hymenoptera and Diptera species (Davis, 1983). Within sown field margins certain plant compositions favoured particular arthropod groups. Tussocky grasses enhanced overwintering densities of Carabidae, Staphylinidae, Chrysomelidae, Collembola, Diptera, Homoptera and Hymenoptera among other arthropods (Luff, 1966; Thomas *et al.*, 1991). Syrphidae abundance was related to the presence of mayweed (*Matricaria* spp.), whilst pollinating insects favoured legumes and labiates such as white clover and white dead nettle (Marshall & Moonen, 2002). Perennial grasses provide a food source and oviposition site for many butterflies in farmland.

1.2.3 Habitat structure and microclimate

Plants form some of the major structural attributes of a boundary and will vary substantially between field boundary types. Together, vegetation structure and additional features influence the microclimatic conditions and the structural complexity of a linear feature and contribute strongly to the arthropod community structure and composition (Pollard *et al.*, 1974; Forman & Baudry, 1984; Maudsley, 2000; Brose, 2003) .

(i)   Habitat structure and microclimate

A field boundary may be composed of three vegetation layers: a herbaceous flora, a dense and continuous woody canopy and emergent trees (Forman & Baudry, 1984). A well-managed hedgerow will support all three and thereby provide a dense, stockproof barrier. Hedgerow degradation through lack of, or inappropriate, management can result in increasing gappiness of the canopy and woody species may begin to regain their natural shape (Barr *et al.*, 1993). Consequently, the lower two metres (or less) of the

canopy may cease to be stockproof frequently leading to the use of ancillary fencing in livestock areas. In the absence of a woody canopy, stockproofing may be achieved using post and wire fencing. Permanent fences will be associated with a narrow margin of herbaceous vegetation either through design or the inability to plough directly adjacent to the fence (Smith *et al.*, 1993). Whilst post and wire habitats are predominately herbaceous, some may support soft woody climbers or emergent trees.

The vertical structure of a field boundary will strongly influence microclimatic conditions by altering wind velocity and solar radiation (Pollard *et al.*, 1974, Forman & Baudry, 1984; Maudsley, 2000; Viaud *et al.*, 2001). For example, a tall canopy will alter air-flow by reducing velocity but increasing turbulence on the windward side (Lewis, 1969). A structurally complex boundary, and hedgerow intersections, will provide a greater range of microclimatic conditions and buffer disturbance caused by field boundary management or farming operations (Pollard *et al.*, 1974; Forman & Baudry, 1984). Gappy and thin woody canopies or boundaries lacking a woody canopy will experience increased levels of solar radiation and air-flow with subsequent effects on the ground cover of herbaceous vegetation. Field boundary orientation will influence the interception of solar radiation with east-west hedgerows supporting sunny and shady aspects.

All field boundaries will support a narrow verge of herbaceous vegetation due to inability to cultivate right up to the boundary edge. In addition, most field boundaries will be raised slightly above the field level. Generally, the presence and structure of additional features will vary independently of field boundary types. Field margins adjacent to field boundaries vary in width and may be composed of natural regeneration or sown with grass or wildflower seed mixtures. They may be created to serve an agronomic or wildlife function, or result from being positioned on land that is marginal or difficult to cultivate. Banks are typically composed of rocks and stones, covered with soil and support herbaceous or woody vegetation. It is on such banks that hedgerows are frequently planted or develop. The presence of banks can result in good drainage and provide a drier habitat compared to fields in winter. Ditches may form naturally or be constructed and

can vary seasonally in wetness. They provide a strong contrast to moisture conditions in other parts of a boundary and may support characteristic arthropod communities (Blomqvist *et al.*, 2003).

(ii)   Habitat structure, microclimate and arthropod biodiversity

Structural complexity within a boundary will provide a greater range of microhabitats and thereby augment the number of niches that may be occupied by different arthropod species (Southwood, 1978; Morris & Webb, 1987). Greater structural complexity achieved by the inclusion of several vegetation layers and a range of additional features in field boundaries have been associated with increased arthropod diversity (Pollard, 1968a; Forman & Baudry, 1984; Menneer, 1994; Maudsley *et al.*, 1997). Each structural component may provide characteristics that support a distinct component of the overall community, though movements between structural elements have been observed (Pollard, 1968a).

Structurally complex boundaries supporting a broad range of microclimatic conditions have the potential to support a more diverse arthropod fauna. Hedgerows have been described as a 'woodland edge' habitat and ecotone, supporting species originating from both closed and open habitat (Pollard *et al.*, 1974; Thiele, 1977; Barr *et al.*, 1995; Duelli *et al.*, 1990). As such, hedgerows are considered to provide a refuge for woodland species in addition to field species and thereby support a more diverse arthropod fauna. Herbaceous linear features are considered to be colonised predominately by open-habitat species. Factors that enhance shade, shelter, soil moisture and humidity (such as height, width, density, the presence of three vegetation layers, bank and ditch) will influence the suitability of a habitat for species of woodland origin (Petit, 1994; Charrier *et al.*, 1997; Petit & Burel, 1998). In addition, shelter afforded by large impermeable habitats will enable species sensitive to disturbance to be buffered from field boundary management or detrimental agronomic practice. Hedgerow intersections have been shown to support increased diversity of butterflies (Dover & Sparks, 2000), canopy invertebrates and greater abundance of the ground dwelling carabid beetle *Nebria brevicollis* compared to middle sections (Joyce *et al.*, 1999; Joyce 2000). Simultaneously, shade may be a

limiting factor for certain groups such as Heteroptera, possibly through a reduction in host plant numbers (Greatorex-Davis *et al.*, 1994). Degraded hedgerow canopies that have become increasingly gappy (10-30% gaps, some up to 15m width) supported lower abundance of canopy dwelling invertebrates than continuous features (Joyce *et al.*, 1997). Passively dispersing arthropods or weak fliers are likely to accumulate in woody canopies orientated to face the prevailing wind and in the eddies and vortices associated with the leeward side (Lewis, 1969; Joyce, 2000).

Epigeal arthropods in field boundaries will be strongly influenced by microclimatic (particularly soil moisture and humidity) and microhabitat conditions at the ground level (Thiele, 1977; Atienza *et al.*, 1996). Consequently, alterations in microclimate and herbaceous vegetation through deterioration of a hedgerow canopy will impact the ground arthropod fauna. Structurally complex boundaries and the presence of banks or ditches that enhance humidity and soil moisture may influence the diversity of soil-dwelling arthropods (e.g. collembola), carabids, staphylinids and other arthropod taxa of woodland origin (Sotherton, 1985; Dennis & Fry, 1992; Asteraki *et al.*, 1995; Alvarez *et al.*, 1997; Blackshaw & DarcyBurt, 1997).

1.2.4 Management

The importance of field boundary management is recognised in the U.K. Biodiversity Action Plan which aims for positive management of 50% of Ancient and/or Species Rich Hedgerows by 2005. English Nature has estimated that only 10% are currently under favourable management, whilst findings from the Countryside Survey 1990 (Barr *et al.*, 1993) indicated considerable hedgerow 'loss' was attributable to management rather than direct removal.

(i) Woody

Traditional management of hedgerows is by laying every ten to twelve years to create a dense, strong, stockproof barrier (Henry *et al.*, 1994; Maudsley *et al.*, 2002). However, the majority of hedgerows are managed using tractor mounted flails (Barr *et al.*, 1995; Britt, 2001). Current recommendations to maintain the wildlife value of

hedgerows are to cut every two to three years in late winter (Maudsley *et al.*, 2002; DEFRA, 2003a). However, most hedgerows are still cut annually (Britt, 2001). While flailing enables affordable and routine management, it can lead to increased gappiness in the hedge canopy if undertaken too intensively or at inappropriate times of the year. Restoration of degraded hedgerows includes laying, coppicing or planting-up to fill in gaps in the canopy, combined with ancillary fencing to protect exposed shoots from domestic or wild grazing (Henry *et al.*, 1994; Maudsley *et al.*, 2002; DEFRA, 2003a). More frequently, ancillary fencing is added to degraded hedgerows in the absence of restorative techniques to make them stockproof. This has been regarded as rendering the hedge effectively obsolete and making management difficult. However, fencing may prevent overgrazing or over-trimming of the canopy and hedge-bottom flora and encourage bird-mediated plant dispersal, through use of posts as perching sites (Barr *et al.*, 1995).

(ii) Herbaceous

The herbaceous flora of field boundaries has commonly been managed with annual or biannual trimming and occasional herbicide applications to control pernicious and invasive weeds. Approximately 30% of plants found in field boundaries can also occur as weeds in the field, with species such as cleavers, barren brome, couch-grass, creeping thistle and field bindweed presenting the highest risk of crop infestation. Appropriate field boundary management can minimise the occurrence of weed species. Current recommendations aim to develop a dense perennial sward and restrict colonisation by competitive weed species which could later spread into the field (Marshall & Moonen, 2002). This is achieved by minimising disturbance and application of non-selective herbicides and fertiliser. With a diverse local species pool and seedbank, natural regeneration of the field margin may be encouraged (Smith *et al.*, 1993). However, in the absence of a diverse local flora, or to achieve a specific agronomic or wildlife objective various seed mixtures are recommended.

(iii) Management and arthropod biodiversity

The traditional approaches to hedge management such as laying and coppicing are considered to be beneficial for arthropod diversity in the long term due to the enhanced structural complexity with new vegetative growth (Henry *et al.*, 1994; Maudsley *et al.*, 2000). Conversely, mechanical flailing of a woody canopy is associated with declines in arthropod abundance. Greater insect numbers, especially predatory species, are found on uncut or 'wild' hedgerows compared to those which have recently been cut (van Emden, 1963; Sotherton *et al.*, 1981). Maudsley *et al.* (2000) demonstrated that the abundance of mobile insect groups such as Diptera and Hymenoptera was negatively affected by regular cutting. Reduced flowering, berry production and shelter were thought to be contributory factors in the decline. However, this response to cutting is not universal among arthropods. Some herbivorous groups (e.g. Hemiptera) were more abundant on annually cut hedges (Maudsley *et al.*, 2000) and overall invertebrate diversity was greater on cut compared with uncut or remnant hedges (Sotherton *et al.*, 1981) possibly due to new vegetative growth stimulated by cutting (Maudsley *et al.*, 2000). Research into the effects of trimming on the hedge-bottom overwintering fauna is lacking, though this is thought to be minimal (Maudsley, 2000). Trimming is more likely to affect epigeal arthropods through alterations in habitat structure and microclimatic conditions. The timing of hedge cutting will affect different arthropod groups at different times depending on their resource requirements (Menneer, 1994; Maudsley *et al.*, 2000). A recent study of hedgerow management recommended a variety of management times and techniques on a rotational basis at a farm-scale to maintain arthropod biodiversity (Maudsley *et al.*, 2002).

Tussocky grasses such as cocksfoot, yorkshire fog (*Holcus lanatus*) and timothy (*Phleum pratense*) are recommended to encourage overwintering populations of natural enemies of crop pests and to provide oviposition sites for hoverflies (Thomas *et al.*, 1992; DEFRA, 2003a). Sown wildflower mixtures can result in high floral diversity and target particular beneficial invertebrates such as natural enemies (e.g. hoverflies, parasitoids), pollinators (e.g. honey and bumble bees) and species of conservation interest (e.g. butterflies) (Smith *et al.*, 1993; Hickman & Wratten, 1996; DEFRA, 2003). Mechanical cutting of the herbaceous vegetation in summer reduced epigeal arthropod diversity and

abundance, though a May cut was less detrimental than a mid-summer cut (Morris & Lakhani, 1979). Certain herbivorous species benefited from regular cutting though this may increase crop pest populations (Morris & Rispin, 1988). Annual cutting in autumn/winter alters the vegetation structure, especially of tussocky grasses, with detrimental effects on the survival of overwintering polyphagous predators (Dennis *et al.*, 1994). Consequently, once tussock forming grasses have established, biennial or triennial cutting is recommended (Marshall & Moonen, 2002).

Management of adjacent land may affect field boundary arthropod communities directly through spray drift or cultivations too close to the boundary (Vickerman et al., 1987; Greig-Smith, 1992; Moreby & Southway, 1999). Indirect effects through reductions in the quantity and diversity of floral resources and the structure of the herbaceous vegetation will impact herbivorous arthropods directly and affect carnivores through depleted prey numbers (Boatman *et al.*, 1989; Chiverton & Sotherton, 1991). For example, herbicide treatments have been shown to reduce the abundance and diversity of carabid beetles in the herbaceous vegetation (Pollard, 1968c; Asteraki *et al.*, 1995).

Disturbance caused by field and field boundary management may have a detrimental effect on the abundance or occurrence of species of poor dispersal powers (Den Boer, 1987). Species with poor mobility are restricted in their ability to disperse away from, and recolonise, disturbed areas. Field boundary types are likely to differ in the intensity of management they receive, with degraded hedgerow exposed to little or no management disturbance. Additionally, a structurally complex boundary may ameliorate some of the effects of disturbance for arthropods enabling sensitive species to persist.

1.2.5 Field boundary network

Within the farmed landscape, field boundaries may form a network of linear habitat features connecting other non-crop habitat patches such as woodland (Fry, 1994). The spatial pattern of field boundaries in the landscape has been shown to influence physical and biological processes locally. These processes include microclimate, surface and sub-surface water flow, soil erosion and run-off of nutrients and pollutants, as well as

dispersal and colonisation processes of plants, arthropods and higher fauna (Forman & Baudry, 1984; Baudry *et al.*, 2000; Viaud *et al.*, 2001).

Cyclical disturbance experienced by arthropods through field cultivations and field boundary management, may result in frequent extinctions of local sub-populations that can be refounded by dispersing individuals from extant sub-populations (Den Boer, 1981). Therefore the processes of dispersal and recolonisation are essential to maintain arthropod biodiversity and gene flow. Recolonisation will be determined by the regional species pool and species dispersal ability, the latter often constrained by landscape structure (Burel & Baudry, 1992). For open-field species field boundary permeability is critical for population persistence (Sherrat & Jepson, 1993), whilst species of woodland origin within woody boundaries are more likely to be influenced by connectivity of the field boundary network (Burel, 1989; Petit, 1994; Charrier *et al.*, 1997).

(i) Field boundaries as corridors for movement

Models have indicated the conservation value of corridors by enhancing the persistence and stability of small isolated populations through dispersal or interaction within a metapopulation (Fahrig & Merriam, 1985; Hanski, 1999). Empirical evidence shows that carabid dispersal improves the persistence of both local and metapopulations (den Boer, 1970). In landscapes where hedgerow removal has resulted in a sharp decrease in connectivity, declines in the abundance of *Abax ater*, a characteristic woodland carabid, have been observed (Petit, 1994). Studies using observation, mark-release-recapture and telemetry techniques have demonstrated that linear landscape features are used as corridors for movement by butterflies (Dover, 1990) and carabid beetles (Burel, 1989; Charrier *et al.*, 1997; Petit & Burel, 1998). Three main attributes determine the use of linear features as movement corridors: habitat suitability, width and spatial continuity (Bennet, 1990; Forman & Moore, 1992). Habitat suitability refers to the availability and abundance of essential resources such as abiotic conditions, food, or protection from predators. It has been demonstrated that woodland carabids would use hedgerows to move between forest fragments providing they were of suitable habitat quality (Petit, 1994). Width is a measure of the area available to the organism and will influence

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microclimatic conditions and disturbance levels. Spatial continuity refers to lack of gaps in a linear feature and connectedness between boundaries to form a network and between the network and other non-crop habitat. Increasing gappiness of the woody canopy through hedgerow deterioration will lessen both the habitat suitability and the effectiveness of the linear feature as a movement corridor.

Some gaps in field boundaries are essential for farm machinery access and movement of livestock, but may restrict the role of linear features as corridors for arthropod movement. Gap width and habitat type are thought to be the main determinants of the extent to which individual species will be affected. For example, the carabid *Nebria brevicollis* was able to cross gaps of 7-9m along a hedgerow during its summer aestivation period, the usual width of farm gateways (Joyce *et al.*, 1998). However, gaps of 100-200m may be too great for most carabid species to cross (Gruttke, 1994; Gruttke & Kornacker, 1995). It was speculated that ground cover within the gap may exert some influence on permeability and that this is likely to be species-specific.

(ii) Field boundaries as barriers to movement

Flying insects may encounter field boundaries as impediments to flight between fields and this will be influenced by height, density and gappiness of a canopy (Fry & Robson, 1992; Fry & Main, 1993; Harwood *et al.*, 1994; Wratten *et al.*, 2003). Therefore gaps in boundary vegetation have been recommended to allow butterflies to disperse through the landscape.

Simulation models have shown that dispersal rate between fields is a critical parameter affecting survival of metapopulations of open habitat carabids in agricultural landscapes, where insecticides are routinely applied to fields (Sherrat & Jepson, 1993). The permeability of field boundaries has important implications for pest control using polyphagous predators such as the Carabidae. The rate at which recolonisation can occur from adjacent fields or refuge populations in the field boundary may be influenced by the permeability of the field boundary habitat. Long delays in recolonisation may enable pest populations to build up beyond threshold levels. Alternatively, reduced prey abundance

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following a disturbance may result in starvation of early recolonising individuals. Linear landscape features including rivers, roads, tracks, woody and non-woody field boundaries represent barriers of varying permeability to carabid beetles (Mader *et al.*, 1990; Mauremooto *et al.*, 1995; Garcia *et al.*, 2000; Thomas *et al.*, 2001a; Brown 2000). Habitat structure and width of linear features can have important effects on their permeability. Hard-surfaced and gravel or dirt tracks considerably reduced transmission of ground beetles, whilst grassy field tracks had no significant effect (Mader *et al.*, 1990). Lack of cover, as found with bare tracks, has been found to restrict dispersal of *P. melanarius* more than physical barriers to movement presented by vegetation structure (Brown, 2000). The effect of herbaceous margins on the movement of ground beetles was less consistent and may have been influenced by margin width (Duelli *et al.*, 1990; Kopp, 1998). However, there was little difference in the permeability of field boundaries of differing width to *P. melanarius* (Frampton *et al.*, 1995; Brown, 2000). An increase in the physical (structural) complexity of the vegetation, increasing in the order bare ground, crop stubble, barley crop and hedgerow, reduced transmission rates of *P. melanarius, P. madidus* and *H. rufipes* within experimental arenas (Mauremooto *et al.*, 1995). Vegetation structure at the ground level has been shown to strongly influence foraging and movement behaviour of carabids (Baars, 1979; Wallin & Ekbom, 1994). Large scale mark-release-recapture studies have produced contrasting results. A two metre wide hedgerow restricted between field movement of *P. melanarius* and *Nebria brevicollis* in a study in Somerset (Garcia *et al.*, 2000; Thomas *et al.*, 2001a). In contrast, a multi-field study in Hampshire showed that 75% of *P. melanarius* and 78% of *P. madidus* crossed through a hedgerow (Holland *et al.*, *in press*). Joyce *et al.* (1999) found that *N. brevicollis* moves readily between fields through gaps in hedgerows and hedge-bottoms, and indicated that differences in gap vegetation structure may affect their suitability. The fractal geometry of the ground surface may be important in increasing the effective distance dispersed by an epigeal arthropod (Weins *et al.*, 1993; Mauremooto *et al.*, 1995; Thomas *et al.*, 2001a).

Studies of field boundary permeability have focused on large to medium sized open habitat carabids, but small carabids e.g. *Bembidion* spp are likely to respond differently to

vegetation structure, cover, microclimate and fractal geometry. For example, impeded between-field movement was implicated in the slow population recovery of *B. obtusum* following insecticide use (Çigli *et al.*, 1993). In addition, there may be significant population exchange between fields when species overwinter, aestivate or take refuge in field boundaries (Garcia *et al.*, 2000).

1.2.6 Landscape structure

Landscape heterogeneity has been shown to contribute to higher invertebrate diversity at the landscape scale and to the effectiveness of natural enemies (Marino & Landis, 1996; Colunga-Garcia *et al.*, 1997; Bommarco, 1998a; Holland & Fahig, 2000). The diversity and quality of different habitat types encountered in relation to the dispersal capacity of a species within its lifetime will influence the long term persistence of the species (Kareiva, 1990). Bommarco (1998a) found that fecundity and body size of a carabid generalist predator was positively correlated with the degree of landscape heterogeneity within its range of mobility. A mosaic landscape of small-sized crop fields, with a high density of woody field boundaries was reported to maximise arthropod diversity and biological control, and decrease the probability for overall extinction, even of rare species (Marino & Landis, 1996; Colunga-Garcia *et al.*, 1997; Bommarco 1998a). Rapid recolonisation of crop fields observed in heterogeneous landscapes may lessen the impact of agronomic disturbance (Good & Giller, 1991a). The presence of field boundaries with several vegetation layers and additional features will enhance the diversity of habitat elements, whilst the maintenance of a range of field boundary types will maximise habitat heterogeneity in the landscape.

Long-term studies on the regional distribution and population dynamics of carabids in the Denthe area of The Netherlands have contributed to the understanding of habitat fragmentation and dispersal processes (Den Boer, 1977, 1987, 1990; Turin & Den Boer, 1986). Increasing fragmentation of suitable habitat through increases in the amount of land in cultivation has resulted in a 14% decline in carabid populations. Isolation of populations in habitat fragments may intensify natural selection against high dispersal ability. Due to the increased distance between suitable habitat patches, dispersing

individuals are unable to encounter suitable habitat and fail to re-found populations. Continued loss of dispersing individuals from the population could result in a selection against dispersal. Consequently, isolated populations may be more at risk of permanent extinction from disturbance or stochastic events, and from the negative effects of genetic isolation. Local populations of species with poor dispersal power may survive for 40 to 50 years in disturbed areas, but these species may become extinct if changes in the distribution and extent of suitable habitat accelerate. However, Maelfait *et al.* (1994) found there was no relationship between dispersal power and the degree of decline of a species over time. Declining species were regarded as the more stenotopic species, and they were either good or poor dispersers.

A recent study examining the carabid assemblage of forest remnants, found that small isolated forest remnants in farmland supported few closed habitat species and was characterised by a carabid assemblage similar to a recently created hedgerow and crop habitat. The absence of woodland species was attributed to their poor dispersal power and isolation of the forest habitat (Fournier & Loreau, 2001). Declines in the distribution and extent of natural and semi-natural habitat in farmland will generally benefit open-field species. The ubiquitous nature, soft-edge response and high dispersal power of many open habitat carabids enables them to colonise most habitats in farmland, including wooded habitats. Consequently, although alpha diversity of habitat elements in farmland was found to be high, species turnover between habitat elements was low (Fournier & Loreau, 2001).

1.3   FIELD BOUNDARIES AS OVERWINTERING HABITAT FOR POLYPHAGOUS PREDATORS

Favourable field boundary habitat is essential to the persistence of the majority of farmland arthropods, many of which perform beneficial functions in farmland. For example, arthropods associated with field boundaries provide prey items for game birds and other fauna of economic or conservation concern (Thomas *et al.*, 2001b; Wilson *et*

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al., 1999), and contribute to soil dynamics, nutrient recycling (Alvarez *et al.*, 1997; Lagerlof *et al.*, 2002) pollination (Lagerlof *et al.*, 1992; Carreck & Williams, 1997) and the biological control of crop pests (Kopp, 1998; Lee & Landis, 2002). Consequently, field boundaries are integral to the maintenance of arthropod biodiversity on farmland and the provision of arthropods that contribute to sustainable agriculture. Both may be enhanced through the mechanism of conservation biological control (Landis *et al.*, 2000). Maximising the overwintering survival of polyphagous predators in field boundaries may be critical to the provision of biological control of arable crop pests the following growing season. However, the relative potential of different field boundary types to enhance arthropod biodiversity in farmland and augment overwintering populations of polyphagous predators, such as species of Carabidae and Staphylinidae, is poorly understood.

1.3.1   Conservation biological control

Intensive arable and horticultural farming covers 30.3% of the land in England and Wales (Haines-Young *et al.*, 2000) and represents a major economic sector of agricultural production. Aphids are a representative example of pests found in cereal ecosystems. Cereal aphid pests (*Sitobion avenae, Metapolophium dirhodum,* and *Rhopalosiphum padi:* Homoptera) cause substantial damage and yield loss both directly and through transmission of Barley Yellow Dwarf Virus (BYDV) (Vickerman & Wratten, 1979; Carter *et al.*, 1989; Dixon, 1989; Tatchell, 1989). Generally, control of aphids is achieved through prophylactic use of broad-spectrum organo-phosphorus pesticides such as dimethoate and pyrethroids, although more selective insecticides such as pirimicarb are recommended (Wratten *et al.* 1995). However, the decreasing value of cereal crops has lowered the cost-effectiveness of insecticide control. Furthermore, recognition of the detrimental side-effects of pesticide use on farmland biodiversity within intensive farming systems has lead to renewed interest in the development of integrated pest management (IPM) systems (Greig-Smith, 1992; Holland *et al.*, 1994b; Wratten *et al.*, 1995; Robinson & Sutherland, 2002). IPM may be achieved by reliance on the natural enemy complex to suppress populations, combined with optimised spray regimes to prevent pest outbreaks when climatic conditions encourage rapid pest

population growth. Field trials have shown that fungal pathogens, aphid specific predators, parasitoids and polyphagous predators can considerably reduce peak aphid numbers and/or yield loss both individually and as a community of natural enemies (Edwards *et al.*, 1979; Carter *et al.* 1982; Chambers *et al.*, 1986; Chiverton, 1986, 1987; Ostman *et al.*, 2003).

Conservation biological control represents one of the most cost-effective and sustainable techniques to augment natural enemy populations in annual cropping systems. The technique acts to manipulate farmland habitats to enhance the survival, fecundity, longevity and behaviour of natural enemies to increase their effectiveness (Landis *et al.*, 2000). Within-crop habitat manipulation measures include the use of green mulches, intercropping amd undercropping. Manipulation of the uncropped habitat aims to augment populations of natural enemies through the provision of suitable overwintering sites, alternative prey or food resources, oviposition sites and refuge. For example, overwintering densities of polyphagous predators, such as aphidophagous Carabidae and Staphylinidae, have been augmented by creating field margins or beetle banks sown with tussock forming grasses such as *Dactylis glomerata*, with subsequent increases in field activity-densities during crop growth (Coombes & Sotherton, 1986; Dennis, 1991; Dennis & Fry, 1991, 1992). In addition, the creation of weed strips around arable fields has been shown to enhance the within-field activity-density of carabid polyphagous predators, as well as increase the availability of food for predators and their subsequent fecundity (Lys, 1994; Zangger, 1994). Field margin strips have also been sown with a variety of floral seed mixtures to provide sources of nectar and pollen to enhance fecundity and population densities of natural enemy groups such as parasitoid and syrphid populations in famland (Powell, 2000; Holland *et al.*, 1994a; Hickman & Wratten, 1996).

1.3.2 Polyphagous predators

Within annual cropping systems generalists rather than specialists tend to dominate, which may explain the numerical importance of polyphagous predators in the natural enemy complex of agricultural systems (Sunderland *et al.*, 1997). The polyphagous

predatory group is dominated by members of Carabidae: Coleoptera (ground beetles) and Staphylinidae: Coleoptera (rove beetles) and Linyphiididae: Araneae (money spiders) and Lycosidae: Araneae (wolf spiders), but some species are also found in Dermaptera (earwigs), Opiliones: Arachnida (harvestmen), Chrysopidae: Neuroptera (lacewings) and Acari: Arachnida (mites) (Wratten & Powell, 1990). Sunderland *et al.* (1985) recorded more than 390 species of polyphagous predator and parasitoid in U.K. cereals, of which 100 may be common during the summer months. It has been estimated that there are on average 30 species of Carabidae active within a crop habitat in one season (Lovei & Sunderland, 1996; Luff, 2002). In total 150 staphylinid species have been recorded in cereal fields across northern Europe (Good & Giller, 1988). Carabid and staphylinid comunities in crop and pasture habitats tend to be dominated by a few species. For example, ten species can account for up to 95% of the carabid fauna, whilst single staphylinid species may compose 20% of the staphylinid fauna (Good & Giller, 1988; Luff, 2002). Therefore, these dominant species can have a considerable ecological impact.

Many open habitat species of Carabidae and Staphylinidae in farmland are generalist predators that contribute to the suppression of arable crop pests. The majority of these species require field boundary habitat at some stage in their life cycle. For adult overwintering Carabidae and Staphylinidae that show seasonal migration between crop and semi-natural habitats, suitable field boundary overwintering habitat has been shown to enhance their richness and abundance in adjacent cereal fields at the time when aphid populations establish (Dennis 1991; Dennis & Fry, 1991). Within intensively managed cropping systems polyphagous predators overwintering in field boundary habitat are more likely to persist and even dominate the arthropod fauna compared to other natural enemies (Wissenger, 1997; Ribera *et al.*, 2001). The requirement of field boundary habitat by polyphagous predators makes them amenable to augmentation through manipulation of the non-crop habitat via conservation biological control techniques.

Polyphagous predators have several ecological characteristics that enable them to be effective natural enemies:

(i) The large number of polyphagous predators common to agricultural systems follow a range of life-history strategies differing in phenology and habitat preferences (Den Boer & Den-Danje, 1990). Whilst some species may be susceptible to certain agronomic practices, others within the complex will be less affected. For example, autumn breeding carabids are sensitive to winter crop cultivations which favour spring-breeding species, and the reverse is true for spring cultivations (Hance *et al.*, 1990).

(ii) Many polyphagous predators (e.g. *Agonum dorsale, Bembidion lampros, Demetrias atricapillus, Tachyporus spp.*) show early spring migration from field boundary overwintering sites into fields (Wallin, 1985; Chiverton, 1986; Coombes & Sotherton, 1986; Dennis, 1991; Pedersen *et al.*, 1990) resulting in established populations prior to aphid colonisation when the suppression of aphid population growth is most effective (Edwards *et al.*, 1979).

(iii) A polyphagous species has the potential to consume large quantities of the pest species as it becomes abundant (Sopp & Wratten, 1986; Sunderland *et al.*, 1987), but can switch to alternative prey when pest numbers are low. Therefore, predator populations can be maintained independently of pest population numbers.

(iv) Polyphagous predators restricted to the ground surface have been implicated in aphid control as they predate live aphids which would otherwise return to the canopy (Griffiths *et al.*, 1985; Winder, 1990). In addition, active foraging on the crop plant or climbing of plants for night flights by more agile polyphagous predators (e.g. *Tachyporus* spp. and *D. atricapillus*) contributed to aphids falling from the crop plant, thereby making them available to ground foraging predators (Sunderland & Vickerman, 1980; Dennis *et al.*, 1990).

(v) Some generalist predators exhibit an aggregative numerical response to aphid spatial heterogeneity (Bryan & Wratten, 1984).

(vi) Species that disperse by flight from overwintering sites in field boundaries (most staphylinid polyphagous predators) show a rapid and even field colonisation in early spring (Coombes & Sotherton, 1986; Pedersen *et al.*, 1990). Species overwintering in field boundaries that disperse by walking may be more limited in their field penetration and restricted to field edges (Hance *et al.*, 1990; Dennis & Fry, 1992), but the creation of

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beetle banks through large arable fields may enhance mid-field densities of ground active carabids and staphylinids.

1.3.3 Factors influencing polyphagous predator survival over winter

The effectiveness of polyphagous predators is in part attributable to their consumption of alternative prey items. Observation and gut disections have indicated that alternative invertebrate prey include the eggs, larvae and/or adults of Collembola, Acari, Araneae (particularly the small Linyphiidae), small Coleoptera, Mollusca, Lepidoptera and Diptera (Hengeveld, 1980; Sunderland *et al.*, 1987; Good & Giller, 1991b). Certain groups such as *Tachyporus* spp. (Staphylinidae) also consume fungal material (Dennis *et al.*, 1991). Additionally, species of the genera *Harpalus* and *Amara* (Carabidae) contribute significantly to the consumption of weed seeds in arable crops (Tooley & Brust, 2002). Carabid and staphylinid species vary in the degree of polyphagy they exhibit, but several studies have indicated the value of a mixed diet in maximising growth and survival (Toft, 1995; Jorgensen & Toft, 1997; Toft & Wise, 1999). Prey availability will also influence fecundity of polyphagous predators (Wallin *et al.*, 1992; Bommarco, 1998b). A diverse arthropod fauna supplying generalist predators with mixed diets and a continuity of food sources will enable polyphagous predator populations to be maintained when the pest is absent or present at low levels (Settle *et al.*, 1996). This applies in early spring prior to the colonisation of cereal fields by aphids, and over winter.

Availability of prey in field boundaries in autumn and early winter enables beetles to build up fat reserves essential to maintain respiration, for the production of cryoprotectants and for movement either to find overwintering sites or prey (Leather *et al.*, 1993). Consequently, fat reserves may contribute to the overwintering survival of polyphagous predators (Mols, 1988; Van Dijk, 1994). Overwintering mortality in the absence of freezing was related to starvation in adult overwintering Coccinellidae (Watanabe, 2002). Additionally, lack of available prey was considered a determining factor in weight loss and subsequent mortality of active beetles (Petersen *et al.*, 1996; Petersen, 1999). Although certain species e.g. *C. melanocephalus* (Vlijm *et al.*, 1968) and

B. lampros (Petersen, 1999) can survive periods of starvation, survival may be dependent on their physiological condition.

Abiotic and biotic conditions such as temperature and moisture and the availability of prey have been shown to influence overwintering survival and condition (Luff, 1966b; Bossenboek *et al.*, 1977; Mills, 1981; Van Dijk, 1994; Zhou *et al.*, 1995; Petersen, 1999; Wanatabe, 2002). Microclimatic conditions of an overwintering site will determine body temperature, metabolic rate, biochemical and physiological responses of an organism and regulate the timing of its various activities (Casey, 1981; Leather *et al.*, 1993; Atienza *et al.*, 1996). Reduction in temperature fluctuations have been shown to enhance overwintering survival of *B. lampros* and *T. hypnorum* (Dennis *et al.*, 1994; Petersen *et al.*, 1996). For example, populations of *B. lampros* and *T. hypnorum* were reduced by up to 90% where temperatures fluctuated between +2°C and –6°C, compared to more stable temperature regimes at +2°C or below 0°C. Additionally, mortality was greatest where temperatures fluctuated weekly rather than daily as a result of cold declimatisation (Petersen *et al.*, 1996; Petersen, 1999). Abiotic factors such as temperature have been considered more important in determining overwintering mortality (due to changes in the supercooling point of individuals), whilst pre-winter food levels influence overwintering condition. However, stressful abiotic conditions over winter experienced by *B. lampros*, *T. hypnorum* (Petersen, 1999) and *Coccinella septempunctata* (Zhou *et al.*, 1995) led to a decrease in fat content. Additionally, mild winter temperatures may result in the depletion of fat reserves through increased metabolic activity. For example, fat reserves in *C. septempunctata* reduced by 30% in harsh cold temperatures and >50% in less cold overwintering conditions (Zhou *et al.*, 1995), whilst high mortality of *B. lampros* was observed at constant temperatures of 6°C, close to the lower threshold for feeding activity of about 9°C for this species (Chiverton, 1988; Petersen, 1997). The temperature values and fluctuations experienced as stressful by overwintering polyphagous predators are poorly understood and likely to be species-specific. In addition, sedentary individuals overwintering in the soil substrate risk suffocation by water-logging or ice-nucleation when soil water freezes, causing many species to seek drier overwintering conditions (Sotherton, 1985; Leather *et al.*, 1993).

Distribution patterns of arthropods and polyphagous predators result from either differential survival or differential selection of overwintering sites (Thomas *et al.*, 1992b; Dennis *et al.*, 1994). Differential overwintering survival has been demonstrated for a range of overwintering polyphagous predators, whilst site selection has generally been inferred. It is generally accepted that individuals will show a preference for habitats that optimise their survival and fecundity (Orians, 1980). Therefore it is likely that many of the variables shown to influence overwintering survival may also act as stimuli in site selection. Thiele (1977) indicated the importance of microclimate, particularly temperature, relative humidity and substrate moisture in determining the distribution of Carabidae. The heterogenous distributions of some carabid and staphylinid species may be due to spatial differentiation in abiotic factors providing a mosaic of microclimates within a particular site (Grum, 1971). Availability of prey and other food items may also be determining factors in arthropod overwintering distributions.

1.3.4 Overwintering habitats of carabid and staphylinid polyphagous predators

Research into the overwintering of arthropods in field boundaries has focused on carabid and staphylinid species identified as important polyphagous predators of cereal aphids (Sunderland & Vickerman, 1980). Limited information exists on the overwintering habitat requirements of other field boundary residents such as woodland species, coleopteran families or arthropods generally. A succession of studies have demonstrated the importance of field boundary habitat in farmland for supporting a range of overwintering arthropods in comparison to winter sown cereals, crop stubbles, temporary and permanent pasture and woodland. Arthropod taxa found in higher densities and diversities in field boundary habitat include Carabidae, Staphylinidae, Coccinellidae, other Coleoptera adults, Coleoptera larvae, Araneae, Hemiptera, Diptera adults and larvae, Dermaptera, Chilopoda, Diplopoda, Myriapoda and Isopoda (Descender, 1982; Sotherton, 1984; Kromp & Steinberger, 1992; Thomas *et al.*, 1994; Andersen, 1997; Pfiffner & Luka, 2000; Thomas & Marshall, 2000). In particular, the ability of field boundaries to support high densities of overwintering polyphagous predators has been emphasised.

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(i) Distribution patterns between field boundary types

Field boundaries vary in the overwintering density and diversity of arthropods (Thomas *et al.*, 1994; Pfiffner & Luka, 2000; Thomas & Marshall, 2000) and polyphagous predators (Sotherton, 1985; Thomas *et al.*, 1992a) they support. There is no clear pattern in the relative importance of woody and non-woody field boundary types. For example, the greatest abundance of overwintering arthropods was associated with the hedgerow field boundary and lower numbers were found in adjacent herbaceous field margins (Thomas *et al.*, 1994; Thomas & Marshall, 2000). In contrast, Pfiffner & Luka (2000) found total abundance of overwintering arthropods was higher in sown wildflower strips compared to hedgerows. Equally, there was no consistent pattern of overwintering arthropod abundance between margins sown with grass and wildflower seed mixtures and those left to naturally regenerate (Thomas *et al.*, 1994; Thomas & Marshall, 2000).

A study conducted on a Hampshire farm found higher overwintering densities of polyphagous predators at hedge banks and shelterbelts compared to grass banks and grass strips (both with post and wire fences), but these findings were not replicated at a Sussex farm (Sotherton, 1985). Subsequent studies found no differences in predator densities between a range of field boundary types including hedgebanks, shelterbelts, grassbanks and grass strips (Dennis *et al.*, 1992; Thomas *et al.*, 1992a), although species specific differences were observed for *Bembidion* spp., *Tachyporus* spp., other staphylinids and linyphiids (Dennis *et al.*, 1992). Studies that have formally compared the arthropod fauna of field boundary types (Sotherton, 1985; Thomas *et al.*, 1992a; Dennis *et al.*, 1994) may be criticised for failing to describe and classify the field boundaries quantitatively and create a field boundary typology for application to other sites.

(ii) Distribution patterns within field boundaries

Polyphagous predators and other arthropod taxa have been demonstrated to have heterogenous distributions across farmland (Descender, 1982; Sotherton, 1984) and within farmland habitats both over winter (Maudsley *et al.*, 2002) and during the summer (Thomas *et al.*, 2001a). Variations in the distribution, composition and community

structure of overwintering Coleoptera have been associated with a range of microhabitat characteristics including bare ground, vegetation type and height, depth of the root layer, leaf litter, bank height, soil depth, boundary width, distance from the field boundary edge, orientation, adjacent land-use and prey availability (Descender, 1982; Sotherton, 1985; Pedersen *et al.*, 1990; Dennis & Fry, 1992; Thomas *et al.*, 1992a, b; Dennis *et al.*, 1994; Riedel, 1995; Andersen, 1997; Maudsley *et al.*, 2002). Arthropod taxa and polyphagous predators may show a collective response to certain variables, whilst others are more species-specific depending on a species biology and ecology.

A negative relationship has been found between the distribution of bare ground and the diversity of overwintering arthropods and density of polyphagous predators (Pollard, 1968a; Thomas *et al.*, 1991; Dennis & Fry, 1992). This is thought to be a result of the greater amplitude of seasonal and diurnal temperature changes on bare ground due to unimpeded solar radiation and reduced relative humidity compared to vegetated ground (Geiger, 1965). The presence of vegetation cover is associated with higher overwintering densities of carabids and staphylinids, although this is strongly dependent on vegetation type (Thomas *et al.*, 1991; Dennis & Fry, 1992; Thomas *et al.*, 1992b). Tussocky grasses such as *Dactylis glomerata* and *Holcus lanatus* have been found to support the greatest overwintering densities of *Tachyporus hypnorum, Demetrias atricapillus* and other polyphagous predators compared to rosette or mat-forming grasses, or loose plant structures such as dicotyledonous plants (e.g. *Ranunculus repens*) (Luff, 1965, 1966a; Bossenboek, 1977; Thomas *et al.*, 1991, 1992a,b; Dennis *et al.*, 1994). The high biomass of live and dead plant matter associated with tussocky grasses acts to buffer fluctuations in temperature and thereby provide improved overwintering conditions (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b). A similar relationship has been observed in dicotyledonous plants. Species with a loose plant structure such as *Agrostemma githago* or *Chenopodium polyspermum* were associated with higher diurnal temperature fluctuations and lower arthropod densities compared to plants providing greater ground cover such as *Achillea millefolium* and *Arctium minus* (Burki & Hausamann, 1993). Reduced temperature fluctuations were considered to enhance overwintering survival of *T. hypnorum* and other overwintering predators (Luff 1966b;

Burki & Hausamann, 1993; Dennis *et al.*, 1994) and may act as stimuli for overwintering site selection (Thomas *et al.*, 1992b). In addition, the mean depth of the root layer associated with grassy vegetation has been positively related to high densities of overwintering carabids and *T. hypnorum* (Descender, 1982; Dennis *et al.*, 1994).

In the absence of ground vegetation, leaf-litter may provide shelter and ground cover for overwintering arthropods. Overwintering densities of *T. chrysomelinus* and *Forficula auricularia* (earwig) sampled from hedgebanks, grassbanks and shelter belts were positively correlated to deciduous leaf litter cover (Thomas *et al.*, 1992a). The biomass of leaf litter on the ground was positively associated with high densities of overwintering carabids and staphylinids (Maudsley *et al.*, 2002) and may insulate individuals from temperature fluctuations. However, no relationship with leaf litter cover was found for a range of carabid and staphylinid species overwintering in field boundaries in the U.K. or Norway (Dennis & Fry, 1992; Dennis *et al.*, 1994).

Where field boundaries are raised above the level of the field, better drainage and drier soils may result in higher densities of polyphagous predators (Sotherton, 1985; Dennis *et al.*, 1994). Substrate moisture content is likely to affect overwintering survival of arthropods through increased risk of suffocation or ice-nucleation when soil water freezes (Leather *et al.*, 1993). Wider field boundaries with an east-west orientation favoured higher overwintering densities of *T. hypnorum* (Dennis *et al.*, 1994), however, width of the hedge-base was negatively correlated to carabid abundance in the soil, and it was suggested that limited numbers of carabids spread out to fill the available habitat area (Maudsley *et al.*, 2002).

The spatial distribution of overwintering species in relation to distance from the boundary edge may vary as a result of differential microclimatic conditions, environmental resistance from vegetation or field boundary structure or dispersal behaviour of migrating individuals (Lipkow, 1966; Pedersen *et al.*, 1990; Mauremooto *et al.*, 1995; Riedel, 1995; Brown, 2001). Cold intolerant species such as *T. obtusus* overwintered in higher densities in the middle of hedge-banks and hedgerows, whilst the

more cold tolerant *T. hypnorum* overwintered at the boundary edges (Lipkow, 1966; Pedersen *et al.*, 1990). Higher overwintering densities of *B. lampros* and *T. hypnorum* on the southern side of a newly established grassy ridge and hedgerow respectively reflected drier and warmer conditions considered to result from increased solar radiation (Pedersen *et al.*, 1990; Riedel, 1991). Structural complexity such as dense vegetation and a deep litter layer have been shown to restrict the movement patterns of Carabidae and Coccinellidae (Greenslade, 1964; Rivard, 1965; Klazenga & de Vries, 1994; Mauremooto *et al.*, 1995). Differences in spatial distributions may also result from dispersal behaviour. For example, homogenous overwintering distributions were shown by carabid and staphylinid species that predominately disperse by flying, whilst species showing an edge preference tend to disperse by walking (Riedel, 1995). However, Maudsley *et al.* (2002) found *B. lampros* to be evenly distributed through a hedgerow although this species predominately disperses by walking (Coombes & Sotherton, 1986).

Adjacent crop type may influence numbers of Carabidae and Staphylinidae migrating to field boundaries to overwinter (Andersen, 1997). For example, carabids and *Tachyporus* spp. were more abundant in boundaries bordering crop compared to those bordering grass fields. Differential densities were thought to be caused by more suitable overwintering conditions present in pasture compared to crop resulting in lower emigration rates to field boundaries in autumn (Andersen, 1997).

The importance of food availability over the winter period for adult overwintering polyphagous predators has been demonstrated using gut dissections (Thomas *et al.*, 1992b). Demonstrating the relationship between prey availability and overwintering distributions of polyphagous predators is complicated by temporal variations and possible time lags in prey and predator distributions, and the high degree of polyphagy shown by carabid and staphylinid species (e.g. Thomas *et al.*, 1992b). Generally, the diversity of prey items such as Collembola and small soil-dwelling arthropods, increases or shows a unimodal response to densities of polyphagous predators in field boundaries (Dennis & Fry, 1992). The observed decrease in diversity associated with highest predator densities was thought to result from dominance by a single species or group due to optimal site

conditions. In addition, densities of general arthropods and polyphagous predators show similar patterns within a range of grass plant structures (Luff, 1966a) and vegetation types (Lys, 1994; Thomas *et al.*, 1994). Plant diversity, dense herbaceous vegetation and leaf litter may influence the distributions of soil dwelling species that form prey items for polyphagous predators (Altieri & Letourneau, 1982; Dennis *et al.*, 1994).

Gut dissection and feeding experiments demonstrate the importance of food availability to *D. atricapillus* for overwintering survival. Laboratory based feeding experiments with *D. atricapillus* resulted in increased mortality with starvation (49.4%) compared to fed cohorts (19.6%) (Thomas *et al.*, 1992b). Field trials demonstrated higher mortality of *D. atricapillus* in bare ground sites where prey was initially removed and no further prey items added (Dennis *et al.*, 1994). However, the experimental treatments were confounded by the immigration of prey into soil enclosures reserved for unfed *D. atricapillus*. In both sets of experiments, increased mortality was observed towards the end of the winter period (Thomas *et al.*, 1992b; Dennis *et al.*, 1994). This reflects highest mortality rates with duration of winter observed by Riedel & Steenberg (1998) and Petersen *et al.* (1996).

Overwintering arthropods will also differ in their vertical distribution, burrowing down or entering the soil through crevices to find more sheltered overwintering sites at greater depths. Temperature is considered a determining factor in the vertical migration of soil arthropods (Dowdy, 1944) and temperature fluctuations are greatly reduced at a soil depth of 5cm compared to the bare soil surface (Thomas *et al.*, 1991). However, there is a trade-off between energy expenditure of burrowing and increased survival at greater soil depths, an additional cost being the exit of the individual from the soil in springtime (Leather *et al.*, 1993). Most overwintering arthropods will be found at depths of less than 40cm and abundance will decrease sharply with soil depth. Large carabids such as *Harpalus* spp. and *Pterostichus* spp. may overwinter at 25 to 45cm depth in soil (Maudsley *et al.*, 2002).

1.4   AIMS

Field boundaries provide essential semi-natural habitat for farmland arthropods and are especially important in the provision of overwintering sites for many polyphagous predators that contribute to sustainable agricultural production. Recent nationwide surveys have classified field boundaries into seven major types, many of which are typical of lowland farmland. This typology is primarily based on differences in structural characteristics (that are readily observable in the field) and which reflect plant species composition and management regimes. Arthropod assemblages may be influenced by the differences in field boundary habitat used within this typology, in addition to factors operating within the field boundary network and landscape. This study adopted a farm-scale approach to examine arthropod assemblages in relation to field boundaries. This was done in order to minimise the effect of non-field boundary factors (i.e. those that operate at the regional or landscape scale). This also allowed the study to be conducted at a scale which is directly relevant to their management; most operational decisions are made on a 'farm by farm' basis. To determine the effects of field boundary type on arthropod communities it was necessary to describe and classify the field boundaries selected for this study (Chapter Two). Habitat characteristics that distinguish between field boundary types could then be investigated in relation to the composition of the overwintering arthropod fauna that they support (Chapter Three). Examination of key functional groups within this overwintering arthropod fauna (polyphagous predators, woodland specialists and poor dispersers) will enable an assessment of the potential of different field boundary types to contribute to the natural enemy complex, and the conservation of vulnerable taxa at a farm-scale.

Understanding the ecology of field boundaries is frequently complicated by the variability in structural and 'additional' features exhibited. Elucidating the relative contribution of such features to the overwintering epigeal arthropods within and between field boundary types, together with the underlying habitat characteristics, may enable targeted habitat manipulation to enhance arthropod biodiversity or beneficial agronomic

services. Hence, arthropod assemblages in relation to such features were investigated (Chapter Four).

Field boundaries may contribute to conservation biological control by providing microhabitats that enhance the overwintering survival of polyphagous predator populations. Mortality overwinter is in general caused by unsuitable microclimatic conditions and lack of available prey, both of which will be influenced by microhabitat characteristics of a field boundary. Microclimatic conditions and prey availability are difficult to measure in a biologically meaningful way. Instead, surrogate measures of beetle condition may be used to determine the quality of field boundary habitat for overwintering arthropods. This study investigated the condition of selected polyphagous beetles using fat content as the surrogate measure to determine whether field boundary type influenced overwintering survival (Chapter Five).

Within field boundary habitat, polyphagous predators typically show heterogeneous spatial distributions at the micro-scale that have been correlated with microhabitat characteristics. These heterogeneous distributions may be the result of differential survival overwinter, differential site selection, or a combination of both. Whilst certain microhabitat characteristics have been shown to influence overwintering mortality, the role of active microhabitat selection has generally been inferred. Consequently, experiments described in Chapter Six examined whether polyphagous predatory species of Carabidae and Staphylinidae actively select overwintering sites. The microhabitat characteristics of 'preferred' sites were described. The degree to which spatial distributions of overwintering species differ between boundary types and between species was also examined. Between-field movement has been recognised as an important parameter in the persistence of open-habitat species such as polyphagous predators. However, field boundaries are considered to represent barriers of variable permeability to epigeal beetles. The effect of different field boundary types on permeability overwinter remains unquantified and will also be examined (Chapter Six).

The results of this study were discussed in relation to optimal field boundary management at the farm-scale in order to benefit arthropod biodiversity and enhance conservation biological control by carabid and staphylinid polyphagous predator populations (Chapter Seven).

CHAPTER TWO: DESCRIPTION OF FIELD BOUNDARY TYPES

2.1 INTRODUCTION

Within a single species pool, a complex array of factors will determine the arthropod fauna associated with a field boundary. Different species of arthropods vary in their habitat preferences and some will be mutually exclusive. However, maximising the range and continuity of resources, microclimate and microhabitats will enhance the potential of a field boundary to support a diverse arthropod community (Greaves & Marshall, 1987). The diversity of woody and herbaceous species within a field boundary will influence arthropod diversity through direct host-plant interactions, attraction of secondary consumers and increased architectural complexity (Bowden & Dean, 1977; Thomas & Marshall, 2000). Habitat structure or complexity will determine the range of microclimatic conditions and microhabitats found at a field boundary (Forman & Baudry, 1986; Maudsley, 2000). A tall, wide, dense canopy without gaps will maximise microclimatic extent and shelter, as will the presence of banks, margins and ditches. Additionally, mature emergent trees are more likely to have dead wood to support saprolytic species (Clements & Toft, 1992a). Increased width of a boundary will provide a buffer to farming operations and reduce the disturbance levels at the boundary interior. Factors acting outside the field boundary habitat can influence arthropod communities that develop locally. These include connectivity to the boundary network, orientation, elevation above sea level and adjacent land-use (Forman & Baudry, 1984). The potential of different field boundary types to support overwintering arthropods remains poorly understood and forms the focal point of this study. In order to understand patterns in species-habitat relationships, field boundary habitats need to be described in terms of their plant species composition, structure and additional features, which allows classification and subsequently facilitates interpretation.

The most comprehensive survey of linear features in the U.K was conducted as part of the Countryside Survey 2000 (CS2000) by the Centre for Ecology and Hydrology (Haines-Young *et al.*, 2000). This survey identified seven major field boundary types based on their structural features (see Table 1.1.1 for definitions), which were regarded as

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decreasing in ecological value in the order: hedge > remnant hedge > wall > relict hedge with fence/line of trees or shrubs > relict hedge/line of trees or shrubs > bank/grass strip/margin > fence. Hedgerows and their derivatives (remnant and relict hedgerows and lines of trees or shrubs) were differentiated by the openness of the lower 2m of the woody canopy as defined by earlier Countryside Surveys that sampled only woody boundaries (Barr *et al.*, 1991). Non-woody boundaries were generally defined according to their dominant structural feature such as fence, bank or wall. The botanical composition, additional features or field boundary network structure were not included in these definitions.

Hedgerows are considered to be the traditional field boundary type in lowland farmland, although they comprise only 35.8% of the field boundary stock in England and Wales (Haines-Young *et al.*, 2000). Where hedgerows have been removed they are frequently replaced by fences, which form 33.7% of field boundary stock. The remainder of field boundaries are composed of remnant and relict hedgerows, lines of trees or shrubs, banks, vegetation strips and walls. Both within and between these field boundary types, botany, structure and additional features, such as margins, ditches and banks, will vary.

The Hedgerow Evaluation and Grading System (HEGS) (Clements & Toft, 1992b), has been used to classify hedgerows according to their perceived ecological and wildlife value. This system measures field boundary characteristics demonstrated to influence associated floral and faunal assemblages, including woody species richness, young and mature emergent trees, height, width, gappiness of the woody canopy, banks, ditches and margins more than 2m in width, field boundary length and connectivity. The majority of these characteristics may be applied to woody and non-woody linear features alike and form the basis of the survey conducted for this study. Although the herbaceous species composition was noted in HEGS it did not form part of the grading system due to the seasonality of many herbaceous plant species and level of taxonomic expertise required for accurate identification. However, comparison of the herbaceous species composition between boundary types provides information on both wildlife value and

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habitat condition and was therefore surveyed according to methodologies used in the Countryside Surveys (Barr, 1998). Additional landscape characteristics such as orientation, elevation and adjacent land-use were also recorded.

British hedgerows have been divided into eleven categories based on their dominant woody species (Cummins & French, 1994; French & Cummins, 2001). The four principal types are: hawthorn dominant, mixed hawthorn, mixed hazel dominant and blackthorn dominant. More woody species may be found depending on the hedgerow's origin (Rackham, 1986) and age (Hooper, 1970). Woody species that are good hedgerow colonisers include: *Sambucus nigra, Corylus avellana, Acer campestre,* and *Cornus sanguinea,* with *Fraxinus excelsior, Rosa* spp. and *Prunus spinosa* occupying intermediate positions in terms of colonisation (Dowdeswell, 1987). The CS2000 found that 86% of hedgerows had more than two species, whilst a quarter supported more than five woody species in a standard 30m length of hedge (Haines-Young *et al.*, 2000). The ecological value of woody species richness is reflected in the protection of hedgerows with more than five woody species (in a standard 30m length) within the amended Hedgerow Regulations (Anon., 1997; DEFRA, 2003b), and the creation of a Biodiversity Action Plan to conserve such ancient and/or species rich hedgerows (Anon., 1995).

Hedgerows, remnant and relict hedgerows, lines of trees and shrubs and fences vary along a continuum of woody species representation. Both woody species composition and the continuity of the canopy are of prime importance in determining the ecological and wildlife value of a boundary and in distinguishing between boundaries (Clements & Toft, 1992b). Consequently, in the current study, the relative abundance (%) of woody species within a boundary (as a measure of woody species richness and the gappiness or openness of a canopy) was used to describe field boundary habitat and compare field boundary types.

Although a positive correlation has been reported between plant diversity in the canopy and herbaceous flora (Cummins & French, 1994; French & Cummins, 2001), Bunce *et al.* (1994), showed there was limited correlation between classification of

hedgerows based on woody species compared to herbaceous plants. The herbaceous flora of field boundaries generally colonises naturally (except where field margins have been sown), and strongly reflects field boundary management and adjacent land-use (French & Cummins, 2001; Maudsley *et al.*, 2002; Marshall & Moonen, 2002). French & Cummins (2001) used TWINSPAN (Hill, 1979) to identify four herbaceous communities in hedgerows that may be applied to field boundaries generally due to the strong associations with land-use. The indicator species for these four communities are shown in Table 2.1.1a. 'Intensive arable' communities were typified by species of disturbed or fertile ground, 'rotational' communities supported the most varied flora with species indicative of low management intensity and some shade-tolerant species, 'grassland' flora was typical of intensively fertilised or sown grass or intensively grazed pasture, whilst 'woodland' supported the highest occurrence of shade tolerant species and were typified by species of low intensity field boundary management and adjacent land use. With regards to management, where it is less intensive tall plants may develop, whilst frequent cutting, grazing or flailing encourages finer leaved grasses and rosette forming species (see Table 2.1.1b for indicator species of management intensity) (Dowdeswell, 1987). Some differences in the herbaceous flora due to the presence or absence of a woody boundary have been observed (see Table 2.1.1c for indicator species) (Boatman *et al.*, 1994). Consequently, the botanical composition may give indications regarding field boundary and adjacent land-use and management.

a) Intensive arable	Rotational	Grassland	Woodland
Arrhenatherum elatius	*Anthriscus sylvestris*	*Lolium perenne*	*Digitalis purpurea*
Bromus sterilis	*Rubus* spp.	*Poa annua*	*Hedera helix*
Convolvulus arvensis	*Stachys* spp.		*Holcus mollis*
Elymus repens	*Vicia* spp.		*Pteridium aquilinum*
Galium aparine			
Agrostis stolonifera			
Poa trivialis			
Urtica dioica			

b) Intensive management	Less-intensive management
Agrostis capilaris	*Agropyron repens*
Festuca spp.	*Dactylis glomerata*
Ranunculus repens	*Holcus lanatus*
Plantago major	*Arrhenatherum elatius*
Taraxacum spp.	*Anthriscus sylvestris*
	Heracleum spondylium
	Conium maculatum

c) Woody canopy absent	Woody canopy present
Agrostis stolonifera	*Anthriscus sylvestris*
	Galium aparine
	Glechoma hederacea
	Hedera helix
	Heracleum spondylium
	Urtica dioica

Table 2.1.1 Indicator species of field boundary herbaceous communities associated with a) different land-use types (French & Cummins, 2001; Boatman *et al.*, 1994), b) intensive and less intensive field boundary management (Dowdeswell, 1987), and c) presence or absence of a woody boundary (Boatman *et al.*, 1994).

In addition, the herbaceous flora is highly influenced by (and indicative of) underlying environmental gradients. Ellenberg (Ellenberg, 1988) environmental indicator scores (adapted for British conditions, Hill *et al.*, 1999) and autecological accounts (Grime, 2001) may be used to describe habitat conditions based on herbaceous species composition. The purpose of the Ellenberg values is to define an ecological niche held by an individual plant species. Ellenberg defined scales for seven factors based on plant species compositions in central Europe. Values for five of these scales (light, moisture, pH, nitrogen/fertility and salt) have now been re-calculated or re-estimated (where necessary) to apply to much of the flora of the British Isles (Hill *et al.*, 1999; Hill *et al.*, 2000). The use of Ellenberg values may be more indicative of site conditions through time and space than physical measurements of abiotic variables, as these can be problematic to record accurately. Values for light, moisture, pH and fertility are likely to differ between boundary types. For example, shading of the hedge-base may encourage species with low light requirements to grow. A dense canopy may enhance soil moisture, though this may be counteracted by increased drainage from a hedge-bank. Woody field boundaries might have been expected to support plants of higher fertility requirements due to the larger biomass of organic matter accumulating from leaf litter. Indeed, hedge plots were found to have higher fertility scores than other vegetation plots in all vegetation classes identified by the Countryside Surveys (Bunce *et al.*, 1999).

The abiotic conditions of a locality are not the only determinants for a plant species' presence within a community. The two principal external factors that influence vegetation are stress and disturbance. Stress refers to processes that restrict photosynthetic production, for example, through shortages of limiting factors such as light, water or nutrients, or sub-optimal temperatures. Disturbance relates to partial or total destruction of the plant biomass for example through herbivore grazing, pathogens, wind damage, frost or human activities. Through the evolution of plant strategies, three plant types may be recognised in relation to stress and disturbance (Grime, 2001):

(i) Competitors – capable of exploiting conditions of low stress and low disturbance.

(ii) Stress-tolerators – associated with high stress and low disturbance.

(iii) Ruderals – characteristic of low stress and high disturbance.

Through a combination of field surveys and autecological studies, much of the U.K. flora has been evaluated in terms of individual species' propensity for competition, stress-tolerance or ruderal strategies to develop the Competitor-Stress tolerator-Ruderal (CSR) model. The mean CSR scores of a community at a particular location give an indication of the processes of stress, disturbance and competition operating there. This can be useful in assessing the management of individual field boundaries and their adjacent land, and in comparing the relative intensities of stress and disturbance to which different field boundary types are subjected. Generally, plants growing in arable situations will have strong ruderal strategies, enabling them to colonise bare ground. Grassland and herb communities are likely to support a high proportion of competitive plants, showing vigorous growth and competitive-ruderal strategies. Woodland and underscrub communities tend to have a relatively high proportion of competitive-stress tolerators (Bunce *et al.*, 1999).

Comprehensive description of the botanical and habitat characteristics of a field boundary will produce a large array of quantitative and categorical variables, which can be difficult to interpret meaningfully. In addition, it is unlikely that any single attribute will be primarily responsible for determining the arthropod fauna overwintering in a boundary. It is more likely that a combination of characteristics will reflect some underlying latent variable influencing arthropod populations. Understanding the underlying factors describing the essential characteristics of different field boundary types could then be used to determine the influence of boundary type on the associated arthropod composition.

This study aimed to investigate relationships between field boundary type and arthropod assemblages. Consequently, it was necessary to conduct an initial classification and robust categorization of field boundaries on the study farm in order to allow comparisons to be made in subsequent chapters. Hence, this chapter is concerned with the classification and description of field boundaries within the study area.

2.1.1 Aims

(i) Select a representative sample of field boundaries on the Seale-Hayne Farm, Newton Abbot, Devon.

(ii) Describe selected field boundaries in terms of their botanical composition, habitat structure, field boundary network structure and landscape characteristics.

(iii) Identify underlying habitat characteristics of different field boundary types in order to allow comparison with arthropod communities.

2.2 METHODS

2.2.1 Field surveys

To minimise the influence of regional differences in floral and faunal assemblages, soil type, landscape structure and land-use, the examination of different field boundary types was conducted at the farm-scale. The Seale-Hayne farm (Newton Abbot, Devon) is characterised by a mixture of arable rotation and pastoral farming over 200 hectares. Winter wheat is the main arable crop grown in rotation with barley, maize and grass. Livestock include dairy cows and sheep. Most of the estate is on well drained, shallow clay loam. The land has undulating topography and few fields are level. Elevation ranges from 45 metres to 176 metres above sea level (Anon., 2002).

The farm has an extensive network of field boundaries including hedgerows, remnant and relict hedgerows, fences and a grassy bank. Boundaries vary in the representation of hedge-banks, margins and ditches. Hedgerows are managed by alternately flailing either side and the top, annually in winter. Where hedgerows have started to degrade flailing occurs in between emergent trees. Where hedgerows reach a more advanced stage of degradation, management has generally ceased. Most hedgerows, remnant and relict hedgerows and lines of trees and shrubs have ancillary fencing to ensure stockproofing. Herbaceous vegetation of post and wire fences and margins is generally strimmed biannually, in spring and autumn.

Eighteen field boundaries were examined. Selection criteria used were:

(i) Field boundaries on the farm perimeter were excluded.

(ii) Field boundaries adjacent to roads or buildings were excluded.

(iii) Field boundaries in the part of the farm south of the A386 were excluded due to difficult access.

(iv) Field boundaries were selected to represent a subset of those recorded on the estate.

(v) Selected field boundaries representing different field boundary types were evenly distributed across the estate.

A preliminary survey was conducted to categorise all selectable boundaries on the Seale-Hayne farm according to the CS2000 definitions (Table 1.1.1). Of the 59 boundaries identified, 24 were hedgerows, 16 were fences, 18 were a combination of remnant and relict hedges or line of trees and shrubs and there was one bank. To represent these proportions and create a balanced experimental design six hedgerows and six fences were selected. The remaining six boundaries were composed of two remnant, two relict and two lines of trees or shrubs which were grouped together to form a 'degraded' hedgerow category. A map of the Seale-Hayne Estate shows selected boundaries (labelled 1 to 18) (Figure 2.2.1). The eighteen selected field boundaries were surveyed to describe their structural, botanical and landscape characteristics. A description of the characteristics measured can be found in Table 2.2.1.

Figure 2.2.1 Map of the Seale-Hayne farm showing selected study field boundaries (labeled 1-18).

Orientation (degrees from north)	The compass bearing of the line of a field boundary measured as degrees from north measured from 1:10,000 scale O.S. map.
Average elevation (m)	Height above sea level (m) of field boundary averaged from five measurements recorded equidistantly the entire field boundary length from 1:10,000 scale O.S. map.
Elevation range (m)	The difference in height above sea level (m) between the highest point and lowest point of a field boundary taken from 1:10,000 scale O.S. map.
Connections	The number of linear features or woodland to which a selected field boundary is connected. A count of 1 given to a connection with another field boundary and 2 given to a connection with a woodland.
Field boundary length (m)	End-points of a field boundary defined by intersections or obvious changes in structure.
Field boundary width (m)	Width of all field boundary components including canopy, bank, margin, ditch and grassy track where applicable.
Canopy height (m)	Height of woody canopy from field level to top of canopy excluding new shoot growth.
Canopy width (m)	Width of woody canopy excluding new shoot growth.
Canopy gaps (%)	Calculated by subtracting the sum of the % woody species abundance from 100 to give the % gaps in the woody canopy.
Bank height (m)	Measured from the field level to the highest point on the bank.
Margin width (m)	Width of margin measured from canopy/fence/track edge to field edge.
Ditch width (m)	Width of ditch measured at field level between the two slopes.
Ditch depth (m)	Depth of ditch measured from field level to the the the upper surface of sediment.
Grassy track (2.4m width)	Presence (1) or absence (0) of grassy track (positioned between the canopy and margin).
Post and wire fence	Recorded as 1 for present and 0 for absent.
Mature emergent trees (100m-1)	Emergent trees were those which extend above the height of the canopy (if present), have maintained their natural tree shape and were positioned within any field boundary component (canopy, bank, margin, ditch or track). Trees were considered mature if the trunk diameter at a height of 1.5m from the ground was >0.1m. Counted along the entire length of the field boundary and then calculated per 100m.
Young emergent trees (100m-1)	Emergent trees (meeting the specifications above) were considered young if the trunk diameter at 1.5m from ground was <0.1m. Counted along the entire length of the field boundary and then calculated per 100m.
Canopy woody species richness	The number of woody species recorded in the 30m sample length.
Total woody species richness	The number of woody species recorded in the 30m sample length and as emergent trees within the field boundary (no double counting of species).
Herbaceous species richness	The number of herbaceous species recorded in the 10m sample length for the field boundary as a whole (no double counting of species).
Woody species richness (ET)	The number of woody species recorded within the emergence tents used to sample overwintering arthropod biodiversity (see Chapter 3).
Herbaceous species richness (ET)	The number of herbaceous species recorded in the emergence tents (see Chapter 3).
Herbaceous ground cover (%) (ET)	Estimated as the proportion of the ground surface area within the emergence tents (see Chapter 3) supporting rooted herbaceous vegetation.
Soil moisture (%) (ET)	Average soil moisture (%) of five soil cores from emergence tents (see Chapter 3) on 9th May. Samples were weighed, oven dried at 105 °C for 24 hours and reweighed. Calculated as the difference between dry weight and wet weight, divided by wet weight and multiplied by 100.
Adjacent land use	Classified as arable, permanent ley, temporary ley and other for each adjacent field.

Table 2.2.1 Description of the landscape, structural and botanical variables recorded at each field boundary.

Three survey methods were used, based on those employed by the Countryside Survey 2000 (Haines-Young *et al.*, 2000) and the Hedgerow Evaluation and Grading System (Clements & Toft, 1992b):

(i) A standard 30m sample length was used for recording % woody species abundance. The sample was positioned centrally along the field boundary length but avoiding gateways. All woody species were recorded, including climbing species since these add to the structural dimensions of a canopy (Barr *et al.*, 1995). Identification was to species level. Percentage gaps in the canopy were estimated and then the % abundance of each woody species in the remaining canopy sample length estimated. Each sample length was surveyed in January and May 1999.

(ii) A standard 10m sample section was used for recording herbaceous species presence-absence data (recorded as 1-0 respectively). This section was positioned centrally in the 30m sample length used above. The presence of all herbaceous species was recorded for each side of the field boundary separately. The dividing line between the two field boundary sides was defined as the centre-line of the woody canopy or the post and wire fence-line where field boundaries were non-woody. Identification was to species level. Herbaceous species were surveyed in May and September 1999 and the results were combined into a single data set.

(iii) The entire field boundary length was surveyed to record structural and landscape data. All structural attributes (see Table 2.2.1) were measured at five points equidistantly along the length of the field boundary and measurements then averaged. Measurements were recorded using 30m tape measures and 5m bamboo poles where necessary. Additional features (e.g. margins, ditches etc.) on both sides of a field boundary were included in the assessment of a field boundary habitat. Surveys were conducted in January 1999.

2.2.2 Analysis

Means for total woody abundance (raw data) and herbaceous species richness ($\log_{10}n+1$ transformed) for post and wire fences, hedgerows and degraded boundaries were compared separately using one-way anova with Tukey's post-hoc test. A general linear model was used to test whether adjacent crop type (summarised as arable, permanent ley, temporary ley and other) or aspect (the direction a field boundary side faces measured as degrees from north) influenced the herbaceous species richness. Crop type and field boundary type were fixed factors and aspect was used as a co-variate. Since each side of a field boundary forms a non-independent paired sample which may influence the interaction, one side of a boundary was selected at random for input into the analysis (hence n=18). Statistical tests were calculated using SPSS version 11.0.

Twinspan analysis was used to compare field boundaries in terms of their relative woody species composition (%) (using cut levels of 0, 2, 5, 10, 15 and 20% abundance) and their herbaceous species composition (presence-absence data). For the woody composition analysis, two post and wire field boundaries (PW13 and PW17) were omitted from the data set due to absence of woody species. The analysis was therefore based on 16 samples. Twinspan classification based on herbaceous composition combined presence-absence records from each side of a boundary. For both Twinspan analyses the maximum level of divisions was six, the minimum size of group to be divided was five and analysis was conducted using the Community Analysis Package version 1.3 (Pisces Conservation Ltd.).

Using the herbaceous species composition Ellenberg scores for light, pH, moisture and nitrogen/fertility were calculated for each field boundary to indicate the abiotic and biotic conditions prevalent at these localities. The scales for Ellenberg scores range from 1 to 9 for light, pH and fertility with 1 indicating extreme shade, acidity or infertility and 9 indicating bright light, alkaline or fertile conditions respectively. For moisture the scale ranges from 1 for extreme dryness to 12 for submerged plants (Hill *et al.*, 1999). Additionally, Grime's (2001) triangular CSR model for classifying British

vegetation was used to determine life history strategies by calculating relative scores for competitors, stress-tolerators and ruderal species found in each field boundary. MAVIS (Modular Analysis of Vegetation Information System, MAVIS Plot Analyser Version 1.0) was used to calculate the Ellenberg (light, moisture, pH and fertility) and CSR scores for each field boundary habitat.

Factor analysis was conducted using variables that described field boundary habitat structure and botany in order to investigate underlying environmental pattern. Variables describing network and landscape structure were omitted from the analysis since the study aims to examine the effect of field boundary type on the overwintering arthropod community. To perform factor analysis, variables must be sufficiently correlated to each other (correlation coefficients >0.3, correlation matrix determinant < 1.0×10^{-5}) without causing redundancy or colinearity in the data set. In a preliminary analysis, those variables that did not meet the requirements were excluded. The data set must also meet assumptions of sphericity (Bartletts test <0.05) and sampling adequacy (KMO measure of sampling adequacy >0.05) (Kinnear & Gray, 2000) and these parameters were checked. Varimax rotation was conducted on the eigenvalues produced by the analysis to determine simple structure and facilitate an ecological understanding of the analysis (Kinnear & Gray, 2000). Factor analysis was conducted using SPSS version 11.0.

2.3 RESULTS

2.3.1 Woody composition

Post and wire boundaries supported less than 15% total woody abundance (composed of soft woody species and *S. nigra*) and two supported no woody species at all (Table 2.3.1). Hedgerows supported > 84% total woody abundance, indicating few gaps in the canopy. Degraded boundaries supported between 49% and 74% woody abundance indicating the variation in canopy continuity between remnant hedgerows, relict hedgerows and lines of trees and shrubs. As expected, total woody abundance differed significantly between all three boundary types being greatest in hedgerows, intermediate in degraded boundaries and lowest in post and wire fencelines (Figure 2.3.1).

Field boundary type		Post and wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Acer campestre	Field maple							8	30	25	35	5	20	5		2	2		6
Cornus sanguinea	Dogwood											4	2			2			
Corylus avellana	Hazel							15		5			20		8	2	15	30	2
Crataegus monogyna	Hawthorn							38	16	5	5	13	5	20	25	30	15	8	2
Euonymus europaeus	Spindle							4	5	3		7	5		2				
Fagus sylvatica	Beech																		10
Fraxinus excelsior	Ash								5	2	4	5		2	8	1	2		2
Ilex aquifolium	Holly										5	5		20	5			2	5
Prunus spinosa	Blackthorn							13	18	40	25	25	20	2	8	15	4	12	8
Quercus robur	Oak									4	5	5			2			4	2
Salix caprea	Goat willow																	4	
Salix cinerea	Grey willow											15						4	5
Sambucus nigra	Elder			5					5				5						
Rosa arvensis	Field rose							3	8	2	5	2			2		2	4	
Rosa canina	Dog rose			2				2	8	2	3	2	2		5	5	5	3	10
Rosa rubiginosa	Sweet briar	5																	
Rubus fruticosus	Bramble		15	5			5	9	5	8	9	8	5		8	10	6	3	7
Viburnum opulus	Guelder rose																2		
Total woody species abundance (%)		5	15	12	0	0	5	92	100	96	96	96	84	49	73	67	53	74	59

Table 2.3.1 Relative abundance (%) of each woody species present in a 30m sample length of field boundary.

Thirteen tree and five woody climbing species were recorded in the survey. All woody boundaries supported five or more tree species. *P. spinosa* and *C. monogyna* were the most abundant and ubiquitous tree species occurring in all hedgerows and degraded boundaries. Hedgerows were dominated by *P. spinosa, C. monogyna* and *A. campestre* but most supported high proportions of other species. Degraded boundaries were typically dominated by *C. monogyna* or *C. avellana* and one degraded boundary supported equivalent proportions of *C. monogyna* and *I. aquifolium*. Amongst the soft woody climbing species *R. fruticosus* was the most common, occurring in 14 out of the 18 field boundaries including all woody boundaries. *R. canina* and *R. arvensis* also occurred frequently.

Twinspan classification did not distinguish clearly between boundary types (Figure 2.3.2). Post and wire fences were separated from hedgerows and degraded boundaries at the first two divisions based on the presence of *R. rubignosa* and absence of *C. monogyna*. Subsequently, four degraded boundaries and a hedgerow were separated from the remainder based on the presence of *I. aquifolium* and *S. cinerea*. The remaining six linear features were divided into a group of three hedgerows supporting a high proportion of *A. campestre*, and a group of two degraded boundaries and a hedgerow with only a low relative abundance of this species.
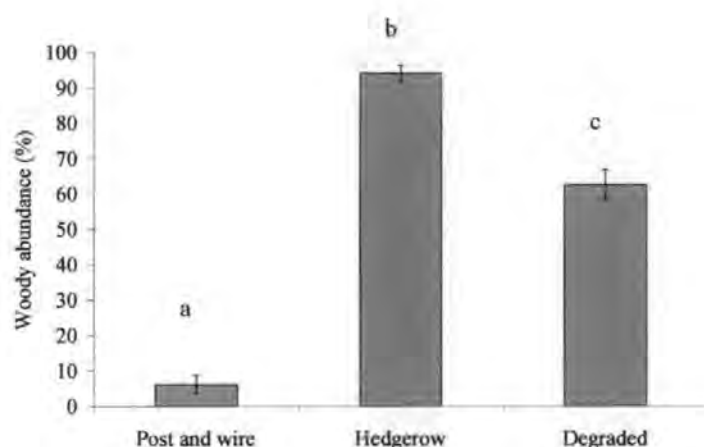
Figure 2.3.1 Woody species abundance (%, ±1 s.e.) in post and wire, hedgerow and degraded field boundary types. Mean woody abundance differed significantly between boundary types (F=200.16, df=2,15, P<0.001), same letter denotes no difference between types (Tukey's test).
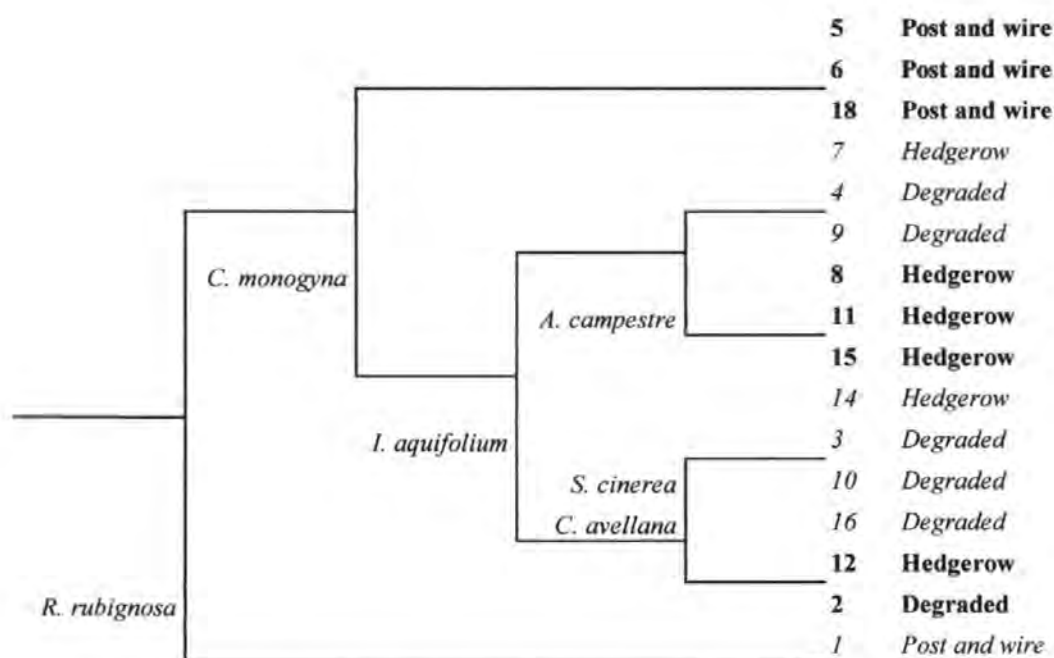
Figure 2.3.2 Classification (TWINSPAN) of field boundaries based on the relative (%) woody species abundance showing indicator species for each division, boundary number and type. Field boundary groupings at the final division are indicated using alternately bold and italic font.

2.3.2 Herbaceous composition

In total, 154 herbaceous species were recorded in the field boundary surveys (Table 2.3.2). *U. dioica* was the only plant ubiquitous to all field boundaries. Twenty species were recorded from more than half the boundaries including: *R. obtusifolius, C. temulentum, D. glomerata, L. perenne, C. arvense, G. hederacea, R. repens, T. repens* and *A. stolonifera*. Sixty species (39% of total) were found at one boundary only, indicating a high level of heterogeneity in herbaceous composition between samples. Herbaceous species richness per field boundary ranged from 8 to 47 species. Mean herbaceous species richness did not differ between field boundary types (Figure 2.3.3). Neither adjacent land-use nor aspect was found to influence species richness on either side of a boundary (arable: $F=0.038$, $df=2,13$, n.s.; permanent ley: $F=0.011$, $df=1,13$, n.s.; aspect $F=1.871$, $df=1,13$, n.s.).

All field boundaries supported herbaceous species indicative of all four land-use type communities (intensive arable, rotational, grassland and woodland), though a greater frequency of plants indicative of woodland were recorded at degraded boundaries (Table 2.3.3). Hedgerow and degraded boundaries supported higher frequencies of species indicative of the presence of a woody canopy.

Generally, the classification based on herbaceous composition did not distinguish between boundary types (Figure 2.3.4). The first TWINSPAN division separated a group of two post and wire fencelines and one hedgerow that lacked *S. asper* or *C. vulgare*, both of which were distributed ubiquitously across the other boundaries. The second division clustered together four degraded boundaries based on the strong representation of *G. mollugo* and *D. purpurea* and by the low representation of *R. repens* and *P. pratense*. *R. repens* and *P. pratense* were particularly well distributed in hedgerows with partial representation in post and wire boundaries. In contrast, *G. mollugo* was found almost exclusively in degraded boundaries (D3, D4 & D16) and one other hedgerow (H15), whilst *D. purpurea* is present at all four degraded boundaries, one other hedgerow (H15) and, surprisingly, two post and wire boundaries (PW13 & PW17). At the third division another group of two post and wire fences and one hedgerow was positioned in the

dendrogram such that the four post and wire boundaries are adjacent. The strong presence of *S. officinale* identified this grouping, a species otherwise only found in one degraded boundary (D4). The positioning of boundaries in the dendrogram indicated strong similarities in herbaceous composition between the post and wire habitats and also emphasised a polarity in composition between the post and wire boundaries located at the bottom of the dendrogram and the degraded boundaries clustered at the top. The final division segregated a group of three hedgerows and one degraded adjacent to the post and wire grouping, and two post and wire, one hedgerow and one degraded boundary adjacent to the degraded cluster. This latter group supported *A. tenuis*, which was absent from the former boundary grouping.

Field boundary type		Post and wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Achillea millefolium	Yarrow	1	1	1				1					1						
Aethusa cynapium	Fools Parsley				1														
Agropyron repens	Couch Grass			1	1		1		1	1	1	1	1		1	1		1	
Agrostis gigantea	Black Bent			1					1		1								
Agrostis stolonifera	Creeping Bent	1			1	1	1	1	1			1	1		1	1		1	1
Agrostis tenuis	Common Bent		1	1		1	1			1			1	1	1	1		1	1
Alopecurus geniculatus	Floating /Marsh Foxtail								1										
Alopecurus pratensis	Meadow Fox-Tail				1														
Anagallis arvensis	Scarlet Pimpernel							1											
Angelica sylvestris	Angelica																		1
Anthriscus sylvestris	Cow Parsley	1	1					1		1		1	1				1	1	1
Apium graveolens	Wild Celery										1								
Arctium minus	Lesser Burdock					1	1	1			1								
Arrenatherum elatius	False (Tall) Oat Grass	1	1		1					1		1	1		1		1		
Artemisia absinthum	Wormwood						1												
Arum maculatum	Lords-and-Ladies							1					1			1	1		
Asplenium scolopendrium	Harts-tongue Fern							1										1	
Aster lynosyris	Goldilocks aster														1				
Atriplex longipes	Long-stalked Orache							1										1	
Atriplex patula	Common Orache			1															
Avena ludoviciana	Winter Wild Oat						1						1						
Bellis perennis	Daisy												1						
Brachypodium sylvaticum	Wood False Brome																	1	
Brassica nigra	Black Mustard			1	1														
Bromus commutatus	Meadow Brome			1		1									1				
Bromus mollis	Soft Brome					1													
Bromus secalinus	Rye Brome			1															
Bromus sterilis	Barren Brome				1	1	1				1	1	1					1	
Calamintha sylvatica	Common Calamint							1			1								1
Calystegia sepium	Hedge Bindweed									1			1		1	1		1	
Cardamine flexuosa	Wavy Bitter-cress									1								1	
Carex sylvatica	Wood Sedge	1																	
Cerastium fontanum	Common Mouse-ear							1											
Chaerophyllum temulentum	Rough Chervil		1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	
Chamomilla recutita	Scented Mayweed						1				1								
Chamomilla suaveolens	Pineappleweed							1		1	1							1	
Chenopodium album	Fat Hen					1		1			1								
Chenopodium ficifolium	Fig-leaved Goosefoot				1														
Chrysanthemum leucanthemum	Oxeye Daisy	1																	

Table 2.3.2 Herbaceous species presence-absence (1-0) recorded from both sides of a 10m sample length of each field boundary (continued overleaf).

Field boundary type		Post and wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Cirsium acaulon	Dwarf Thistle							1	1							1		1	1
Cirsium arvense	Creeping Thistle	1	1	1	1	1	1		1			1	1	1	1	1			1
Cirsium eriophorum	Woolly Thistle		1							1			1					1	1
Cirsium palustre	Marsh Thistle																		1
Cirsium vulgare	Spear Thistle		1			1	1	1		1	1	1	1	1		1	1	1	
Conium maculatum	Hemlock					1	1				1	1							
Conopodium majus	Pignut											1							
Convolvulus arvensis	Field Bindweed	1	1	1	1	1	1				1		1					1	1
Coronopus didymus	Lesser Swine-cress							1								1	1		
Crepis biennis	Rough Hawksbeard									1									
Crepis capillaris	Smooth Hawksbeard								1								1		1
Dactylis glomerata	Cocksfoot	1	1	1	1	1	1	1		1	1	1			1	1	1	1	1
Digitalis purpurea	Foxglove				1	1							1	1	1	1			1
Dryopteris filix-mas	Male Fern											1					1		1
Epilobium hirsutum	Great Willowherb	1			1														
Epilobium montanum	Broad-leaved Willowherb	1		1					1				1					1	1
Equisetum arvense	Field Horsetail														1			1	1
Festuca ovina	Sheeps Fescue		1	1			1						1		1				
Foeniculum vulgare	Fennel	1																	
Fumaria parviflora	Fine-leaved Fumitory									1									
Galium aparine	Cleavers	1		1				1		1	1	1	1					1	1
Galium verum	Ladies Bedstraw										1								1
Gallium mollugo	Hedge Bedstraw												1		1	1			1
Geranium colobinum	Long-stalked Crane's-bill			1															1
Geranium molle	Doves-foot Crane's-bill														1				
Geranium pyrenaicum	Hedgerow Crane's-bill				1					1									
Geranium robertianum	Herb Robert				1	1		1	1	1	1	1	1			1	1	1	1
Geranium rotundifolium	Round-leaved Crane's-bill					1				1								1	1
Glechoma hederacea	Ground Ivy	1		1			1	1		1		1	1	1	1	1	1	1	1
Hedera helix	Ivy							1	1	1	1	1	1		1	1	1	1	1
Helictotrichon pubescens	Hairy Oat Grass									1								1	
Heracleum spondylium	Hogweed	1					1			1		1					1	1	1
Hieracium perpropinquum	Hawkweed									1									
Holcus lanatus	Yorkshire Fog	1	1	1			1	1	1		1	1	1				1		1
Holcus mollis	Creeping Soft Grass										1				1		1	1	
Hordeum murinum	Wall Barley					1													
Hordeum secalinum	Meadow Barley Grass													1	1				

Table 2.3.2 Herbaceous species presence-absence (1-0) recorded from both sides of a 10m sample length of each field boundary (cont.)

Field boundary type		Post and wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Hyacinthoides non-scriptus	Bluebell							1										1	
Hydrocotyle vulgaris	Marsh Pennywort														1				1
Hypercium tetrapterum	Square-stalked St. John's Wort								1										
Hypericum perforatum	Perforate St John's Wort	1	1																
Hypochoeris radicata	Common Cats-ear										1								
Juncus effusus	Soft Rush																	1	
Lamium album	White Dead Nettle						1												
Lamium purpureum	Red Dead Nettle								1									1	
Lapsana communis	Nipplewort			1		1		1	1		1	1			1				1
Leontodon autumnalis	Autumn Hawkbit		1												1				
Leontodon hispidus	Rough Hawkbit							1											
Linaria vulgaris	Common Toadflax		1																
Lolium perrene	Perennial Rye Grass			1	1	1		1	1	1	1	1	1	1	1	1	1	1	1
Lotus corniculatus	Common Birds-foot Trefoil	1																	
Lotus uliginosus	Greater Birds-foot Trefoil								1										
Malva moschata	Musk Mallow								1						1				
Matricaria perforata	Scentless Mayweed												1						
Mentha aquatica	Water Mint																	1	
Mentha arvensis	Corn Mint							1			1								
Mercurialis perennis	Dogs Mercury								1									1	1
Oenanthe crocata	Hemlock Water-dropwort										1								
Papaver rhoeas	Common Poppy				1														
Papaver somniferum	Opium Poppy				1														
Pastinaca sativa	Wild Parsnip	1																	
Persicaria lapathifolia	Pale Persicaria							1											
Petroselinum crispum	Garden Parsley										1								
Petroselinum segetum	Corn Parsley																		1
Phleum bertolonii	Small Cats Tail				1				1										
Phleum pratense	Timothy		1	1		1	1	1	1		1	1	1				1		
Pimpinella major	Greater Burnet-Saxifrage		1																
Plantago lanceolata	Ribwort Plantain	1								1	1							1	
Plantago media	Hoary Plantain			1				1		1	1							1	1
Poa annua	Annual Meadow Grass			1	1			1			1								
Poa pratensis	Smooth Meadow Grass										1						1		
Poa trivialis	Rough-stalked Meadow Grass							1		1	1				1			1	1
Polygonum aviculare	Cornfield Knotgrass				1			1			1				1				
Potentilla erecta	Tormentil										1							1	
Potentilla reptans	Creeping Cinquefoil										1								

Table 2.3.2 Herbaceous species presence-absence (1-0) recorded from both sides of a 10m sample length of each field boundary (cont.)

Field boundary type		Post and wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Primula veris	Cowslip	1																	
Pteridium aquilinum	Bracken														1	1			
Pulicaria vulgaris	Small Fleabane							1											
Ramunculus acris	Meadow Buttercup							1											
Ramunculus bulbosus	Bulbous buttercup										1		1						
Ramunculus parviflorus	Small Flowered Buttercup												1						
Ramunculus repens	Creeping Buttercup	1	1		1		1	1	1	1	1	1	1				1	1	1
Ramunculus sardous	Hairy Buttercup		1		1			1		1									
Rumex conglomeratus	Clustered dock												1				1		
Rumex obtusifolius	Broad-leaved Dock	1		1	1	1	1	1	1	1	1	1	1		1	1	1	1	1
Salvia pratensis	Meadow Clary													1					
Saponaria officinalis	Soapwort								1										
Senecio jacobaea	Ragwort		1				1			1				1				1	1
Sherardia arvensis	Field Madder											1							
Silene dioica	Red Campion		1		1									1	1	1	1		
Sison amomum	Stone Parsley	1																	1
Sisymbrium officinale	Hedge Mustard				1	1				1						1			
Solanum nigrum	Black Nightshade																	1	
Sonchus asper	Prickly Sow Thistle		1		1		1	1		1	1			1			1	1	1
Sonchus oleraceus	Smooth Sow-thistle											1							
Stachys arvensis	Field Woundwort											1				1			
Stachys sylvatica	Hedge Woundwort		1						1				1					1	1
Stellaria graminea	Lesser Stichwort												1						1
Stellaria holostea	Greater Stichwort			1					1						1				
Stellaria media	Chickweed						1			1							1	1	1
Taraxicum officinale	Dandelion										1								
Thlaspi arvense	Field Pennycress				1														1
Trifolium pratense	Red Clover		1			1	1			1								1	
Trifolium repens	White Clover	1	1	1	1	1			1	1	1	1	1			1	1	1	
Umbilicus rupestris	Wall Pennywort														1				
Urtica dioica	Stinging nettles	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Veronica chamaedrys	Germander Speedwell																		1
Veronica montana	Wood Speedwell		1					1					1		1	1			
Veronica persica	Common Field Speedwell		1				1	1				1	1				1		
Veronica serpyllifolia	Thyme-leaved Speedwell						1												1
Vicia cracca	Common Vetch										1								
Vicia hirsuta	Hairy Tare	1																	
Vicia sepium	Bush Vetch	1	1					1	1										
Viola riviniana	Common Dog Violet														1				

Table 2.3.2 Herbaceous species presence-absence (1-0) recorded from both sides of a 10m sample length of each field boundary.
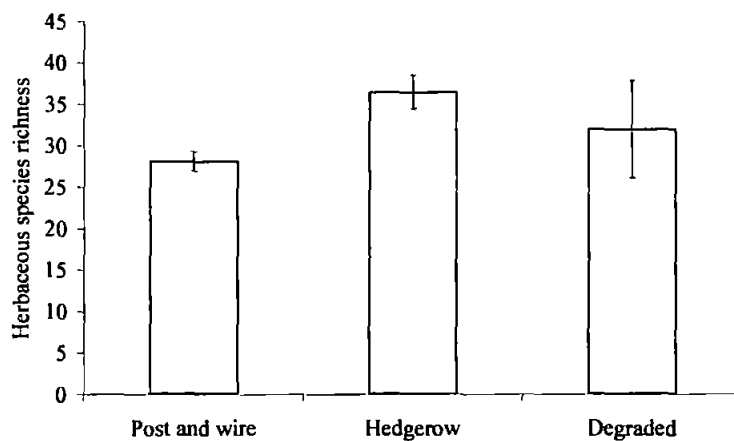
Figure 2.3.3 Herbaceous species richness (%, ±1 s.e.) in post and wire, hedgerow and degraded field boundary types. Using ANOVA no significant differences in herbaceous species richness ($\log_{10}n+1$) were found between boundary types (F=0.881, df=2,15, n.s.).

2	**Degraded**
3	**Degraded**
4	**Degraded**
16	**Degraded**
5	*Post and wire*
10	*Degraded*
15	*Hedgerow*
18	*Post and wire*
7	**Hedgerow**
9	**Degraded**
12	**Hedgerow**
14	**Hedgerow**
11	*Hedgerow*
13	*Post and wire*
17	*Post and wire*
1	**Post and wire**
6	**Post and wire**
8	**Hedgerow**

Indicator species labels in dendrogram: *G. mollugo*, *D. purpurea*, *S. asper*, *C. vulgare*, *R. repens*, *P. pratense*, *A. tenius*, *S. oficinale*
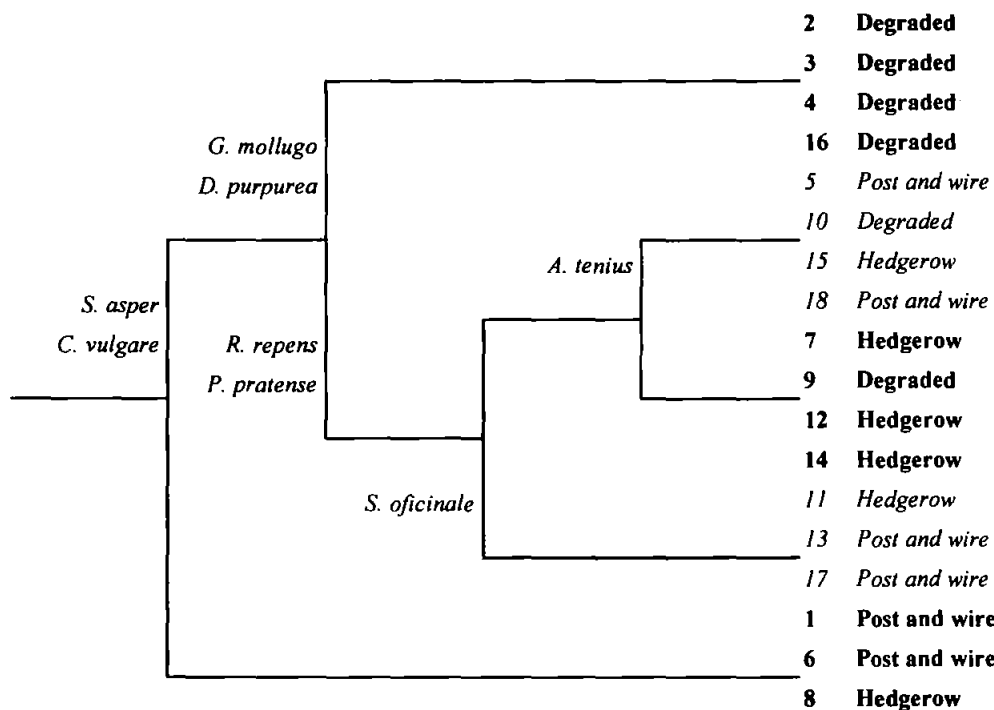
Figure 2.3.4 Classification (TWINSPAN) of field boundaries based on herbaceous species presence-absence showing indicator species at each division, boundary number and type. Field boundary groupings at the final division are indicated using alternately bold and italic fonts.

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	Post and wire	Hedgerow	Degraded
Intensive arable	24	28	22
Rotational	6	10	6
Grassland	5	8	6
Woodland	2	8	14
Intensive management	7	8	4
Less-intensive management	22	25	18
Woody canopy absent	4	4	4
Woody canopy present	15	27	26

Table 2.3.3 Frequency of occurrence of indicator species identified with adjacent land-use (intensive arable, rotational, grassland or woodland), intensity of field boundary management and presence or absence of a woody canopy (Boatman *et al.*, 1994; French & Cummins, 2001).

2.3.3 Habitat condition

Herbaceous vegetation associated with post and wire habitat had a measurably greater light requirement than either hedgerows or degraded boundaries (Figure 2.3.5a). Post and wire boundaries supported herbaceous vegetation associated with well-lit habitats but also occurring in partial shade such as *A. elatius,* though similar species such as *P. trivialis* and *V. cracca* (Hill *et al.,* 1999) were absent from post and wire habitat whilst present at hedgerow and degraded boundaries. In contrast, woody boundaries supported semi-shade plants in the shadow footprint of the canopy (e.g. *H. non-scripta,* Hill *et al.,* 1999), but light scores would have been elevated by the presence of herbaceous vegetation in adjacent margins that were well illuminated.

Mean moisture scores between field boundary categories showed a small but measurable difference increasing in the order post and wire < hedgerow < degraded (Figure 2.3.5b). Moisture scores in the range recorded at all field boundary types were indicative of fresh soils with average dampness supporting such species as *A. sylvestris,* *H. non-scripta* and *S. nigum.* As moisture content increases, species such as *A. stolonifera* are likely to be found (Hill *et al.,* 1999). Soil at all field boundary types was fairly neutral though measurably more acidic at degraded boundaries and more basic at post and wire and hedgerow habitats (Figure 2.3.5c). Field boundary categories could all be described as intermediate to richly fertile (Figure 2.3.5d). Field boundary categories did not differ in their competitor (Figure 2.3.6a), stress-tolerator (Figure 2.3.6b) or ruderal (Figure 2.3.6c) scores.
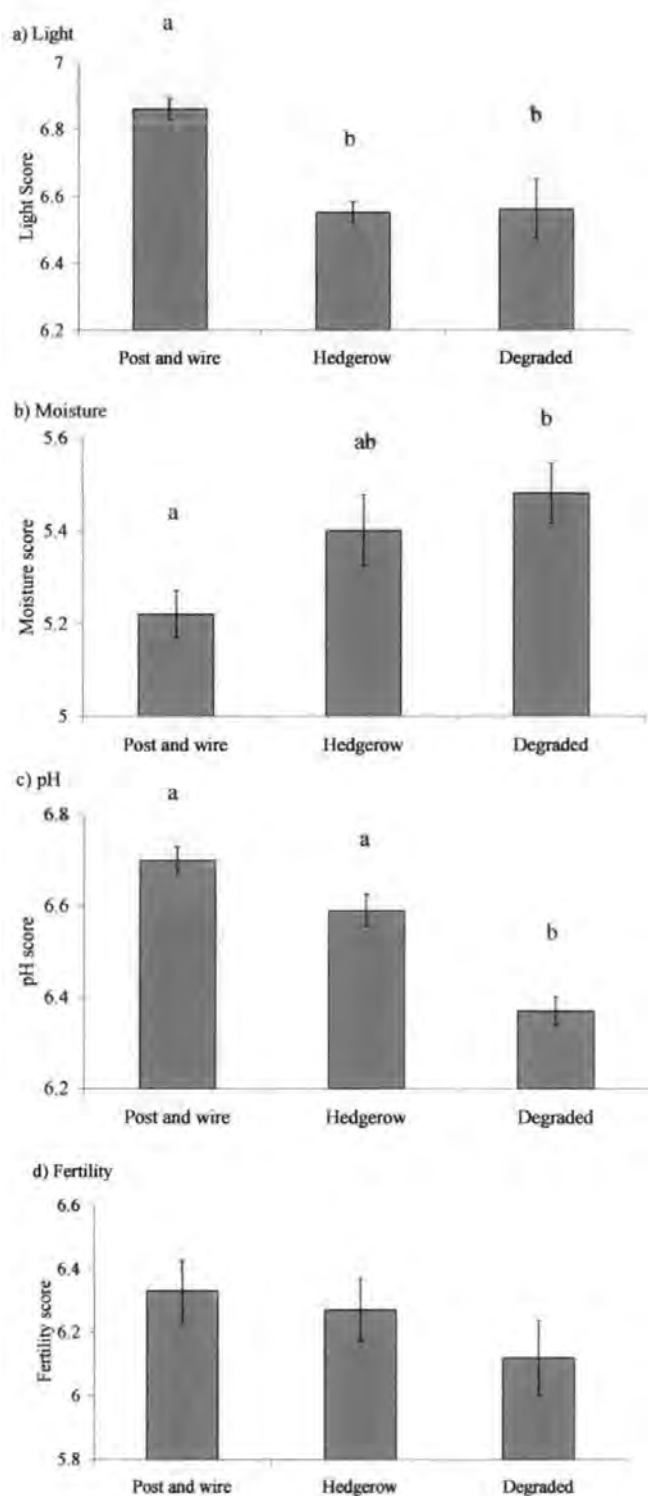
Figure 2.3.5 Mean Ellenberg scores for a) Light, b) Moisture, c) pH and d) Fertility for each field boundary type (±1 s.e). Scores for light (F=9.14, df=2,15, P<0.01), moisture (F=4.4, df=2,15, P<0.05) and pH (F=28.78, df=2,15, P<0.001) were significantly different between field boundary types. Field boundary categories did not differ in their fertility scores (F=1.04, df=2,15, n.s.). Same letters denote no difference between boundary types (Tukey's test).

a) Competitor

b) Stress-tolerator
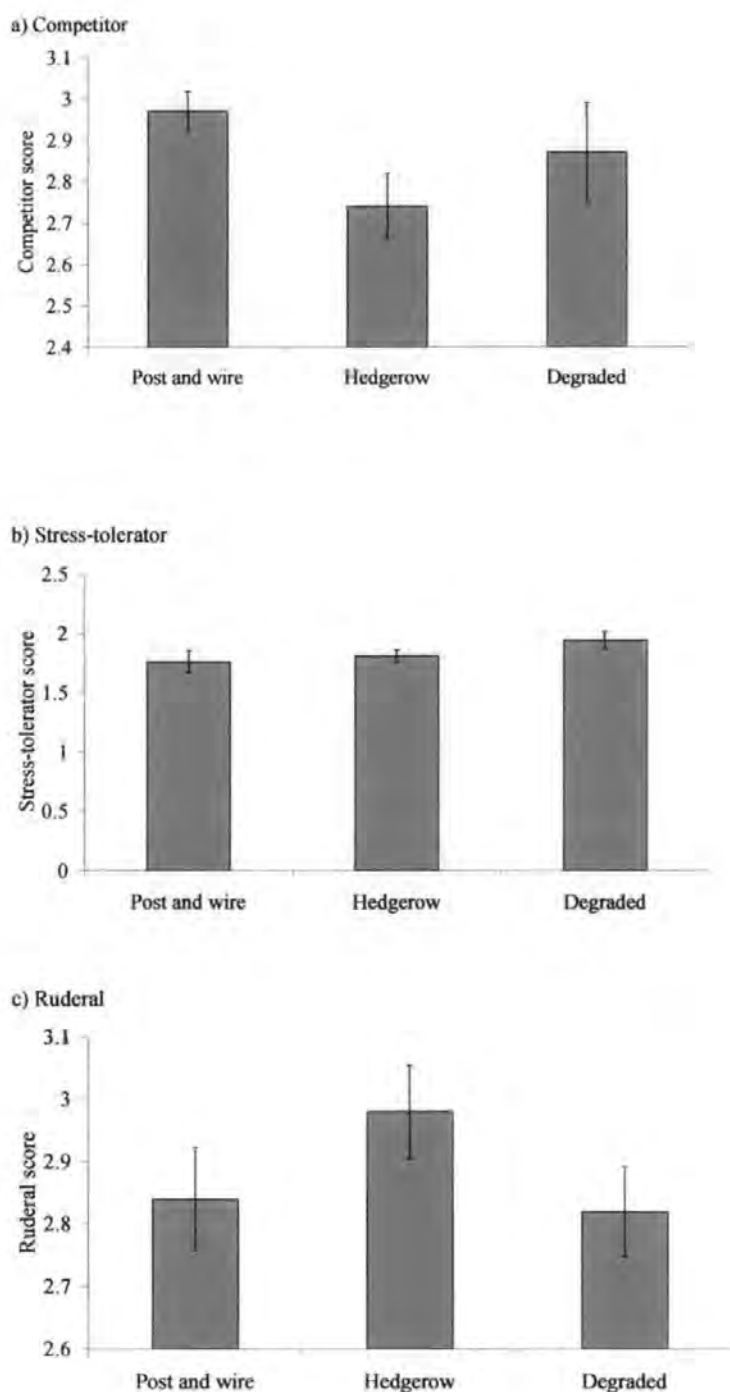
c) Ruderal

Figure 2.3.6 Mean CSR model scores for a) Competitor, b) Stress-tolerator and c) Ruderal plant strategies for each field boundary type (± 1 s.e.). The scores did not vary significantly between field boundary types (competitor: F=1.6, df=2,15, n.s.; stress-tolerator: F=1.5, df=2,15, n.s.; ruderal: F=1.3, df=2,15, n.s.).

2.3.4 Structure

Quantitative and categorical variables describing landscape characteristics, habitat structure and plant species richness of each field boundary and averaged for each field boundary type are shown in Table 2.3.4 and Table 2.3.5 respectively. Within each boundary type, selected linear features vary fully in orientation. The average elevation of field boundaries varies from 65m to 167.5m above sea level, with hedgerows generally found at lower levels and more post and wire fencelines positioned on slopes (elevation range). Most linear features had three or four connections to other field boundaries.

The entire field boundary width can be broken down into composite features including width of canopy, margin, ditch and grass track. The widest field boundaries supported all three additional features, the narrowest were post and wire fence lines associated with a grass strip. Both hedgerows and degraded boundaries were positioned on large banks and frequently had adjacent ditches. In contrast, no post and wire boundaries had ditches and they were only slightly raised above field level. Herbaceous strips adjacent to field boundaries vary from 0.2m to 4.0m, though only those >2.0m were classed as margins (Clements & Toft, 1992b). Where verges were <0.6m they generally were formed through an inability to plough to the boundary edge. Often they were sown with *L. perenne,* but in any case tended to support a dense stand of grassy vegetation. Wider margins were frequently associated with land too steep to cultivate and supported a natural regeneration vegetation. Only two hedgerows had grassy tracks positioned between the canopy and margin.

All post and wire, four hedgerows and three degraded boundaries had post and wire fences. In addition all field boundary types were associated with mature emergent trees, though numbers of mature and young emergent trees were considerable greater at degraded boundaries. Amount of herbaceous ground cover notably decreased in the order post and wire > degraded > hedgerow.

Field boundary type	Post and wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Orientation (degrees from north)	125	50	145	140	30	95	100	20	160	80	50	160	80	110	85	110	170	85
Elevation average (m)	87.5	167.5	110	70	100	107.5	82.5	82.5	72.5	70	67.5	65	135	125	130	67.5	67.5	82.5
Elevation range (m)	5	15	40	20	10	5	5	5	5	10	15	10	10	10	0	5	5	25
Connections	3	7	4	4	3	3	4	4	3	3	6	4	3	4	4	4	4	3
Field boundary length (m)	60	140	150	120	80	100	80	160	100	160	180	130	80	90	50	140	140	80
Entire field boundary width (m)	4	2.6	0.6	0.4	0.2	2.5	3.2	4.4	10.1	10.4	3.2	3	3.6	3.8	3.3	4.4	5.8	6.9
Canopy height (m)	0	0	0	0	0	0	2.9	2.8	3	3	2.6	2.8	0	3.5	3	2.4	4.2	4
Canopy width (m)	0	0	0	0	0	0	3	3.4	3.6	3.6	3	2.8	3.6	3.3	2.8	3.2	4.3	4.5
Canopy gaps (%)	95	85	88	100	100	95	8	0	4	4	4	16	51	27	33	47	26	41
Bank height (m)	0	0.3	0	0	0	0.5	0.8	0.5	1	1	0.6	0.1	0.5	1.1	0.7	1.2	0.4	0.5
Margin width (m)	4	2.6	0.6	0.4	0.2	2.5	0.2	0.2	3.3	3.3	0.2	0.2	0	0.5	0.5	0.2	0.2	2
Ditch width (m)	0	0	0	0	0	0	0	0.8	0.8	1.1	0	0	0	0	0	1	1.3	0.4
Ditch depth (m)	0	0	0	0	0	0	0	0.5	0.4	0.4	0	0	0	0	0	1	1.1	0.2
Grassy track (2.4m width) (1-0)	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Post and wire fence (1-0)	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0	0	1
Mature emergent trees (100m^{-1})	0	8.6	0	0	1.3	0	2.5	1.9	1	0.59	3.3	1.5	6	5.6	0	0	5.7	6.2
Young emergent trees (100m^{-1})	0	0	0	0	0	0	0	0	13	0	3.8	10	20	5.6	2	13.6	6.4	16.3
Canopy woody species richness	1	1	3	0	0	1	8	9	10	9	12	9	5	10	8	9	10	11
Total woody species richness	1	4	3	0	1	1	8	9	10	9	12	9	5	10	8	9	11	11
Herbaceous species richness	28	29	23	32	28	29	43	28	37	37	35	39	8	36	26	30	49	43
Woody species richness (ET)	0	0	0	0	0	0	3	3	2	1	2	1	0	3	4	2	1	1
Herbaceous species richness (ET)	9	10	3	6	2	7	7	11	10	12	5	10	5	8	9	5	10	8
Herbaceous ground cover % (ET)	75	70	90	90	85	80	35	45	35	40	45	65	80	45	55	55	55	65
Soil moisture (%)	31.658	30.023	23.67	24.38	32.525	37.993	30.455	34.29	24.178	27.378	31.685	30.643	28.655	25.49	30.428	38.058	31.448	26.245

Table 2.3.4 Landscape, structural and botanical characteristics of each field boundary.

	Post and wire		Hedgerow		Degraded	
	mean	s.e.	mean	s.e.	mean	s.e.
Orientation (degrees from north)	49.2	8.1	45.0	12.0	66.7	11.7
Elevation average (m)	107.1	13.5	73.3	3.1	101.3	13.1
Elevation range (m)	15.8	5.4	8.3	1.7	9.2	3.5
Connections	4.0	0.6	4.0	0.4	3.7	0.2
Field boundary length (m)	108.3	14.2	135.0	15.9	96.7	14.8
Entire field boundary width (m)	1.7	0.6	5.7	1.4	4.6	0.6
Canopy height (m)	0.0	0.0	2.9	0.1	2.9	0.6
Canopy width (m)	0.0	0.0	3.2	0.1	3.6	0.3
Canopy gaps (%)	93.8	2.5	6.0	2.2	37.5	4.3
Bank height (m)	0.1	0.1	0.7	0.1	0.7	0.1
Margin width (m)	1.7	0.6	1.2	0.7	0.6	0.3
Ditch width (m)	0.0	0.0	0.5	0.2	0.5	0.2
Ditch depth (m)	0.0	0.0	0.2	0.1	0.4	0.2
Grassy track (frequency)	0		2		0	
Post and wire fence (frequency)	6		4		3	
Mature emergent trees ($100m^{-1}$)	1.7	1.4	1.8	0.4	3.9	1.2
Young emergent trees ($100m^{-1}$)	0.0	0.0	4.5	2.3	10.7	2.9
Canopy woody species richness	1.0	0.4	9.5	0.6	8.8	0.9
Total woody species richness	1.7	0.6	9.5	0.6	9.0	0.9
Herbaceous species richness	28.2	1.2	36.5	2.0	32.0	5.9
Woody species richness (ET)	0.0	0.0	2.0	0.4	1.8	0.6
Herbaceous species richness (ET)	6.2	1.3	9.2	1.1	7.5	0.8
Herbaceous ground cover (%) (ET)	81.7	3.3	44.2	4.5	59.2	4.9
Soil moisture (%)	30.0	2.2	29.8	1.4	30.1	1.9

Table 2.3.5 Mean (±1 s.e.) landscape, structural and botanical descriptions of post and wire fences, hedgerows and degraded boundaries.

2.3.5 Factor analysis

A subset of 15 variables describing field boundary habitat were used to extract four latent factors describing 78% of the observed variation between field boundaries (Table 2.3.6). The loadings of the field boundary variables were used to describe each of the extracted factors. The scores generated for Factors 1 and 2 (F1 and F2) differed significantly between boundary categories, whilst scores for Factors 3 and 4 (F3 and F4) were not measurably different (Table 2.3.7). Post and wire boundaries had low F1 scores compared to degraded and hedgerow boundaries which had increasingly high F1 scores respectively. Scores for F2 were lowest in post and wire habitats and measurably highest in degraded habitats whilst hedgerows had an intermediate score (closer to post and wire than degraded).

Factor 1

Factor loadings indicated that field boundaries with a high score for F1 tended to have a high woody species richness with a tall, wide and continuous woody canopy. Additionally, the canopy was set on a tall bank with low herbaceous ground cover underneath the canopy. Hedgerows are frequently defined by these characteristics and were found to support the highest F1 scores. Post and wire boundaries contrast strongly with hedgerows in these characteristics and consequently had the lowest F1 scores. This factor will be referred to as describing 'hedgerow' characteristics.

Factor 2

Boundaries with high F2 scores supported high numbers of young emergent trees along their length. This was characteristic of boundaries in the first stages of deterioration as indicated by the measurably higher F2 scores associated with degraded boundaries compared to post and wire fencelines or hedgerows. This factor will be referred to as describing 'initial degradation' of hedgerow characteristics.

Factor 3

Field boundaries with high F3 scores supported wide margins associated with high herbaceous species richness. This factor would not be expected to vary with

boundary type since linear features were not selected with regards to additional features such as margins. However, degraded boundaries with lowest mean margin width had the lowest F3 scores. It is interesting to note that herbaceous richness was correlated with margin width. This factor will be referred to as describing 'margin' characteristics.

Factor 4

F4 describes habitats with a large number of mature emergent trees as found within the degraded hedgerow category. This factor will be referred to as describing 'advanced degradation' of hedgerow characteristics.

	Factor 1	Factor 2	Factor 3	Factor 4
Cummulative variance %	52.1	64.2	73.8	81.3
Canopy height (m)	0.933			
Canopy width (m)	0.795			
Canopy gaps (%)	-0.918			
Bank height (m)	0.650			
Margin width (m)			0.870	
Ditch width (m)				
Post and wire fence (1-0)				
Mature emergent trees (100m^{-1})				0.818
Young emergent trees (100m^{-1})		0.907		
Canopy woody species richness	0.899			
Total woody species richness	0.900			
Herbaceous species richness	0.617			
Woody species richness (ET)	0.853			
Herbaceous species richness (ET)			0.717	
Herbaceous ground cover % (ET)	-0.909			

Table 2.3.6 Factor loadings (where >0.6 in order to show important values) for each field boundary characteristic entered into the analysis used to describe Factors 1 to 4. The cumulative variance (%) explained by Factors 1 to 4 is shown.

		Post and wire	Hedgerow	Degraded		
Factor 1	mean	-1.16	0.82	0.35	F	23.664
	s.e.	0.06	0.13	0.34	df	2, 15
		a	b	b	P	<0.001
Factor 2	mean	-0.61	-0.23	0.84	F	4.976
	s.e.	0.07	0.35	0.46	df	2, 15
		a	ab	b	P	<0.05
Factor 3	mean	0.11	0.21	-0.33	F	0.466
	s.e.	0.42	0.52	0.30	df	2, 15
					P	n.s.
Factor 4	mean	-0.45	-0.01	0.15	F	0.097
	s.e.	0.34	0.30	0.60	df	2, 15
					P	n.s.

Table 2.3.7 Mean scores for Factors 1 to 4 (±1 s.e.) for each field boundary type. Scores for Factors 1 and 2 differed significantly between boundary types (ANOVA) described by Tukey's test (same letter denotes no difference).

2.4 DISCUSSION

The proportions of different field boundary types found on the farm and selected for study reflect those typically found in England and Wales by the Countryside Surveys (Haines-Young *et al.*, 2000). Strong differences observed between field boundary types were attributable to the abundance, dimensions and continuity of the woody canopy and the presence of emergent trees. Herbaceous species richness did not differ between post and wire, hedgerow or degraded boundaries, though there was a high species turnover between linear features. Margins were generally wider at post and wire fence-lines and narrowest at degraded boundaries. Variations in herbaceous composition appeared to be more strongly related to field boundary type than adjacent land-use.

In total, 18 woody and 154 herbaceous species were identified from surveys of the 18 field boundaries. Although the origins of hedgerows on the Seale-Hayne farm are not known, all selected boundaries pre-date early O.S. maps from 1889 (Landmark Information Group Ltd). All selected field boundaries were probably hedgerows, with replacement by post and wire features or degradation likely to have occurred after this time. The presence of *C. monogyna* and *P. spinosa* in all woody boundaries suggested that hedgerows may have been planted with these species and additional species have since colonised (French & Cummins, 2001). *A. campestre* and *C. avellana* are both regarded as good colonisers (Dowdeswell, 1987) which may explain their strong presence in hedgerows and degraded boundaries. All woody boundaries supported more than five woody species in a standard 30m length and, therefore, would be protected from removal under the Hedgerow Regulations (Anon., 1997; DEFRA, 2003b) and categorised as priority habitats for conservation according to the U.K. Biodiversity Action Plan (Anon., 1995). Observed differences in total woody abundance reflect the importance of this characteristic in the definition of field boundary types. However, the component woody species differed within hedgerows and degraded boundaries primarily based on the presence or absence of increasingly infrequent species such as *I. aquifolium, A. campestre, C. avellana* and *S. cinerea*.

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Herbaceous composition of the field boundaries was fairly heterogeneous, with only 20 species out of 154 occurring at more than half of the field boundaries surveyed. Six of these species (*U. dioica, D. glomerata, L. perenne, C. arvense, G. hederacea*, and *A. stolonifera*) were among the 15 most frequently occurring species in another survey of 103 field boundaries across nine farms in southern England (Boatman *et al.*, 1994). Measurements of relative abundance of herbaceous species may have indicated greater homogeneity between boundaries, with those species occurring most frequently also tending to dominate the ground flora. Few similarities in field boundary classification were found between woody or herbaceous composition. However, classification based on herbaceous composition identified two clusters of post and wire and degraded boundaries, indicating some pattern in species occurrences within these boundary types. Degraded boundaries supported herbaceous communities with lower light requirements and higher moisture preference and may be associated with more basic soils compared to post and wire boundaries. Generally, hedgerows were intermediate between degraded and post and wire boundaries in terms of habitat condition. The presence of *D. purpurea* in post and wire habitat was unexpected since this species is typical of wooded boundaries that are more shaded (Boatman *et al.*, 1994; French & Cummins, 2001). Degraded boundaries supported a notably higher frequency of species indicative of woodland communities, whilst post and wire boundaries showed a distinctly low frequency of species typical of boundaries supporting a woody canopy. Therefore, despite the strong evidence in the literature for the importance of adjacent land-use in determining the herbaceous composition of field boundaries (e.g. French & Cummins, 2001; Marshall & Moonen, 2002), variations in herbaceous species presence-absence appeared to be influenced more by field boundary type than crop type at the farm-scale. Field boundaries were found to support plant species indicative of all land-use categories as may be expected on a mixed arable-livestock farm (Boatman *et al.*, 1994; French & Cummins, 2001). However, the lack of difference in CSR scores between field boundary types suggested that all boundaries experience equivalent levels of stress and disturbance on the farm. For example, run-off from the addition of slurry and fertiliser to fields throughout the farm may counteract any difference attributable to field boundary type. The importance of field boundary structure in determining herbaceous species composition

will prove an important consideration in subsequent studies investigating the arthropod communities emerging from overwintering at different field boundary types.

These analyses confirm that the classification into post and wire fences, hedgerows and degraded hedgerows is robust and will allow detailed comparison of arthropod assemblages between boundary types. The selection of field boundaries maximised differences in habitat structure and plant species composition between boundary types, whilst minimising confounding factors such as network and landscape structure or adjacent land-use that may otherwise influence arthropod communities. Factor scores provided a quantitative measure of field boundary traits and were used in subsequent analyses to examine the effect of field boundary type on arthropod communities emerging from overwintering (Chapter 3).

CHAPTER THREE: COMMUNITY STRUCTURE AND COMPOSITION OF ARTHROPODS OVERWINTERING IN DIFFERENT FIELD BOUNDARY TYPES AT THE FARM-SCALE

3.1 INTRODUCTION

Agricultural reform in the U.K., primarily through the Common Agricultural Policy of the European Union is attempting to encourage sustainable and environmentally beneficial farming (Curry, 2002). As a result, features of the farmed landscape that provide beneficial agronomic services or enhance biodiversity are increasingly encouraged within agri-environment schemes. Field boundaries provide farmland arthropods with a range of resources, including overwintering sites and refuge from detrimental agronomic practices that are vital for their continued persistence in farmland. Research into the arthropod fauna of field boundaries has focussed on either hedgerows or field margins (e.g. Lagerlof *et al.*, 1992; Smith *et al.*, 1993; Maudsley *et al.*, 1997; Dover & Sparks, 2000). As a result, most agri-environment schemes now support prescriptions for hedgerow creation in place of post and wire fences, hedgerow restoration and management, and options for the introduction and maintenance of field margins (DEFRA, 2003a). However, the dominant field boundary types in lowland farmland include hedgerows, post and wire fencelines and degraded hedgerows (Haines-Young *et al.*, 2000), yet the relative contribution of each to farmland biodiversity or agronomic services remains largely unquantified.

Arthropods associated with field boundaries are beneficial as prey items for game birds and other fauna of economic or conservation concern (Thomas *et al.*, 2001b; Wilson *et al.*, 1999); contributors to soil dynamics and nutrient recycling (Alvarez *et al.*, 1997; Lagerlof *et al.*, 2002); pollinators (Lagerlof *et al.*, 1992; Carreck & Williams, 1997); and biological control agents of crop pests (Kopp, 1998; Lee & Landis, 2002). The maintenance of biodiversity and the provision of beneficial functions are inextricably linked (Naeem *et al.*, 1995; Cardinale *et al.*, 2003). For example, a diverse community of the natural enemies of cereal aphids may provide a greater range of control through space and time. This reduces the likelihood of the pest finding a refuge for population growth to economically damaging levels (Sunderland, 2002; Sunderland *et al.*, 1997). In addition, a diverse natural enemy

complex will have a wider amplitude of ecological properties (in response to changing abiotic conditions) than each species individually, and therefore may exert more consistent control of the pest under changing conditions (Altieri & Letourneau, 1982; Altieri, 1999). The natural enemy complex of cereal aphids in lowland farmland includes nearly 400 species from several families within Coleoptera, Araneae, Diptera, Dermaptera and Hymenoptera (Sunderland *et al.*, 1985). Polyphagous predators such as the Carabidae and Staphylinidae (Coleoptera) feed on alternative prey items in the absence of cereal aphids, enabling predator population levels to be maintained independently of aphid populations (Hengeveld, 1980; Sunderland *et al.*, 1987; Good & Giller, 1991b). Generalist natural enemies feeding on a diverse range of alternative prey show greater fecundity than those receiving a single prey species diet (Toft, 1995; Jorgensen & Toft, 1997; Toft & Wise, 1999). As a consequence, a diverse arthropod fauna also contributes to the maintenance of effective biological control of cereal pests. By maintaining aphid populations below economically damaging levels, natural enemies minimise the necessity for aphicides and broad-spectrum pesticides as part of an integrated pest management programme, thereby reducing the detrimental side-effects of agro-chemical usage on farmland biodiversity (Edwards *et al.*, 1984; Holland *et al.*, 1994b).

This study aims to compare the arthropod fauna overwintering in the three dominant field boundary types of lowland farmland: post and wire fencelines, hedgerows and degraded boundaries, within the scale of a single farm. Special reference will be made to the Coleoptera, and the coleopteran families Carabidae and Staphylinidae. These taxa are numerically important and speciose in farmland and provide a range of beneficial agronomic services. Many species of Carabidae and Staphylinidae overwintering in field boundaries are polyphagous predators known to restrict aphid population growth (Symondson *et al.*, 2002; Sunderland, 2002).

3.1.1 Community structure and composition

When comparing similar habitats, species-rich, equitable communities are considered to indicate greater habitat quality. Within field boundaries, species richness may be determined by botanical diversity, habitat complexity and disturbance from management (Maudsley, 2000). High plant diversity will provide a wider variety and continuity of resources; structurally complex habitats provide a

greater range of microclimatic conditions and microhabitats; disturbance may reduce abundance and subsequent occurrence of species. High equitability within a community suggests low interspecific competition and high biological activity (e.g. productivity) (Legendre & Legendre, 1998). Studies examining different field boundary types have revealed no clear patterns in general invertebrate diversity (Thomas *et al.*, 1994; Pfiffner & Luka, 2000), whilst many Carabidae and Staphylinidae show species–specific variation in habitat preference. In terms of equitability, several studies have demonstrated the dominance of polyphagous predatory carabids and staphylinids overwintering in grassy field boundary habitats (Sotherton, 1985; Thomas *et al.*, 1992a; Dennis *et al.*, 1994). In these previous studies, absence of a formal classification of field boundaries confounded the assessment of the arthropod community overwintering in different field boundary types.

Community structure and composition may be examined at any taxonomic level. The use of higher taxon richness (Order and Family) provides a broad-scale measure of invertebrate diversity across a wide range of life traits and may be a useful surrogate for speeding biodiversity assessments (Williams & Gaston, 1994). The use of lower taxonomic resolution (genus and species) enables a more precise interpretation of their biological and ecological characteristics.

3.1.2 Functional composition of Carabidae and Staphylinidae

Uncropped habitat in farmland can be managed to enhance the potential of polyphagous predator populations within integrated pest management systems (Holland *et al.*, 1994b; Lee & Landis, 2002). Grassy field margins, particularly those sown with *Dactylis glomerata*, and field boundaries raised above the level of the field, have been demonstrated to enhance densities of overwintering polyphagous predatory carabids and staphylinids (Sotherton, 1984; Thomas *et al.*, 1992a, b; Dennis *et al.*, 1994). Additionally, reduced hedgerow management has been shown to result in a proportional increase in predatory arthropods (Van Emden, 1963; Sotherton, 1981). However, the relative overwintering densities of polyphagous predators supported by the field boundary types that predominate in lowland farmland remains poorly understood.

There are many factors that determine the effectiveness of a polyphagous predator, including the timing of activity within the pest population growth cycle, field penetration from boundary overwintering sites, the ability to aggregate at patches of high pest density, feeding rate, prey preference and field density (Wratten *et al.*, 1984; Sunderland *et al.*, 1997). However, their presence is clearly a pre-requisite for any predatory activity, followed by abundance. It should be noted that resources provided by different field boundaries may also influence migration rates into the crop by aphidophagous populations. This study assesses the potential of different field boundary types to support overwintering populations of polyphagous predators by comparing the density of aphidophagous carabid and staphylinid species captured; the efficacy of each species captured is beyond the scope of this thesis.

The functional composition of a community can provide an ecological understanding of the processes occurring in a habitat type (Tilman *et al.*, 1997; Southwood & Henderson, 2000). Two functional groupings identified in the Carabidae of relevance to this study are related to habitat preference and dispersal power. The habitat preference of carabid species may be categorised as open, closed or ubiquitous and their dispersal power defined as high, medium or low (Ribera *et al.*, 1999; Fournier & Loreau, 2001). Although some associations have been recognised between the two functional classifications (closed-habitat species are more likely to be poor dispersers whilst open-habitat and ubiquitous species tend to have medium to high dispersal power) there are many exceptions. In addition, each functional classification indicates different ecological processes. Therefore a separate analysis for each is instructive.

The relative composition of carabid assemblages in terms of habitat preference will provide an indication of the ability of woody boundaries to act as a refuge for woodland species. Hedgerows have long been recognised as supporting a carabid fauna similar to that found in woodland or woodland edge (Pollard, 1968a; Thiele, 1977). Closed habitat species vary in their ability to colonise woody boundaries, and most require a continuous tree or shrub layer within hedgerow networks for woodland species to disperse from connected forest remnants (Burel, 1989; Charrier *et al.*, 1997; Petit & Burel, 1998). Fournier & Loreau (2001) found that recently planted hedgerows were dominated by open-field carabids with very few closed-habitat

species present. However, with increasing age and stability of a hedgerow, more closed-habitat species may colonise (Den Boer, 1987; Terrell-Nield, 1990). Within arable landscapes, fragmentation of woodland and hedgerows may result in the loss of species associated with closed habitat as populations become locally extinct and cannot be refounded due to habitat isolation (den Boer, 1981, 1990; Ricklefs, 1987). Consequently, habitat suitability alone may not be sufficient to support species of woodland origin in farmland (Fournier & Loreau, 2001).

Community composition, in terms of dispersal power, may be influenced by several factors including age, degree of openness, stability and disturbance of a habitat (Den Boer, 1977, 1987; Ranta & As, 1982; Roff, 1994; Gutierrez & Menendez, 1997). In ephemeral and highly disturbed farmed landscapes, species with high dispersal power are more likely to colonise and persist (Den Boer, 1981, 1990; Sherratt & Jepson, 1993). In the short-term, high dispersal ability enables an individual to respond rapidly to changes in the environment, for example toward prey patches or away from unfavourable conditions. In the longer term, fragmentation of suitable habitat and frequent disturbance increases the likelihood of small isolated populations becoming extinct through stochastic or demographic events. Therefore, the persistence of a species depends on recolonisation of empty patches by dispersing individuals (Den Boer, 1981, 1990). Species with low dispersal power may persist in undisturbed, woody boundary networks, especially where they are connected to woodlots that act as sources of colonising individuals (Petit & Burel, 1998). In terms of age, openness and stability the three field boundary types may be ranked in increasing order post and wire < degraded < hedgerow, with hedgerows representing the most stable and closed habitats over the longest temporal scale compared to degraded boundaries. However, in terms of habitat disturbance, degraded boundaries receive the least direct management followed by hedgerows and post and wire boundaries. In addition, post and wire habitats are more exposed to farming operations in adjacent fields. Therefore, degraded boundaries are more likely to maintain populations of species with a low dispersal power, whilst post and wire habitats will be dominated by species with high dispersal ability. However, in highly fragmented arable landscapes, species with poor dispersal power may be rare in all habitats regardless of disturbance levels (Fournier & Loreau, 2001).

3.1.3 Field boundary factors influencing arthropod communities

An understanding of the determinants of arthropod biodiversity in field boundaries could be used to develop ecologically based agri-environment policy regarding field boundary management. This can subsequently be used as a tool to enhance farmland arthropod biodiversity (Lee & Landis, 2002). Habitat structure (including vegetation and additional features), botanical composition and features that affect microclimate and shelter are likely to be of prime importance in influencing overwintering communities (see sections 1.2 and 1.3).

Canonical Correspondence Analysis (CCA) (ter Braak, 1995) provides a measure of the amount of variance in species composition that may be explained by environmental variables (Legendre & Legendre, 1998). It is used in this study to examine the relationship between the arthropod assemblages at each taxonomic level, and the botanical and structural characteristics of the field boundaries. Arthropod species are likely to respond to a set of related characteristics rather than a single variable. For example, a species of woodland origin may be associated with a tall, wide and continuous woody canopy and a high hedge bank. In addition, arthropods may not be responding directly to variables used to describe field boundary characteristics but to some underlying variable. Hence, the above set of hedgerow characteristics may provide damp and shady conditions similar to a woodland edge environment. Botanical and structural characteristics of the eighteen study field boundaries were used to generate four latent variables using factor analysis (see Chapter 2). Factor 1 (F1) relates to optimal hedgerow canopy structure; Factor 2 (F2) to the presence of young trees, an indication of low management and the initial stages of degradation of the canopy structure; Factor 3 (F3) describes herbaceous margins; and Factor 4 (F4) the presence of mature trees and advanced deterioration of a hedgerow. These four factors were used as environmental variables to examine differences in assemblages of each taxonomic group between field boundaries in a partial canonical correspondence analysis (partial CCA). To eliminate potential differences in boundary composition relating to landscape or network characteristics, the variables orientation, altitude, connectivity and field boundary length were used as covariables. CCA is generally regarded as an ordination method for unimodal data though it can be used with linear data and is preferable when analysing compositional data with many zero values (ter Braak & Smilauer, 2002).

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3.1.4 Field boundary classification based on Carabidae and Staphylinidae

Arthropod assemblages are considered useful indicators of habitat type due to their wide spectrum of feeding habits and other life traits, range of generalists and specialists and short generation times. Arthropods are considered to be more sensitive to variation in habitat, landscape and farming systems than plants and vertebrates (Burel et al., 1998). Community composition of Carabidae and Staphylinidae has frequently been used to classify habitat types and to indicate changes in habitats. For example, carabid beetle assemblages have been shown to respond to changes in habitat structure (Fournier & Loreau, 1999), landscape structure (Den Boer, 1987; Burel & Baudry, 1995; de Vries, 1996; Burel et al., 1998; Tischendorf et al., 1998), and agricultural practices (Carcamo et al., 1995; Holland et al., 2002). Carabid composition has been successfully used to classify grassland and cereal crop types using classification (TWINSPAN) and ordination (DCA) techniques (Luff et al., 1992; Luff, 1996). The scale at which assemblages are examined may be important: carabid composition differed measurably between habitats within a landscape but did not provide a suitable indication of land-type diversity in Vermont, USA (Rykken et al., 1997). For Staphylinidae, clear differences in composition have been observed between grass and cereal fields (Good & Giller, 1991a), open and wooded pasture (Hunter et al., 1991) and raspberry plantation and adjacent semi-natural sites (Levesque & Levesque, 1995). Staphylinid species also differed in their overwintering densities between field and field boundary habitat (Andersen, 1997). In this current study, TWINSPAN was used to classify the eighteen field boundaries according to their combined carabid and staphylinid composition.

3.1.5 Farm-scale representation of Carabidae and Staphylinidae

Within agroecology, most studies are conducted at the plot, field or landscape scale (e.g. McLaughlin & Minneau, 1995; Burel et al., 1998; Holland & Fahrig, 2000). However, at an intermediate level, the farm-scale provides a practical unit for investigation into arthropod representation. Firstly, the farm represents the scale at which many ecological processes such as species movement and population dynamics are thought to occur and is more likely to provide a single arthropod species pool from which the composition of a boundary habitat will be drawn. Therefore, arthropod composition is more likely to reflect differences attributable to field

boundary habitat. Evidence of distinctive arthropod communities from different field boundary types has implications for the representation of those arthropods at the farm-scale through the addition, removal or alteration of those habitats. Secondly, the farm is the unit at which agri-environmental policies are implemented and management decisions are made and has been recognised as the key scale for the conservation of plants and arthropods (Weibull *et al.*, 2003). Current and future agri-environment schemes aim to produce whole-farm plans for the maintenance of field boundaries (Curry, 2002; DEFRA, 2003a). However, decisions about which field boundaries to maintain, restore, remove or create can be arbitrary. Therefore, it is relevant to understand the relative contributions that different field boundaries make to the arthropod community at the farm-scale.

Emerging methods of systematic reserve selection for biodiversity conservation were used to provide a novel examination of arthropod representation at the farm-scale, with implications for the farm-scale management of field boundaries. Computer programs based on iterative algorithms may be used to prioritise field boundaries according to their complimentarity in contributing species not found at other sites. As a result, the minimum number of field boundaries required for complete species representation (near-minimum-area algorithm) may be established (Pressey *et al.*, 1993; Williams *et al.*, 1997). The process begins by selecting areas richest in the rarest taxa, where these are equivalent, areas richest in the next rarest taxa are selected, and so on, until the representation goal is achieved. In this case the goal is at least one representation of all species or genera. Further selection methods include 'hotspot-areas' and a 'random' selection process. Hotspot-areas selects those areas with the highest species richness. A random selection process selects a specified number of areas at random that are scored for richness, the mean expected scores for sets of areas chosen is then calculated (± 2 s.d.) and the boundaries reordered by complementary taxon richness. For this study, the manual selection method was used to illustrate the accumulation of species within each field boundary type, which was reordered by complementary taxon richness. Using these analyses, the importance of each landscape element in achieving full representation of an assemblage can be identified. Such knowledge will enable the informed development of field boundary management plans at a farm-scale aimed at enhancing arthropod biodiversity and sustainable farming.

3.1.6 Aims

i) Describe the arthropod composition and community structure associated with hedgerows, degraded hedgerows and post and wire fencelines.

ii) Compare the functional composition of different field boundary types in terms of carabid and staphylinid polyphagous predator densities and the habitat preference and dispersal ability of carabid species.

iii) Identify relationships between arthropod composition and the structural and botanical composition of the field boundary types.

iv) Classify field boundaries according to their carabid and staphylinid assemblages.

v) Identify the contribution of different field boundaries to arthropod representation at a farm-scale.

3.2   METHODS

3.2.1 Field survey

Eighteen field boundaries on the Seale-Hayne farm were surveyed to determine post-overwintering arthropod assemblages. The field boundaries correspond to those examined in the previous chapter and are classified as hedgerows, degraded hedgerows and post and wire fencelines.

To sample arthropods emerging from overwintering, representative portions of each boundary were enclosed in custom-made tents. Each tent was positioned centrally along the field boundary length and enclosed a 1m length and the entire width and height of boundary vegetation. Tents were constructed from 85% agricultural shade material (Tildenet, Bristol) and supported vertically using bamboo canes and guy ropes. At the base of the tents, the shade material was buried to a depth of 0.2 m to minimise arthropod emigration or immigration. At post and wire boundaries it was not possible to isolate sections of fence within a tent. Therefore, tents were positioned alongside the fence enclosing a representative portion of the associated non-crop vegetation.

Within each enclosure, four pitfall traps were positioned close to the four corners of the tent. Pitfall traps followed a standard design (Southwood & Henderson, 2000). Sleeves constructed from lengths of drainage pipe (6.8 cm diameter and 10 cm

length) were set in the soil with the top of the pipe just below the soil surface and no gaps between the outside of the pipe and the soil. White plastic cups (#8, A.W. Gregory & Co. Ltd., London) were positioned inside the sleeves with the rim of the cup resting on the upper edge of the sleeve such that the cup was flush with the soil. Raincovers were constructed from 10cm diameter lids (#11, A.W. Gregory & Co. Ltd., London) attached to 12 cm length dowelling using metal tacks, thereby enabling the lid to be rotated away from the pitfall when checking traps. Raincovers were supported approximately 8 cm above the pitfall cup by pushing the dowelling into the soil close to the pitfall sleeve. Pitfall cups were one-third filled with a trapping solution (97.5% water: 2.5% detergent). Access into the enclosures to check and reset pitfall traps was via a Velcro opening sewn into one side seam of the tents.

All emergence tents were in position by the 25th February 1999 and pitfall trapping was continuous from the 1st March 1999 to the 9th May 1999. Pitfalls were reset every four days during March and then on a weekly basis. Collected samples were transferred to 70% alcohol preservation fluid (7.0 industrial methylated spirits: 2.5 water: 0.5 glycerol) while awaiting subsequent identification.

Arthropods collected for this study were sorted into four groups based on differing levels of taxonomic resolution. Individuals were identified to a practicable taxonomic level since estimates of richness do not require groups to be of equivalent taxonomic rank (Williams & Gaston, 1994):
(i) Higher arthropod taxa – all specimens were identified to the taxonomic level of class, order, sub-order or super-family where appropriate.
(ii) Coleopteran families – all Coleoptera were identified to family level.
(iii) Staphylinidae (Coleoptera) taxa – all staphylinids were identified to species level where possible, otherwise they were recorded to genus level.
(iv) Carabidae (Coleoptera) species – all carabids were identified to species level.

Identification of arthropods to Order and Family was based on Chinery (1993). Nomenclature for Coleopteran families was based on Joy (1976); for Staphylinidae, Joy (1976) and Tottenham (1954); for Carabidae, Lindroth (1945). Additional assistance in identification was provided by Dr. J. Holland (The Game Conservancy

Trust) and J. Ashby (Rothamsted Research). All analyses were conducted separately at each level of taxonomic resolution unless otherwise stated.

Pitfall trap captures per tent were converted to density (m^{-2}) to correct for differences in the size of emergence tents. Enclosing a known area of boundary habitat and pooling data for the entire trapping period minimised discrepancies in pitfall trap catches due to differential dispersal abilities either inherent in the invertebrate species or resulting from the permeability of the different habitat types (Baars, 1979; Luff, 1996; Dufrene & Legendre, 1997). As each emergence tent was used to isolate a representative portion of the field boundary habitat, the number of taxa captured represents the richness of that habitat relative to other habitats for overwintering arthropods. To test the efficiency of emergence tents at isolating portions of field boundary habitat the permeability of the shade material to arthropods with a range of body sizes was investigated in a preliminary study that demonstrated their effectiveness in preventing invertebrate ingress or egress.

3.2.2 Analysis
(i) Community structure and composition

Richness and density values for taxa at each taxonomic level were compared between field boundary types using one-way analysis of variance and Tukey's test on $log_{10}(n+1)$ transformed data. The density of the most abundant taxa as a proportion of the total density for a taxonomic level were also calculated to compare dominance structures between boundary types, with less abundant taxa combined as 'Other'.

Measures of richness and abundance or density form the basic units of community structure and may be combined to describe the diversity of a community. Many diversity indices are available to represent species richness and equitability as a single value. Whilst they facilitate comparisons between communities, the indices vary in the relative weighting they give to richness and evenness. As a result, communities may be ranked differently according to the diversity index employed (Magurran, 1988). To avoid such bias, diversity ordering generates the weighting produced by different indices by changing the value of a single parameter (Southwood & Henderson, 2000). In this way, the diversity profile of a community may be displayed graphically by plotting the diversity values generated against the parameter

value progressing from species rarity at the origin to species dominance along the x axis (Tóthmérész, 1995). The use of diversity ordering allows comparison between communities of the relative balance of rare, sub-dominant and dominant species. Where the diversity profiles intersect, communities are defined as non-comparable. Rényi diversity ordering (Rényi, 1961) compares favourably against other ordering families (Tóthmérész, 1995) and is defined as:

$$H_\alpha = \frac{\log \sum_{i=1}^{s} p_i^\alpha}{1-\alpha}$$

The Rényi diversity expression produces values from 0 to 4, where $\alpha = 0$ is equivalent to the number of species, $\alpha = 1$ is equivalent to the Shannon-Weiner equation weighted toward rare species, $\alpha = 2$ reflects Simpson's D index that is weighted toward the most abundant species in a sample and is less sensitive to species richness (Magurran, 1988). For the scale parameter $\alpha = 3$ and 4, the indices calculated are most sensitive to changes in abundance of the commonest species, i.e. dominance (Magurran, 1988).

Rarefaction was used to estimate the species richness (S_R) that would be expected based on the lowest abundance value observed for a field boundary type (Hassan & Rashid, 2003). Abundance values were from pooled pitfall trap data for all field boundaries belonging to a particular type. ANOVAs were performed using SPSS version 11.0, Rényi diversity ordering was performed using Species Diversity and Richness II (Pisces Conservation Ltd) and rarefaction estimates calculated with Biodiversity Pro software.

(ii) Functional composition of Carabidae

Carabidae and Staphylinidae were categorised as polyphagous predators of cereal aphids according to Sunderland *et al.* (1987), Chiverton (1988) and Mundy *et al.* (2000). Total densities of polyphagous predators found at each field boundary type were compared using a one-way ANOVA on $\log_{10}(n+1)$ transformed data. Carabid species were categorised for habitat preference according to Ribera *et al.* (1999) and for dispersal power according to Ribera *et al.* (1999) and Fournier & Loreau (2001).

Species that could not be categorised were eliminated from the data set. For each functional group category, the relative (%) density of carabids belonging to a field boundary type was determined and one way ANOVA performed (on arcsine transformed data) to test the difference in relative density of a single functional category between the three boundary types.

(iii) The influence of field boundary factors on arthropod communities

Partial-CCA requires equivalent data matrices for composition, environmental variables and co-variables. Composition data was separated for each taxonomic group (after exclusion of species occurring at a density of $<1m^{-2}$ across all field boundary sites) and an additional table produced to summarise richness and density for each taxonomic group per boundary. Environmental data was composed of factor scores for the four latent variables for each boundary. Covariables included values for the four landscape and network descriptors: orientation, altitude, connectivity and length. Preliminary analysis indicated that the four environmental variables, factors F1 to F4, were not correlated to each other, whilst covariables showed no correlation greater than 0.49. The analysis maximised inter-species distances and employed biplot scaling. The importance of the latent variables was determined using automatic forward selection and tested with Monte Carlo permutation test (999 permutations) under the full (or null) model (ter Braak & Šmilauer, 2002). Species-conditional biplots (of species and environmental variables) display only those species with a high degree of weight (>10%) within the analysis (ter Braak & Verdonschot, 1995). Arrows for environmental variables point in the direction of maximum change in magnitude of that variable. The projection of species points perpendicularly onto the arrow indicates the magnitude of the variable at which the species is most abundant. The origin represents the mean of a variable; therefore species points lying behind the origin from the direction in which an arrow is pointing are found at below average values for that variable. The arrow length is proportional to the maximum rate of change of a variable but also indicates the importance of that variable in explaining variation in species data (in the absence of other variables). Relationships between arrows indicate correlations between environmental variables. Interpretation of ordination diagrams followed ter Braak & Verdonschot (1995). Partial inter-set correlation coefficients between environmental variables and the four canonical axis, species eigenvalues and cumulative % variance described by the species-environment

relation for each axis were reported, in addition to overall species inertia, covariable inertia and canonical eigenvalues (variation explained by species-environment relation). Partial canonical correspondence analysis was conducted using CANOCO 4.5 and ordination plots produced with CanoDraw (ter Braak & Šmilauer, 2002).

(iv) Classification of field boundaries based on Carabidae and Staphylinidae

TWINSPAN (Hill, 1979) was used to classify the eighteen field boundaries using the % density (m^{-2}) of carabids and staphylinids (both assemblages combined) collected at each site. The use of rare species as indicators of a habitat type will not facilitate the identification of that habitat type in future studies and their presence can influence multivariate procedures. Therefore, species occurring at a density of $<1 m^2$ were deleted. This removed nine staphylinid and six carabid species. The percentage occurrence of each species from the total catch at each site was used for the analysis (Luff et al., 1992; Rykken et al., 1997). Standard cut levels of 0, 2, 5, 10 and 20% were used (Hill, 1979; Luff et al., 1992). TWINSPAN was performed using the Community Analysis Package (CAP) version 1.3 (Pisces Conservation Ltd).

(v) Farm-scale representation of Carabidae and Staphylinidae

The presence or absence of Carabidae and Staphylinidae (78 taxa in total) was used to assess the complementarity of field boundaries at the farm-scale. The analysis was conducted using WorldMap version 4.17.06 (Williams, 1997).

3.3   RESULTS

3.3.1 Community structure and taxonomic composition

The composition (density, m^{-2}) of higher arthropods, coleopteran families, Carabidae and Staphylinidae communities emerging from overwintering at each field boundary (grouped by field boundary type) are summarised in Tables 3.3.1 to 3.3.4 respectively. For each taxonomic level, the overall density and richness at a boundary is summarised at the bottom of each table. In total 16,048 arthropod specimens were collected from 28 orders, sub-orders or families from the classes Arachnida, Crustacea, Myriapoda and Insecta. Of these, 3,802 specimens belonged to 26 families of Coleoptera. Carabidae and Staphylinidae dominated the Coleoptera numerically with 2,202 individuals belonging to 34 Staphylinidae taxa and 857 specimens belonging to 43 Carabidae species.

(i) Higher arthropod taxa

Collembola, Coleoptera, Crustacea, Myriapoda, Arachnida and Diptera comprised more than 80% of arthropod captures at all field boundary types (Figure 3.3.1a). Relative arthropod composition between the boundary types was similar. Hedgerow and degraded boundaries supported proportionately more Collembola, whilst Coleoptera formed the largest group numerically in post and wire fences. Post and wire fences appeared to support a more even density distribution among the five principle arthropod groups. There was no difference in higher arthropod richness between the boundary types (F=0.56, df=2, 15, n.s., Figure 3.3.1b) but post and wire fencelines supported measurably greater arthropod density (excluding Coleoptera) than hedgerow or degraded boundaries (F=4.74, df=2, 15, P<0.05, Figure 3.3.1c). Rényi diversity ordering illustrated that the distribution of individuals amongst taxa was more equitable in post and wire boundaries (α=4), although the proximity of profiles between the three boundary types suggests they are essentially similar in their arthropod diversity (Figure 3.3.1d).

(ii) Coleopteran families

The numerical dominance of Staphylinidae and Carabidae relative to other coleopteran families (Figure 3.3.2a) emphasises their ecological importance in terms of biodiversity and ecosystem services and justifies their use as model taxa for this study. Staphylinidae represented about 60% of Coleoptera collected in post and wire and degraded boundaries, and c.50% in hedgerows. This numerical dominance may be partly explained by the abundance and ubiquity of Aleocharinae (see Figure 3.3.4a). Hedgerows supported proportionately more Carabidae than post and wire or degraded boundaries. Coleopteran family richness did not differ between field boundary types (F=1.75, df=2, 15, n.s., Figure 3.3.2b) but coleopteran density (excluding Carabidae and Staphylinidae) was significantly greater in post and wire fences compared to hedgerows or degraded boundaries (F=6.93, df=2, 15, P<0.01, Figure 3.3.2c). Degraded boundaries supported a marginally higher richness (α=0) but the main differences between boundaries was related to the distribution of individuals amongst coleopteran families (Figure 3.3.2d). In terms of equitability, field boundary types can be ranked hedgerow> degraded> post and wire.

(iii) Carabid species

In degraded boundaries, less abundant taxa combined together as 'other' species compose about 40% of carabids collected (Figure 3.3.3a) and proportions of the more numerous species were evenly distributed. The proportional density of 'other' carabids decreased for degraded> hedgerows> post and wire fences. The most abundant single species in degraded boundaries were *M. obscurogutattus, T. quadristriatus, B. lampros, D. atricapillus, N. brevicollis* and *P. cupreus*. In hedgerows, *B. lampros* was the numerically dominant single carabid species (representing 31.3% of total individuals) followed by *T. quadristriatus, M. obscurogutattus, D. atricapillus, N. brevicollis* and *P. cupreus*. Post and wire boundaries supported highest densities of *N. brevicollis*, equivalent proportions of *P. cupreus*, and *B. lunulatum*, followed by decreasing proportions of *B. lampros* and *B. guttula*. Neither carabid richness ($F=1.4$, $df=2$, 15, n.s., Figure 3.3.3b) nor density ($F=1.79$, $df=2$, 15, n.s., Figure 3.3.3c) differed significantly between boundary types, despite an apparently greater density of carabids at post and wire boundaries. However, the large standard error demonstrated the inherent variability in carabid density between post and wire boundaries. Degraded boundaries supported a far more equitable carabid community than hedgerows, whilst post and wire fencelines showed lowest carabid diversity overall with lowest richness ($\alpha=0$) and greatest dominance ($\alpha=4$) in the distribution of individuals among species (Figure 3.3.3d). Boundaries differed considerably in the diversity of the carabid community they supported and were ranked degraded> hedgerow> post and wire, although the interception ($\alpha=0.5$) by hedgerow and degraded profiles means that they were essentially non-comparable.

(iv) Staphylinid taxa

The numerically dominant Aleocharinae showed highest numbers in hedgerows> degraded> post and wire boundaries (Figure 3.3.4a). After Aleocharinae, the most abundant staphylinids in post and wire habitats were *Stenus* spp., *T. signatus*, 'other' and *Anotylus* spp., in hedgerows *Anotylus* spp., 'other', *T. signatus* and *P. litoralis*, whilst in degraded boundaries the subsequent most numerous taxa were *Anotylus* spp. and *T. signatus*. Field boundary types did not differ in staphylinid richness ($F=1.27$, $df=2$, 15, n.s., Figure 3.3.4b) but post and wire habitats supported a significantly greater density than hedgerows or degraded boundaries ($F=13.92$, $df=2$, 15, $P<0.001$, Figure 3.3.4c). Generally, Rényi diversity profiles for the three boundary

types were similar (Figure 3.3.4d). The only observable difference was the marginally greater number of rare Staphylinidae in degraded and hedgerow boundaries ($\alpha=0$) and fractionally greater equitability in the staphylinid assemblage of post and wire boundaries ($\alpha=4$).

Rarefaction estimates showed post and wire boundaries to support consistently lower taxon richness compared to observed values at each taxonomic level (Table 3.3.5). However, the estimates of richness were similar to observed numbers. Therefore despite differences in density between post and wire and woody boundaries, the observed richness values provided an accurate description of the community at each taxonomic level.

Field boundary type		Post and Wire						Hedgerow						Degraded					
Field boundary number		1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Arachnida	Acari	46.36	73.00	15.00	63.16	28.00	24.00	6.48	4.31	14.18	8.48	15.29	27.39	17.00	1.71	4.86	51.88	23.68	38.58
Arachnida	Araneae - Linyphiidae	41.82	87.00	30.00	68.42	55.00	12.00	2.16	3.16	18.39	12.73	18.18	5.65	25.75	4.29	5.71	24.38	14.74	7.10
Arachnida	Araneae - Lycosidae	11.82	13.00	2.50	141.05	18.00	10.00	0.93	2.01	7.66	4.24	12.40	4.78	3.75	2.29	4.00	2.50	2.63	5.86
Arachnida	Araneae other	9.09	7.00	1.25		1.00	4.00		3.74	1.92	0.61	2.48	0.87	1.25	0.57	1.43	6.25	1.58	1.85
Arachnida	Opiliones	1.82	1.00	1.25	9.47	1.00	2.00	0.93	0.29	1.53		1.24	0.87	3.00		0.57	2.50	4.21	2.78
Arachnida	Psuedoscorpionida							0.31	0.29	0.77								1.25	0.53
Crustacea	Isopoda	207.27	23.00	60.00	717.89	27.00	50.00	13.27	16.67	25.29	75.15	49.59	42.61	2.75	36.57	31.71	28.75	124.21	70.06
Myriapoda	Chilopoda	8.18	8.00	2.50	92.63	23.00	53.00	2.78	8.05	11.49	33.94	15.70	23.91	0.75	3.14	2.00	15.63	18.42	165.43
Myriapoda	Didlopoda	7.27	1.00		2.11	1.00		12.35	6.61	4.98	7.27	19.01	2.17		0.86	0.57	55.00	11.05	3.09
Insecta	Coleoptera	140.03	251.00	157.48	623.57	239.00	188.00	28.72	38.51	58.59	126.69	47.93	81.25	102.50	46.32	38.91	127.58	140.54	55.58
Insecta	Collembola	130.00	143.00	167.50	307.37	56.00	276.00	61.42	61.78	127.59	123.64	129.34	173.04	68.25	34.29	33.14	216.25	177.37	241.36
Insecta	Dermaptera			1.25	1.05			0.93	1.15		2.42		1.30	1.75	0.57		0.63		3.70
Insecta	Diptera	50.91	17.00	16.25	49.47	109.00	64.00	8.33	9.48	17.62	26.67	24.38	23.91	30.00	17.43	16.00	30.63	11.05	21.91
Insecta	Diptera larvae	2.73	4.00	6.25		32.00	3.00	0.62	0.86	0.38	0.61	0.41	0.43	0.75	0.29	0.29	17.50	1.05	
Insecta	Heteroptera	0.91	1.00	1.25	5.26	1.00	4.00		0.29	0.38		1.24			0.29	0.86	3.75		0.62
Insecta	Homoptera - Aphididae	8.18	6.00				28.00			5.75	0.61			0.25	0.57	0.57	2.50		3.09
Insecta	Homoptera other	57.27	8.00	1.25	21.05	27.00	9.00			2.68	1.21	0.83	3.48	1.00	0.86	0.29	3.75		1.23
Insecta	Hymenoptera - Apoidea				1.05								0.43	0.25	0.29	0.29			
Insecta	Hymenoptera - Formicidae		155.00	7.50	56.84	15.00	2.00	0.31	2.30	2.68		0.83	12.17	24.50	3.14	4.86	0.63	0.53	3.70
Insecta	Hymenoptera - Parasitica	11.82	2.00	6.25	1.05	12.00	3.00	0.31	0.57	2.68		0.83	2.17	3.25	0.86	0.29	3.13	1.58	5.25
Insecta	Lepidoptera - Heterocera									0.38	1.21		0.87						
Insecta	Lepidoptera - Rhopalocera									1.15									
Insecta	Lepidoptera larvae	9.09	1.00	2.50	6.32		2.00		0.86	2.68	1.21		0.43				3.13	2.11	0.62
Insecta	Neuroptera									0.38									0.31
Insecta	Orthoptera					1.00										0.29			
Insecta	Psocoptera	0.91									3.64		2.17		0.29				1.23
Insecta	Thysanoptera														0.57				
Insecta	Thysanura		1.00																
Arthropod density m^{-2}		745.48	802.00	479.98	2167.76	646.00	734.00	139.85	160.93	309.15	430.33	339.68	409.90	286.75	155.20	146.64	597.62	535.28	633.35
Richness		18	19	17	17	17	17	15	18	22	17	16	20	17	20	19	20	16	20

Table 3.3.1 Density (m^{-2}) of arthropod taxa emerging from overwintering at each field boundary.

Field boundary type	Post and Wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Anistomidae	0.91	1.00	8.75	1.05		3.00	2.47	0.57	3.83	0.61	1.24	1.74	1.25		1.14	3.75	1.05	2.78
Anobiidae					1.00		0.31											
Byrrhidae		1.00		5.00			0.31			0.61			0.25					
Carabidae	13.65	11.00	40.00	283.13	18.00	17.00	8.96	20.12	18.75	46.07	14.87	10.85	16.50	9.17	6.59	13.17	23.17	7.43
Chovelidae						1.00									0.86			0.62
Chrysomelidae	6.36		5.00	5.26	3.00	2.00		0.86	5.75	12.73	0.83	13.48	1.25	2.86	1.43	5.63	13.68	1.85
Coccinelidae	27.27	1.00		15.79	4.00	5.00			0.77	1.21			0.25	0.29		1.25	1.58	0.62
Corylophidae					1.00													
Cryptophagidae				1.05														0.62
Cucujidae		1.00												0.29				
Curculionidae	1.82	3.00	6.25	15.79	37.00	39.00	0.62	1.72		2.42	0.83	2.17	0.25	2.57		11.88	4.74	8.02
Elateridae				1.05	4.00	1.00												
Helophoridae								0.29										
Histeridae					1.00								0.25		0.29			
Hydrophilidae	0.91			2.11	2.00				0.77				1.50	0.29	0.57	0.63	1.05	
Lathrididae		2.00			1.00	1.00				0.61	1.65	0.43			0.57		0.63	0.62
Leiodidae										1.15			0.75					0.31
Phalarcridae										0.38								
Pselaphidae																	0.53	
Ptilidae	0.91			2.11	2.00		0.31	0.29	3.45	0.61	0.41	2.61		0.57		0.63	1.05	3.09
Scaphididae												0.43						
Scarabaeidae		5.00	5.00	8.42	5.00	1.00	0.31		1.15		0.83	3.04	21.00	1.14	4.00	0.63	0.53	0.93
Silphidae			1.25										0.25					
Sphaeridiidae	1.82	1.00			1.00			0.57					0.75					
Staphylinidae	86.38	225	91.23	287.81	154	118	15.44	14.08	22.6	61.83	27.27	46.49	58.25	28.58	24.03	89.41	93.16	28.71
Density m^{-2}	140.03	251.00	157.48	623.57	239.00	188.00	28.72	38.51	58.59	126.69	47.93	81.25	102.50	46.32	38.91	127.58	140.54	55.58
Family richness	9	10	7	11	15	10	8	8	10	9	8	9	13	10	8	10	10	12

Table 3.3.2 Density (m^{-2}) of Coleoptera families emerging from overwintering at each field boundary.

Field boundary type	Post and Wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Acupalpus meridianus				2.11														
Agonum dorsale				1.05				1.15							0.29			
Agonum muelleri				1.05														
Agonum sexpunctatum				1.05														
Agonum vidum/moestrum											0.41							
Amara aenea	1.82		2.50					0.29					4.75	0.29				
Amara communis			3.75	4.21	2.00					1.21		0.43	0.25					
Amara familiaris				2.11	4.00								1.25	0.29				
Amara montivaga										1.21								
Amara ovata				1.05										0.29				
Amara plebeja		2.00				1.00			0.38	2.42	0.41		1.75					
Amara similata	1.82			1.05	1.00					0.61			0.50					
Asphidion flavipes								0.29		0.61	0.83							
Badister bipustulatus	3.64							0.29	0.38		0.83					1.25	0.53	
Bembidion biguttatum								0.29									0.53	
Bembidion guttula				20.00				0.57										
Bembidion harpaloides	0.91							0.29			0.41							
Bembidion lampros		7.00	1.25	38.95	1.00	9.00	3.09	4.31	6.51	19.39	3.72	0.43	0.25	1.71	1.43		3.16	0.62
Bembidion lunulatum				57.89	2.00			0.57								0.63		
Bembidion obtusum				12.63			0.31				0.41							
Calathus fuscipes												0.43	1.25					
Clivinia fossor				1.05				1.72		1.82								

Table 3.3.3 Density (m^{-2}) of Carabid (Coleoptera) species emerging after overwintering at each field boundary (continued overleaf).

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Field boundary type	Post and Wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Demetrias atricapillus			13.68	1.00	4.00		0.31		2.68		0.41			0.86		1.88	3.68	0.93
Dromius linearis						1.00		0.29	0.38				0.25	0.29	0.29	0.63		0.31
Dromius melanocephalus								0.38									0.53	
Dromius meridionalis										0.61								
Dromius quadrinotatus								0.38						0.29			1.05	
Harpalus rufipes				1.00														
Leistus ferrugineus			1.05														0.53	
Leistus fulvibarbis							0.31	0.86	0.38		1.24			0.29		0.63	4.21	
Leistus rufescens											0.41				0.29		1.05	
Loricera pilicornis			2.50					1.44	0.38				0.25	0.29		0.63	1.05	
Metabletus obscurogutattus			4.21					0.29	4.60	6.67	1.24	0.87	0.25	1.71	1.43	2.50	2.11	0.93
Nebria brevicollis	4.55	1.00	20.00	57.89	2.00		2.16	2.01	0.38	0.61	0.41	0.43	1.50	0.57	1.14	1.88		0.31
Notopillis bigutattus													0.25	0.29				0.93
Pterostichus cupreus			2.50	48.42	3.00	1.00	0.93	2.01		1.82			1.50	0.57		0.63	0.53	
Pterostichus madidus		1.00			1.00					1.21			1.00		0.29			2.47
Pterostichus melanarius				1.05									1.00					0.62
Pterostichus strennus	0.91		3.75	5.26				1.44			2.07		0.25			0.63	1.05	
Pterostichus vernalis								0.57									0.53	
Stomis pumicatis								0.29										
Trechus quadristriatus			3.75	7.37		1.00	1.85	2.30	0.77	7.88	2.07	8.26	0.25	1.14	1.43	1.88	2.63	0.31
Trechus rubens														0.29				
Carabid density m^{-2}	13.65	11.00	40.00	283.13	18.00	17.00	8.96	20.12	18.75	46.07	14.87	10.85	16.50	9.17	6.59	13.17	23.17	7.43
Species richness	6	4	8	21	10	6	7	19	13	13	14	6	17	15	8	11	15	9

Table 3.3.3 Density (m^{-2}) of Carabid (Coleoptera) species emerging after overwintering at each field boundary.

Field boundary type	Post and Wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Actobius spp.	0.91						0.31											
Aleocharinae spp.	42.73	129.00	43.73	65.26	60.00	60.00	9.88	7.47	10.34	40.00	14.46	33.48	5.75	20.86	13.43	55.00	64.74	18.21
Anotylus spp.	1.82	13.00	8.75	16.24	5.00	10.00	1.54	1.44	4.98	11.52	4.13	5.65	1.25	4.00	2.86	13.13	17.89	3.70
Anthobium unicolor															0.29			
Lathrobrium spp.					1.00			0.29										0.31
Lesteva longoelytrata								0.29		0.61								
Mycetoporus splendidus																	0.53	
Omalium rivulare																	1.58	
Omalium tricolor								0.29							0.29			
Othius punctulatus								0.57										
Paederus litoralis	1.82	1.00	8.75	27.37	2.00	2.00	0.31	0.29	1.92	0.61	3.31	0.87	0.25	0.29	1.14	2.50	1.05	
Philonthus cognatus	4.55	3.00	3.75		4.00	3.00			0.38				7.00		0.29		0.53	0.31
Philonthus cruentatus		1.00						0.29										
Philonthus decorus		4.00				1.00						0.43	1.75			0.63		
Philonthus fuscipennis													0.25					
Philonthus laminatus				1.00								0.43	23.50		0.29			
Philonthus roundicollis		1.00																
Philonthus splendens							0.31					0.43	7.50		0.29			
Philonthus varius			5.00	1.05	1.00						0.41	1.30	2.00		0.29		1.05	
Proteinus spp.														0.29				

Table 3.3.4 Density (m^{-2}) of Staphylinid (Coleoptera) species emerging from overwintering in each field boundary (continued overleaf).

Field boundary type	Post and Wire						Hedgerow						Degraded					
Field boundary number	1	5	6	13	17	18	7	8	11	12	14	15	2	3	4	9	10	16
Rugilus rufipes								0.29										
Rugilus orbiculatus		1.00	2.50	6.32	2.00					0.61			0.25					
Staphylinus olens				1.00														
Stenus spp.	10.91	3.00		78.94	54.00	5.00			0.38	1.21	1.24		3.50	0.57	1.71	2.50	0.53	0.62
Tachinus rufipennis		2.00				1.00							0.25					
Tachinus signatus	5.45	59.00	12.50	21.05	2.00	4.00	1.54		1.92	2.42	0.83	1.30	1.75	1.14	0.29	9.38	1.58	0.62
Tachyporus chrysomelinus	14.55	2.00	1.25	4.21	6.00	7.00	0.93	0.57	0.77	1.82	0.41	0.43	1.25	0.29	0.86	1.25	1.05	1.54
Tachyporus hypnorum	2.73	4.00	2.50	14.74	6.00	12.00		0.86	0.38	1.82	1.24		0.25	0.57	0.57	0.63		1.85
Tachyporus nitidulus	0.91			3.16	1.00	3.00		0.57			0.83	0.43	0.75		0.29	0.63		0.62
Tachyporus obtusus		1.00															1.05	
Xantholinus glabratus				1.05													0.63	
Xantholinus linearis			2.50	36.84	8.00	10.00	0.62	0.86	0.77	1.21	0.41	1.74	0.25	0.57	1.14	3.13	1.58	0.93
Xantholinus longiventris		1.00		11.58					0.38				0.75					
Xylodromus spp.									0.38									
Staphylinid density m^{-2}	86.38	225.00	91.23	287.81	154.00	118.00	15.44	14.08	22.60	61.83	27.27	46.49	58.25	28.58	24.03	89.41	93.16	28.71
Richness	10	15	10	13	15	12	8	13	11	10	10	11	18	9	15	11	12	10

Table 3.3.4 Density (m^{-2}) of Staphylinid (Coleoptera) species emerging from overwintering in each field boundary.

a) Percentage density (m^{-2}) of dominant taxa

Others
Heteroptera
Hymenoptera
Diptera
Arachnida
Crustacea / Myriapoda
Coleoptera
Collembola

b) Richness

c) Density (m^{-2}) (without coleoptera)

d) Renyi diversity ordering
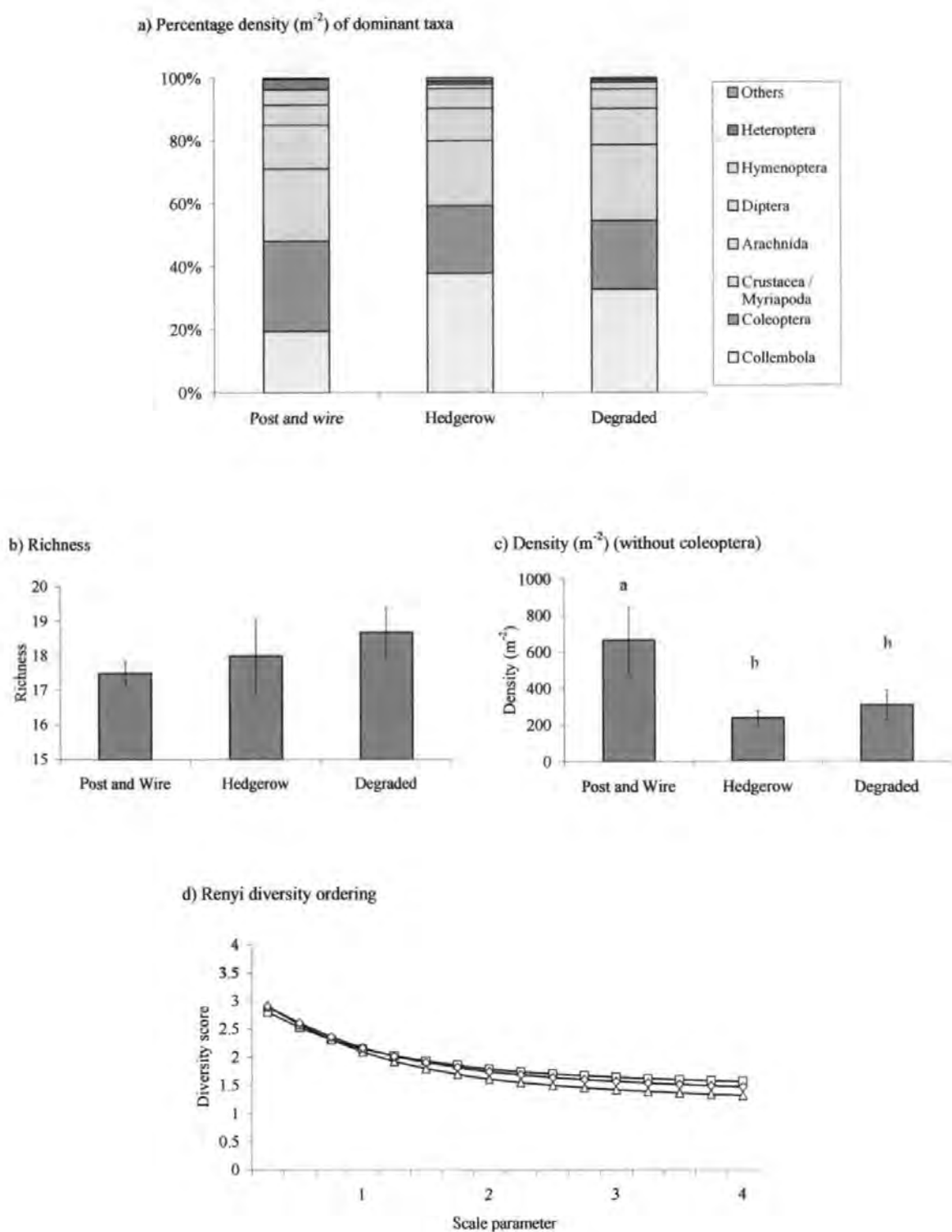
Figure 3.3.1 Higher arthropod community structure in post and wire, hedgerow and degraded field boundary types described by: a) Percentage density of dominant taxa, b) Richness (F=0.56, df=2, 15, n.s.), c) Density (F=4.74, df=2, 15, P<0.05, same letter denotes no significant difference with Tukey's test) and d) Renyi diversity ordering. Symbols represent □ = Post and wire, Δ= Hedgerow and ◊ = Degraded field boundary.

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a) Percentage density (m^{-2}) of the dominant families

Legend:
- Ptilidae
- Coccinelidae
- Anistomidae
- Others
- Scarabaeidae
- Curculionidae
- Chrysomelidae
- Carabidae
- Staphylinidae

b) Richness

c) Density (m^{-2}) (without Carabidae/Staphylinidae)

d) Renyi diversity ordering
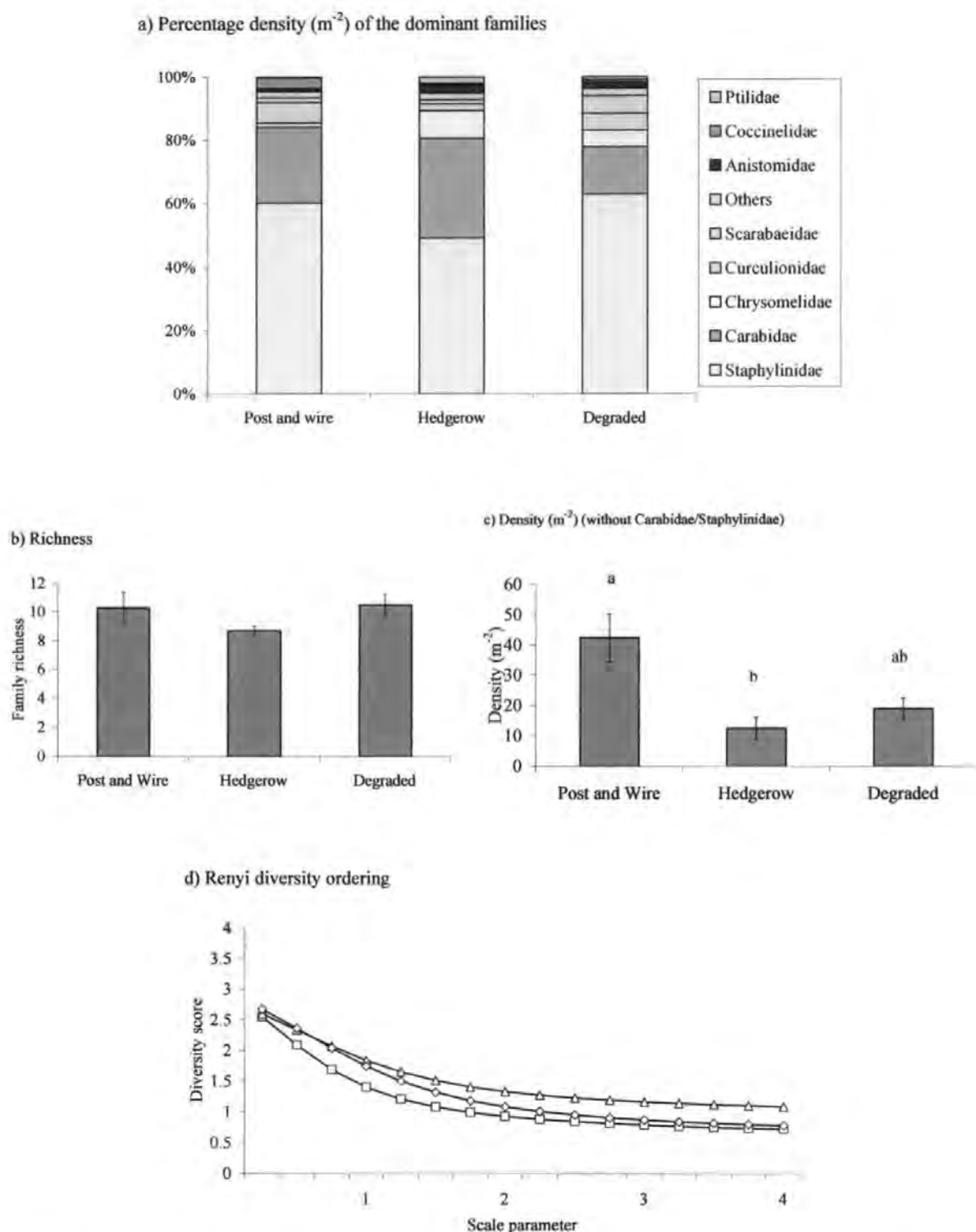
Figure 3.3.2 Coleopteran family community structure in post and wire, hedgerow and degraded field boundary types described by: a) Percentage density of dominant families, b) Richness (F=1.75, df=2, 15, n.s.), c) Density (F=6.93, df=2, 15, P<0.01, same letter denotes no significant difference with Tukey's test) and d) Renyi diversity ordering. Symbols represent □ = Post and wire, ∆= Hedgerow and ◊ = Degraded field boundary.

a) Percentage density (m^{-2}) of the dominant species

Legend:
□ B. obtusum
■ B. guttula
▣ P. strennus
□ B. lunulatum
▥ D. atricapillus
□ P. cupreus
□ M. obscuro.
□ T. quadrist.
□ N. brevicollis
▣ B. lampros
□ Others

b) Richness

c) Density (m^{-2})

d) Renyi diversity ordering
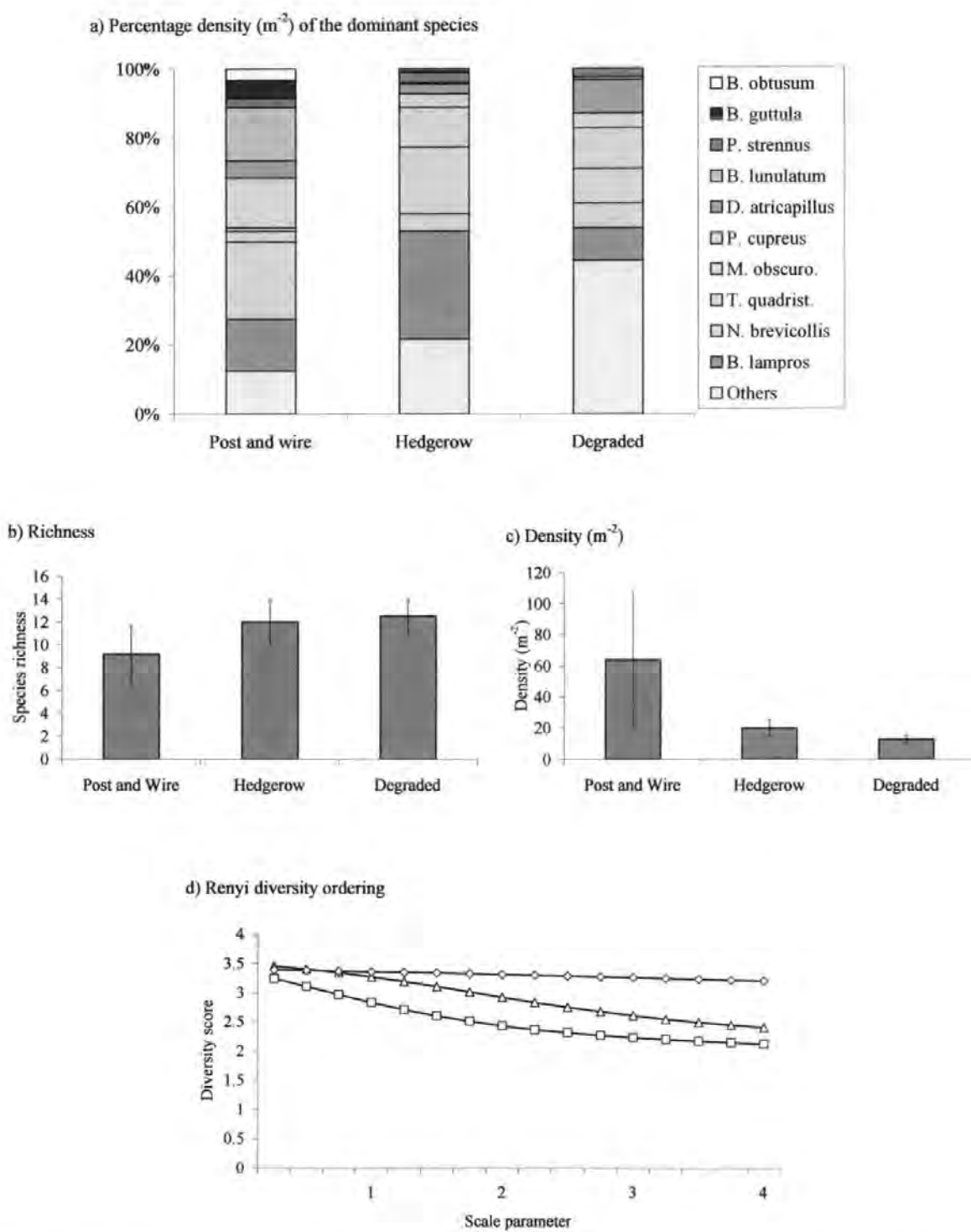
Figure 3.3.3 Carabidae community structure in post and wire, hedgerow and degraded field boundaries (n=18) described by: a) Percentage density of dominant species, b) Richness (F=1.4, df=2, 15, n.s.), c) Density (F=1.79, df=2, 15, n.s.) and d) Renyi diversity ordering. Symbols represent □ = Post and wire, Δ= Hedgerow and ◊ = Degraded field boundary.
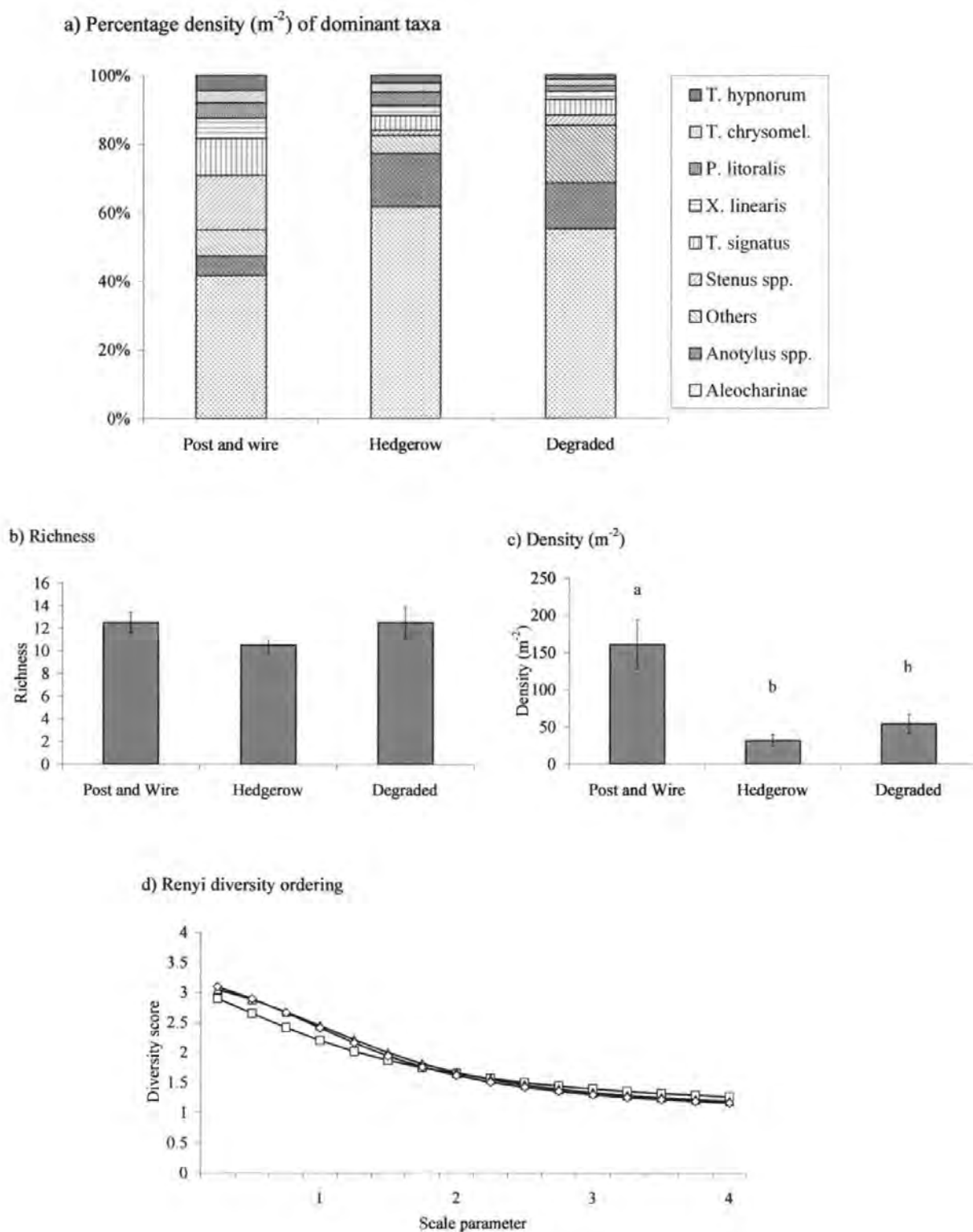
Figure 3.3.4 Staphylinid community structure in post and wire, hedgerow and degraded field boundary types described by: a) Percentage density of dominant taxa, b) Richness (F=1.27, df=2, 15, n.s.), c) Density (F=13.92, df=2, 15, P<0.001, same letter denotes no significant difference with Tukey' tests) and d) Renyi diversity ordering. Symbols represent □ = Post and wire, Δ= Hedgerow and ◊ = Degraded field boundary.

		Post and wire	Hedgerow	Degraded
Higher arthropod taxa	N	5446	4295	6228
	S	23	25	25
	S_R	22.1	25	24.2
Coleopteran families	N	1551	892	1359
	S	20	17	19
	S_R	16.9	17	17.3
Carabidae species	N	362	285	210
	S	29	33	30
	S_R	24.1	29.7	30
Staphylinidae taxa	N	939	433	830
	S	23	24	26
	S_R	18.5	24	21.3

Table 3.3.5 Rarefaction estimates of richness (S_R) for each taxonomic group, with observed abundance (N) and richness (S) values, for each field boundary type.

3.3.2 Functional composition of Carabidae and Staphylinidae

Post and wire habitats supported higher densities of polyphagous predators compared to hedgerows or degraded boundaries (Figure 3.3.5). However, standard errors were large indicating high variability within this boundary category. One post and wire boundary (FB13) supported densities of Carabidae an order of magnitude higher than all other field boundaries and also relatively high densities of Staphylinidae (Tables 3.3.3 and 3.3.4). Even with the removal of this boundary from the analysis, the mean density of polyphagous predators supported by post and wire boundaries (54.64±11.49) was still significantly greater than densities supported by hedgerows and degraded boundaries (F=7.56, df=2, 14, P<0.01).

There were no measurable differences between field boundary types in the proportion of carabids belonging to a habitat preference category. At all three boundary types, open habitat carabids composed about 50% of individuals collected, ubiquitous species formed c. 30% to 35% and closed habitat species between 10% and 15% of the carabid composition (Figure 3.3.6a, b and c respectively).

Carabids with high dispersal power formed the majority (between 45% to 60%) of specimens collected at all field boundary types (Figure 3.3.7a). The proportion of carabids categorised as high and medium powered dispersers (Figure 3.3.7b) did not differ between boundary types. However, the proportional density of carabids categorised as low powered dispersers was significantly greater in degraded boundaries and hedgerows (Figure 3.3.7c). Carabid species with low dispersal powers formed about 30% of the carabid density in degraded boundaries, 15% in hedgerows and <5% in post and wire habitats.
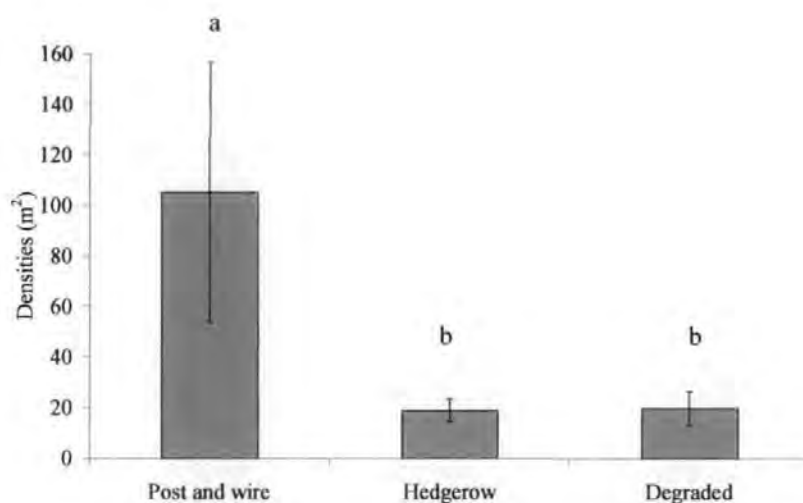
Figure 3.3.5 Carabidae and Staphylinidae polyphagous predator densities (m^{-2}) emerging from overwintering in each field boundary type. Post and wire boundaries supported significantly higher densities of polyphagous predators (F=8.443, df=2,15, P<0.01). Same letter denotes no significant difference between boundary type (Tukey's test).

a) Open habitat
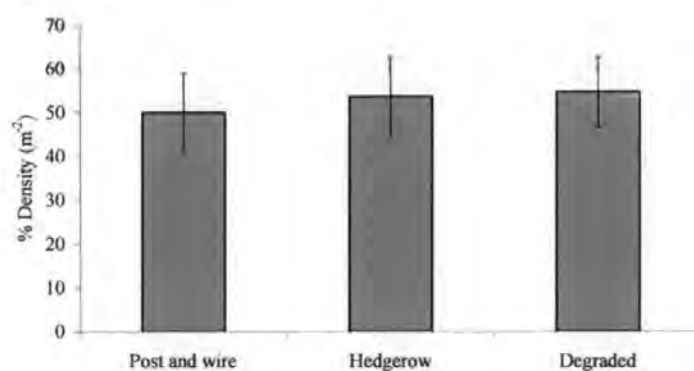
b) Closed habitat
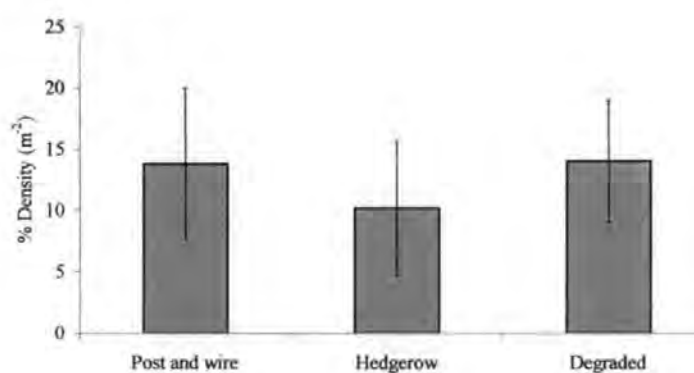
c) Ubiquitous habitat
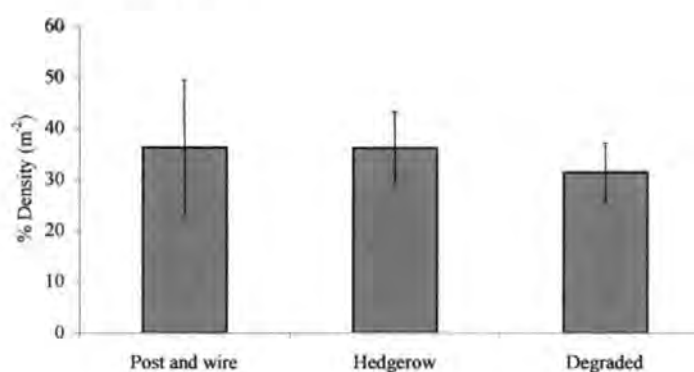
Figure 3.3.6 Habitat preference: Relative (%) density (m^{-2}, ± 1 s.e.) of carabids within each field boundary type that are classified as having a preference for a) Open habitat, b) Closed habitat or c) Ubiquitous habitat.. Using one-way ANOVA (performed on arcsin-square root transformed proportional data) no differences in relative density between field boundary types were found for open habitat (F=0.1, df=2,15, n.s.), closed habitat (F=0.33, df=2,15, n.s) or ubiquitous habitat (F=0.03, df=2,15, n.s.).

a) High dispersal power
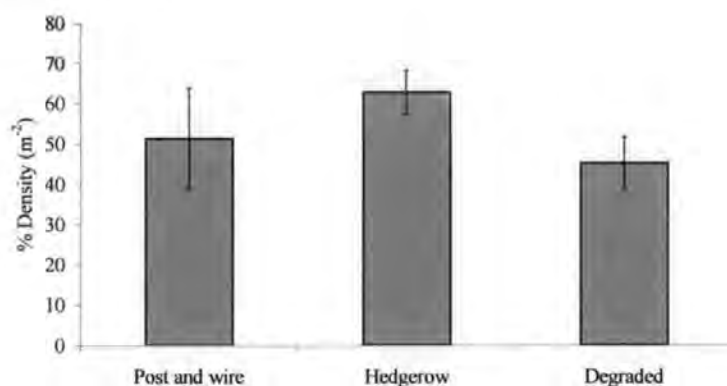
b) Medium dispersal power
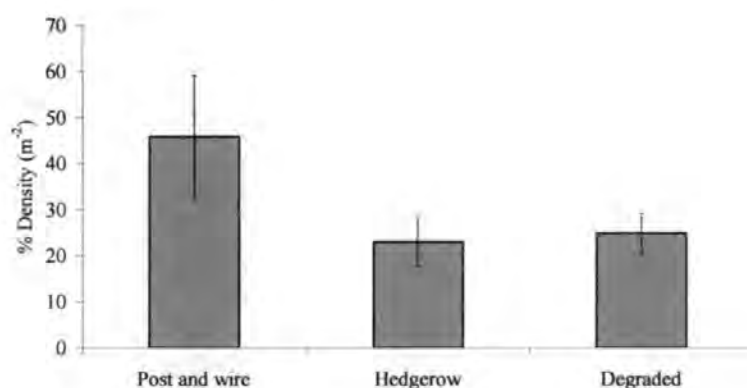
c) Low dispersal power
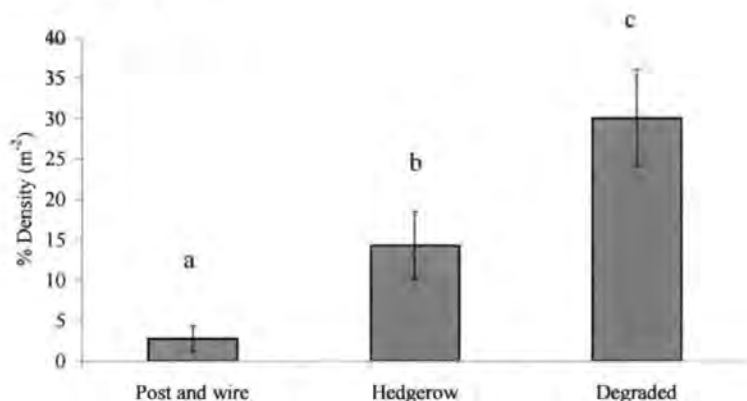
Figure 3.3.7 Dispersal power: Relative (%) density (m^{-2}, ± 1 s.e.) of carabids within each field boundary type that are classified as having a) High dispersal power, b) Medium dispersal power, or c) Low dispersal power. Using one-way ANOVA (performed on arcsin-square root transformed proportional data) a significant difference in relative density between field boundary types was found for low dispersal power ($F=13.3$, $df=2,15$, $P<0.001$). Field boundary types supporting densities that do not differ are indicated by the same letter (Tukey's test). No differences were found for high dispersal power ($F=0.93$, $df=2,15$, n.s.) or medium dispersal power ($F=1.77$, $df=2,15$, n.s.).

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3.3.3 Field boundary factors influencing arthropod communities

Summarised richness and density for each taxonomic group differed little between boundaries as indicated by the low total species inertia (Table 3.3.6). Landscape and network variables (covariable inertia) explain a greater proportion of the variance in composition than habitat factors (canonical eigenvalues) for higher arthropod taxa and coleopteran families. In contrast, carabid and staphylinid composition were more influenced by habitat factors although landscape and network variables contributed considerably towards determining field boundary arthropod composition.

(i) Community structure

Woody canopy structure (F1) was highly significant in explaining differences in overall richness and density of each taxonomic group (Figure 3.3.8c). Richness of all four taxonomic groups was strongly associated with a dense woody canopy (F1) such as that found in hedgerows (Figure 3.3.8a). The density of higher arthropods, Coleoptera and Staphylinidae showed little variation amongst field boundaries. In contrast, carabid density was strongly associated with the presence of mature trees, though this factor shows only a weak correlation (0.3) with axis 2 (Figure 3.3.8b).

(ii) Higher arthropod composition

The first two canonical axes showed no clear environmental gradients since both showed strong correlations (>0.48) to the environmental variables F1, F2 and F4 (Table 3.3.7; Figure 3.3.9b). The presence of mature trees (F4) and woody canopy structure (F1) explained a significant proportion of the variation in higher arthropod composition (Figure 3.3.9c). Most higher arthropod taxa were fairly ubiquitous in their distribution across field boundaries, though several were positioned behind the environmental variables in ordination space indicating the importance of other unmeasured factors in determining higher arthropod composition of field boundaries (Figure 3.3.9a).

(iii) Coleopteran family composition

None of the habitat variables were significant in explaining the coleopteran family composition (Figure 3.3.10c), which varied little between field boundaries as indicated by the small eigenvalues (Figure 3.3.10b). Of twenty-one families included

in the analysis only ten families fit the explanatory model by >10% and so were displayed in the biplot (Figure 3.3.10a).

The fungal feeding (Unwin, 1988) Leodidae, and (to a lesser extent) Ptilidae which are associated with bark, decaying wood and other plant matter and the exclusively phytophagous Chrysomelidae showed a preference for tall woody structures. Hence, their presence could be attributed to the presence of decomposing leaf litter and the wide variety and abundance of plant material respectively. Coccinellidae were associated with wide and rich herbaceous margins.

The dung, carrion, fungi or decaying plant matter feeding families (Joy, 1976; Unwin, 1988) Scarabaeidae, Cryptophagidae and Silphidae were associated with sites characterised by high soil moisture and presence of mature trees, characteristics typical of degraded boundaries. It was noted during the study that degraded boundaries were directly exposed to dung from grazing animals when compared to hedgerows with dense canopies and tall banks which excluded grazing animals.

(iv) Carabid composition

Woody canopy structure (F1) explained a significant amount of the variation in carabid species composition (Figure 3.3.11c) and was strongly correlated to axis 1 (Figure 3.3.11b). The factors describing herbaceous margins (F3) and presence of young trees (F2) were also correlated to axis 1, though not as strongly as F1. Axis 1 therefore, suggested a gradient of increasing canopy density and dimensions and boundary structural complexity (with woody canopy, herbaceous vegetation and emergent trees). Axis 2 was strongly correlated to factors (F2 and F4) describing the the presence of young trees and mature emergent trees. These factors indicate increasing levels of hedgerow degradation and lack of management. Axis 2 was also negatively correlated to F3 describing the herbaceous margin. Axis 2 therefore described a gradient from predominantly herbaceous boundaries through to degraded woody boundaries.

Ordination of the field boundary carabid composition indicates four groups of carabids (Figure 3.3.11a):

(a) Species strongly associated with a large and dense woody canopy (F1) that are typical of woody habitats, and autumn breeders (hence adults are mature individuals overwintering for a second year). These species include *L. fulvibarbis, L. rufipennis,* and *D. quadrinotatus* commonly found as permanent hedgerow residents.

(b) Species abundant at boundaries with a large number of young and mature emergent trees (F2 and F4), such as degraded boundaries: *Amara aenea* (a spring breeder), *C. fusipennis, Pterostichus madidus* and *P. melanarius* (all late summer and early autumn breeders, overwintering predominately as larvae) and *N. biguttatus* (regarded as having an irregular life cycle with instances of bivoltinism having been recorded resulting in variable proportions overwintering as adults (Den Boer & Den-Danje, 1990)). With the exception of *N. biguttatus*, these species will be active in adjacent fields during the summer where the larval population overwinters, whilst mature adults will migrate to field boundaries to overwinter.

(c) Widely distributed species not positively associated with any of the factors describing field boundary habitat: *Amara communis, Acupalpus meridionalis, Agonum muelleri, A. sexpunctatum, Bembidion guttula, , B. obtusum, N. brevicollis* (open field species with medium dispersal power), *B. lunulatum* (categorised as preferring closed habitat) and *P. cupreus* (high dispersal power). The majority of species are spring breeders, overwintering as adults apart from *B. obtusum* (a winter breeder) and the autumn breeding and winter active *N. brevicollis* (Penney, 1966). This group was composed primarily of species exhibiting seasonal migration between field and boundary habitat where they overwinter as adults.

(d) Widely distributed species associated with a woody canopy structure (F1) and herbaceous margin (F3): *A. dorsale, Badister bipustulatus, Bembidion harpaloides, B. lampros, Demetrias atricapillus, Dromius linearis, M. obscuroguttatus, P. vernalis* and *T. quadristriatus*. This group includes species belonging to all categories of habitat preference and dispersal power. Most are spring breeders and autumn overwinterers except for *T. quadristriatus*, which breeds in autumn.

(v) Staphylinidae composition

The number of young emergent trees (F4) and woody canopy structure (F1) explained a significant amount of the variation in staphylinid composition (Figure 3.3.12c). Axis 1 was positively correlated to the presence of young trees (F2) and negatively (and weakly) correlated to herbaceous margin (F3) and therefore described

a degradation gradient from post and wire to degraded boundaries (Figure 3.3.12b). No young trees were found in post and wire boundaries, only a low number in hedgerows and a measurably greater number of young trees were recorded in degraded boundaries (see Chapter 2). A considerable proportion of the variance in staphylinid composition was explained by this axis. Axis 2 was strongly correlated to woody canopy structure (F1) and the presence of young trees described a gradient of increasingly tall, dense, woody boundaries.

Most staphylinid taxa showed a fairly ubiquitous distribution across field boundaries indicated by their position in ordination space close to the origin (Figure 3.3.12a). *Philonthus* species formed two groups defined by their relationship to axis 1 describing the degradation gradient. The three species *P. cognatus, P. decorus and P. varius* were more widely distributed whilst *P. laminatus* and *P. splendidus* were characteristic of highly degraded boundaries supporting a large number of young trees. These species are typically found in dung, carrion and rotting vegetation (Joy, 1976) and their preference for degraded boundaries is consistent with trends for species with similar life histories described above. The distribution of *Tachyporus* spp. in ordination space are defined by Axis 2 with *T. obtusus> T. chrysomelinus> T. hypnorum* associated with a tall, dense woody canopy. *O. rivulare* is strongly associated with tall, dense woody boundaries and *Omalium* spp. are typical of decaying plant matter and damp, shady conditions (Joy, 1976).

	Total inertia	Covariable inertia	Canonical eigenvalues
Community structure	0.123	0.039	0.050
Higher Arthropod	0.535	0.225	0.154
Coleoptera	0.548	0.174	0.161
Carabidae	2.237	0.555	0.675
Staphylinidae	1.136	0.378	0.463

Table 3.3.6 Partial-CCA examining variation in community structure: summary inertia and eigenvalues for each taxonomic group. Total inertia is the total variation in composition data. Covariable inertia is the variation in composition data described by the covariables. Canonical eigenvalues refer to the variation in composition data described by the environmental variables.
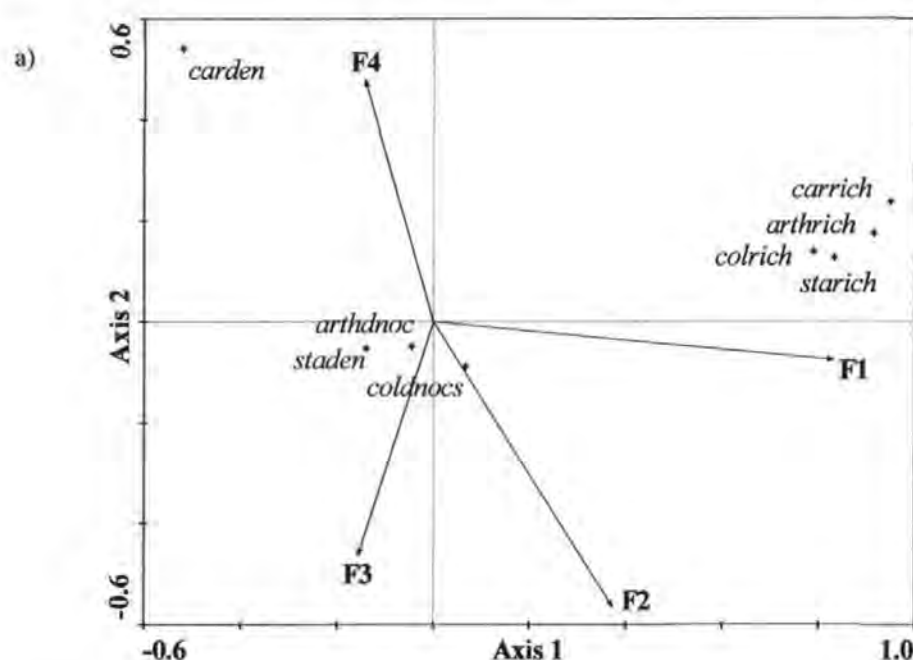
a)

b) Partial inter-set correlations, eigenvalues and cum. % canonical variance					c) Conditional effects		
	A1	A2	A3	A4		λ_a	P
F1	0.866	-0.049	0.221	-0.024	F1	0.03	0.001 ***
F2	0.363	-0.342	0.126	0.351	F3	0.01	0.209 n.s.
F3	-0.149	-0.273	0.400	-0.315	F4	0.01	0.202 n.s.
F4	-0.144	0.299	0.504	0.163	F2	0.00	0.289 n.s.
Eigenvalues	0.037	0.009	0.004	0.000			
Cum. % canonical variance	74.0	92.0	99.3	100.0			

Figure 3.3.8 Partial-CCA examining variation in richness and density of each taxonomic group explained by the four latent variables (factors F1 to F4) describing field boundary habitat, with 4 covariables (connectivity, field boundary length, orientation, altitude) to minimise effects of field boundary network and landscape characteristics.
a) Species-conditional biplot displaying richness and density variables and four factors. Codes in italics represent summarised data for Arthropod density (excluding Coleoptera) (*arthdnoc*) Arthropod richness (including Coleoptera) (*arthrich*), Coleoptera density (excluding Carabidae and Staphylinidae) (*coldnocs*), Coleoptera richness (including Carabidae and Staphylinidae) (*colrich*), Carabid density (*carden*), Carabid richness (*carrich*), Staphylinid density (*staden*) and Staphylinid richness (*starich*).
b) Partial inter-set correlation coefficients between environmental variables and four axes, species eigenvalues and cumulative % variance described by species-environment relation for each axis.
c) The amount of variation explained by each variable added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation tests (999 permutations) are shown with asterix to indicate significance ***=<0.001 and n.s.= non-significant.

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Higher arthropods		Coleoptera		Carabidae		Staphylinidae	
acari	Acari	*cara*	Carabidae	*amer*	*Acupalpus meridianus*	*aleo*	*Aleocharinae* spp.
aphid	Aphididae	*chry*	Chrysomelidae	*ador*	*Agonum dorsale*	*anot*	*Anotylus* spp.
arano	Araneae other	*cocc*	Coccinelidae	*amue*	*Agonum muelleri*	*orivu*	*Omalium rivulare*
butter	Rhopalocera	*cryp*	Cryptophagidae	*asex*	*Agonum sexpunctatum*	*plito*	*Paederus litoralis*
chilo	Chilopoda	*hydr*	Hydrophilidae	*aaen*	*Amara aenea*	*pcogn*	*Philonthus cognatus*
coleop	Coleoptera	*leod*	Leodidae	*acom*	*Amara communis*	*pdeco*	*Philonthus decorus*
collem	Collembola	*ptil*	Ptilidae	*bbip*	*Badister bipustulatus*	*plami*	*Philonthus laminatus*
dermap	Dermaptera	*scar*	Scarabaeidae	*bgut*	*Bembidion guttula*	*psple*	*Philonthus splendens*
diplo	Didlopoda	*silp*	Silphidae	*bhar*	*Bembidion harpaloides*	*pvari*	*Philonthus varius*
diptlar	Diptera larvae	*staph*	Staphylinidae	*blam*	*Bembidion lampros*	*rorbi*	*Rugulus orbiculatus*
heterop	Heteroptera			*blun*	*Bembidion lunulatum*	*sten*	*Stenus* spp.
homop	Homoptera other			*bobt*	*Bembidion obtusum*	*tchry*	*Tachyporus chrysomelinus*
isopod	Isopoda			*cfus*	*Calathus fuscipes*	*thypn*	*Tachyporus hypnorum*
lycos	Lycosidae			*datr*	*Demetrias atricapillus*	*tobtu*	*Tachyporus obtusus*
opil	Opiliones			*dlin*	*Dromius linearis*	*xglab*	*Xantholinus glabratus*
orthop	Orthoptera			*dqua*	*Dromius quadrinotatus*	*xlini*	*Xantholinus linearis*
psocop	Psocoptera			*lful*	*Leistus fulvibarbis*	*xlong*	*Xantholinus longiventris*
psued	Psuedoscorpionida			*lruf*	*Leistus rufescens*		
				mobs	*Metabletus obscurogutattus*		
				nbre	*Nebria brevicollis*		
				nbig	*Notopillis bigutattus*		
				pcup	*Pterostichus cupreus*		
				pmad	*Pterostichus madidus*		
				pmel	*Pterostichus melanarius*		
				pver	*Pterostichus vernalis*		
				tqua	*Trechus quadristriatus*		

Table 3.3.7 Taxon codes for partial-CCA ordination plots.
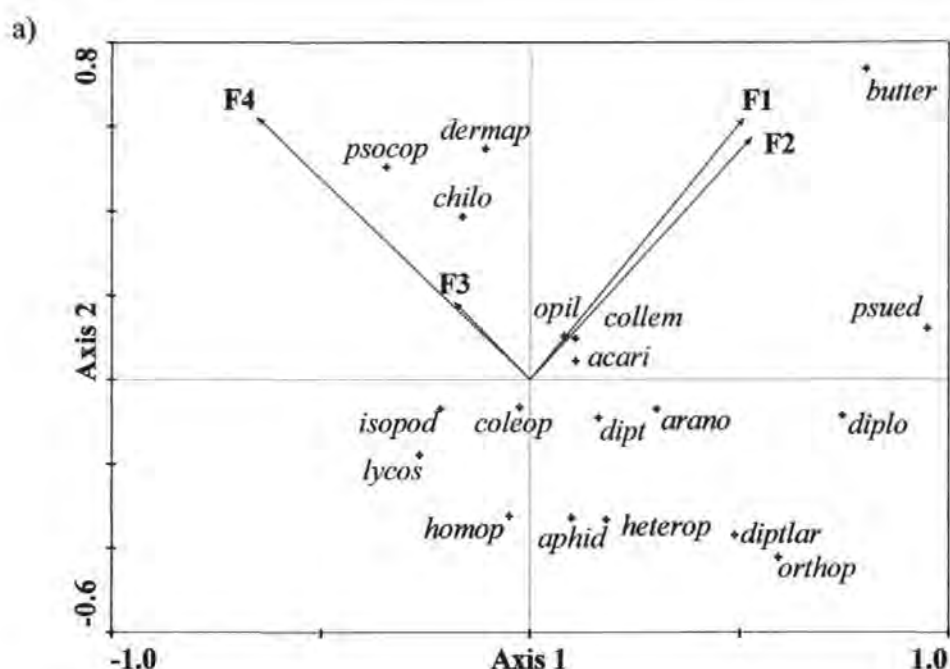
a)

b) Partial inter-set correlations, eigenvalues and cum. % canonical variance					c) Conditional effects		
	A1	A2	A3	A4		λ_a	P
F1	0.500	0.567	0.007	-0.278	F4	0.06	0.015 *
F2	0.480	0.486	-0.095	0.373	F1	0.05	0.003 **
F3	-0.161	0.153	-0.778	-0.206	F3	0.03	0.310 n.s.
F4	-0.616	0.546	0.177	-0.002	F2	0.01	0.335 n.s.
Eigenvalues	0.076	0.050	0.018	0.010			
Cum. % canonical variance	49.3	81.8	93.6	100.0			

Figure 3.3.9 Partial-CCA examining variation in higher arthropod composition caused by four latent variables (Factors F1 to F4) describing field boundary habitat, with 4 covariables (connectivity, field boundary length, orientation, altitude) to minimise effects of field boundary network and landscape characteristics.
a) Species-conditional biplot displaying higher arthropod taxa (with >10% weight) and four factors. Taxa are labelled using abbreviated italics (see Table 3.3.7).
b) Partial inter-set correlation coefficients between environmental variables and four axes, species eigenvalues and cumulative % variance described by species-environment relation for each axis.
c) The amount of variation explained by each variable added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation tests (999 permutations) are shown with asterix to indicate significance *= <0.05, **=<0.01 and n.s.= non-significant.
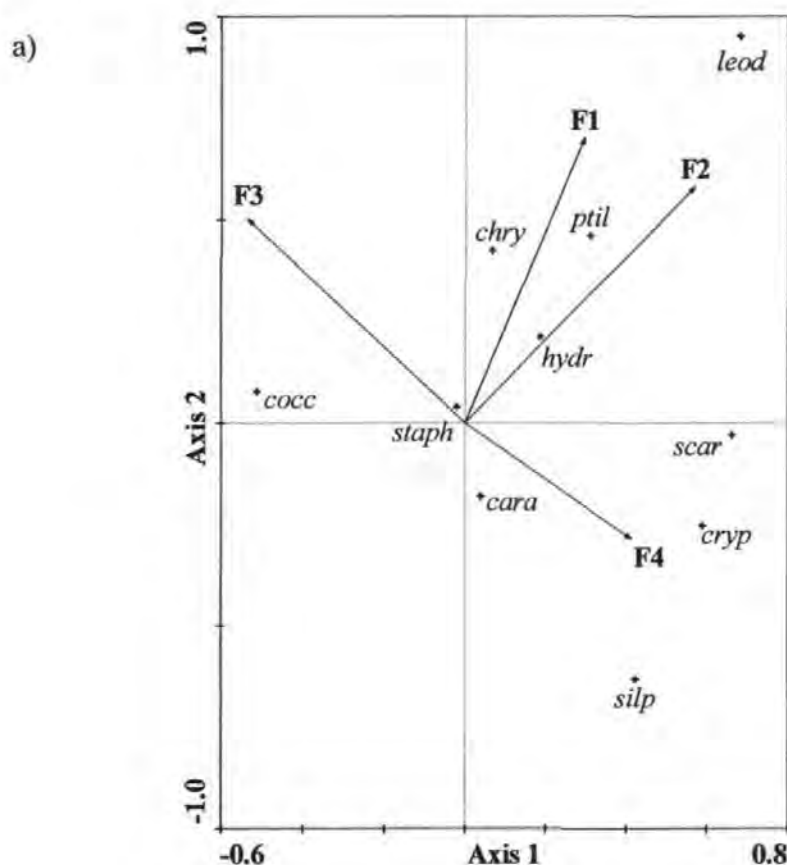
a)

b) Partial inter-set correlations, eigenvalues and cum. % canonical variance					c) Conditional effects		
	A1	A2	A3	A4		λ_a	P
F1	0.271	0.626	0.027	0.379	F3	0.05	0.092 n.s.
F2	0.492	0.492	0.107	-0.348	F2	0.04	0.111 n.s.
F3	-0.461	0.423	-0.424	-0.021	F4	0.05	0.082 n.s.
F4	0.389	-0.264	-0.537	0.111	F1	0.02	0.316 n.s.
Eigenvalues	0.059	0.052	0.034	0.016			
Cum. % canonical variance	36.9	69.3	90.2	100.0			

Figure 3.3.10 Partial-CCA examining variation in coleopteran family composition caused by four latent variables (Factors F1 to F4) describing field boundary habitat, with 4 covariables (connectivity, field boundary length, orientation, altitude) to minimise effects of field boundary network and landscape characteristics.
a) Species-conditional biplot displaying coleopteran families (with >10% weight) and four factors. Families are labelled using abbreviated italics (see Table 3.3.7).
b) Partial inter-set correlation coefficients between environmental variables and four axes, species eigenvalues and cumulative % variance described by species-environment relation for each axis.
c) The amount of variation explained by each variable added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation tests (999 permutations) are shown with n.s. to indicate non-significance.
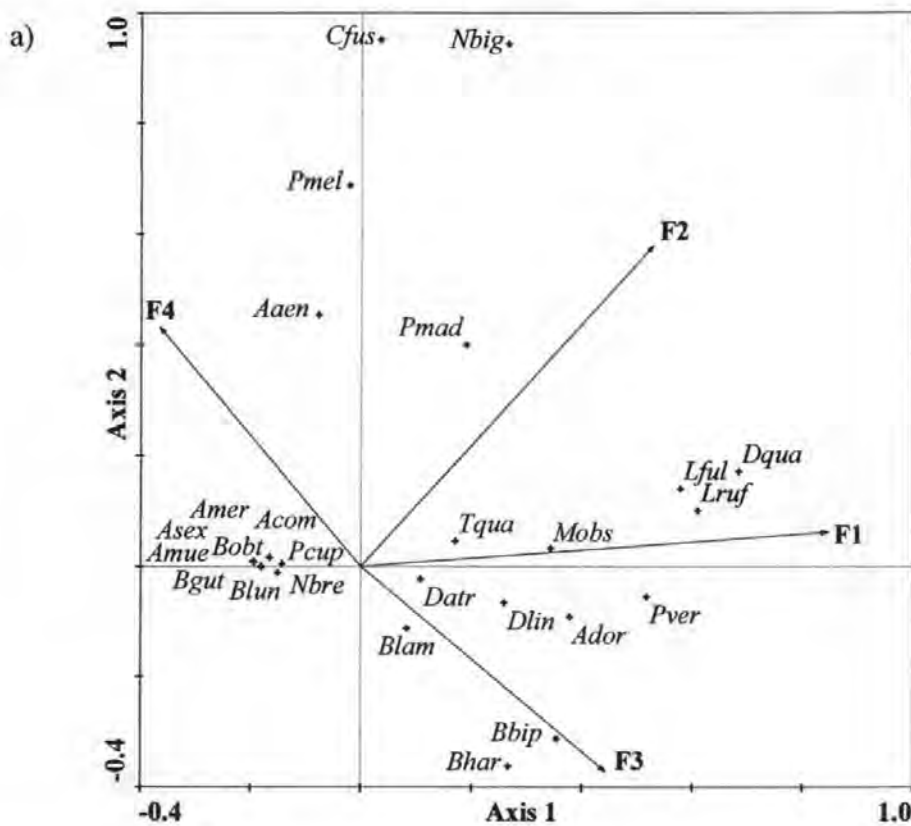
a)

Axis 2

1.0

Cfus. Nbig.

Pmel.

F2

F4 Aaen. Pmad.

Lful. Dqua
Lruf

Amer Acom Tqua Mobs F1
Asex Bobt. Pcup
Amue
Bgut Blun Nbre Datr
Dlin Ador Pver
Blam

Bbip
Bhar. F3

-0.4

-0.4 Axis 1 1.0

b) Partial inter-set correlations, eigenvalues and cum. % canonical variance	A1	A2	A3	A4	c) Conditional effects	λ_a	P
F1	0.881	0.065	-0.192	-0.216	F1	0.30	0.001 ***
F2	0.564	0.618	0.034	0.331	F2	0.13	0.270 n.s.
F3	0.509	-0.428	0.634	-0.040	F3	0.12	0.362 n.s.
F4	-0.373	0.440	0.447	-0.423	F4	0.13	0.353 n.s.
Eigenvalues	0.335	0.176	0.091	0.075			
Cum. % canonical variance	49.5	75.5	88.9	100.0			

Figure 3.3.11 Partial-CCA examining variation in carabid composition caused by four latent variables (Factors F1 to F4) describing field boundary habitat, with 4 covariables (connectivity, field boundary length, orientation, altitude) to minimise effects of field boundary network and landscape characteristics.
a) Species-conditional biplot displaying carabid species (with >10% weight) and four factors. Species are labelled using abbreviated italics (see Table 3.3.7).
b) Partial inter-set correlation coefficients between environmental variables and four axes, species eigenvalues and cumulative % variance described by species-environment relation for each axis.
c) The amount of variation explained by each variable added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation tests (999 permutations) are shown with asterix to indicate significance ***=<0.001 and n.s.= non-significant.

a)

b) Partial inter-set correlations, eigenvalues and cum. % canonical variance					c) Conditional effects		
	A1	A2	A3	A4		λ_a	P
F1	-0.031	0.830	0.336	0.057	F2	0.21	0.005 **
F2	0.624	0.534	-0.097	-0.158	F1	0.14	0.008 **
F3	-0.380	0.356	-0.607	0.200	F4	0.05	0.143 n.s.
F4	0.252	-0.142	0.070	0.515	F3	0.06	0.117 n.s.
Eigenvalues	0.280	0.158	0.020	0.005			
Cum. % canonical variance	60.4	94.6	99.0	100.0			

Figure 3.3.12 Partial-CCA examining variation in staphylinid composition caused by four latent variables (Factors F1 to F4) describing field boundary habitat, with 4 covariables (connectivity, field boundary length, orientation, altitude) to minimise effects of field boundary network and landscape characteristics.
a) Species-conditional biplot displaying staphylinid taxa (with >10% weight) and four factors. Taxa are labelled using abbreviated italics (see Table 3.3.7).
b) Partial inter-set correlation coefficients between environmental variables and four axes, species eigenvalues and cumulative % variance described by species-environment relation for each axis.
c) The amount of variation explained by each variable added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation tests (999 permutations) are shown with asterix to indicate significance **=<0.01 and n.s.= non-significant.

3.3.4 Field boundary classification based on Carabidae and Staphylinidae

The TWINSPAN classification of field boundaries based on combined relative carabid and staphylinid density divided the sites into three groups of six boundaries in each (Figure 3.3.13). These divisions generally distinguish between post and wire boundaries and woody boundaries. One degraded field boundary (D2, in an advanced stage of hedgerow degradation which could be best described as a line of trees with a grass sward typical of post and wire boundaries) was positioned with the post and wire cluster, whilst one post and wire boundary (PW18, characterised by a wide, natural regeneration margin with several patches of brambles along its length) was positioned in an adjacent cluster with woody boundaries. However, the proximity of PW18 to other post and wire boundaries in the dendrogram indicated similarities in carabid and staphylinid composition. There was considerable mixing between hedgerow and degraded boundaries in the woody boundary clusters.

Field boundary site	Field boundary type
3	**Degraded**
8	**Hedgerow**
9	**Degraded**
10	**Degraded**
11	**Hedgerow**
14	**Hedgerow**
4	*Degraded*
7	*Hedgerow*
12	*Hedgerow*
15	*Hedgerow*
16	*Degraded*
18	*Post and wire*
1	**Post and wire**
2	**Degraded**
5	**Post and wire**
6	**Post and wire**
13	**Post and wire**
17	**Post and wire**
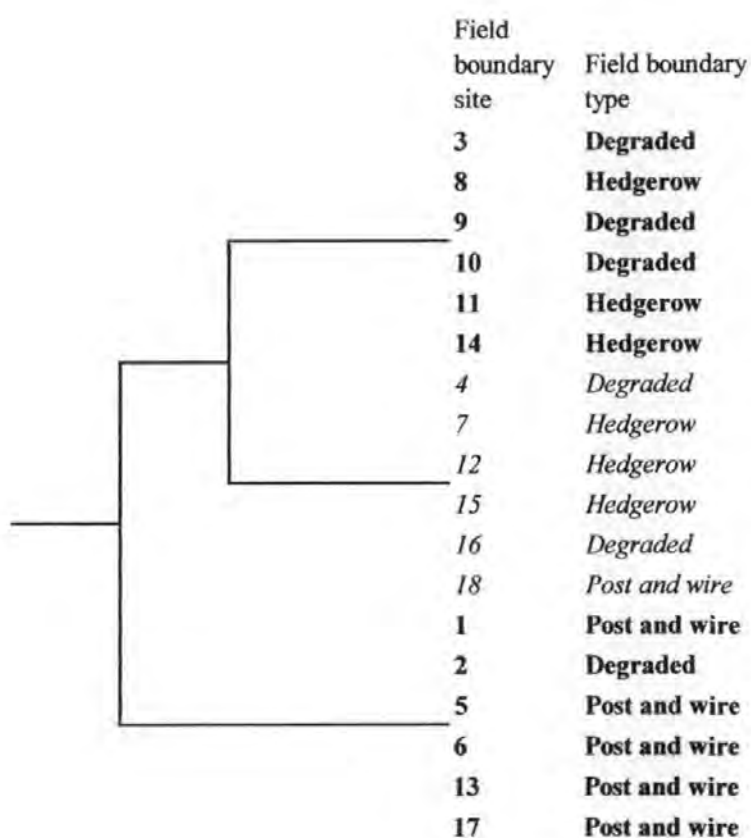
Figure 3.3.13 Classification of field boundaries based on the relative (%) density of Carabidae and Staphylinidae. TWINSPAN groupings are shown using alternately bold and italic font for the field boundary sites and types at the right-hand-side of the dendrogram.

3.3.5 Farm-scale representation of Carabidae and Staphylinidae

Using the near-minimum-area algorithm, twelve field boundaries were necessary for complete representation of the 78 Carabidae and Staphylinidae species (Figure 3.3.14). Subsequent site selection using hotspot-areas and random selection were based on 12 sites to compare the three methods. The hotspot-areas selection was virtually equivalent to the near-minimum-area set, but achieved a marginally lower % representation of species. However, this was significantly better than a random selection of 12 field boundaries which supported about 79% of carabid and staphylinid species. When considered individually, post and wire, degraded and hedgerow boundaries supported 68%, 72% and 74% respectively, of complete species representation. Hedgerows as a single group provide the greatest species representation, and post and wire boundaries the poorest. However, this was lower than the 79% species representation achieved by random selection from all field boundary types.

Examination of the types of field boundary selected by the near-minimum-area (Table 3.3.15) revealed that all field boundary types were required. In addition they were selected in direct proportion to their presence in the original 18 sites. Eleven sites from all three boundary types contribute unique species.
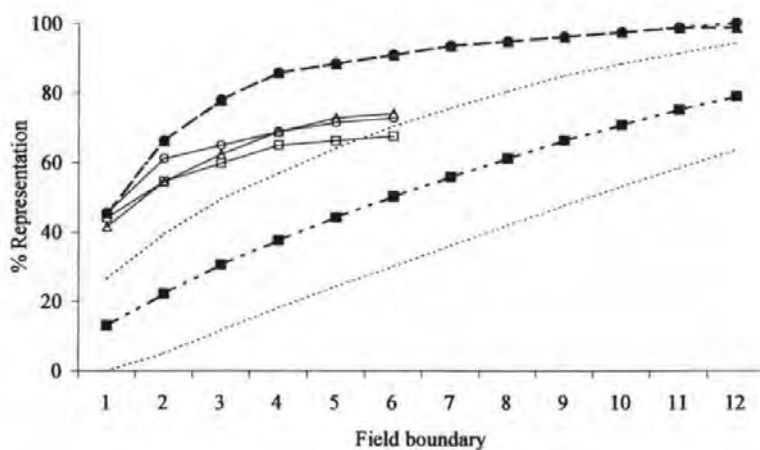
Figure 3.3.14 Complimentary analysis: Selection of (12 from 18) field boundaries to achieve full species representation using near-minimum-area algorithm (●, with dotted line). Selection of 12 boundaries as hotspots (▲, with dashed line) and randomly (■, with dash-dot line). The accumulation of species represented by post and wire (□), hedgerow (Δ) and degraded (○) boundaries separately is also shown.

Field boundary site	Field boundary type	Near-minimum-area set	Unique species	Species richness
3	Degraded	7th	1	24
8	Hedgerow	2nd	2	32
9	Degraded		0	22
10	Degraded	4th	2	27
11	Hedgerow	10th	1	24
14	Hedgerow	8th	1	24
4	Degraded	11th	1	23
7	Hedgerow		0	15
12	Hedgerow	5th	2	23
15	Hedgerow		0	17
16	Degraded		0	19
18	Post and wire		0	18
1	Post and wire	12th	0	16
2	Degraded	1st	1	35
5	Post and wire	9th	1	19
6	Post and wire		0	18
13	Post and wire	3rd	3	34
17	Post and wire	6th	2	25

Figure 3.3.15 Field boundary selection using the near-minimum-area algorithm, with the number of unique species contributed and combined carabid and staphylinid richness of each boundary.

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3.4 DISCUSSION

Examination of arthropod representation in field boundaries at a farm-scale indicated the importance of habitat heterogeneity in the maintenance of farmland biodiversity. Observed differences in the arthropod composition and community structure of the three dominant field boundary types in lowland farmland could have important consequences for farmland biodiversity and the provision of beneficial agronomic services. In summary, post and wire habitats were the most productive (in terms of emergence of overwintering arthropods), whilst both hedgerows and degraded boundaries supported a more diverse arthropod community. Differences in the composition of Carabidae and Staphylinidae and functional composition were evident between boundary types. Within this study, some advances have been made in understanding the field boundary habitat requirements of different arthropod groups that could promote beneficial management. However, arthropod composition, particularly at higher taxonomic levels, was strongly influenced by characteristics of the landscape and field boundary network which warrants further study.

Post and wire boundaries supported measurably greater densities of higher arthropods, Coleoptera, Staphylinidae and polyphagous predators compared to hedgerows and degraded boundaries. Whilst arthropod densities were approximately one-third lower in woody boundaries, these boundaries were on average three times wider than post and wire habitats. Consequently, overall abundances of higher arthropods, Coleoptera and Staphylinidae supported by different field boundary types may be similar, when the ground surface area of the field boundary is accounted for. Post and wire boundaries may be capable of supporting a 'tightly packed' overwintering distribution, whilst arthropods 'spread-out' to fill the available space in woody boundaries (Maudsley *et al.*, 2002). However, densities of polyphagous predators differed by an order of magnitude between post and wire and woody boundaries. The dominance of these taxa may be indicative of strong competitive interactions between species in a habitat with limited resources and to which some species are better suited than others (Loreau, 1984). In intensively farmed arable landscapes, maximising yield of polyphagous predators in the minimum field boundary width would be an advantage. The productivity of post and wire habitat could be used as a tool to promote the biological control of cereal aphid pests and the spread of BYDV as part of an integrated pest management regime in much the same

way as field margins, conservation headlands and beetle banks (Wratten, 1988; Sotherton, 1990; Collins *et al.*, 1997; Kopp, 1998; de Snoo *et al.*, 1999; Lee & Landis 2003). Hedgerows and degraded boundaries supported more equitable communities of Coleoptera, Carabidae and Staphylinidae than post and wire boundaries. Although observed taxon richness of higher arthropods, Coleoptera, Carabidae and Staphylinidae was similar between boundary types, rarefraction estimates suggested higher taxon richness in hedgerows and degraded boundaries compared to post and wire fence-lines based on equivalent densities.

Higher carabid richness in hedgerows and degraded hedgerows was not due to their suitability as a refuge for species of woodland origin. All boundaries supported similar proportions of closed habitat species despite the greater habitat suitability of woody boundaries (Burel, 1989). The presence of tall, dense woody canopies in hedgerows and young and mature emergent trees in degraded boundaries provide microclimatic conditions favoured by closed habitat species (Thiele, 1977; Fournier & Loreau, 2001). Many closed habitat species will use woody boundaries as dispersal corridors to move between breeding populations at hedgerow intersections or woodland (Burel, 1989; Charrier *et al.*, 1997; Petit & Baudry, 1998). Reproductive sites may also be more suitable for overwintering individuals. In addition, typical carabid forest species are known to be autumn breeders that overwinter as larvae (Fournier & Loreau, 2001). If closed habitat species overwinter predominantly at intersections or in the larval stage, it is unlikely that the sampling conducted for this study would have detected their presence. Processes operating at a landscape scale may also influence the representation of closed habitat species locally (den Boer, 1981, 1990; Ricklefs, 1987). Within the study landscape, woodlands were small and sparsely distributed. In addition, none of the woody boundaries were directly connected to woodland. Without a source of individuals to colonise the field boundary network and refound populations, it may not be possible for closed habitat species to persist in woody boundaries (Burel, 1989; Charrier *et al.*, 1997; Petit & Baudry, 1998). In farmed landscapes where suitable habitat is highly fragmented, hedgerows and remnant woodlands have been colonised by species of open or ubiquitous habitat preference with a loss of closed habitat species (Fournier & Loreau, 2001).

Habitat fragmentation in farmland makes recolonisation of suitable habitat difficult for species with poor dispersal power. This suggests that woody boundaries supporting higher proportional densities of species with low dispersal power provide shelter from disturbance that might result in local extinctions (Den Boer, 1981). Within this study, field boundary types represented a gradient of increasing disturbance in the order degraded< hedgerow< post and wire boundaries. Den Boer (1987) suggests that a high dispersal power may be preferentially selected in dimorphic or polymorphic species populations living in unstable environments (high environmental stochastity) or in suitable but too small environments (high demographic stochastity). Future work to compare wing development of dimorphic but ubiquitous species such as *B. lampros* between field boundary types may provide information regarding disturbance independent of habitat preference.

Degradation of a habitat may temporarily result in higher arthropod diversity as new species colonise. For example, opening up of the ground layer as trees regain their natural shape will enable greater access by grazing livestock. This interaction between boundary structure and adjacent land-use may have enabled colonisation by staphylinid dung and carrion feeders. Simultaneously, existing species persist in a degrading habitat through a delayed population response to habitat change (Petit & Burel, 1998). For example, time lags of thirty years have been observed between carabid species distributions and the fragmentation of hedged networks in Western France (Burel, 1993). Consequently, by allowing a habitat to degrade an extinction debt may be created, though the time scale over which populations persist may be considerable (Den Boer, 1977). This provides time for either restoration work to the field boundary habitat or to the field boundary network to facilitate colonisation, though deciding which if either are required is clearly complex.

Greater arthropod diversity of woody boundaries may result from their greater structural complexity. The environmental variables describing hedgerow (woody canopy structure) and degraded (emergent trees) habitat structure were most important in determining the richness of all four taxonomic groups and the composition of higher arthropods, Carabidae and Staphylinidae. The habitat complexity of woody boundaries will provide a greater range of microclimates and microhabitats and a greater variety and continuity of resources for arthropods (Forman & Baudry, 1986;

Maudsley, 2000). Whilst habitat factors play a key role in determining arthropod diversity and composition between field boundary types, landscape and field boundary network variables are highly influential, particularly for higher arthropods and coleopteran composition.

Woody boundaries and post and wire fencelines could be classified based on their carabid and staphylinid compositions. However, no such distinction was possible between hedgerows and degraded boundaries. Together with evidence from the community structure and functional composition, this suggests that post and wire fencelines represent habitats that are ecologically different from hedgerows and degraded boundaries. Woody boundaries represented a gradient in canopy density, presence of emergent trees and herbaceous ground cover. The distinction between hedgerows and degraded boundaries, whilst important in terms of management, is not clearly defined ecologically. The classification of field boundary types based on vegetation structure is more applicable than one based on carabid and staphylinid composition. However, carabid and staphylinid composition may provide more detailed knowledge of previously classified habitats and will highlight field boundary characteristics of ecological importance, such as differences in disturbance levels (Refseth, 1980).

To maintain and enhance arthropod biodiversity at a farm-scale, field boundary heterogeneity is essential. Each field boundary type contributes unique or rare species. Therefore degraded boundaries do not support a sub-set of those expected in hedgerows, nor do post and wires support a sub-set of species expected in woody boundaries. This contradicts the perception of different field boundary types with regards their ecological value (Haines-Young et al., 2000). The removal, replacement or alteration of any of the eleven field boundaries contributing unique species could result in a decrease in farm-scale richness. In addition, the majority of species were represented in fewer than five boundaries. Therefore, the viability of species at the farm-scale would be affected by the loss of any boundary. It could be hypothesised that the U.K. agricultural landscape might be close to this threshold where the loss of landscape features causes an amplified decline in richness due to lack of representation in other sites. If conservation policy and agri-environment schemes support the creation of single landscape features (at the expense of, or to

replace others) the result would be a contribution to or acceleration of biodiversity loss at the farm-scale.

CHAPTER FOUR: THE DISTRIBUTION OF OVERWINTERING COLEOPTERA IN DIFFERENT FIELD BOUNDARY FEATURES

4.1 INTRODUCTION

Studies examining the use of field boundaries by overwintering Coleoptera have generally regarded a boundary as a single homogenous habitat (e.g. Sotherton, 1985; Thomas *et al*, 1992a; Dennis *et al*, 1994; Andersen, 1997). However, such studies reported high variability in coleopteran densities, suggesting that overwintering distributions are heterogeneous. Several studies have shown strongly aggregated distribution patterns of carabid species in hedgerows, both over winter (Maudsley *et al.*, 2002) and during the summer (Thomas *et al.*, 2001a). Spatial heterogeneity in microclimatic conditions, particularly temperature and moisture, is considered to be the determining factor in the distribution of carabid and staphylinid species in field boundaries (Grum, 1971). Microclimatic conditions will be determined by the structural and vegetation characteristics of a field boundary (Sotherton, 1985). In order to provide practical advice on optimal field boundary management, the contribution of recognisable field boundary features to overwintering distributions of Coleoptera needs to be examined.

Field boundaries are composed of a range of structural and additional features including woody components, fences, margins and banks. These composite features of a field boundary may vary in microhabitat characteristics and consequently their suitability as overwintering sites. Several carabid species, including *Agonum dorsale* and *Dromius* spp. are known to overwinter gregariously and anecdotal evidence suggests they may aggregate in high densities at particular habitat features such as rocks or the base of tree trunks (Thiele, 1977; Dennis & Fry, 1992; Maudsley *et al.*, 2002). Other species such as those within the genus *Bembidion* are regarded as lithophilous and take refuge under stones (Andersen, 1985). Additionally, the position of features will vary in relation to distance from the field boundary edge. The spatial distribution of overwintering species in relation to distance from the boundary edge may vary as a result of differential microclimatic conditions or dispersal behaviour of migrating individuals (Lipkow, 1966; Pedersen *et al.*, 1990; Riedel, 1995). Some features may consistently provide optimal overwintering conditions, relative to other features both within and between boundary types. Habitat features are easily

recognisable and understanding their suitability as overwintering sites for Coleoptera may enable targeted enhancement of boundary habitats for species of beneficial or conservation concern within habitat restoration or management schemes.

Variations in the distribution, composition and community structure of overwintering Coleoptera have been associated with a range of microhabitat characteristics including bare ground, leaf litter, vegetation type and height, bank height and distance from the field boundary edge (Sotherton, 1985; Pedersen *et al.*, 1990; Dennis & Fry, 1992; Thomas *et al.*, 1992a, b; Dennis *et al.*, 1994; Riedel, 1995; Andersen, 1997; Maudsley *et al.*, 2002). These habitat characteristics may all vary between field boundary features and thereby influence their suitability as overwintering sites. Additionally, features within and between different boundary types will vary in the presence or absence of a woody canopy, the presence of dead plant stubble from trimmed herbaceous vegetation and moss cover, with consequent variations in microclimatic conditions experienced by overwintering Coleoptera.

A negative relationship has been found between the distribution of bare ground and the diversity of overwintering arthropod and density of polyphagous predators (Pollard, 1968a; Thomas *et al.*, 1992b; Dennis & Fry, 1992). This is thought to be a result of the greater amplitude of seasonal and diurnal temperature changes on bare ground due to unimpeded solar radiation and reduced relative humidity compared to vegetated ground (Geiger, 1965). The presence of vegetation cover is associated with higher overwintering densities of carabids and staphylinids, although this is strongly dependent on vegetation type. Tussocky grasses such as *Dactylis glomerata* and *Holcus lanatus* have been found to support the greatest overwintering densities of *Tachyporus hypnorum*, *Demetrias atricapillus* and other polyphagous predators compared to rosette or mat forming grasses, or loose plant structures such as dicotyledonous plants (e.g. *Ranunculus repens*) (Luff, 1965, 1966a; Bossenboek, 1977; Thomas *et al.*, 1991, 1992a, b; Dennis *et al.*, 1994). The high biomass of live and dead plant matter associated with tussocky grasses acts to buffer fluctuations in temperature and thereby provide improved overwintering conditions (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b). Dicotyledonous plants will also vary in their ability to buffer temperatures. Species with a loose plant structure such *as Agrostemma githago* or *Chenopodium polyspernum* were associated with higher diurnal

temperature fluctuations and lower arthropod densities compared to plants providing greater ground cover such as *Achillea millefolium* and *Arctium minus* (Burki & Hausamann, 1993). Reduced temperature fluctuations were considered to enhance overwintering survival of *T. hypnorum* and other overwintering predators (Luff 1966b; Burki & Hausamann, 1993; Dennis *et al.*, 1994) and may act as stimuli for overwintering site selection (Thomas *et al.*, 1992b). In addition, the mean depth of the root layer associated with grassy vegetation has been positively related to high densities of overwintering carabids and *T. hypnorum* (Descender, 1982; Dennis *et al.*, 1994). Where field boundaries are raised above the level of the field, better drainage and drier soils may result in higher densities of polyphagous predators (Sotherton, 1985; Dennis *et al.*, 1994).

Adjacent crop type may influence numbers of Carabidae and Staphylinidae migrating to field boundaries to overwinter (Andersen, 1997). In addition, the degree to which migrating individuals penetrate the field boundary will influence overwintering distributions at different field boundary features. The extent to which individuals move into the field boundary habitat from the field will be influenced by habitat suitability, environmental resistance from vegetation or field boundary structure (Thiele, 1977; Mauremooto *et al.*, 1995; Brown, 2000) and species-specific dispersal behaviour (Riedel, 1995). Species that disperse by flight are likely to show a more homogenous distribution pattern than those that migrate to field boundaries by walking (Riedel, 1995).

Many species of carabid and staphylinid are morphologically adapted for burrowing and respond positively to thigmotactic stimuli (body contact or pressure) in autumn and winter (Thiele, 1977). As a result, they are able to take refuge from adverse climatic conditions by burrowing or following crevices and fissures into the soil. Temperature is considered a determining factor in the vertical migration of soil arthropods (Dowdy, 1944) and temperature fluctuation has been shown to decrease with soil depth (Thomas *et al.*, 1991). Energetic trade-offs in the cost of burrowing in and out of the soil against the benefits of more stable and less severe microclimatic conditions at increased depth have been discussed by Leather *et al.* (1993). Optimal microclimatic conditions associated with particular structural features within a boundary type may reduce the depth at which Coleoptera overwinter (Dowdy, 1944;

Thiele, 1977; Maudsley *et al.*, 2002). Furthermore, the literature suggests contrasting patterns in the vertical distributions of Carabidae between woody and non-woody field boundaries. Maudsley *et al.* (2002), studying a single hedgerow, found carabid abundance decreased with soil depth (with the exception of *H. rufipes*) with most individuals found in the upper 10cm of soil and in the leaf litter. By contrast, Dennis *et al.* (1994) reported an even distribution of carabids to a soil depth of 35cm in grassy margins. Vertical distribution of staphylinids was similar between field boundary types; highest densities were captured in the upper 10cm of soil in the hedgerow (Maudsley *et al.*, 2002) and the upper 15cm of soil in grassy margins (Dennis *et al.*, 1994).

Previous studies examining the distributions of adult overwintering beetles in field boundaries have focused on the dominant polyphagous predators. However, Maudsley *et al.* (2002) demonstrated that community composition may vary considerably between different sides of a hedgerow despite similarities in the most abundant species. Additionally, little is known about the overwintering habitat requirements of coleopteran families in general or species of Carabidae and Staphylinidae. Understanding the overwintering microhabitat preferences of a broad range of taxa will provide the foundation for field boundary management that is more sympathetic to the conservation of farmland arthropods.

This study will compare habitat features in post and wire and hedgerow boundaries, both with and without margins. Hedgerows and fences form the dominant boundary types in lowland farmland and represent strongly contrasting habitats, whilst margins represent a versatile means of augmenting field boundary functions and may influence the overwintering distribution of Coleoptera in a pre-existing boundary. Selected features represent the range of structural (trunk, fence-post and fence-wire), additional (bank top, bank slopes and margin) and incidental (rock) features typical of these boundary-margin combinations.

4.1.1 Aims

(i) Describe and compare the microhabitat characteristics of habitat features typical of different field boundary-margin types.

(ii) Quantify and compare the richness and density of Coleoptera, with special reference to Carabidae and Staphylinidae, overwintering at different substrate depths and in different features, both within and between boundary types.

(iii) Assess the relative importance of different microhabitat characteristics in determining the composition of coleopteran families, Carabidae and Staphylinidae.

4.2 METHODS

4.2.1 Field work

Eight field boundaries were selected for study on the Seale-Hayne farm: four each of post and wire (PW) or hedgerow (H). Each boundary type was represented by two boundaries without margin (-M) and two with margin (+M). Botanical, structural and landscape characteristics of the eight field boundaries studied are described in Chapter 2 (PW-M 6 and 13; PW+M 18 and 5; H-M 7 and 14; H+M 11 and 12). Overwintering Coleoptera were captured using substrate searches. Three transects of substrate searches for Coleoptera were conducted perpendicular to each field boundary. Transects were a minimum of 40 m apart and positioned equidistantly along the length of the field boundary. Transects were conducted in rotation, resulting in the first transect at each field boundary being completed before the second set of transects was conducted. Each set of transects took one month to complete, and were all conducted between November 1999 and January 2000.

Each transect was composed of a series of quadrats targeted to sample defined structural and additional features of the four field boundary types. Transects were replicated within, but differed by necessity between, boundary types to reflect their differing habitat complexity. All transects included a quadrat taken at 20m into each adjacent field from the field boundary-field edge (one arable field quadrat and one ley field quadrat) and one quadrat taken from the inside edge of the boundary (one arable edge quadrat and one ley edge quadrat). Within the boundary interior, quadrats were taken at the base of fence-posts and tree trunks, underneath fence-wire and rocks, from bank slopes (both sides), bank top and margins where these features were present within a boundary type. Consequently, seven quadrats were conducted in PW-M transects, eight at PW+M, 11 at H-M and 12 quadrats taken in H+M transects. The field boundary profiles and position of quadrats is shown in Figure 4.2.1. The features sampled in each field boundary type are described in Table 4.2.1.
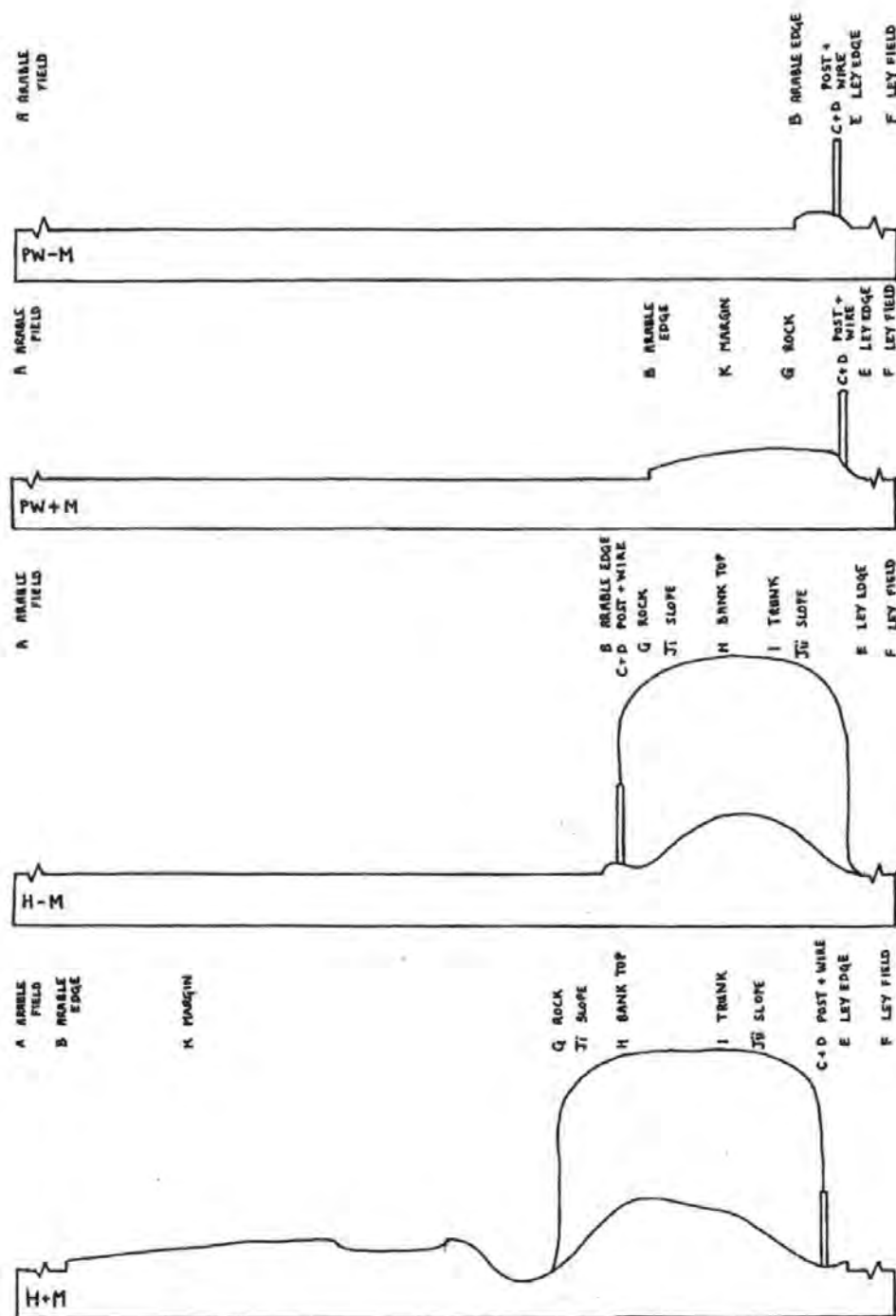
Figure 4.2.1 Profiles of field boundary types investigated showing feature locations.

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Code	Name	Description	Field boundary-margin			
			PW-M	PW+M	H-M	H+M
A	Arable field	Quadrat positioned 20m from the uncultivated boundary edge into the arable field (or ley field in the one exception).	X	X	X	X
B	Arable edge	Placed at the uncultivated boundary edge adjacent to arable field.	X	X	X	X
C	Fence-post	Post placed centrally within the quadrat and soil and vegetation sampled round the edge of post to the limits of the sample area.	X	X	X	X
D	Fence-wire	Quadrat positioned beneath fence wire centrally between two posts, to the left of the sampled post.	X	X	X	X
E	Ley edge	Placed at the uncultivated boundary edge adjacent to ley field.	X	X	X	X
F	Ley field	Quadrat positioned 20m from the uncultivated boundary edge into the ley field.	X	X	X	X
G	Rock	Rock placed centrally within the quadrat and soil and vegetation sampled round the edge and underneath rock to the limits of the sample area. Selected rocks did not exceed 60% of quadrat surface area and were those nearest to the line of the transect.	X	X	X	X
H	Bank top	Sample taken from the uppermost part of the bank.			X	X
I	Trunk	Woody trunk not exceeding 12cm diameter (similar to post) and placed centrally within the quadrat. Soil and vegetation sampled round the edge of the trunk to the limits of the sample area. Selected trunks were those nearest to the line of the transect.			X	X
Ji	Bank slope (arable)	Quadrat placed halfway up bank on the boundary side adjacent to the arable field.			X	X
Jii	Bank slope (ley)	Quadrat placed halfway up bank on the boundary side adjacent to the ley field.			X	X
K	Margin	Quadrat positioned midway across margin width and following the line of the transect.		X		X

Table 4.2.1 Description of features sampled in each field boundary-margin combination (indicated by a X) with codes used in the analysis.

Each quadrat was 0.04m^2 (0.2m by 0.2m) and soil searches were conducted to a depth of 0.2m. The quadrat area was marked using a metal square and habitat characteristics recorded (Table 4.2.2). The vegetation and leaf litter on the soil surface and the upper 5cm of soil ('Depth 1') were removed into a plastic container using a trowel and secateurs. Soil from 5-20cm depth ('Depth 2') was subsequently removed and placed into a second plastic container. Each sample of soil and/or vegetation and litter was systematically searched for 20 minutes in the field. Coleoptera were captured with the aid of a pooter and specimens were placed in labelled sample bags for freezing and later identification. Throughout the first transect conducted in each field boundary a soil sample of approximately 40 grams was collected from Depth 2 of each quadrat to measure gravimetric soil moisture and organic matter content (see Table 4.2.2 for methods). Carabidae were identified to species and Staphylinidae to species or genus. All other Coleoptera captured were identified to family level (for details of taxonomic references see 3.2.1).

Microhabitat characteristics	Code	Description
Canopy height (m)	*canht*	Average height of woody canopy.
Bank height (m)	*bankht*	Height of quadrat position above field level.
Ground vegetation height (m)	*veght*	Height of ground vegetation within the quadrat area.
Distance from arable edge (m)	*dist-a*	Measured from the centre of the quadrat to the uncultivated boundary edge adjacent to the arable field.
Distance from ley edge (m)	*dist-l*	Measured from the centre of the quadrat to the uncultivated boundary edge adjacent to the ley field.
% Soil moisture content	*moist*	Soil samples collected, after searching for Coleoptera, from depth two of each quadrat in transect one. Samples weighed and oven dried at 105°C for 24 hours and reweighed. Calculated as the difference between the dry weight and wet weight of the soil samp
% Soil organic matter content	*organ*	After oven drying (see above) the soil sample burnt in muffle furnace at 500°C for 3 to 4 hours. The remining ash content is allowed to cool in a dry environment and reweighed. Calculated as the difference between the ash weight and original wet weight, d
% Bare ground	*.bare*	Amount of quadrat that is bare ground estimated as a % of the total quadrat surface area.
% Monocot cover	*.mono*	Amount of quadrat supporting monocot vegetation estimated as a % of the total quadrat surface area.
% Dicot cover	*.di*	Amount of quadrat supporting dicot vegetation estimated as a % of the total quadrat surface area.
Dead plant stubble index (0-3)	*dead*	Presence of dead plant stems and stubble recorded as 0=none, 1=low, 2=medium and 3=high.
Leaf litter index (0-3)	*litter*	Presence of leaf litter recorded as 0=none, 1=low, 2=medium and 3=high.
Moss cover index (0-3)	*moss*	Presence of moss cover recorded as 0=none, 1=low, 2=medium and 3=high.

Table 4.2.2 Description of microhabitat characteristics recorded at each feature location, with codes used in the analysis.

4.2.2 Analysis

Three sets of analyses were conducted. The first investigated variation in habitat characteristics between features within and between each field boundary-margin combination (i.e. PW-M, PW+M, H-M and H+M). The second compared mean richness and density values of coleopteran families (excluding Carabidae and Staphylinidae), Carabidae and Staphylinidae between features within each field boundary-margin combination. The third set of analyses examined the relative importance of habitat characteristics in influencing the composition of Coleoptera, Carabidae and Staphylinidae.

Quantitative habitat characteristics recorded at each quadrat were compared with a repeated measures GLM using the six transects from each field boundary-margin combination as replicates, except for soil moisture and soil organic matter content where only two replicates were available. Differences between features and depth were tested using Tukey's test as appropriate. Categorical habitat characteristics (leaf litter, dead plant stubble and moss cover) were compared using the non-parametric Friedman test for repeated samples based on the Chi-squared statistic. These analyses aimed to describe features within each field boundary-margin combination, therefore arable-field and ley-field quadrats were omitted.

A principal components analysis (PCA) was used to summarise the habitat descriptors for each feature and illustrate the similarity or otherwise of the same habitat feature sampled from different field boundary-margin types. Features sampled in the first set of transects conducted at each field boundary ('Transect One') were used in the analysis as this transect recorded all possible habitat characteristics including soil moisture and soil organic matter content. PCA is most suited to linear data of quantitative measurements rather than compositional data with many zeros that follows a unimodal relationship (Jongman *et al.*, 1995). For descriptive purposes large departures from the normal data structure (uncorrelated and with normal distribution) may be tolerated (Gauch, 1982). Within a PCA biplot showing habitat characteristics and features, the habitat characteristics increase linearly along the direction of the arrow. By projecting a feature point perpendicularly onto the arrow of a habitat characteristic it is possible to rank features supporting the greatest magnitude of that variable (furthest from the origin in the direction the arrow in pointing). Where

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features are positioned behind the origin from a habitat characteristic, the feature supports below average values for that variable (Jongman *et al.*, 1995).

Variation in the mean richness and density of Coleoptera, Carabidae and Staphylinidae between features within each boundary-margin combination were compared using the six transects as replicates. Using GLM, data were analysed with feature treated as a between-subject factor and soil depth as a within subject repeated measure. The density of *B. lampros* (the most abundant species captured) was also compared between features within each boundary-margin type. Differences between features and depth were tested using Tukey's pairwise comparisons as appropriate. This analysis aimed to examine overwintering distributions in field boundary habitat, therefore quadrats taken from the arable-field and ley-field were omitted. All GLM and Friedmans tests were performed using SPSS 11.0.

Multivariate analysis was used to compare habitat characteristics of features between boundary-margin combinations and to examine the relationship between overwintering compositions and habitat characteristics from features in all boundary-margin types. Detrended Correspondence Analysis (DCA) was used to compare the relative utilisation of all features (including field samples) by coleopteran families (including Carabidae and Staphylinidae) between boundary-margin combinations. Coleopteran family density for each quadrat was transformed to describe the utilisation of each feature as a proportion of the total transect population. This transformation was conducted to eliminate any potential bias caused by differing abundances of Coleoptera in transects, field boundaries or boundary types. Values of relative utilisation per transect were then summed for each field boundary-margin combination. When data are plotted using DCA (with detrending by segments) the axes are measured in standard deviation (S.D.) units of species turnover. Therefore the length of the DCA axes are an approximate measure of the length of the ecological gradient, in species turnover units. A gradient length of >4 S.D. units represents a complete turnover in species composition between samples, whilst a half-change in species composition occurs within approximately 1 to 1.4 S.D units (ter Braak, 1995). A gradient length of >4 S.D. suggests that species composition shows a strong unimodal response to the sampled environmental gradient, whereas a gradient length of <3 S.D. suggests a linear response (ter Braak & Šmilauer, 2002). With a short

gradient length species composition may not necessarily respond in a linear fashion to the environment if sites sampled do not encompass the full range of the environmental gradient to which species are responding.

Canonical Correspondence Analysis (CCA) was used to determine the amount of variation in compositional data explained by the recorded habitat characteristics. CCA is generally regarded as an ordination method for unimodal data though it can be used for both unimodal and linear data. In addition, CCA is preferable to RDA when analysing compositional data with many zero values (ter Braak & Šmilauer, 2002). Composition data was analysed in three taxonomic groups: Coleopteran families (excluding Carabidae and Staphylinidae), Carabidae species and Staphylinidae taxa (species or genus). Density data per quadrat for each taxonomic group were transformed to describe the relative utilisation of a field boundary feature as a proportion of the total population in a transect (field samples were omitted). An equivalent data matrix included all quantitative and categorical habitat variables. For each taxonomic group two CCAs were conducted. The first, termed 'All Transects', included all field boundary quadrats taken from the three sets of transects (n=180), used month as a covariable and 11 environmental variables. The second analysis, termed 'Transect One', used all samples from the first transect (n=60) with the 11 original environmental variables (as for 'all transects') plus the variables % soil moisture and % soil organic matter content that were only measured in the first transect taken from each boundary. The analysis maximised inter-species distances and employed biplot scaling. The importance of environmental variables was determined using automatic forward selection and tested with Monte Carlo permutation test (999 permutations) under the full (or null) model (ter Braak & Šmilauer, 2002). CCA ordination plots display only those taxa with a high degree of weight (>20%) within the analysis. Weights represent the percentage of the weighted-average (from the ordination calculation) of the taxa with the largest impact on the analysis results (ter Braak & Šmilauer, 2002). Interpretation of ordination diagrams followed ter Braak & Verdonschot (1995). All detrended and canonical correspondence analysis was conducted using CANOCO 4.5 and ordination plots produced with CanoDraw (ter Braak & Šmilauer, 2002).

4.3   RESULTS

4.3.1   Habitat characteristics

All environmental variables differed significantly between features in at least one field boundary type with the exception of soil moisture and soil organic matter content (Tables 4.3.1 to 4.3.4). The habitat characteristic canopy height showed a dichotomous trend between post and wire and hedgerow boundaries and may be used as a clear indication of field boundary type. Within field boundary-margin combinations, greatest bank height was associated with the fence line in post and wire boundaries, and the bank top, bank slope and trunk features in hedgerows. Margin features had intermediate bank height. Edge sites were consistently close to field level at all boundary types. Other environmental variables characterise certain features. For example, high levels of bare ground, litter and moss were characteristic of bank top, bank slopes, trunk and rock features in hedgerows, whilst maximal vegetation height and dead plant stubble, with low bare ground cover were typical of the fence-post and fence-wire features of all field boundary types. Distance of features from the ley and arable edge varies in all boundary-margin combinations. Interpretation of these habitat characteristics was complicated by increasing field boundary width in the order PW-M (0.5m) < PW+M (2.55m) < H-M (3.0m) < H+M (10.25m). As a result, maximal values for 'distance to arable edge' (>7m) referred to the arable slope, rock, bank top, trunk, fence-post, fence-wire, ley slope and ley edge features of H+M boundaries. Maximal 'distance to ley edge' values (>8m) refer to margin and arable edge features of H+M boundaries. Features at all other field boundary types were located at <3m for both distance to ley or arable edge.

The PCA biplot illustrated strong similarities in the habitat characteristics of same features across different boundary-margin combinations (Figure 4.3.1). These similarities were particularly evident for bank slopes characterised by bare ground and moss cover and bank tops typified by high leaf-litter cover. Fence-post and fence-wire features supported a range of characteristics but were particularly associated with dicot vegetation and high soil moisture content. All margin features were characterised by a high cover of dead plant stubble left over from summer annuals, tall vegetation and greatest distance from the ley edge. The latter resulted from the positioning of margins adjacent to arable crops, rather than pasture where they would be heavily grazed. Ley edge sites tended to have more monocot vegetation or bare

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Environmental variables		Post and wire, without margin					Repeated measures GLM	
		Arable edge	Post	Wire	Ley edge	Rock		
Distance to arable edge	mean	0.17	0.33	0.33	0.43	0.33	df	4, 20
	s.e.	0.07	0.04	0.04	0.07	0.05	F	6.48
							P	<0.01
Distance to ley edge	mean	0.43	0.27	0.27	0.17	0.27	df	4, 20
	s.e.	0.07	0.04	0.04	0.07	0.05	F	6.48
							P	<0.01
Bank height	mean	0.05	0.08	0.08	0.05	0.05	df	1, 5
	s.e.	0.00	0.01	0.01	0.00	0.00	GG	3.96
							P	n.s.
Vegetation height	mean	0.16	0.23	0.20	0.13	0.08	df	4, 20
	s.e.	0.02	0.04	0.01	0.02	0.02	F	6.48
							P	<0.01
% Bare ground	mean	36.67	7.50	21.67	25.00	15.00	df	4, 20
	s.e.	11.16	1.71	6.54	7.64	6.71	F	1.93
							P	n.s.
% Monocot cover	mean	29.17	25.83	36.67	60.00	16.67	df	4, 20
	s.e.	8.98	9.52	15.85	7.75	4.22	F	3.91
							P	<0.05
% Dicot cover	mean	34.17	16.67	41.67	15.00	8.33	df	4, 20
	s.e.	9.17	3.33	9.80	6.71	3.07	F	4.81
							P	<0.01
% Soil moisture	mean	27.68	31.60	28.28	27.44	28.60	df	1, 5
	s.e.	2.08	2.31	2.44	4.30	2.43	GG	3.45
							P	n.s.
% Soil organic matter	mean	7.38	10.68	9.60	6.90	6.94	df	1, 5
	s.e.	1.12	0.39	1.14	0.87	1.18	GG	2.79
							P	n.s.
Dead plant stem index	mean	0.50	1.67	1.17	0.67	0.33	df	4, 20
	s.e.	0.50	0.42	0.60	0.49	0.21	F	1.31
							P	n.s.
Leaf litter index	mean	0.00	0.00	0.00	0.00	0.00	df	1, 5
	s.e.	0.00	0.00	0.00	0.00	0.00	GG	1
							P	n.s.
Moss cover index	mean	0.17	0.00	0.00	0.00	0.00	df	1, 5
	s.e.	0.17	0.00	0.00	0.00	0.00	GG	1
							P	n.s.

Table 4.3.1 Microhabitat characteristics (±1 s.e.) recorded at features within PW-M boundaries. Microhabitat characteristics are summarised over all transects data with the exception of % soil moisture and % soil organic content summarised over transect one. Results of GLM (degrees of freedom, F-ratios or GG-ratios and P values) are shown.

Environmental variables				Post and wire, with margin				Repeated measures GLM	
		Arable edge	Post	Wire	Ley edge	Rock	Margin	df	1, 5.1
Distance to arable edge	mean	0.10	2.35	2.35	2.45	0.95	1.50	df	1, 5.1
	s.e.	0.00	0.20	0.20	0.20	0.28	0.00	F	68.61
								P	<0.001
Distance to ley edge	mean	2.45	0.20	0.20	0.10	1.60	1.05	df	1, 5.1
	s.e.	0.02	0.00	0.00	0.00	0.28	0.02	F	68.61
								P	<0.001
Bank height	mean	0.07	0.52	0.48	0.04	0.16	0.24	df	1.49, 7.43
	s.e.	0.01	0.02	0.01	0.01	0.03	0.01	GG	147.71
								P	<0.001
Vegetation height	mean	0.17	0.22	0.21	0.09	0.20	0.23	df	2, 10.2
	s.e.	0.03	0.07	0.05	0.03	0.07	0.02	F	1.37
								P	n.s.
% Bare ground	mean	28.33	3.33	20.00	33.33	8.33	26.67	df	5, 25
	s.e.	13.27	2.11	8.94	11.45	4.01	2.47	F	1.91
								P	n.s.
% Monocot cover	mean	27.50	16.67	50.00	50.00	18.33	34.17	df	5, 25
	s.e.	11.95	3.33	5.16	8.56	6.01	5.23	F	3.65
								P	<0.05
% Dicot cover	mean	44.17	20.00	30.00	16.67	8.33	39.17	df	1.8, 9
	s.e.	13.19	3.65	5.16	4.94	3.07	3.75	F	4.42
								P	<0.05
% Soil moisture	mean	29.07	36.88	37.29	31.25	31.22	29.07	df	1, 1
	s.e.	0.76	0.07	0.92	0.52	4.54	0.76	GG	3.58
								P	n.s.
% Soil organic matter	mean	8.14	13.70	13.83	5.86	8.43	8.14	df	1, 1
	s.e.	0.25	0.03	0.09	0.35	0.37	0.25	GG	149.39
								P	n.s.
Dead plant stem index	mean	0.83	1.00	2.00	0.00	0.33	2.00	df	5, 25
	s.e.	0.31	0.45	0.52	0.00	0.21	0.26	F	8.2
								P	<0.001
Leaf litter index	mean	0.00	0.50	0.50	0.50	0.00	0.00	df	1, 5
	s.e.	0.00	0.50	0.50	0.50	0.00	0.00	GG	1
								P	n.s.
Moss cover index	mean	0.00	0.00	0.00	0.00	0.17	0.00	df	5, 25
	s.e.	0.00	0.00	0.00	0.00	0.17	0.00	GG	3.65
								P	<0.05

Table 4.3.2 Microhabitat characteristics (±1 s.e.) recorded at each feature sampled within PW+M boundaries. Microhabitat characteristics are summarised over all transects data with the exception of % soil moisture and % soil organic content summarised over transect one. Results of the GLM (degrees of freedom, F-ratios or GG-ratios and P values) are shown.

Environmental variables		Arable edge	Post	Wire	Ley edge	Rock	Bank top	Trunk	Slope (arable)	Slope (ley)	Repeated measures GLM	
					Hedgerow, without margin							
Distance to arable edge	mean	0.10	0.20	0.20	2.90	1.33	1.70	2.20	1.00	2.40	df	1, 5
	s.e.	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	F	78.88
											P	<0.001
Distance to ley edge	mean	2.90	2.80	2.80	0.10	1.67	1.30	0.80	2.00	0.60	df	1, 5
	s.e.	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	F	78.88
											P	<0.001
Bank height	mean	0.07	0.08	0.08	0.04	0.27	0.70	0.51	0.58	0.54	df	1.3, 6.7
	s.e.	0.00	0.10	0.10	0.00	0.05	0.04	0.02	0.06	0.06	GG	60.69
											P	<0.001
Vegetation height	mean	0.16	0.22	0.19	0.13	0.06	0.05	0.22	0.10	0.06	df	1.4, 6.8
	s.e.	0.02	0.05	0.04	0.02	0.03	0.02	0.16	0.02	0.03	F	1.4
											P	n.s.
% Bare ground	mean	25.00	12.50	50.83	46.67	26.67	72.50	30.00	72.50	71.67	df	2, 10
	s.e.	7.64	3.59	4.90	12.82	6.67	15.48	3.65	9.98	13.27	F	6.21
											P	<0.05
% Monocot cover	mean	45.83	5.83	5.00	25.00	6.67	1.67	3.33	0.83	10.00	df	2.3, 11.4
	s.e.	6.88	3.27	2.24	7.19	4.94	1.67	2.11	0.83	10.00	F	7.94
											P	<0.01
% Dicot cover	mean	29.17	21.67	44.17	28.33	5.00	9.17	6.67	26.67	18.33	df	3.3, 16.4
	s.e.	10.52	4.94	5.83	7.92	3.42	5.54	3.33	10.22	10.46	F	3.85
											P	<0.05
% Soil moisture	mean	31.08	34.41	37.96	32.81	32.07	33.21	29.24	32.74	25.58	df	1, 1
	s.e.	3.03	0.80	0.00	0.00	2.33	1.25	3.70	2.70	0.00	GG	2.76
											P	n.s.
% Soil organic matter	mean	7.75	9.45	9.36	8.03	7.65	10.75	11.95	8.44	9.34	df	1, 1
	s.e.	1.91	0.04	0.00	0.00	1.77	1.91	1.20	0.03	2.01	GG	1.06
											P	n.s.
Dead plant stem index	mean	0.33	0.67	0.67	0.33	0.00	0.17	0.17	0.17	0.33	df	3.4, 17
	s.e.	0.21	0.33	0.33	0.21	0.00	0.17	0.17	0.17	0.21	F	1.04
											P	n.s.
Leaf litter index	mean	0.17	0.83	1.67	0.67	1.00	1.50	1.67	1.50	1.67	df	2.8, 14.1
	s.e.	0.17	0.48	0.33	0.33	0.45	0.43	0.33	0.22	0.42	GG	2.39
											P	n.s.
Moss cover index	mean	0.17	0.00	0.00	0.00	0.17	0.83	0.50	0.00	1.17	df	2.4, 11.8
	s.e.	0.17	0.00	0.00	0.00	0.17	0.40	0.34	0.00	0.48	GG	3.29
											P	n.s.

Table 4.3.3 Microhabitat characteristic means (±1 s.e.) recorded at each feature sampled within H-M boundaries. Microhabitat characteristics are summarised over all transects data with the exception of % soil moisture and % soil organic content summarised over transect one. Results of the GLM (degrees of freedom, F-ratios or GG-ratios and P values) are shown.

		Arable edge	Post	Wire	Ley edge	Rock	Bank top	Trunk	Slope (arable)	Slope (ley)	Margin	Repeated measures GLM	
Distance to arable edge	mean	0.10	8.85	8.85	10.15	7.42	8.00	8.68	7.35	9.25	1.50	df	1,4, 7
	s.e.	0.00	0.65	0.65	0.07	0.31	0.00	0.24	0.02	0.07	0.00	F	128.4
												P	<0.001
Distance to ley edge	mean	10.15	1.40	1.40	0.10	2.83	2.25	1.57	2.90	1.00	8.85	df	1,4, 7
	s.e.	0.07	0.58	0.58	0.00	0.34	0.07	0.24	0.04	0.00	0.11	F	127.55
												P	<0.001
Bank height	mean	0.08	0.06	0.06	0.05	0.34	0.99	0.75	0.83	0.81	0.34	df	1.9, 9.7
	s.e.	0.00	0.00	0.01	0.00	0.04	0.02	0.06	0.02	0.03	0.02	GG	209.13
												P	<0.001
Vegetation height	mean	0.13	0.18	0.10	0.13	0.09	0.05	0.10	0.11	0.09	0.19	df	2.6, 12.8
	s.e.	0.03	0.04	0.02	0.03	0.02	0.02	0.01	0.01	0.02	0.02	F	3.65
												P	<0.05
% Bare ground	mean	23.33	23.33	55.00	31.67	35.00	90.00	26.67	61.67	81.67	6.67	df	3.4, 17
	s.e.	12.02	4.77	7.64	9.46	13.10	5.16	2.11	11.38	7.03	3.33	F	11.11
												P	<0.001
% Monocot cover	mean	60.00	13.33	11.67	41.67	0.00	0.00	0.00	10.00	1.67	60.83	df	2.8, 14.2
	s.e.	12.91	6.67	8.33	15.37	0.00	0.00	0.00	10.00	1.67	9.35	F	9.15
												P	<0.001
% Dicot cover	mean	16.67	13.33	33.33	16.67	15.00	10.00	13.33	28.33	16.67	32.50	df	3.3, 16.6
	s.e.	6.67	4.77	8.43	7.60	3.42	5.16	2.11	7.92	6.15	7.93	F	1.85
												P	n.s.
% Soil moisture	mean	26.92	29.54	31.84	29.66	30.33	30.07	33.07	34.88	29.59	28.77	df	1, 1
	s.e.	8.26	5.71	2.51	0.14	1.06	0.00	2.55	7.10	1.46	5.26	GG	0.24
												P	n.s.
% Soil organic matter	mean	7.81	11.79	10.95	8.95	10.57	8.88	11.02	11.98	12.52	10.43	df	1, 1
	s.e.	0.39	5.55	2.08	0.04	0.89	0.00	0.35	3.30	2.76	1.90	GG	0.61
												P	n.s.
Dead plant stem index	mean	1.00	0.83	0.50	0.50	0.33	0.00	0.17	0.17	0.00	1.17	df	2.2, 11.2
	s.e.	0.52	0.54	0.50	0.34	0.33	0.00	0.17	0.17	0.00	0.17	F	1.66
												P	n.s.
Leaf litter index	mean	0.17	1.00	0.83	0.67	0.33	1.33	1.00	1.50	1.33	0.17	df	3.1, 15.6
	s.e.	0.17	0.37	0.40	0.42	0.33	0.33	0.26	0.43	0.33	0.17	GG	2.41
												P	n.s.
Moss cover index	mean	0.17	0.33	0.00	0.00	0.50	0.83	0.33	1.00	0.83	0.17	df	2.7, 13.6
	s.e.	0.17	0.33	0.00	0.00	0.34	0.40	0.33	0.52	0.48	0.17	GG	1.2
												P	n.s.

Table 4.3.4 Microhabitat characteristic means (±1 s.e.) recorded at each feature sampled within H+M boundaries. Microhabitat characteristics are summarised over all transects data with the exception of % soil moisture and % soil organic content summarised over transect one. Results of the GLM (degrees of freedom, F-ratios or GG-ratios and P values) are shown.

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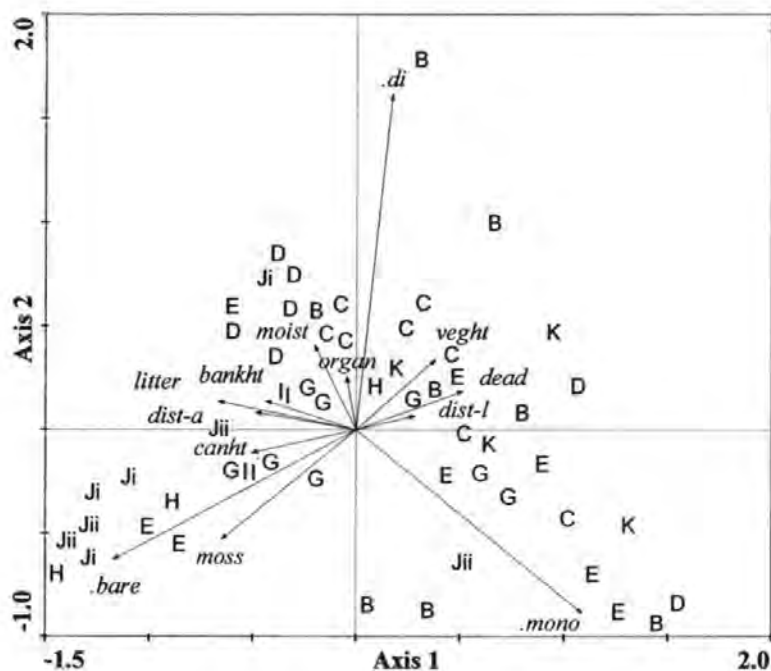
Figure 4.3.1 PCA biplot of features sampled in each field boundary-margin
combination in relation to recorded habitat characteristics from transect one data.
Codes for features B to K are: B = arable edge, C = post, D = wire, E = ley edge, G =
rock, H= bank top, I = trunk, Ji = slope (arable), Jii = slope (ley), K = margin. Codes
of habitat characteristics (in italics) are listed in Table 4.2.2.

ground, whilst arable edge features tended to be dominated by either dicot or monocot vegetation. However, these last two features showed greater variation in their habitat characteristics across boundary-margin combinations compared to other features. Similarly, several rock features, four positioned on hedge-banks and one at a post and wire boundary, had high leaf litter cover. Rock features located at other post and wire boundaries supported more monocot vegetation and dead plant stubble.

4.3.2   Density and richness

Mean density of Coleoptera and Staphylinidae, and richness of all three taxonomic groups differed significantly between features in post and wire fences both with and without margin (carabid density was evenly distributed between features in post and wire without margin boundaries) (Table 4.3.5 and 4.3.6). Generally, for post and wire boundary types (both with and without margin), the features margin, fence-post and fence-wire supported highest relative densities and richness values, rock features supported intermediate levels and arable and ley edge supported lowest relative densities and richness values for all three taxonomic groups. In contrast, field boundary features in hedgerows with and without margins supported homogenous richness and density of Coleoptera, Staphylinidae, Carabidae and *B. lampros* (Table 4.3.7 and 4.3.8). Clear preferences were shown by Coleoptera, Staphylinidae and Carabidae for Depth 1 compared to Depth 2, across features in all four field boundary types. *B. lampros* densities were also higher in Depth 1 of all features in post and wire boundaries but showed a homogenous vertical distribution in hedgerows.

In PW-M boundaries, coleopteran and Staphylinidae density and richness, and Carabidae richness differed significantly between features, whilst there were no significant differences in Carabidae or *B. lampros* density between features. Pairwise comparisons demonstrated that coleopteran density was higher in fence-wire features compared to arable edge, whilst coleopteran richness was higher in both fence-post and fence-wire sites than edge or rock features (Figure 4.3.2). Staphylinid density was also higher in both fence-post and fence-wire compared to arable edge, whilst staphylinid richness was higher in wire than arable edge sites. More carabid species were found in fence-post and fence-wire features than either arable or ley edge. There were no significant interactions between feature and depth in density or richness

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values. All density and richness values (including *B. lampros* density) were significantly greater in Depth 1 compared to Depth 2.

In PW+M boundaries, there were significant differences between features for mean density and richness values of Coleoptera, Staphylinidae and Carabidae. There were no significant differences in *B. lampros* density between features. Coleopteran density and richness was higher in margin than arable and ley edge features (Figure 4.3.3), whilst fence-post, fence-wire and rock features had intermediate values for Coleoptera density and richness. Highest staphylinid densities were observed in fence-post features, though fence-wire, rock and margin also supported intermediate densities. Edge sites supported lowest staphylinid densities. Staphylinid richness in margin, fence-post and fence-wire features was considerably higher than ley edge sites. Densities of Carabidae were highest in fence-post and margin sites, with significantly higher values in margin compared to arable or ley edge, fence-wire and rock features. Carabid richness was significantly greater in margin sites compared to all other features sampled, and intermediate in fence-post features. All density and richness values (including *B. lampros* density) were significantly greater in Depth 1. Significant feature*depth interactions were observed for Coleoptera and Staphylinidae density and richness, and for carabid richness; Depth 1 consistently supported higher densities and richness values compared to Depth 2 and where features supported high values, greater differences between the two substrate depths were observed.

In H-M and H+M, there were no measurable differences between features for any density or richness variables. In H-M boundaries, Depth 1 supported significantly higher densities of Coleoptera, Staphylinidae and Carabidae and higher richness values for coleopteran families only (Figure 4.3.4). In H+M boundaries, Depth 1 supported significantly higher density and richness values for Coleoptera, Staphylinidae and Carabidae (Figure 4.3.5). There were no significant interactions between feature and depth in density or richness values in H-M or H+M boundaries.

	Post and wire without margin		Feature		Depth		Feature*Depth
a)	Coleopteran family density (0.04m^{-2})	df	4, 20	df	1, 5	df	1.6, 8.1
	(excl. carabids & staphylinids)	s.a. F	4.1	s.a. F	9.8	G-G F	1.5
		P	<0.05	P	<0.05	P	n.s.
	Coleopteran family richness	df	4, 20	df	1, 5	df	4, 20
	(incl. carabids & staphylinids)	s.a. F	7.4	s.a. F	29.6	s.a. F	1.4
		P	<0.01	P	<0.01	P	n.s.
b)	Staphylinidae density (0.04m^{-2})	df	2.1, 10.5	df	1, 5	df	4, 20
		G-G F	5.6	s.a. F	11.9	s.a. F	1.2
		P	<0.05	P	<0.05	P	n.s.
	Staphylinidae richness	df	4, 20	df	1, 5	df	4, 20
		s.a. F	3.4	s.a. F	18.2	s.a. F	1.2
		P	<0.05	P	<0.01	P	n.s.
c)	Carabidae density (0.04m^{-2})	df	1.6, 7.9	df	1, 5	df	4, 20
		G-G F	1.5	s.a. F	7.3	s.a. F	1.7
		P	n.s.	P	<0.05	P	n.s.
	Carabidae richness	df	4, 20	df	1, 5	df	4, 20
		s.a. F	6	s.a. F	9.6	s.a. F	1.5
		P	<0.01	P	<0.05	P	n.s.
d)	B. lampros density (0.04m^{-2})	df	4, 20	df	1, 5	df	1.3, 6.4
		s.a. F	2.2	s.a. F	15.2	G-G F	1.5
		P	n.s.	P	<0.05	P	n.s.

Table 4.3.5 In PW-M: results of repeated measures GLM testing for differences in mean density (0.04m^{-2}) and richness of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* from five features at two depths. Statistics are shown for differences between features, between depths and for interactions between the two main effects. Means (±1 s.e) for density (0.04m^{-2}) and richness values for each of the four derived variables at both depths within each feature are illustrated in Figure 4.3.2.

	Post and wire with margin	Feature		Depth		Feature*Depth	
a)	Coleopteran family density (0.04m⁻²)	df	2, 10	df	1, 5	df	5, 25
	(excl. carabids & staphylinids)	G-G F	6.1	s.a. F	24.7	s.a. F	4.7
		P	<0.05	P	<0.01	P	<0.05
	Coleopteran family richness	df	5, 25	df	1, 5	df	5, 25
	(incl. carabids & staphylinids)	s.a. F	29.4	s.a. F	48.9	s.a. F	5.4
		P	<0.001	P	<0.01	P	<0.01
b)	Staphylinidae density (0.04m⁻²)	df	1.3, 6.9	df	1, 5	df	2.1, 10.4
		G-G F	6.2	s.a. F	67.7	G-G F	13
		P	<0.05	P	<0.001	P	<0.01
	Staphylinidae richness	df	1.5, 7.7	df	1, 5	df	5, 25
		G-G F	15.2	s.a. F	54.9	s.a. F	4.5
		P	<0.01	P	<0.01	P	<0.01
c)	Carabidae density (0.04m⁻²)	df	1.3, 6.5	df	1, 5	df	1.4, 7.2
		G-G F	10.2	s.a. F	19.1	G-G F	4.5
		P	<0.05	P	<0.01	P	n.s
	Carabidae richness	df	5, 25	df	1, 5	df	5, 25
		s.a. F	41.4	s.a. F	18.6	s.a. F	6.3
		P	<0.001	P	<0.01	P	<0.01
d)	B. lampros density (0.04m⁻²)	df	2.6, 13.1	df	1, 5	df	1.9, 9.5
		G-G F	1.9	s.a. F	7.2	G-G F	1.3
		P	n.s	P	<0.05	P	n.s.

Table 4.3.6 In PW+M: results of repeated measures GLM testing for differences in mean density (0.04m⁻²) and richness of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* from six features at two depths. Statistics are shown for differences between features, between depths and for interactions between the two main effects. Means (±1 s.e) for density (0.04m⁻²) and richness values for each of the four derived variables at both depths within each feature are illustrated in Figure 4.3.3.

	Hedgerow without margin	Feature		Depth		Feature*Depth	
a)	Coleopteran family density (0.04m⁻²)	df	2.7, 13.3	df	1, 5	df	2.1, 10.7
	(excl. carabids & staphylinids)	G-G F	2.1	s.a. F	20.5	G-G F	1.2
		P	n.s.	P	<0.01	P	n.s.
	Coleopteran family richness	df	2.5, 12.4	df	1, 5	df	3.1, 15.3
	(incl. carabids & staphylinids)	G-G F	1.2	s.a. F	11.2	G-G F	0.5
		P	n.s.	P	<0.05	P	n.s.
b)	Staphylinidae density (0.04m⁻²)	df	2.7, 13.4	df	1, 5	df	2.9, 14.4
		G-G F	1.7	s.a. F	11.6	G-G F	1.1
		P	n.s.	P	<0.05	P	n.s.
	Staphylinidae richness	df	2.4, 12.4	df	1, 5	df	3.2, 16.1
		G-G F	2.9	s.a. F	3.7	G-G F	1.3
		P	n.s.	P	n.s.	P	n.s.
c)	Carabidae density (0.04m⁻²)	df	1.8, 8.9	df	1, 5	df	1.5, 7.3
		G-G F	1.2	s.a. F	8.6	G-G F	1
		P	n.s.	P	<0.05	P	n.s.
	Carabidae richness	df	2.4, 12.1	df	1, 5	df	3.1, 15.7
		G-G F	2.2	s.a. F	4.6	G-G F	1.7
		P	n.s.	P	n.s.	P	n.s.
d)	B. lampros density (0.04m⁻²)	df	1.4, 7.2	df	1, 5	df	2.4, 12.1
		G-G F	1.7	s.a. F	4.4	G-G F	1
		P	n.s.	P	n.s.	P	n.s.

Table 4.3.7 In H-M: results of repeated measures GLM testing for differences in mean density (0.04m⁻²) and richness of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* from nine features at two depths. Statistics are shown for differences between features, between depths and for interactions between the two main effects. Means (±1 s.e) for density (0.04m⁻²) and richness values for each of the four derived variables at both depths within each feature are illustrated in Figure 4.3.4.

	Hedgerow with margin	Feature		Depth		Feature*Depth	
a)	Coleopteran family density (0.04m^{-2})	df	3.3, 16.7	df	1, 5	df	2.8, 13.9
	(excl. carabids & staphylinids)	G-G F	3.1	s.a. F	23	G-G F	1.9
		P	n.s.	P	<0.01	P	n.s.
	Coleopteran family richness	df	2.8, 14.2	df	1, 5	df	2.7, 13.6
	(incl. carabids & staphylinids)	G-G F	1.9	s.a. F	31.6	G-G F	3.1
		P	n.s.	P	<0.01	P	n.s.
b)	Staphylinidae density (0.04m^{-2})	df	2.3, 11.4	df	1, 5	df	2.8, 13.9
		G-G F	2.7	s.a. F	36.1	G-G F	1.4
		P	n.s.	P	<0.01	P	n.s.
	Staphylinidae richness	df	2.3, 11.7	df	1, 5	df	3.1, 15.4
		G-G F	2.5	s.a. F	18.6	G-G F	1.6
		P	n.s.	P	<0.01	P	n.s.
c)	Carabidae density (0.04m^{-2})	df	2.5, 12.3	df	1, 5	df	2.5, 12.4
		G-G F	0.6	s.a. F	13.3	G-G F	0.9
		P	n.s.	P	<0.05	P	n.s.
	Carabidae richness	df	2.5, 12.5	df	1, 5	df	3.4, 17.1
		G-G F	0.7	s.a. F	18.3	G-G F	1.2
		P	n.s.	P	<0.01	P	n.s.
d)	B. lampros density (0.04m^{-2})	df	3, 14.9	df	1, 5	df	1.8, 8.8
		G-G F	0.8	s.a. F	3	G-G F	1.1
		P	n.s.	P	n.s.	P	n.s.

Table 4.3.8 In H+M: results of repeated measures GLM testing for differences in mean density (0.04m^{-2}) and richness of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* from ten features at two depths. Statistics are shown for differences between features, between depths and for interactions between the two main effects. Means (±1 s.e) for density (0.04m^{-2}) and richness values for each of the four derived variables at both depths within each feature are illustrated in Figure 4.3.5.

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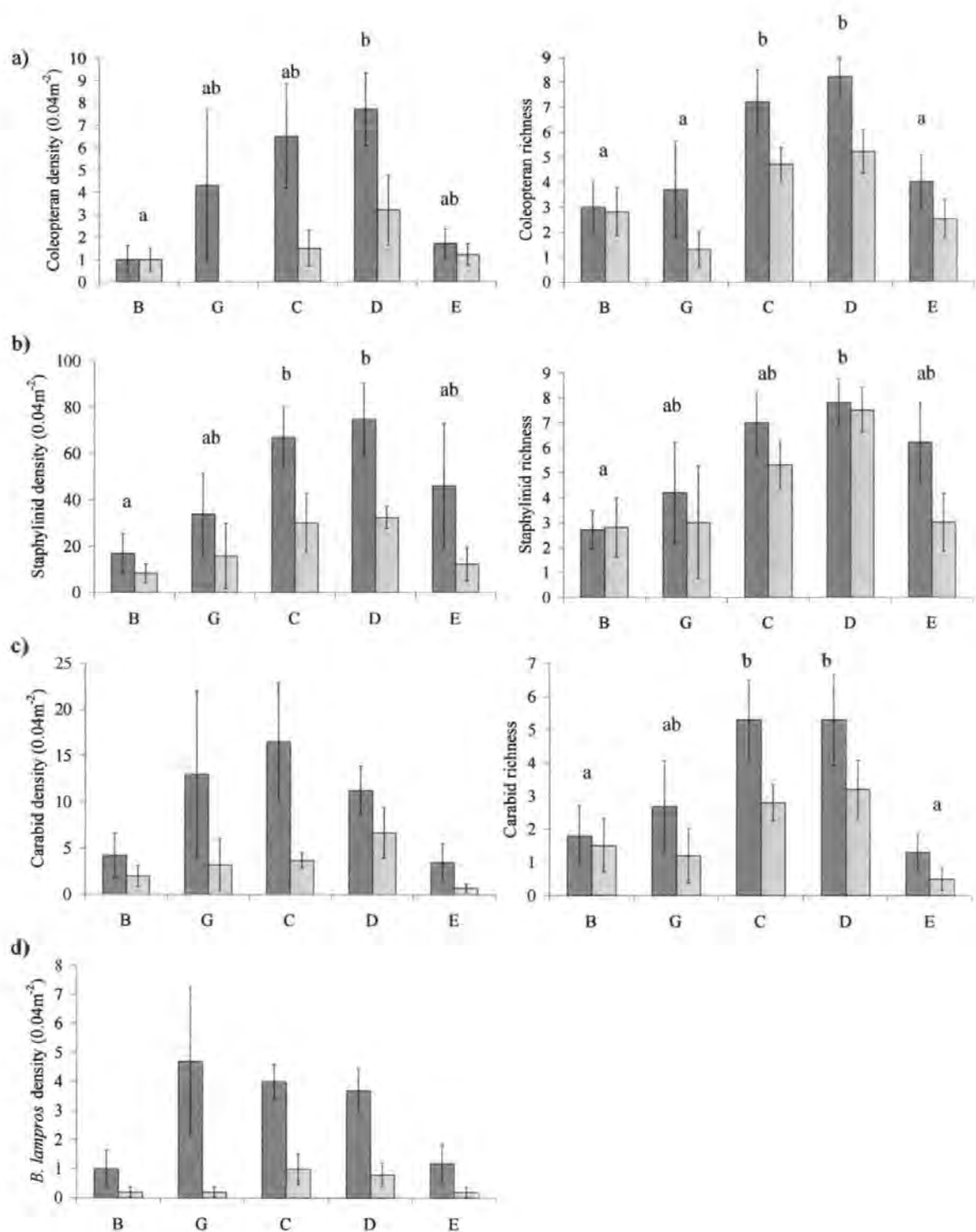
Figure 4.3.2 In PW-M: Mean density ($0.04m^{-2}$) and richness values (± 1 s.e.) of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* in each feature at depth 1 (dark grey) and depth 2 (light grey). The sequence of features labelled B-K represents the boundary profile: B = arable edge, C = fence-post, D = fence-wire, E = ley edge and G = rock. Results of repeated measures GLM testing for difference in means between features and depths are shown in Table 4.3.5. Features with density or richness values that do not differ are denoted by the same letter (Tukey's test).
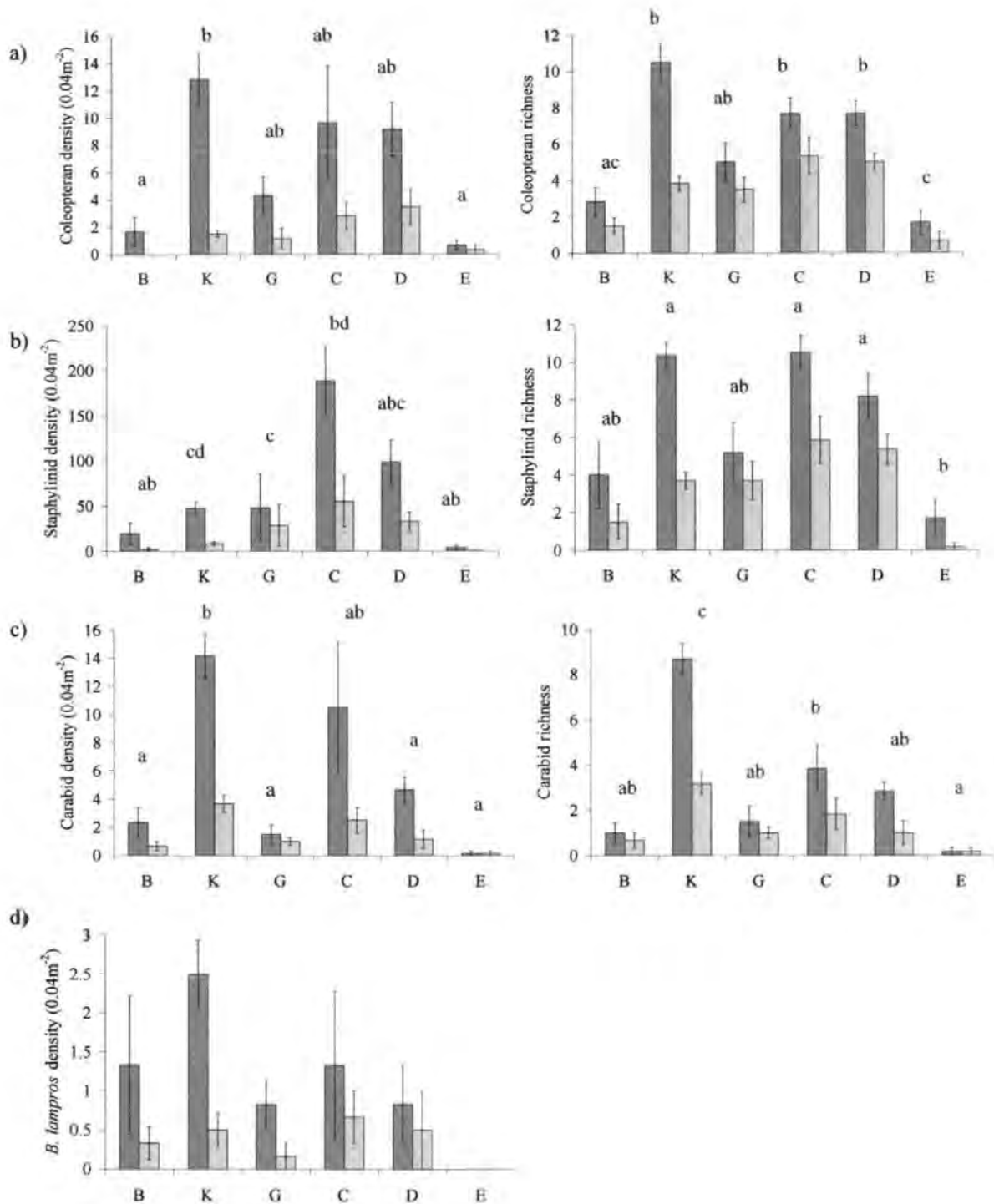
Figure 4.3.3 In PW+M: Mean density (0.04m^{-2}) and richness values (± 1 s.e.) of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* in each feature at depth 1 (dark grey) and depth 2 (light grey). The sequence of features labelled B-K represents the boundary profile: B = arable edge, C = fence-post, D = fence-wire, E = ley edge, G = rock and K = margin. Results of repeated measures GLM testing for difference in means between features and depths are shown in Table 4.3.6. Features with density or richness values that do not differ are denoted by the same letter (Tukey's test).

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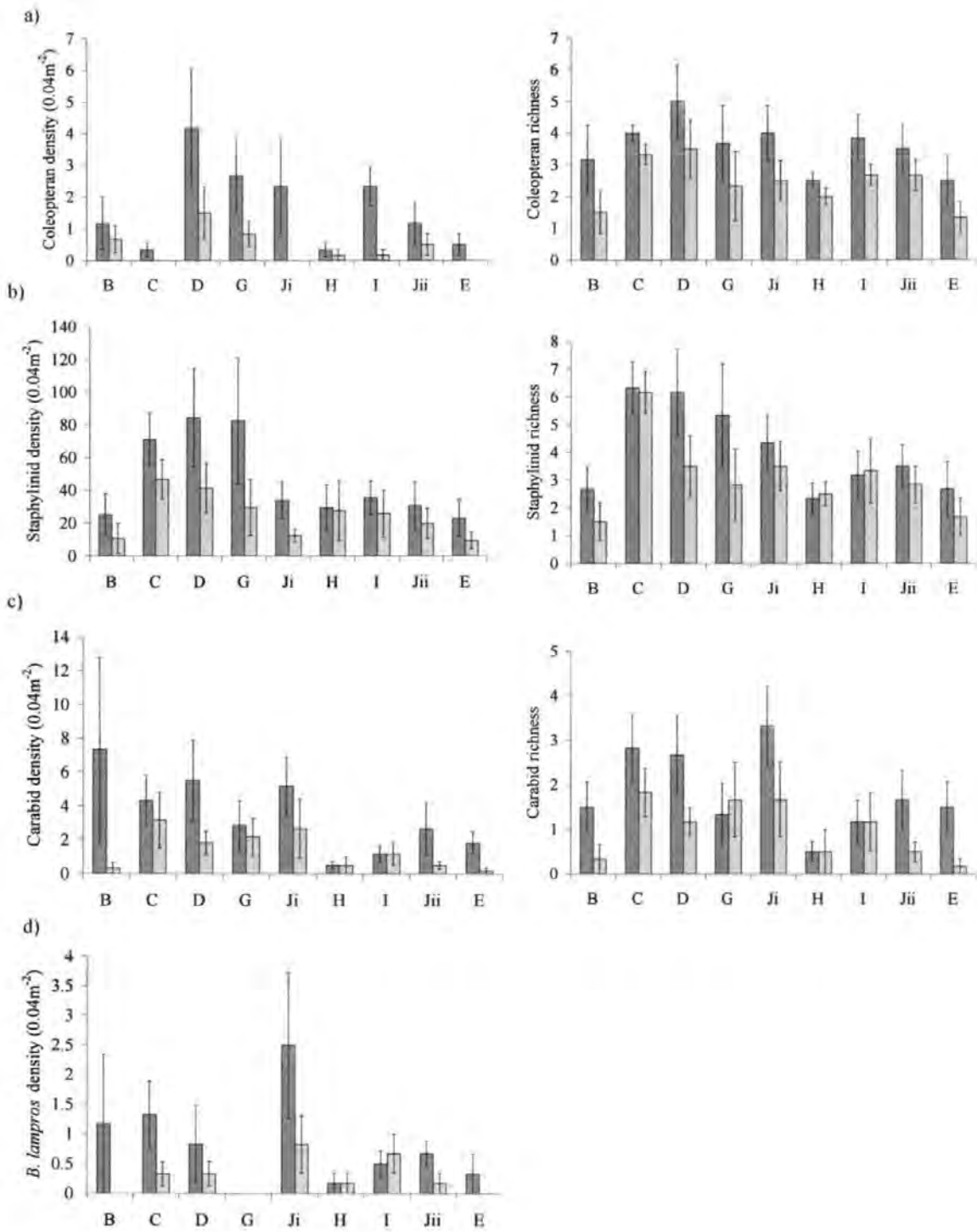
Figure 4.3.4 In H-M: Mean density $(0.04m^{-2})$ and richness values ($\pm$ 1 s.e.) of a) Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* in each feature at depth 1 (dark grey) and depth 2 (light grey). The sequence of features labelled B-Jii represents the boundary profile: B = arable edge, C = fence-post, D = fence-wire, E = ley edge, G = rock, H = bank top, I = trunk, Ji = slope (arable) and Jii = slope (ley). Results of repeated measures GLM testing for difference in means between features and depths are shown in Table 4.3.7.
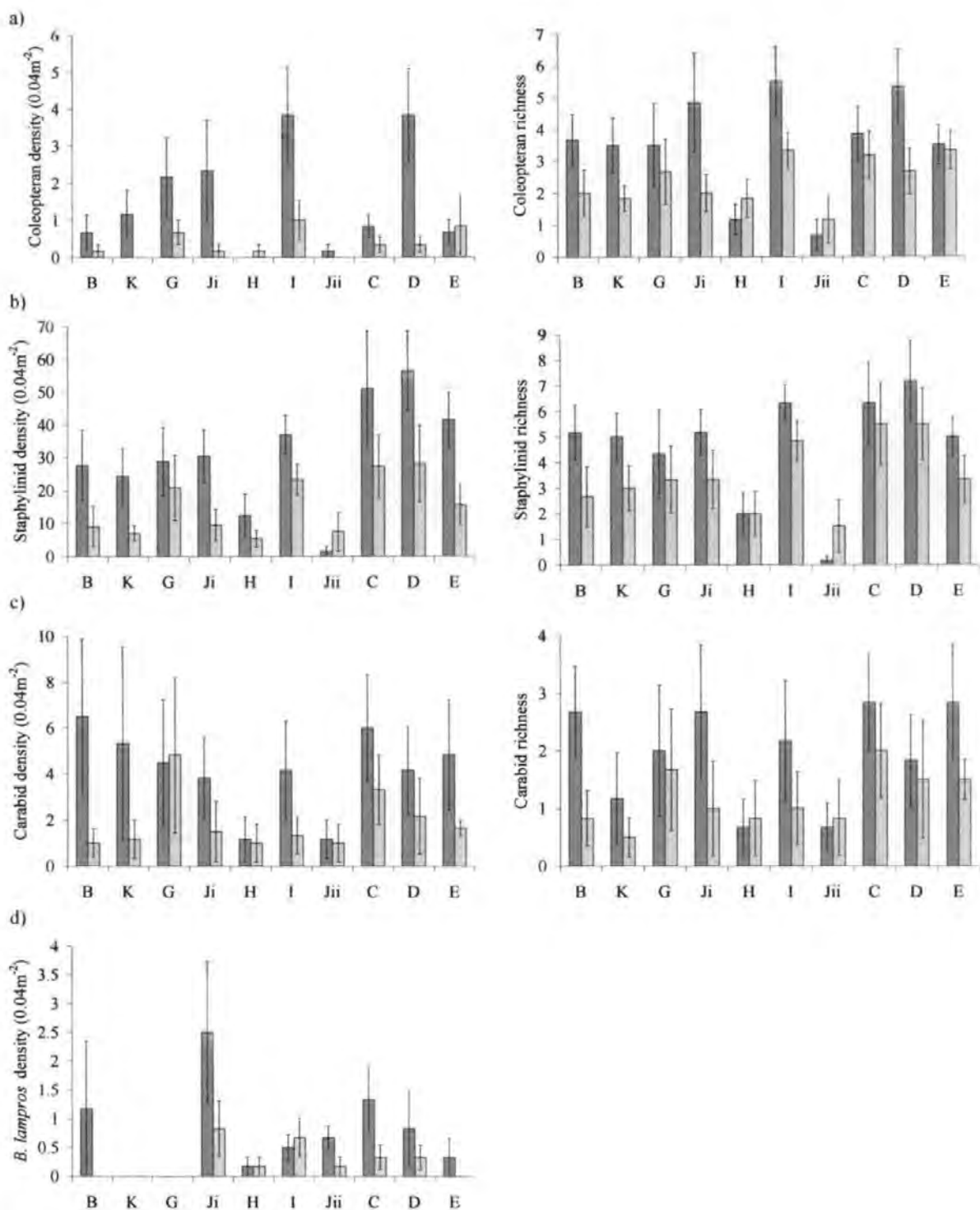
Figure 4.3.5 In H+M: Mean density (0.04m^{-2}) and richness values (± 1 s.e.) of a)
Coleoptera, b) Staphylinidae, c) Carabidae and d) *B. lampros* in each feature at depth
1 (dark grey) and depth 2 (light grey). The sequence of features labelled B-K
represents the boundary profile: B = arable edge, C = fence-post, D = fence-wire, E =
ley edge, G = rock, H = bank top, I = trunk, Ji = slope (arable), Jii = slope (ley) and K
= margin. Results of repeated measures GLM testing for difference in means between
features and depths are shown in Table 4.3.8.

4.3.3   Coleopteran composition in relation to features

The DCA biplot illustrated coleopteran family composition at all features from all boundary-margin combinations (Figure 4.3.6). Gradient lengths of 3.45 and 2.28 were generated for Axis 1 and Axis 2, with each axis describing 18.3% and 9.1% of the total variation in compositional data respectively. Sites positioned along Axis 1 come close to showing a unimodal response, with almost complete species turnover between sites with lowest (wire and bank-slope) and highest (field) Axis 1 scores (Figure 4.3.6a). However, excluding field sites, gradient lengths for field boundary features were reduced demonstrating a linear response in coleopteran composition to changes in field boundary habitat. This does not necessarily mean that coleopteran composition responded linearly to the measured habitat characteristics, rather the range of characteristics encompassed by the study may be too small to show a unimodal relationship.

Polygons representing the ordination space encompassed by each field boundary type overlapped strongly and covered equivalent areas indicating similarity in the type and range of coleopteran composition (Figure 4.3.6a). Samples were more strongly grouped according to feature. Arable and ley fields were clustered together with high Axis 1 scores (>2). The arable edge and ley edge sites from boundaries with margins had higher Axis 1 scores than other field boundary features. Close proximity between these field and edge samples indicated similar coleopteran composition and differentiation from more distant field boundary features. Field samples had a high relative utilisation by coleopteran larvae (Figure 4.3.6b). Heliophoridae and Byrrhidae were mostly found in ley edge sites of PW+M and H+M boundaries respectively. The location of Carabidae, Scarabidae, Curculionidae and Ptilidae close to margin, bank top and rock features indicated their high relative utilisation of these sites in all field boundary types. Staphylinidae and Chrysomelidae were positioned centrally amongst samples indicating a ubiquitous distribution across features and boundary types. The position of Anistomidae, Byrrhidae, Heliophoridae, Histeridae, Hydrophilidae and Lathrididae at the outer edges of the ordination space indicated infrequent occurrence of these families.
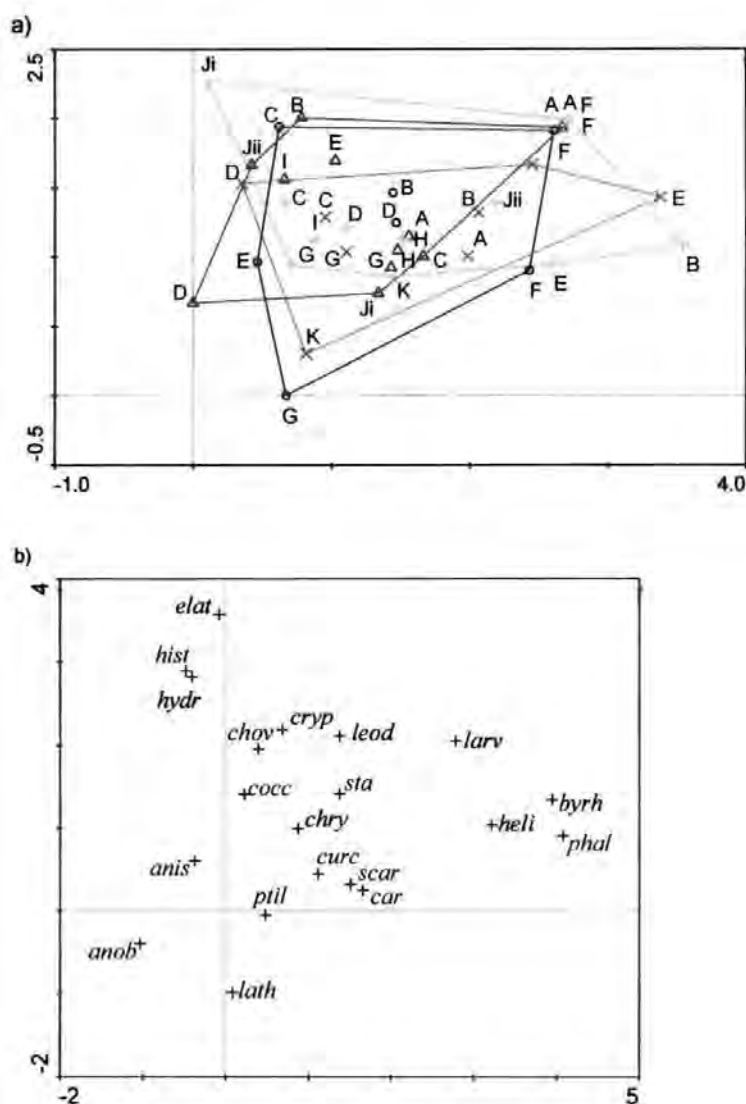
Figure 4.3.6 Detrended correspondence analysis (DCA) based on the summed relative utilisation of features by Coleopteran families within each field boundary type.

a) Plot showing features in each boundary*margin combination. Symbols represent boundary*margin type: ○ = PW-M , × = PW+M , △ = H-M and + = H+M.
Feature labels A-K represent: A = arable field, B = arable edge, C = post, D = wire, E = ley edge, F = ley field, G = rock, H= bank top, I = trunk, Ji = slope (arable), Jii = slope (ley), K = margin. Polygons indicate the ordination space encompassed by a boundary*margin type; the larger the polygon the greater variation in coleopteran composition within a field boundary type. The distance between symbols approximates the dissimilarity of their species compositions.

b) Plot showing Coleopteran family distribution in ordination space. Coleopteran families are illustrated by four letter italics: *anis* = Anistomidae, *byrh* = Brryhidae, *chry* = Chrysomelidae, *cocc* = Coccinellidae, *cryp* = Cryptophagidae, *curc* = Curculionidae, *heli* = Heliophoridae, *hist* = Histeridae, *hydr* = Hydrophilidae, *lath* = Lathrididae, *leod* = Leoidae, *ptil* = Ptilidae, *scar* = Scarabidae, *tcar* = Carabidae, *tlar* = Larvae, *tsta* = Staphylinidae.

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4.3.4 Habitat characteristics influencing composition

Month used as a covariable explained little of the variation in Coleoptera (1.9%), Staphylinidae (0.48%) or Carabidae (0.75%) data suggesting little difference in composition of sites during the winter. A much greater proportion of the variation in species data was explained by the environmental variables recorded in Transect One compared to All Transects data. Hence, CCA analysis for 'transect one' data was displayed to describe the relationship between taxa and habitat characteristics. The total species inertia described the amount of variation found in the compositional data for each taxonomic group; Carabidae composition varied most (7.2), Coleoptera composition was intermediate (4.5) and Staphylinidae composition varied least (3.3). The habitat characteristics recorded best explain the variation in Carabidae composition (43.1%), followed by Coleoptera (39.3%) and Staphylinidae (33.6%) (Tables 4.3.9a to 4.3.11a).

(i) Coleoptera composition

Moss cover, % soil organic matter content, % bare ground cover and leaf litter explained a significant portion of the variation in composition of coleopteran families (Table 4.3.9b). Axis 1 accounted for 32.2% of the coleopteran variation explained by the environmental variables and was strongly and positively correlated to % bare ground (0.48), moss cover (0.47), % moisture content of the soil (0.43) and % organic matter content of the soil (0.40). Axis 2 explained 18.4% of species-environment relation and was strongly and positively correlated to leaf litter (0.53) and % organic matter content of the soil (0.40).

Eleven coleopteran families were recorded in transect one, of these eight have >20% weight in the CCA analysis and were displayed (Figure 4.3.7). Coleopteran families Chrysomelidae, Coccinelidae, Curculionidae (all typically found in herbaceous or grassy vegetation where they feed on leaves and stems or are carnivorous on other small insects), Leodidae, Scarabidae and Coleopteran larvae showed strong association with vegetation height, cover of monocot and dicot vegetation and presence of dead plant stubble typical of boundary edge, margin sites and features in post and wire boundaries. Dead plant stubble during the winter was greatest at features supporting summer annuals such as umbellifers and thistles known

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to support large communities of insects. In contrast, Ptilidae (a fungal feeder frequenting shady and damp habitats) was more closely associated with hedgerow characteristics of bank height, leaf litter and bare ground.

(ii) Carabidae composition

A significant amount of the variation in carabid species composition between features was explained by distance to arable edge, leaf-litter index and vegetation height (Table 4.3.10b). Axis 1 accounted for 18.5% of the variation in the carabid-environment relationship and was positively correlated to distance to arable edge (0.26) and negatively correlated to leaf litter index (-0.42) and % moisture content of the soil (-0.26). Axis 2 explained 17% of species-environment relation and was strongly and negatively correlated to a range of variables including distance to arable edge (-0.76), leaf litter index (-0.53), bank height (-0.5), % organic matter content of the soil (-0.44), % bare ground cover (-0.36), % dicot cover (-0.36) and woody canopy height (-0.35). Axis 2 was also positively correlated to % monocot cover (0.55).

Of the twenty-three carabid species recorded in transect one, nine have >20% weight in the CCA analysis. The three *Bembidion* species all have negative Axis 1 scores and therefore occurred at sites with below average soil moisture levels (Figure 4.3.8). *B. lampros* was most closely associated with this variable. The three *Bembidion* species were positioned along a gradient of increasing monocot ground cover. *B. lampros* was most ubiquitous, *B. guttula* was associated with increasing proportions of monocot relative to dicot vegetation whilst *B. obtusum* (an autumn breeding species known to favour bare ground (Pollard, 1968a) occurred at sites dominated by grassy vegetation. However, monocot vegetation was particularly dominant at arable and ley edge sites therefore associations with this microhabitat may reflect high field activity.

All other carabid species illustrated were found at sites with above average soil moisture. *P. strennus, P. vernalis* and *D. linearis* were found at maximal soil moisture levels. Distributions of *P. strennus* and *P. cupreus* were also associated with high monocot cover, vegetation height and distance to the ley edge, characteristics typical of boundary edge sites (particularly arable edge), margin features and of post and wire boundaries. This result was surprising for *P. strennus* which is categorised as

a woodland species (Thiele, 1977; Lindroth, 1992), although during its activity period
it is found both in wooded sites with leaf litter and sparse ground vegetation
(Lindroth, 1992) and in areas with dense, often weedy vegetation (Thiele, 1977).

M. obscuroguttatus and *D. atricapillus* were both located close to the origin
indicating a widespread distribution with marginally greater utilisation of hedge-bank
sites characterised by bare ground, high soil organic matter and leaf litter cover. *P.
vernalis* (characterised as an open-field species that shows a preference for damp and
shady habitats during its activity period, which is reflected in its overwintering
distribution (Thiele, 1977; Lindroth, 1992)) was associated with high leaf litter,
organic matter content of the soil, bare ground and moss cover. This combination of
characteristics suggested a strong presence in hedge-banks.

(iii) Staphylinidae

Distance to ley edge was the most important habitat characteristic in
explaining variation in the staphylinid composition (Table 4.3.11b). Axis 1 explained
26.2% of the variation in staphylinid composition described by the environmental
variables and was strongly and negatively correlated to distance to ley edge (-0.51)
and positively correlated to distance to arable edge (0.42) and % organic matter
content of the soil (0.35). Axis 2 explained 16.8% of species-environment relation and
was positively correlated to % monocot cover (0.26) and negatively correlated with %
dicot cover (-0.36) and % organic matter content of the soil (-0.29).

Of the thirteen Staphylinidae taxa recorded in transect one, eleven had >20%
weight in the CCA analysis. Most staphylinid taxa showed a ubiquitous distribution
across features and boundary types as indicated by their biplot positions close to the
origin (Figure 4.3.9) as well as low total species inertia values described above.
Strong similarities in staphylinid assemblages across features and field boundary-
margin combinations were observed. Distance to arable and ley edge were strong
determining factors in staphylinid composition with taxa showing a range of
responses to these variables.

P. litoralis and *X. longiventris* occupied features at maximal distances from
the ley edge (and below average distances to the arable edge) typical of arable edge

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and margin sites of H+M boundaries. Both species were also associated with bare ground cover, canopy and bank height, indicative of hedgerows generally. *P. litoralis* was frequently observed basking in sunlight on winter days at the edges of woody canopy branches up to 0.2m from the ground (*pers. obs.*). Such behaviour acts to raise body temperatures above ambient temperatures and enable greater metabolic activity; this species is also known to climb plants to search for aphids (Kollat-Pallenga & Basedow, 2000). *M. splendidus, T. nitidulus* and *X. linearis* occupied sites at maximal distances from the arable edge. Interestingly, two closely related species *X. longiventris* and *X. linearis*, occurred in differing overwintering sites. Whilst *X. longiventris* was found more frequently at arable edge and margin sites of H+M boundaries, *X. linearis* tends to overwinter in the ley edge, bank top and slopes, trunk, rock, post and wire features of H+M boundaries.

a)	Eigenvalues	% variation explained	Cummulative % variance of species data	Cumm. % variance of species-environment relation
Axis 1	0.565	12.7	12.7	32.2
Axis 2	0.323	7.2	19.9	50.6
Axis 3	0.280	6.3	26.2	66.6
Axis 4	0.207	4.6	30.8	78.4
Total inertia of species data (sum of all eigenvalues)	4.467			
Environmental variable inertia (sum of canonical eigenvalues)	1.754	39.3		

b) Marginal effects	λ_1	Conditional effects	λ_a	P	
moss index (moss)	0.28	moss index (moss)	0.28	0.084	n.s.
% soil organic matter content (organ)	0.26	% soil organic matter content (organ)	0.24	0.036	*
% bare ground cover (.bare)	0.26	% bare ground cover (.bare)	0.20	0.032	*
leaf litter index (litter)	0.20	leaf litter index (litter)	0.25	0.028	*
distance to ley edge m^{-1} (dist-l)	0.20	distance to ley edge m^{-1} (dist-l)	0.20	0.072	n.s.
% soil moisture content (moist)	0.20	% dicotyledon cover (.di)	0.17	0.134	n.s.
% dicotyledon cover (.di)	0.18	dead plant stems index (dead)	0.10	0.428	n.s.
distance to arable edge m^{-1} (dist-a)	0.13	distance to arable edge m^{-1} (dist-a)	0.07	0.666	n.s.
% monocotyledon cover (.mono)	0.12	% soil moisture content (moist)	0.07	0.752	n.s.
bank height m^{-1} (bankht)	0.11	ground vegetation height (veght)	0.06	0.752	n.s.
ground vegetation height (veght)	0.10	bank height m^{-1} (bankht)	0.05	0.830	n.s.
woody canopy height m^{-1} (canht)	0.09	% monocotyledon cover (.mono)	0.04	0.946	n.s.
dead plant stems index (dead)	0.07	woody canopy height m^{-1} (canht)	0.02	0.992	n.s.

Table 4.3.9 Canonical Correspondence Analysis (CCA) of Coleopteran family composition explained by 13 microhabitat characteristics based on transect one data.
a) Eigenvalues and % variance explained by the first four axes and overall.
b) Amount of variation explained by microhabitat characteristics singly is shown by their marginal (λ_1) effects, the additional variation explained by each characteristic added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation test (999 permutations) are shown with asterix to indicate significance * = <0.05.

a)	Eigenvalues	% variation explained	Cummulative % variance of species data	Cumm. % variance of species-environment relation
Axis 1	0.578	8.0	8.0	18.5
Axis 2	0.528	7.3	15.3	35.5
Axis 3	0.429	5.9	21.2	49.2
Axis 4	0.375	5.2	26.4	61.3
Total inertia of species data (sum of all eigenvalues)	7.239			
Environmental variable inertia (sum of canonical eigenvalues)	3.121	43.1		

b) Marginal effects	λ_1	Conditional effects	λ_a	P	
distance to arable edge m^{-1} (dist-a)	0.45	distance to arable edge m^{-1} (dist-a)	0.45	0.006	**
leaf litter index (litter)	0.45	leaf litter index (litter)	0.42	0.020	*
ground vegetation height (veght)	0.32	ground vegetation height (veght)	0.33	0.038	*
% soil organic matter content (organ)	0.31	% soil organic matter content (organ)	0.27	0.110	n.s.
woody canopy height m^{-1} (canht)	0.30	% bare ground cover (.bare)	0.27	0.124	n.s.
bank height m^{-1} (bankht)	0.30	% soil moisture content (moist)	0.21	0.242	n.s.
% monocotyledon cover (.mono)	0.29	distance to ley edge m^{-1} (dist-l)	0.18	0.426	n.s.
% bare ground cover (.bare)	0.27	woody canopy height m^{-1} (canht)	0.19	0.310	n.s.
% soil moisture content (moist)	0.22	bank height m^{-1} (bankht)	0.24	0.156	n.s.
distance to ley edge m^{-1} (dist-l)	0.22	dead plant stems index (dead)	0.14	0.678	n.s.
% dicotyledon cover (.di)	0.21	% monocotyledon cover (.mono)	0.15	0.580	n.s.
dead plant stems index (dead)	0.18	% dicotyledon cover (.di)	0.18	0.378	n.s.
moss index (moss)	0.09	moss index (moss)	0.09	0.804	n.s.

Table 4.3.10 Canonical Correspondence Analysis (CCA) of Carabidae composition explained by 13 microhabitat characteristics based on transect one data.
a) Eigenvalues and % variance explained by the first four axes and overall.
b) Amount of variation explained by microhabitat characteristics singly is shown by their marginal (λ_1) effects, the additional variation explained by each characteristic added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation test (999 permutations) are shown with asterix to indicate significance * = <0.05, ** = <0.01.

a)	Eigenvalues	% variation explained	Cummulative % variance of species data	Cumm. % variance of species-environment relation
Axis 1	0.288	8.8	8.8	26.2
Axis 2	0.185	5.6	14.4	43.0
Axis 3	0.160	4.9	19.3	57.5
Axis 4	0.135	4.1	23.4	69.8
Total inertia of species data (sum of all eigenvalues)	3.278			
Environmental variable inertia (sum of canonical eigenvalues)	1.1	33.56		

b) Marginal effects	λ_1	Conditional effects	λ_a	P	
distance to ley edge m^{-1} (dist-l)	0.14	distance to ley edge m^{-1} (dist-l)	0.14	0.050	*
% soil organic matter content (organ)	0.14	dead plant stems index (dead)	0.14	0.066	n.s.
dead plant stems index (dead)	0.13	% soil organic matter content (organ)	0.14	0.086	n.s.
% soil moisture content (moist)	0.13	% soil moisture content (moist)	0.12	0.082	n.s.
distance to arable edge m^{-1} (dist-a)	0.09	% dicotyledon cover (.di)	0.07	0.306	n.s.
% dicotyledon cover (.di)	0.08	leaf litter index (litter)	0.06	0.420	n.s.
bank height m^{-1} (bankht)	0.07	% monocotyledon cover (.mono)	0.07	0.378	n.s.
ground vegetation height (veght)	0.07	ground vegetation height (veght)	0.07	0.360	n.s.
woody canopy height m^{-1} (canht)	0.06	% bare ground cover (.bare)	0.07	0.334	n.s.
% monocotyledon cover (.mono)	0.06	distance to arable edge m^{-1} (dist-a)	0.07	0.324	n.s.
leaf litter index (litter)	0.06	bank height m^{-1} (bankht)	0.05	0.592	n.s.
% bare ground cover (.bare)	0.03	woody canopy height m^{-1} (canht)	0.05	0.520	n.s.
moss index (moss)	0.03	moss index (moss)	0.05	0.550	n.s.

Table 4.3.11 Canonical Correspondence Analysis (CCA) of Staphylinidae composition explained by 13 microhabitat characteristics based on transect one data.
a) Eigenvalues and % variance explained by the first four axes and overall.
b) Amount of variation explained by microhabitat characteristics singly is shown by their marginal (λ_1) effects, the additional variation explained by each characteristic added using the forward selection procedure is shown by their conditional (λ_a) effects. Results (P) of the Monte Carlo permutation test (999 permutations) are shown with asterix to indicate significance * = <0.05.
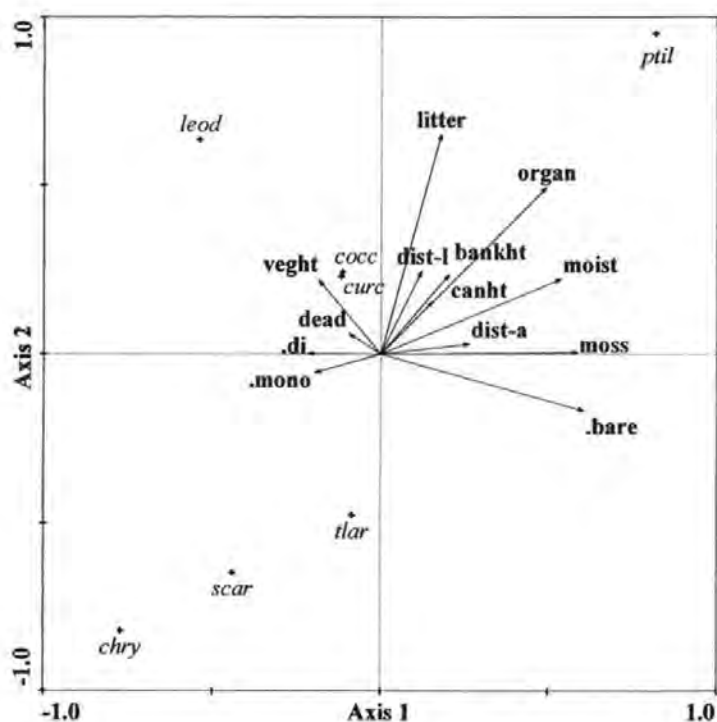
Figure 4.3.7 CCA biplot of coleopteran families (excluding carabidae and staphylinidae) and microhabitat characteristics, based on transect one data and 13 environmental variables (labelled arrows, see Table 4.2.2 for codes). Coleopteran families are illustrated using four letter italics: *chry* = Chrysomelidae, *cocc* = Coccinellidae, *curc* = Curculionidae, *leod* = Leoidae, *ptil* = Ptilidae, *scar* = Scarabidae, *tlar* = Coleoptera larvae.
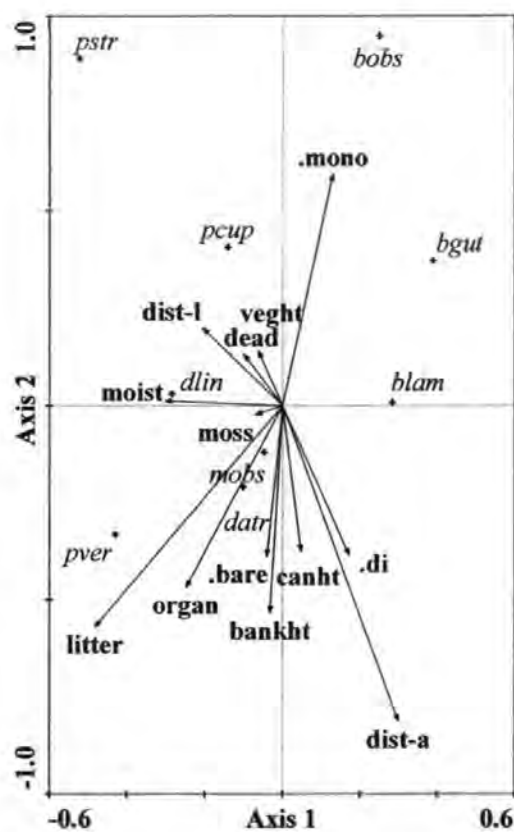
Figure 4.3.8 CCA biplot of carabid species and microhabitat characteristics based on transect one data and 13 environmental variables (labelled arrows, see Table 4.2.2 for codes). Carabid species are illustrated using four letter italics: *blam = Bembidion lampros, bgut = B. guttula, bobs = B. obtusus, datr = Demetrias atricapillus, dlin = Dromius linearis, mobs = Metabletus obscuroguttatus, pcup = Pterostichus cupreus, pstr = P. strennus, pver = P. vernalis.*
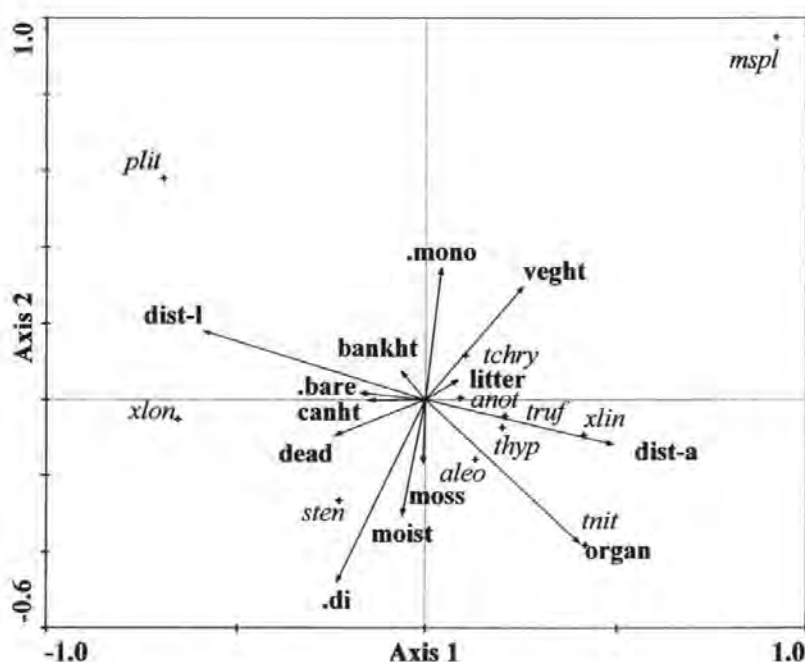
Figure 4.3.9 CCA biplot of staphylinid species and microhabitat characteristics based on transect one data and 13 environmental variables (labelled arrows, see Table 4.2.2 for codes). Staphylinid species are illustrated using four letter italics: *aleo* = Aleocharinae spp., *anot* = *Anotylus* spp., *mspl* = *Mycetoporus splendidus*, *plit* = *Paederus litoralis*, *tchry* = *Tachyporus chrysomelinus*, *thyp* = *T. hypnorum*, *tnit* = *T. nitidulus*, *truf* = *Tachinus rufipes*, *sten* = *Stenus* spp., *xlin* = *Xantholinus linearis*, *xlon* = *X. longiventris*.

4.4   DISCUSSION

The range of habitat features found within field boundary-margin combinations varied in their microhabitat characteristics relative to each other, but across boundary-margin types, the same features frequently supported similar characteristics. This was particularly evident for fence-post, fence-wire, hedge-bank and margin features. Hence, these habitat features may provide consistent overwintering conditions regardless of field boundary type. Furthermore, the features fence-post, fence-wire and margin supported high overwintering densities and richness of Coleoptera, Carabidae and Staphylinidae across all boundary-margin combinations. These features were associated with a high monocot and dicot vegetation cover, vegetation height and dead plant stubble (frequently the remains of tall herbaceous summer annuals). The first two microhabitat characteristics are recognised as supporting high overwintering densities of polyphagous predators and arthropod diversity (Dennis & Fry, 1992; Thomas *et al.*, 1992a; Dennis *et al.*, 1994; Maudsley *et al.*, 2002). Vegetation cover and height act to insulate the ground layer from temperature fluctuations and enhance humidity (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b; Burki & Hausamann, 1993). The results from this study suggest that dead plant stubble may also contribute to optimal microclimatic conditions in field boundaries, particularly margin habitats. Consequently, the use of fencing (as the principal barrier structure or in an ancillary role) and the presence of margins may provide preferred overwintering sites for a wide range of taxa and could be targeted as part of field boundary management, restoration or creation schemes. Furthermore, the use of ancillary fencing may act to protect hedgerows from grazing and adverse management practices (Barr *et al.*, 1995).

The presence or absence of a margin appeared to have little influence on the distribution of taxa in adjacent field boundary features. However, hedgerow and post and wire boundaries showed differences in the distribution of taxa among habitat features. Features that supported low density and richness values for each taxonomic group had similar magnitudes in all boundary-margin types. The difference between hedgerow and post and wire boundaries was in the magnitude of the high density and richness values, which were greater relative to low values in post and wire boundaries compared with hedgerows. These distribution and density patterns suggest that hedgerow and post and wire field boundaries supported similar abundances of

overwintering taxa. In post and wire boundaries, individuals are more tightly packed into preferred overwintering sites, whilst in hedgerows they spread out to fill the available space. This homogenous distribution pattern in hedgerows has been reported in the literature for *B. lampros*, although other carabid species showed more clumped distributions (Maudsley *et al.*, 2002).

The homogeneous distribution of taxa in hedgerows may reflect the high representation of bare ground across all hedgerow features. Within the literature, bare ground is generally regarded as providing sub-optimal overwintering conditions (Pollard, 1968a; Thomas *et al.*, 1992b; Dennis & Fry, 1992). The distribution of overwintering taxa may result from differential survival or differential site selection (Thomas *et al.*, 1992b; Dennis *et al.*, 1994). Evidence in the literature demonstrates that overwintering mortality of *T. hypnorum* in bare ground may be greater than under tussocky grasses as a result of greater fluctuations in temperature (Dennis *et al.*, 1994). It has also been suggested that temperature buffering properties of microhabitat characteristics may act as a stimuli in overwintering site selection (Thomas *et al.*, 1992b). In the absence of positive stimuli for the selection of overwintering sites, searching behaviour may continue resulting in a more homogenous distribution across hedgerows. In addition, the high proportion of bare ground typical of hedgerow features will provide less of an impediment to movement.

Clear vertical distribution patterns were observed, with all taxonomic groups showing a preference for the ground cover and upper 5cm of soil in habitat features across all boundary-margin combinations. This confirms most evidence in the literature indicating the predominant occurrence of overwintering Carabidae and Staphylinidae in the upper soil profile and ground cover (Dennis *et al.*, 1994; Maudsley *et al.*, 2002). The homogenous vertical distribution of *B. lampros* in hedgerows was the only exception to this observed pattern. Previous studies have reported the occurrence of larger carabids (e.g. *Harpalus rufipes*) at greater soil depths (Thiele, 1977; Maudsley *et al.*, 2002) but not small species such as *B. lampros*. Temperature is considered a determining factor in the vertical migration of soil arthropods (Dowdy, 1944) and it is the temperature buffering properties of microhabitat characteristics such as vegetation cover that act to enhance overwintering densities (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b; Burki &

Hausamann, 1993). In the absence of suitable microhabitat characteristics, individuals may show increased burrowing. A higher proportion of bare ground in hedgerow features compared to post and wire boundaries may encourage *B. lampros* in hedgerows to burrow deeper to find suitable overwintering microclimate. At the same time, the presence of woody roots penetrating through the soil horizons may provide movement channels enabling *B. lampros* to overwinter at greater depths in hedgerows.

Overall, coleopteran composition varied little both within and between field boundary types, as evidenced by the low inertia, gradient lengths <4 S.D. and strongly overlapping boundary type polygons. Composition in field boundary features shows a strong linear response to changes in field boundary habitat which may result from a lack of differentiation in habitat suitability between field boundary features or field boundary-margin combinations. This finding may emphasise the ubiquitous habitat preferences of many coleopteran, carabid and staphylinid taxa occurring and persisting in farmland. Many species, particularly staphylinids disperse by flight (e.g. Aleocharinae spp., *Anotylus* spp., *Tachyporus* spp., *Tachinus* spp., *Paederus* spp., *Philonthus* spp., and *Xantholinus* spp.) (Good & Giller, 1991a; Levesque & Levesque, 1995; Andersen & Eltun, 2000), which may result in more homogenous distributions (Riedel, 1995). In addition, composition of all three taxonomic groups varied little during the course of the winter. Further studies are required to determine whether this implies a lack of movement by individuals during the course of the winter or re-emphasises the ubiquitous composition of overwintering taxa.

Within this study considerable advances have been made in understanding the overwintering microhabitat preferences of a broad range of taxa. Species of Carabidae were most specific and variable in their overwintering habitat distribution, Coleoptera were intermediate and Staphylinidae showed most ubiquitous distribution patterns across features and boundary-margin combinations. Coleopteran families and carabid species were mostly of open-habitat origin with a preference for sheltered overwintering sites with high vegetation cover, dead plant stubble and leaf litter. However, the hedgerow interior was favoured by a number of species and families that may be more permanent residents of woody boundaries. For such groups, the reduced disturbance provided by wider, woody boundaries together with moist and shady habitat characteristics are essential. This general information can be used to

devise field boundary management that is more sympathetic to the conservation of farmland arthropods. More detailed information describing habitat preferences will contribute to understanding the ecology of many farmland taxa. However, the degree of complexity regarding habitat requirements of individual species cannot be underestimated. For example, the observed differences between the closely related species *X. longiventris* and *X. linearis* suggest differing distributions during their active reproductive period in the field. In a comparison of staphylinid assemblages of cereal and grass fields, Good & Giller (1991a) found *X. longiventris* preferred dense cereal cover, whilst *X. linearis* was more typical of undisturbed pasture, partially attributed to the poor dispersal ability of this species.

The combination of soil moisture, soil organic matter content and the eleven other microhabitat characteristics proved important in explaining the early winter overwintering distribution of beetles. The observed associations of taxa with different microhabitat characteristics frequently reflects habitat preferences during the active reproductive stage of the species life-cycle as described in the literature (e.g. Joy, 1976; Thiele, 1977; Unwin, 1988; Good & Giller, 1991a; Lindroth, 1992; Levesque & Levesque, 1995; Andersen & Eltun, 2000). Microhabitat characteristics identified as explaining a significant proportion of variation in compositional data vary in the extent to which they are positively associated with component taxa. For example, among the coleopteran families only Ptilidae was positively associated with the microhabitat characteristics (organic matter and leaf litter) significantly explaining compositional differences. Other families were strongly dissociated with these variables. Similarly, most carabid species were negatively associated with distance to the arable edge, and only a few species were positively associated with leaf litter and vegetation height although these three variables were most important in explaining overwintering compositions. The importance of distance to the arable or ley edge relative to other microhabitat characteristics raises important questions regarding the influence of adjacent land-use, the dispersal behaviour of migrants and the selection of overwintering sites. These questions cannot be fully addressed within this study but indicate processes influencing the use of field boundaries by overwintering taxa.

CHAPTER FIVE: THE PHYSIOLOGICAL CONDITION OF CARABIDAE OVERWINTERING IN DIFFERENT FIELD BOUNDARY TYPES

5.1 INTRODUCTION

A long-term objective for integrated approaches to pest management is to enhance the abundance of natural enemies. Population growth may be achieved by limiting mortality and enhancing fecundity. The physiological condition of beetles has been shown to influence fecundity (Sota, 1985; Juliano, 1986; Wallin *et al.*, 1992; Honek, 1993; Van Dijk, 1994) and overwintering survival until reproductive age (Van Dijk & Den Boer, 1992; Van Dijk, 1994; Petersen *et al.*, 1996; Petersen, 1999). Consequently, provided factors such as overwintering survival and adult fecundity are determining factors in a species population growth, enhanced physiological condition may have a positive effect on field populations of natural enemies (Honek, 1989).

Adult feeding is generally considered to provide the majority of resources for reproduction (Wallin *et al.*, 1992; Van Dijk, 1994). However, Bommarco (1998b) found that poor teneral conditions over winter could affect fecundity despite high food levels immediately prior to, and during, reproduction. The lack of post-overwintering fat reserves to transfer to reproductive requirements at the start of the breeding season may be responsible for reducing fecundity (Bommarco, 1998b). Additionally, absence of available prey in early spring may delay the onset of reproduction in the absence of fat reserves.

Overwintering mortality may result from the direct effects of adverse microclimatic conditions or depletion of energy reserves. Most Coleoptera in temperate regions will be freeze intolerant, relying on the production of anti-freeze proteins to lower the freezing point of the haemolymph, and the production of polyols and sugars to enable supercooling (maintaining fluids in an aqueous state below their freezing points) (Leather *et al.*, 1993). The production of these biochemicals is energetically costly; therefore individuals show seasonal changes in their cold-hardiness and supercooling ability (Leather *et al.*, 1993). Alterations in anti-freeze proteins are likely to respond to predictive cues such as photoperiod, whilst production of polyols and sugars may be linked quite closely to changes in temperature. Declimatisation to cold through an increase in the supercooling

temperature would make individuals vulnerable to subsequent frosts or cold periods, resulting in increased mortality (Petersen *et al.*, 1996). For example, fluctuations in temperature between +2°C and –6°C resulted in greater mortality of *Bembidion lampros* and *Tachyporus hypnorum*, compared to more stable temperature regimes at +2°C or below 0°C, and mortality was greatest where temperatures fluctuated weekly rather than daily as a result of cold declimatisation (Petersen *et al.*, 1996). Consequently, many species search out a colder, but more stable microclimate in order to maintain cold-hardiness that would otherwise fluctuate with fluctuating temperatures (Leather *et al.*, 1993).

In previous studies of *B. lampros*, abiotic factors such as temperature have been considered more important in determining overwintering mortality (due to changes in the supercooling point of individuals), whilst pre-winter food levels influence overwintering condition. However, maintenance of cold-hardiness may deplete limited fat reserves and result in death. For example, stressful abiotic conditions over winter experienced by *B. lampros*, *T. hypnorum* (Petersen, 1999) and *Coccinella septempunctata* (Zhou *et al.*, 1995) led to a decrease in fat content. Overwintering mortality in the absence of freezing was related to starvation in adult overwintering Coccinellidae (Watanabe, 2002), whilst individuals of *B. lampros*, *T. hypnorum*, *Calathus melanocephalus* with lower fat reserves and/or body weights all showed increased overwintering mortality (Van Dijk, 1994; Petersen, 1999). Additionally, mild winter temperatures may result in the depletion of fat reserves through increased metabolic activity. For example, fat reserves in *C. septempunctata* reduced by 30% in harsh cold temperatures and >50% in less cold overwintering conditions (Zhou *et al.*, 1995). High mortality of *B. lampros* was observed at constant temperatures of 6°C, close to the lower threshold for feeding activity of about 9°C for this species (Chiverton, 1988; Petersen, 1997).

The energetic costs of maintaining cold-hardiness may limit the duration of the winter period that an individual can survive (Petersen *et al.*, 1996). Previous studies have shown that increasing winter duration can influence weight loss in *B. lampros*, with little weight change observed after ten weeks overwintering, but a 16% weight loss after fourteen weeks (Petersen *et al.*, 1996). Petersen (1999) and Reidel & Steenberg (1998) found the highest rates of mortality in *B. lampros* field populations

were immediately after emergence of beetles from overwintering. Lack of available prey for active beetles in spring was considered a determining factor in weight loss and subsequent mortality (Petersen *et al.*, 1996; Petersen, 1999). Similarly, mortality of Coccinellidae after emergence from hibernation was attributed to the depletion of energy reserves (Mills, 1981). Although certain species e.g. *C. melanocephalus* (Sota, 1985) and *B. lampros* (Petersen, 1999) can survive periods of starvation in early spring, survival may be dependent on their physiological condition at emergence. In contrast, the relative fresh weight of field caught *Pterostichus cupreus* showed a steady increase during spring until the start of the reproductive period in late May (den Nijs *et al.*, 1996). The timing of emergence may influence the condition of individuals and their subsequent survival and fecundity. Additionally, seasonal changes in the net body weight of reproductive females will be affected by growth of ovaries and eggs (Mols, 1988), whilst fat reserves may be converted to egg production (Bommarco, 1998b).

Fat reserves during overwintering are clearly essential to maintain respiration, for the production of cryoprotectants and for movement either to find overwintering sites or prey (Leather *et al.*, 1993). Polyphagous predatory carabids and staphylinids that overwinter as adults generally migrate to field boundary habitats soon after emergence as tenerals in the field; food gathered during the teneral stage will be stored as fat reserves to survive winter (Mols, 1988; Van Dijk, 1994). At this time, crop senescence and harvesting will result in low availability of both pests and alternative prey. Consequently, fat reserves accumulated by adults during overwintering reflect prey availability in the field boundary habitat rather than in the field. Within field boundary habitats, microclimatic conditions experienced by individuals will determine the extent to which fat reserves are depleted. The presence or absence of a woody canopy has been shown to influence microclimatic conditions at ground level (Forman & Baudry, 1984), whilst different herbaceous vegetation types and cover vary in their ability to buffer extreme fluctuations in temperature (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b; Burki & Hausamann, 1993) and influence overwintering mortality (Dennis *et al.*, 1994). Tussocky grasses have been recognised as providing the most stable temperature regime for overwintering polyphagous predators (Thomas *et al.*, 1992b). However, grass tussocks may not in all cases secure overwintering survival for *B. lampros* and *T. hypnorum* (Petersen, 1999).

For example, populations of these two species were reduced by up to 90% where temperatures in grass tussocks fluctuated between thaw and frost. The temperature values and fluctuations experienced as stressful by overwintering polyphagous predators are poorly understood and likely to be species-specific. In addition, demonstrating the availability of prey items for predators both spatially and temporally can be difficult. Therefore, the physiological condition of polyphagous predators emerging from overwintering will be used as an indirect measure of prey availability and microclimatic suitability in field boundary habitats (Juliano, 1986; Van Dijk, 1986; Bommarco, 1998b).

Fat content is most frequently used as an indicator of the physiological condition of individuals. Fat reserves vary intra-specifically and are determined by both the quantity and quality of food availability and by abiotic factors (Wallin *et al.*, 1992; Van Dijk, 1994; Petersen, 1999; Bommarco, 1998b; Ostman *et al.*, 2001). Fat content has been positively correlated to feeding levels (Bommarco, 1998b; Ostman *et al.*, 2001) and has been used as an indication of food availability in the field for *B. lampros, P. cupreus, P. melanarius* and *T. hypnorum* (Petersen, 1999; Bommarco, 1998a; Ostman *et al.*, 2001). In laboratory feeding trials, *B. lampros* fed *ad libitum* had a constant fat content of 23%, whilst a fat content of 7% was observed in individuals that died of starvation (Petersen, 1999). Field caught *B. lampros* had a fat content of 23% indicating that individuals were not food-limited post-overwintering (Petersen, 1999). Consequently, fat content provides a measure of both food availability and abiotic conditions. The most reliable measure of fat content is considered to be lipid content as the percentage of dry body mass (Petersen, 1999).

Alternative and non-destructive measurements of condition include body weight and body size. Within a population of *P. cupreus*, two-fold differences in body weight have been observed (den Nijs *et al.*, 1996). Crucially, body weight was positively correlated to the quality and quantity of the diet for *P. cupreus* and *P. melanarius* with heavier beetles having larger fat reserves (Wallin *et al.*, 1992). Starved *D. atricapillus* had significantly lower body weight and suffered greater mortality than fed cohorts (Thomas *et al.*, 1992b). Body weight (corrected by size) has been used to indicate field-based feeding conditions in *P. cupreus* as confirmed by gut contents (Zangger, 1994). Measures of relative body weight (accounted for by

body size) have been correlated to fat content in *P. cupreus* and *P. melanarius* (Bommarco, 1998b; Ostman *et al.*, 2001), but were also considered to vary with fluid contents of the body (Ostman *et al.*, 2001). Body size is not a suitable indicator of field boundary overwintering habitat quality since adult body size is determined by larval body size, which is in turn influenced by food intake and abiotic conditions during larval development in the field (Nelemans, 1988; Leather *et al.*, 1993; Van Dijk, 1994; Bommarco, 1998b). Variation in body size caused by larval conditions will also confound the use of body weight to indicate condition. For example, large adults experiencing low food availability may still weigh more than small individuals with high food levels. Therefore, body size should be used as a correction factor for variation in body weight (e.g. Juliano, 1986; den Nijs *et al.*, 1996; Bommarco, 1998b; Ostman *et al.*, 2001). Elytral area was found to be a better predictor of beetle size than maximum elytral length and is therefore used as the denominator in calculations of relative fresh weight (fresh weight/elytral area) (den Nijs *et al.*, 1996). A high relative fresh weight indicates a beetle that is heavy for its size and therefore in good condition (den Nijs *et al.*, 1996).

This study aims to investigate the effect of three factors: field boundary type (post and wire or hedgerow), margin (absence or presence) and season (early or late) on the relative fresh weight and fat content of carabid and staphylinid polyphagous predators as they emerge from overwintering.

5.1.1 Aims

(i) Determination of field boundary habitat quality (measured by relative fresh weight and fat content) in terms of food availability and microclimatic conditions experienced by individuals

(ii) To investigate whether temperature profiles of each field boundary-margin combination influences relative fresh weight and fat content.

(iii) To determine whether a relationship between abundance and relative fresh weight or fat content of a species exists to determine whether physiological condition is indicative of numbers surviving the winter or population demographics generally.

5.2 METHODS

5.2.1 Field methods

Eight field boundaries were selected for study on the Seale-Hayne farm: four each of post and wire (PW) or hedgerow (H). Each boundary type was represented by two boundaries without margin (-M) and two with margin (+M). The eight boundaries correspond to those studied in Chapter Four and are described in terms of botanical composition, habitat and landscape structure in Chapter Two (PW-M, 6 and 13; PW+M, 18 and 5; H-M, 7 and 14; H+M, 12 and 11). Adjacent land use was standardised by selecting boundaries with one adjacent field in arable and the other in permanent or temporary ley. Margins were adjacent to arable fields.

Carabidae and Staphylinidae were captured from both sides of each boundary. Ten semi-circular barriers were placed at regular intervals parallel to each side of the selected boundaries resulting in 160 barrier traps in total (Figure 5.2.1). The barrier traps were constructed from 0.1 m high plastic lawn edging and set 0.03 m into the soil so that the edging formed a semi-circular enclosure of 1.0 m diameter. The concave edge was adjacent to the field boundary. Each barrier trap was positioned so that it was at the interface between the field and field boundary, with the ends of the trap within the boundary and the concave part within the field. It was assumed that traps acted as barriers to ground active Coleoptera moving in the direction of the field from the boundary.

Two control traps were added to the ten barrier traps on each field boundary side. Both followed the design of the semi-circular barrier traps but with additional features. The first control trap (CT1) aimed to examine the potential for beetles to climb over the lawn edging from the field side by preventing individuals entering traps from the field boundary side. Additional lawn edging (0.2 m high, set to stand 0.16 m above the soil surface and taped to each end of the semi-circular section of trap) and gutters filled with trapping solution (set to be flush with the soil surface as interception traps for ground-active beetles) were used to close off the open side of the traps facing the field boundary. The second control trap (CT2) aimed to quantify arthropods emerging from soil within the traps and therefore not migrating from field boundary overwintering sites. This was achieved by preventing arthropods from entering the trap area. The second control traps replicated the first with 85%
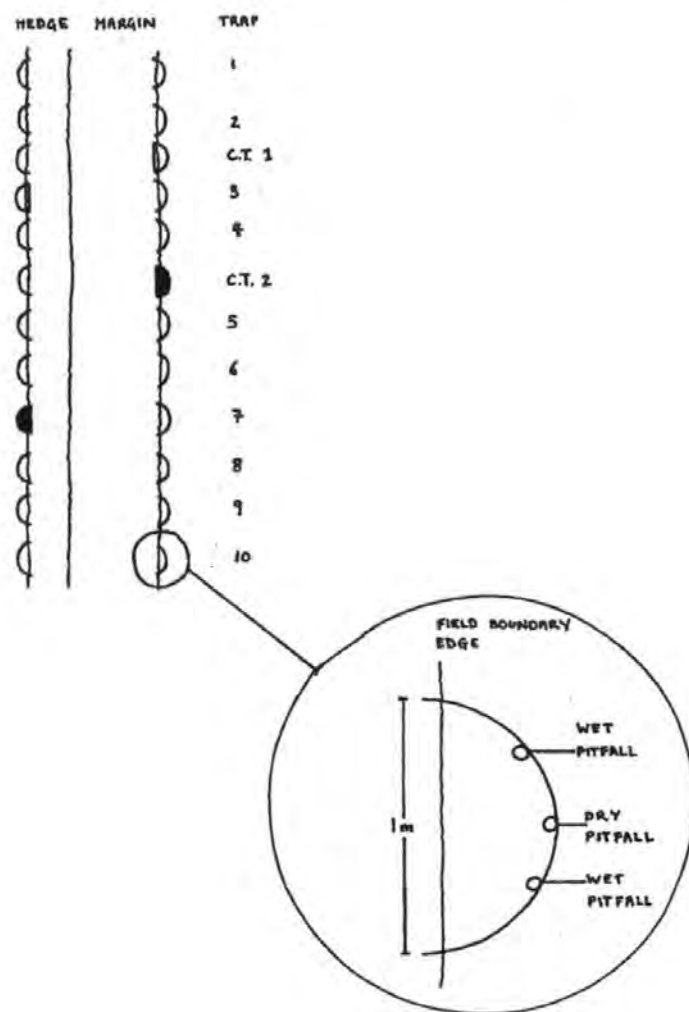
Figure 5.2.1. Arrangement and design of barrier traps along field edge.

agricultural shade material (Tildenet, Bristol) was fitted over the top of the traps and sealed to the lawn edging to prevent entry of beetles.

Three pitfall traps were positioned against the concave edge of the barrier within the field section of the semicircle. The lawn edging acted as a barrier to channel individuals into the pitfall traps. Access to pitfall traps in the second control was via a Velcro opening in the agricultural shade material. Pitfalls within the control traps were treated the same as those in the regular traps. The two outer pitfalls were used as wet traps and quarter filled with a trapping solution (50% ethylene glycol and 50% water with trace of detergent). Wet traps were run continuously from the 7th March to 2nd May 2000 and emptied weekly resulting in eight sampling periods. Captures of carabids and staphylinids were transferred to 70% alcohol preserving fluid and were used to assess abundance of each species.

The middle pitfall was kept dry to collect live individuals for the assessment of relative fresh weigh and fat content. Dry pitfall trapping was conducted from the 14th March until the 2nd May and included eight sampling occasions. Evaporation from beetles in pitfall traps can have considerable influence on their fresh weight (den Nijs *et al.*, 1996; Ostman *et al.*, 2001) and so residence time was kept to a minimum by opening traps for a maximum of twenty-four hours. Dry pitfall traps were opened for one twenty-four hour period on the first day of each sampling week. The pots were filled with crumpled, moist paper to provide shelter, minimise evaporation and deter cannibalism. On collection, beetles were placed in containers with moistened paper and stored in a refrigerator overnight at 4°C; at this temperature physical and metabolic activity was minimised. Beetles collected from the ten traps on one field boundary side were pooled into one container. Control traps were not used for the collection of live specimens. Storage resulted in clean beetles as soil particles were detached. Evaporation by beetles was minimal, thereby reducing weight loss and error. The day after capture the fresh weight of individuals was recorded to within 0.1 mg. Individuals were then placed in labeled bags, killed by freezing (at – 20°C) and species identification confirmed. The left elytron was removed from each specimen and elytral area measured using an image analysis program (Windias) to within 0.1 mm. The relative fresh weight (RFW) (mg. mm^{-2}) was calculated as fresh weight/elytral area (den Nijs *et al.*, 1996).

The remainder of the specimen was used for chemical lipid extraction based on the method by Petersen (1999). Specimens were dried at 60°C for 48 hours and weighed individually to a precision of 0.01mg. Fat was dissolved by soaking specimens for 48 hours in a solution of methanol: chloroform (1:1): 2 ml for smaller specimens (e.g. *B. lampros*) and 6 ml for larger specimens (e.g. *P. cupreus*). Beetles and solution were placed in glass vials and covering with plastic wrap and aluminium foil to prevent evaporation of the solution. Beetles were removed from the solution and dried on tissue paper at room temperature for four hours before being dried at 60°C for a further 48 hours. They were then weighed again to within 0.01 mg. The % fat content (FC) was calculated as the difference between dry weight before and after fat extraction divided by the dry body mass prior to fat extraction and multiplied by 100 (Petersen, 1999).

To examine the effect of seasonality, the first four sampling occasions for abundance (wet traps) and condition (dry traps) were classed as 'early' season, the latter four were combined as 'late' season.

For twelve weeks from 26th November 1999 until 18th February 2000, minimum and maximum temperatures were recorded weekly at the soil surface (using minimum and maximum air thermometers) and at a depth of 10cm into the soil (using temperature probes) at each field boundary. In post and wire boundaries, recordings were taken at a position central between the two uncultivated edges, whilst in hedgerow boundaries temperatures were recorded on the bank top and the base of the bank on either side.

5.2.2 Analysis

Species captured at seven or more boundaries were selected for analysis of condition data. A three factor general linear model was constructed to test for differences in relative fresh weight (mg. mm^{-2}) and fat content (%) of selected species. The three factors were field boundary type (post and wire fence or hedgerow), margin (without margin or with margin) and season (early or late). Pearson's product-moment correlation was used to examine the relationship between relative fresh weight and % fat content of individuals for each species separately.

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Variation in temperature variables (minimum and maximum, soil and air temperature) and the difference between minimum and maximum values was determined using a repeated measures general linear model (GLM). Weekly values (n=12) for each field boundary replicate were used as within subject factors and boundary type (post and wire, PW or hedgerow, H) and margin type (without margin, -M or with margin +M) as between subject factors. Finally, species that showed significant variation in condition measures were selected for analysis of abundance data. Differences in beetle abundance between the three factors (boundary type, margin and season) were tested using a general linear model. Fat content and relative fresh weight were both used as covariates to determine whether they influenced abundance associated with the three factors. Linear regression was used to examine whether either fat content or relative fresh weight could be used to predict abundance.

5.3   RESULTS

In total, 1,022 live specimens were captured, composed of 22 carabid species and 9 staphylinid species. Four carabid adult overwintering species were captured at seven or more field boundary sites and in sufficient numbers to analyse individually: *B. lampros* (36.5 % of total), *Loricera pilicornis* (2.3 %), *P. cupreus* (13.4 %) and *P. strennus* (3.7 %). Additionally, *B. lampros, L. pilicornis* and *P. cupreus* show seasonal migration between field boundaries where they overwinter as adults, and arable fields where they are regarded as potentially effective polyphagous predators of cereal aphids (Wallin, 1985; Coombes & Sotherton, 1986; Sunderland *et al.*, 1987; Chiverton, 1988; Mundy *et al.*, 2000) so they were appropriate for selection in the context of this study. *P. strennus* also overwinters in the adult stage but is more restricted to field boundary habitat and categorised as a closed habitat species (Thiele, 1977; Lindroth, 1992) but analysis was conducted to examine field boundary habitat quality for this woodland species. Adult *Nebria brevicollis* (21.1 % of total) were also captured in high numbers at all eight boundary sites. However this species is an autumn breeder with adults active throughout the autumn and winter (Penney, 1966). The condition of adult *N. brevicollis* captured during the experimental period will reflect both field and field boundary habitat; therefore this species was excluded from the analysis. Few captures within the control traps supported the efficacy of the trapping regime used.

Significant differences in the fat content were observed between *B. lampros* and *P. cupreus*, and in the relative fresh weight of *B. lampros, L. pilicornis* and *P. cupreus* (Table 5.3.1). *P. strennus* showed no differences in either condition measure. The field boundary type (post and wire or hedgerow) at which individuals overwinter had no apparent effect on their post-overwintering condition. Differences in fat content were found for margin and season main effects in *B. lampros* and *P. cupreus*, with strong interactions between field boundary*margin and field boundary*season in *B. lampros*. Strong seasonal differences were also observed in the relative fresh weight of *B. lampros* and *P. cupreus*, with interactions between field boundary*margin for *B. lampros, L. pilicornis* and *P. cupreus*.

The fat content (FC) of *B. lampros* was significantly higher in individuals emerging from post and wire fences without margins compared to those with margins, though there were no differences between hedgerows with or without margins (Figure 5.3.1a). In contrast, boundaries with margins supported *P. cupreus* with consistently and significantly higher fat content, though differences between hedgerows with and without margins were small and not significant (Figure 5.3.1c). Captures of *B. lampros* showed a seasonal increase in fat content at hedgerows, but showed no seasonal difference in post and wire fences. Post and wire without margin boundaries supported *B. lampros* with consistently high fat content throughout the sampling season. For *P. cupreus*, early captures had consistently higher fat contents than late captures across all field boundary and margin combinations. Differences were not observed for *L. pilicornis* and *P. strennus* (Figs 5.3.1b and d).

The relative fresh weights of both *B. lampros* and *L. pilicornis* were highest at post and wire fences without margin and hedgerows with margin (Figures 5.3.2a and 5.3.2b respectively). *P. cupreus* had highest relative fresh weight at hedgerows with margin, and showed no difference between post and wire boundaries with or without margins (Figure 5.3.2c). Early captures of *B. lampros* also had higher relative fresh weights across all field boundary and margin combinations compared to late season individuals. In contrast, *P. cupreus* showed a seasonal increase in relative fresh weight. Differences were not observed for *P. strennus* (Fig 5.3.2d).

Main effects, first order and second order interactions		B. lampros		L. pilicornis		P. cupreus		P. strennus	
df		1,7		1,6		1,7		1,6	
n		373		25		137		37	
		FC	RFW	FC	RFW	FC	RFW	FC	RFW
Field boundary	F	3.07	0.35	0.06	3.6	2.53	0.92	0.31	0.16
	P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Margin	F	8.11	0.003	1.09	2.44	6.52	3.59	1.67	1.11
	P	<0.01	n.s.	n.s.	n.s.	<0.05	n.s.	n.s.	n.s.
Season	F	15.2	14.11	3.33	0.27	5.88	22.53	0.6	3.73
	P	<0.001	<0.001	n.s.	n.s.	<0.05	<0.001	n.s.	n.s.
Field boundary * Margin	F	12.09	15.07	0.06	6.92	1.93	4.06	0.001	2.85
	P	<0.001	<0.001	n.s.	<0.05	n.s.	<0.05	n.s.	n.s.
Field boundary * Season	F	6.94	2.86	0.41	0.74	0.01	0.35	0.12	1.4
	P	<0.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Margin * Season	F	0.42	1.2	1.94	4.25	0.29	0.05	0.06	3.34
	P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Field boundary * Margin * Season	F	2.28	1.59			0.12	0.74		
	P	n.s.	n.s.			n.s.	n.s.		

Table 5.3.1 Results of the 3 factor (field boundary, margin and season) GLM performed on Fat Content (%) and Relative Fresh Weight $(mg.mm^2)$ for *B. lampros, L. pilicornis, P. cupreus* and *P. strennus*. F-statistics and probabilities for main effects, first order and second order interactions, degrees of freedom (df) and number of beetles (n) are shown. Missing values indicate insufficient data.
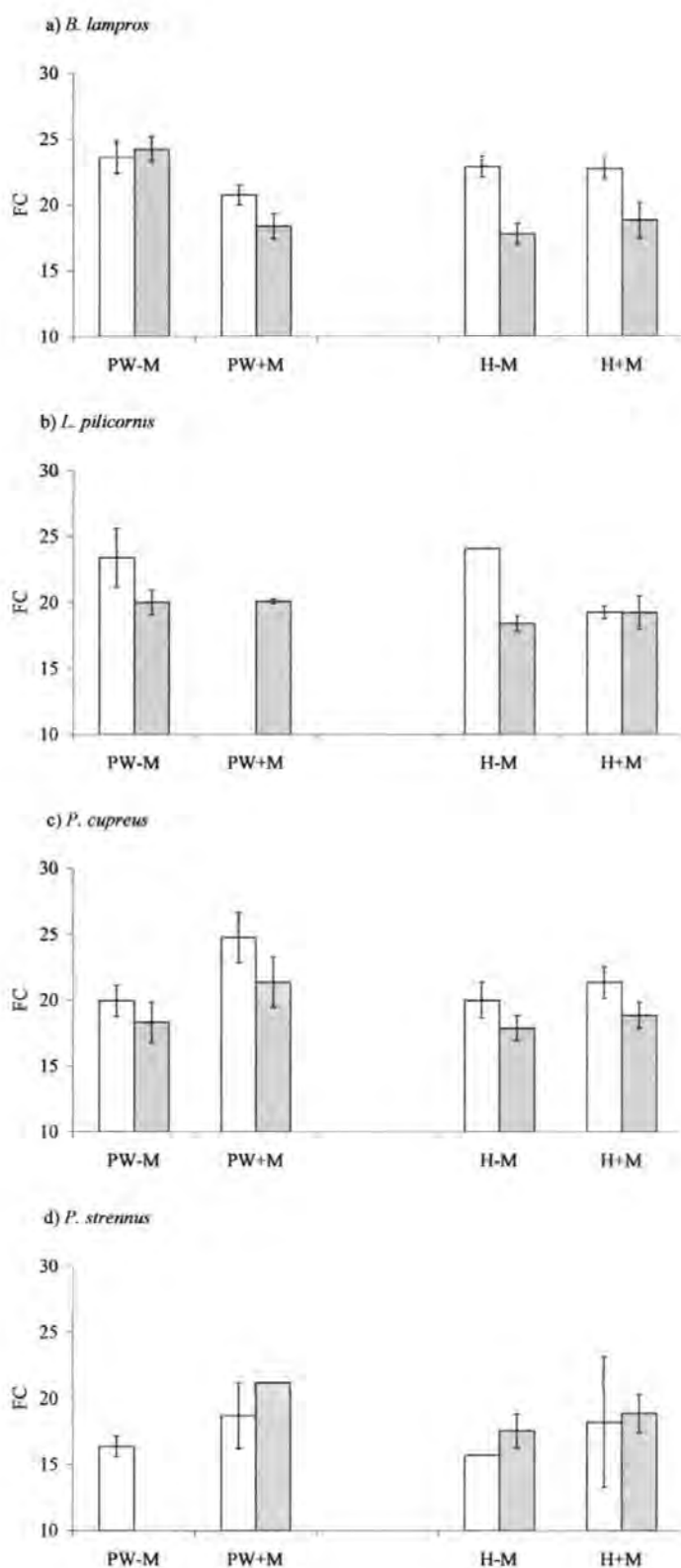
Figure 5.3.1 Mean fat content ± 1 s.e. (FC, %) of four carabid species sampled from two field boundary types, post and wire (PW) or hedgerow (H), without or with margin (-M and +M respectively) from two seasons (early and late represented by open and shaded bars respectively). Missing mean values are due to no captures for a given species. Where standard errors are not represented n=1.
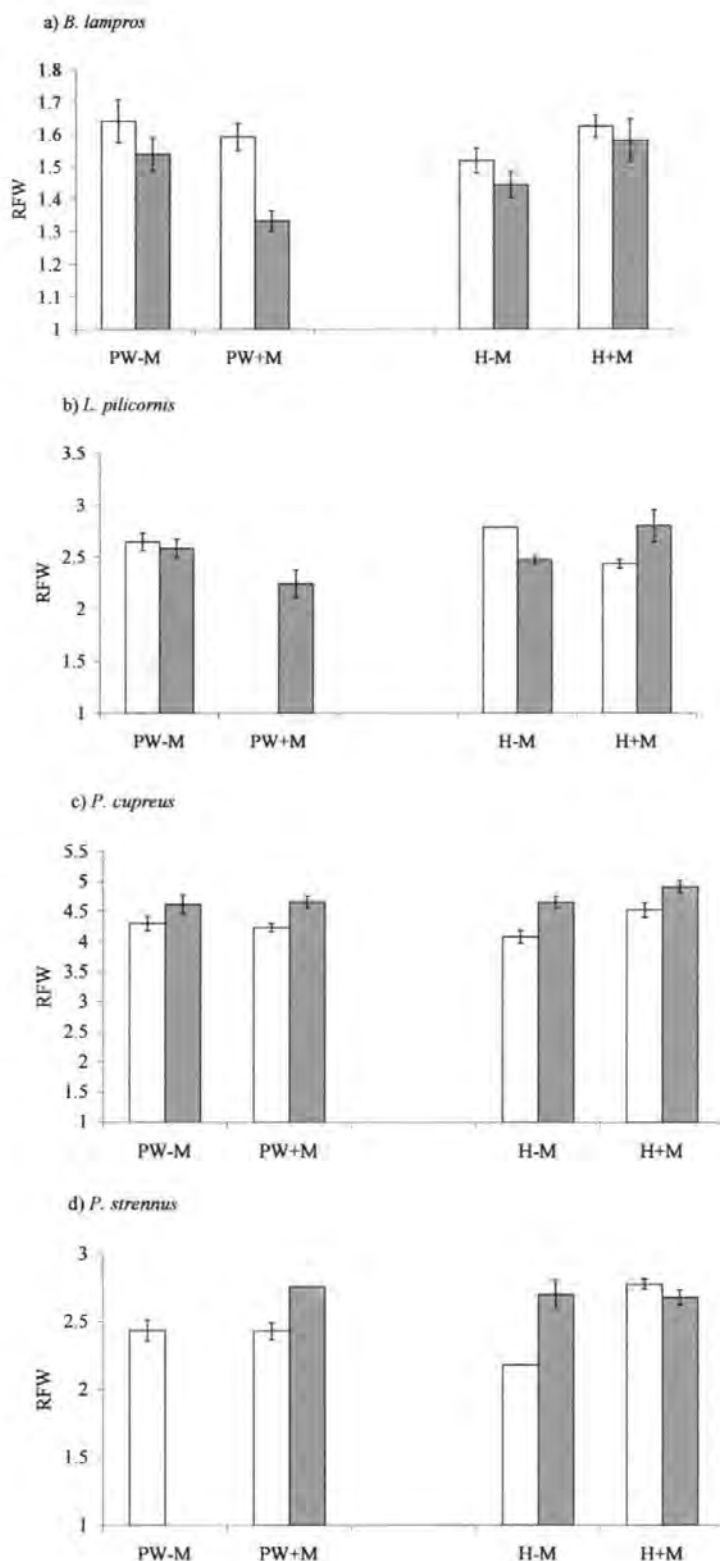
Figure 5.3.2 Mean relative fresh weight ± 1 s.e. (RFW, mg.mm^{-2}) of four species of adult carabid beetle sampled from two boundary types, post and wire (PW) or hedgerow (H), without or with margin (-M and +M respectively) from two seasons (early and late represented by open and shaded bars respectively). Missing mean values are due to no captures for a given species. Where standard errors are not represented n=1.

Relative fresh weight and fat content per specimen showed a significant positive correlation for *B. lampros* only (r=0.137, df=373, P<0.01). There was no association between the two measures of condition for *L. pilicornis* (r=0.264, df=24, n.s.), *P. cupreus* (r=-0.132, df=137, n.s.) and *P. strennus* (r=0.22, df=37, n.s.).

Maximum air temperatures were highest and the difference between minimum and maximum air temperatures largest in post and wire fences with margins and hedgerows without margins resulting in a strongly significant field boundary*margin interactions for both these temperature variables (Table 5.3.2).

Both *B. lampros* and *P. cupreus* differed significantly in physiological condition for the main effects margin and season and so their abundance was investigated. A significantly higher abundance of *B. lampros* was captured emerging from hedgerows compared to post and wire fences (Figure 5.3.3a). However, despite apparently higher mean abundances in boundaries with margins and early compared to late season, neither margin nor seasonal effects were significant. Abundance of *P. cupreus* showed no significant variation with boundary, margin or season, despite consistently lower abundance means late in the season (Figure 5.3.3b). Both relative fresh weight and fat content showed no covariation with abundance (GLM), nor did they predict abundance (linear regression) of *B. lampros* and *P. cupreus* (Tables 5.3.3 and 5.3.4 respectively).

		PW-M	PW+M	H-M	H+M		FB	Margin	FB*Margin
						df	1,4	1,4	1,4
Minimum soil temperature	mean	6.3	5.8	6.58	6.1	F	0.41	0.97	0.00
	s.e.	0.52	0.55	0.34	0.33	P	n.s.	n.s.	n.s.
Maximum soil temperature	mean	9.93	9.67	10.05	10.2	F	3.14	0.09	1.06
	s.e.	0.43	0.47	0.23	0.21	P	n.s.	n.s.	n.s.
Minimum air temperature	mean	-0.21	0.83	-0.42	-0.19	F	4.96	5.55	2.37
	s.e.	0.69	0.54	0.41	0.41	P	n.s.	n.s.	n.s.
Maximum air temperature	mean	13.38	20.67	19.6	15.03	F	0.19	2.62	49.07
	s.e.	0.84	0.93	0.94	0.55	P	n.s.	n.s.	<0.01
Difference in soil temperature	mean	3.63	3.87	3.47	4.1	F	0.00	0.96	0.19
	s.e.	0.33	0.47	0.18	0.2	P	n.s.	n.s.	n.s.
Difference in air temperature	mean	13.58	19.83	20.01	15.22	F	1.00	0.59	33.17
	s.e.	0.61	0.87	0.92	0.57	P	n.s.	n.s.	<0.01

Table 5.3.2 Temperatures (°C, mean ±1 s.e.) at each boundary and margin combination (post and wire PW, hedgerow H, without margin -M and with margin +M). Results (F-statistics and probabilities) are shown of a GLM to test for differences between field bou

a) *B. lampros*
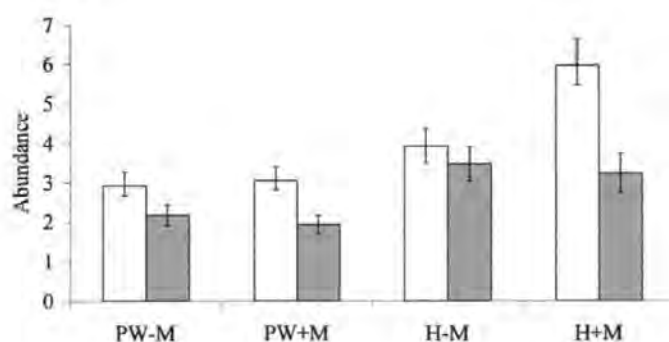
b) *P. cupreus*
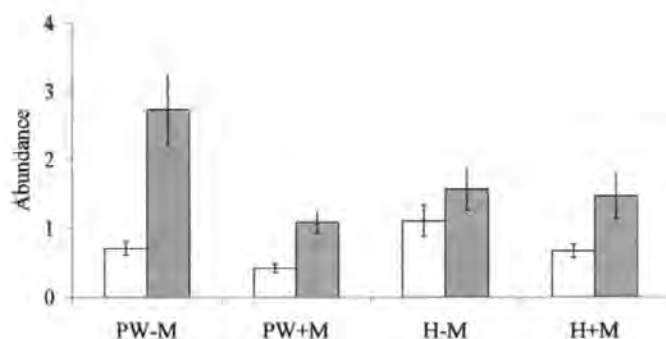
Figure 5.3.3. Abundance (mean ± 1 s.e.) of a) *B. lampros* and b) *P. cupreus* emerging from overwintering at post and wire (PW) or hedgerow (H) boundaries, both without or with margin (–M or +M respectively) in early or late season (represented by open and shaded bars respectively). Results of the GLM testing for differences in abundance means between the three factors: boundary type, margin and season, were significant for *B. lampros* between field boundary type ($F=5.3$, $df=1,7$, $P<0.05$), but were non-significant for *B. lampros* between margin type ($F=0.6$, $df=1,7$, n.s.) and season ($F=3.8$, $df=1,7$, n.s.) and for *P. cupreus* between boundary type ($F=0.1$, $df=1,7$, n.s.), margin type ($F=0.5$, $df=1,7$, n.s.) and season ($F=1.7$, $df=1,7$, n.s.).

		B. lampros		*P. cupreus*	
df		1, 7		1, 4	
		FC	RFW	FC	RFW
Covariable	F	0.009	0.001	0.21	0.25
	P	n.s.	n.s.	n.s.	n.s.
Field boundary	F	4.61	4.58	0.33	0.02
	P	n.s.	n.s.	n.s.	n.s.
Margin	F	0.45	0.51	1.86	1.97
	P	n.s.	n.s.	n.s.	n.s.
Season	F	1.94	2.13	1.64	0.03
	P	n.s.	n.s.	n.s.	n.s.

Table 5.3.3 Results of the GLM testing for differences in the mean abundance of *B. lampros* and *P. cupreus* between the three factors boundary type (hedgerow or post and wire), margin type (without or with) and season (early or late) and using either mean f

		B. lampros	*P. cupreus*
	df	1, 14	1, 12
Fat content (%)	F	0.547	1.01
	P	n.s	n.s
Relative fresh weight (mg.mm^{-2})	F	1.173	1.248
	P	n.s	n.s

Table 5.3.4 Results of linear regression analysis of abundance means for *B. lampros* and *P. cupreus* against means for fat content (FC, %) and relative fresh weight (RFW, mg.mm^{-2}).

5.4 DISCUSSION

Hedgerows and post and wire boundaries provided habitat of suitable and similar quality for polyphagous predators as indicated by the condition of individuals as they emerged from overwintering. The presence of margins adjacent to either boundary type supported populations of *P. cupreus* with higher condition. Boundaries with margins also appeared to be more suitable for *P. strennus*. Although mainly predatory, *P. cupreus* is known to consume seeds and other plant material that may enable individuals to gain condition when prey availability is generally low (Goldschmidt & Toft, 1997). The addition of margins to pre-existing boundaries has previously been recommended on the basis of enhancing overwintering densities of polyphagous predators, which then migrate into adjacent fields (Dennis, 1991; Thomas *et al.*, 1991; Kopp, 1998). This study suggests that margins may also enhance the overwintering condition of some polyphagous predators, with subsequent positive effects on the fecundity and long-term abundance of beneficial species.

The condition of *B. lampros* and *L. pilicornis* appeared to show an association with overwintering temperatures at different field boundary-margin combinations. Low maximum air temperature and small fluctuations in air temperature were particularly favourable. In a previous study, *B. lampros* exposed to constant temperature regimes under laboratory conditions showed greatest overwintering survival; this was attributed to the maintenance of cold-hardiness (low supercooling point) (Petersen *et al.*, 1996). Exposure of *B. lampros* to high winter temperatures was considered to result in greater metabolic activity (Petersen *et al.*, 1996), with subsequent demands on energy reserves that may not be replenished in the absence of available prey. The results of this study suggest that temperature conditions experienced by polyphagous predators may be an important factor determining their overwintering condition.

In this study, the most favourable overwintering temperature regimes were associated with post and wire fences without, and hedgerows with, margins respectively. Microclimatic conditions within a boundary will be influenced by the habitat structure, vegetation type and cover, and landscape effects such as elevation, orientation or exposure to prevailing winds or solar radiation (Forman & Baudry, 1984; Thomas *et al.*, 1992b; Dennis *et al.*, 1994). The narrow verge of vegetation

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associated with post and wire without margin boundaries was dominated by a dense sward of *Lolium perenne*, *Holcus lanatus* and *Dactylis glomerata*. The latter tussock-forming grass species has been shown to buffer temperature fluctuations and therefore provide microclimatic conditions that enhance overwintering survival and density of polyphagous predators (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b; Dennis *et al.*, 1994). This microhabitat characteristic of post and wire without margin boundaries may have been influential in determining temperature profiles and the observed overwintering condition of *B. lampros* and *L. pilicornis*. There were no evident habitat or landscape characteristics to explain why hedgerows with margins should provide more favourable microclimatic conditions than hedgerows without margins (Chapter Two).

Mean fat contents ranged from 18% to 24% for *B. lampros* and *L. pilicornis*, 18% to 25% for *P. cupreus* and 16% to 21% for *P. strennus* respectively. Feeding trials of *B. lampros* reported in the literature demonstrate that individuals fed *ad libitum* maintained constant fat contents of 23% and death by starvation occurred when the fat content of individuals fell below 7% (Petersen, 1999). Comparable measures of fat content in *L. pilicornis*, *P. cupreus* and *P. strennus* are not available in the literature. However, Mols (1988) states that the fat capacity of most beetles will have a maximum threshold due to restrictions in gut size and that this will be proportional to body size. Fat content for *L. pilicornis* and *P. cupreus* was similar to *B. lampros*, whilst populations of *P. strennus* supported a lower range of fat contents. Therefore, individuals of *B. lampros*, *L. pilicornis* and *P. cupreus* with maximal fat reserves are likely to be neither food-limited nor suffering from excessively stressful abiotic conditions. These individuals may be able to find highly suitable overwintering sites in field boundary habitats. Individuals with lower fat reserves suggest poorer quality overwintering habitat in terms of availability of prey or suitability of microclimate. Although these individuals were not threatened by starvation induced mortality, they may be less fecund, with consequences for the long-term population dynamics of these beneficial species. The relative fresh weight of *P. cupreus* (4.1 to 4.9 mg.mm^{-2}) captured within this study compared with values for field caught *P. cupreus* (4.4 to 4.8 mg.mm^{-2} for females and males respectively) from an arable area of The Netherlands during spring (den Nijs *et al.*, 1996).

The poorer condition of *P. strennus* compared to other carabids suggests that all field boundary habitats may be sub-optimal for this species. *P. strennus* is characteristic of closed or woody habitats and has a medium dispersal power. In contrast, the other three carabid species are either ubiquitous (*B. lampros and L. pilicornis*) or prefer open habitat (*P. cupreus*) and have high dispersal power (Thiele, 1977; Lindroth, 1992; Fournier & Loreau, 2001), traits that are regarded as favourable to long-term population persistence in agricultural landscapes (Den Boer, 1981; Fournier & Loreau, 2001).

The condition of polyphagous predators captured was generally 'high' to 'moderate' indicating that starvation induced overwintering mortality is probably not a determining factor in either the abundance of species emerging from overwintering or their long-term population dynamics. This may explain the lack of a relationship between condition measures and abundance. Instead, abundance of *B. lampros* in particular, appeared to be related to the ground surface area that boundaries occupied, being greatest in hedgerows. Larval survival is regarded as an important factor in the population dynamics of *B. lampros* as less than 50% of the population survive this developmental stage (Petersen, 1998). Key-factor analysis on the population dynamics of important natural enemies is required to determine vulnerable life-history stages and subsequently to develop techniques to augment numbers in farmland.

Populations of *B. lampros* emerging from overwintering showed a seasonal decline in condition (both fat content and relative fresh weight). Previous studies have suggested that weight loss observed in post-overwintering *B. lampros* may result from insufficient food to replenish energy reserves consumed by increasingly active individuals (Petersen *et al.*, 1996). Greatest overwintering mortality of this species was observed in early spring (termed post-overwintering mortality), possibly due to a premature declimatisation to cold (Reidel & Steenberg, 1998; Petersen *et al.*, 1996). Stimuli for the elevation of the super cooling point are thought to be temperature related (Leather *et al.*, 1993). However, the maintenance of cold-hardiness through synthesis of cryoprotectants may also have some condition threshold, below which cold-hardiness cannot be sustained. If this is the case, then availability of prey in early spring would have important consequences for post-overwintering survival and subsequent fecundity of polyphagous predatory species. Post and wire without margin

boundaries were the only sites where *B. lampros* showed a slight seasonal increase in condition. Tussocky grasses associated with this habitat (within this study) are known to support high overwintering densities and diversities of alternative prey items for polyphagous predators, including Collembola and other small arthropods. These grass species are already targeted to enhance overwintering densities of polyphagous predators and have been shown to influence overwintering survival (Thomas *et al.*, 1991, 1992b; Dennis *et al.*, 1994) but could also enhance post-overwintering survival, condition and subsequent fecundity. Whilst enhancing post-overwintering condition and survival of polyphagous predators would be beneficial for biological control, further investigation is necessary into the effect of post-overwintering habitat quality on the migration of beneficials into crop fields.

Seasonal changes in the condition of *P. cupreus* vary with the condition measure used. The fat content of *P. cupreus* individuals declined from early to late season, whilst relative fresh weight showed a seasonal increase. Post-overwintering fat reserves may be converted to egg production (Bommarco, 1998b), whilst changes in net body weight in reproductive females will be affected by growth of ovaries and eggs (Mols, 1988) with a corresponding increase in relative fresh weight. Previous studies have also demonstrated a seasonal increase in relative fresh weight of both male and female *P. cupreus*, reaching a maximum at the start of the reproductive period (den Nijs *et al.*, 1996). This contrasting response of relative fresh weight and fat content with season suggests that these two variables may be measuring different aspects of a beetle's overwintering condition. Both measures showed a positive correlation for *B. lampros* but not for the other species examined. It is likely that body weight (and corresponding values for relative fresh weight) will alter more readily in response to environmental conditions such as humidity. Beetles are known to lose body weight through evaporation (e.g. Ostman *et al.*, 2001), and overwintering arthropods may be particularly susceptible to desiccation (Leather *et al.*, 1993). For example, Hemiptera species were found to decrease their water content by 13.7% during hibernation with a resultant decrease in survival, dependent on moisture conditions (Eguagie, 1974). Consequently, relative fresh weight during winter may be more indicative of body fluid levels and desiccation. During the spring relative fresh weight will be increasingly indicative of fecundity.

Relationships between fat content and other non-destructive measures of condition based on body weight (e.g. Juliano, 1986; Bommarco, 1998b; Ostman *et al.*, 2001) have been demonstrated under laboratory conditions. Strict control of humidity levels, use of extreme diets including *ad libitum* and near starvation and the use of indices to estimate fat body sizes will all contribute to the strength of the relationship found. It is unlikely that relative fresh weight can be used as a non-destructive method of estimating energy reserves without a careful examination of the relationship between the two measures in field populations and a greater understanding of the relative determinants of each measure of condition.

The lack of field boundary replicates in this study limited the statistical strength of observed patterns and further work is warranted. The use of condition provided a useful means of assessing habitat quality for polyphagous predators and could provide a means of examining habitat quality for closed habitat species. The condition of arthropods in field boundary habitats may also influence prey quality for game birds, and other birds and small mammals of conservation or economic concern.

CHAPTER SIX: OVERWINTERING MICROHABITAT SELECTION BY CARABIDAE AND STAPHYLINIDAE IN HEDGEROW AND GRASSY MARGIN

6.1 INTRODUCTION

Habitat selection can have a strong impact on the survival, condition and fecundity of Carabidae and Staphylinidae overwintering in field boundaries, and the population dynamics of a species in farmland (Orians & Wittenberger, 1991). The overwintering microhabitat may be described by the abiotic and biotic environment in which a species exists. Microclimatic conditions of an overwintering site will determine body temperature, metabolic rate, biochemical and physiological responses of an organism and regulate the timing of its various activities (Casey, 1981; Leather et al., 1993; Atienza et al., 1996). Microclimatic conditions may also influence prey availability and consequently overwintering energy reserves and the ability of an individual to maintain cold-hardiness or to search for either prey or more suitable overwintering sites (Luff, 1966b; Leather et al., 1993; Zhou et al., 1995). Prey availability and energy reserves may also determine post-overwintering survival, a period when greatest mortalities of carabids and staphylinids have been observed (Riedel & Steenberg, 1998; Thomas et al., 1992b; Petersen, 1999).

Habitat selection is the choice of specific sites by animals orientating to abiotic or biotic factors (habitat cues). Habitat cues include visual stimuli to orientate an individual to major features of the landscape, olfactory stimuli associated with prey, predators or individuals of the same species and abiotic stimuli relating to temperature, humidity, soil moisture and texture. Visual cues (light radiation) and odours elicit a directional kinetic response determined by the direction of the stimuli and preference of the species (Evans, 1983). Most abiotic factors (e.g. temperature, relative humidity and ambient light intensity) elicit a non-directional kinetic response involving reduced locomotion speed and increased turning frequency. This movement behaviour results in aggregation of a population within areas exhibiting the preferred range of stimulus intensity. However, olfactory cues, for example from prey, may also result in an aggregative response by carabids and staphylinids (Bryan & Wratten, 1984) and it has been suggested that they influence overwintering site selection (Thomas et al., 1992b). Consequently, field active carabids and staphylinids may use

visual stimuli to locate field boundaries as overwintering sites (Thiele, 1977; Rijnsdorp, 1980; Colombini *et al.*, 1994) and combined olfactory and abiotic stimuli for the selection of microhabitats. For ground active species, microhabitat selection will be strongly influenced by ground-related habitat factors (Atienza *et al.*, 1996). Carabids were able to detect and express a preference for temperature, substrate moisture, humidity and substrate texture (Thiele, 1977). Mechanical stimulation from vegetation was considered to be an important factor in habitat selection by riparian *Bembidion* spp (Andersen, 1985). Carabids have also been observed to respond to the chemical kairomones emitted by microflora which themselves were distributed according to abiotic factors in the environment (Evans, 1983).

During the active reproductive period of carabid species, the most important factors determining habitat selection are soil moisture and vegetation characteristics (Luff *et al.*, 1989; Rushton *et al.*, 1991; Baguette, 1993; Holopainen *et al.*, 1995; Sanderson *et al.*, 1995). At present, there is little direct evidence of overwintering habitat selection by carabids and staphylinids in field boundaries. However, heterogenous distributions of carabids and staphylinids in field boundaries (Thomas *et al.*, 2001a; Maudsley *et al.*, 2002) suggests that individuals actively select overwintering sites. Microhabitat characteristics associated with high overwintering densities of carabids and staphylinids include the presence and type of vegetation cover, leaf litter biomass and height of a raised bank. These characteristics have been shown to strongly influence temperature, moisture and the availability of prey, and consequently overwintering survival and condition (Bossenboek *et al.*, 1977; Sotherton, 1985; Thomas *et al.*, 1992b; Dennis *et al.*, 1994). Favourable abiotic conditions are likely to act as habitat cues for site selection. These microhabitat characteristics may therefore be actively selected during early to mid-winter at the time of overwintering site selection (Wallin, 1985).

Small fluctuations in temperature overwinter have been shown to enhance overwintering survival of *B. lampros* and *T. hypnorum* (Dennis *et al.*, 1994; Petersen *et al.*, 1996). Variability in temperature has been shown to increase as the complexity and biomass of herbaceous vegetation decreased, with bare earth associated with most extreme temperature fluctuations and tussocky grasses with least variable temperatures (Bossenboek *et al.*, 1977; Thomas *et al.*, 1992b; Burki & Hausamann,

1993). Tussock-forming grasses have been associated with high overwintering densities of polyphagous predators and were shown to reduce mortality rates of overwintering carabids and staphylinids (e.g. *T. hypnorum* and *D. atricapillus*) (Luff, 1966b; Dennis *et al.*, 1994). These temperature buffering properties are also evident during early to mid winter and may be used as stimuli for microhabitat selection (Thomas *et al.*, 1992b). Additionally, relative humidity was lower on bare soil compared with vegetated ground (Geiger, 1965), which may influence preference for vegetated sites. The biomass of leaf litter on the ground was positively associated with high densities of overwintering carabids and staphylinids (Maudsley *et al.*, 2002) and may insulate individuals from temperature fluctuations. During the summer period, many species seek more moist substrate and humidity conditions to prevent dessication of adults, eggs or larvae (Lindroth, 1992). In contrast, during the winter the risk of suffocation by water-logging or ice-nucleation when soil water freezes causes many species to seek drier overwintering conditions (Sotherton, 1985; Leather *et al.*, 1993). Dry and sheltered microhabitats, such as those associated with banks raised above field level, may enhance overwintering survival of *T. hypnorum* (Dennis & Fry, 1992) and contribute to the high densities of polyphagous predators associated with these sites (Sotherton, 1985).

The importance of pre-winter food to build-up energy reserves in overwintering beetles has been recognised. However, the relationship between prey availability and habitat selection of carabid and staphylinid polyphagous predators in field boundaries has yet to be demonstrated (e.g. Thomas *et al.*, 1992b). There is some evidence that microhabitat characteristics such as bare ground providing unfavourable temperature profiles may be more influential in determining overwintering mortality of *D. atricapillus* than prey availability, though this could not be confirmed (Dennis *et al.*, 1994). Difficulties in demonstrating the relationship include assessment of prey availability at the precise moment of habitat selection and quantification of all potential food sources for a generalist feeder (Thomas *et al.*, 1992; Dennis *et al.*, 1994). Generally, the diversity of prey items such as Collembola and small soil-dwelling arthropods, increases or shows a unimodal response to densities of polyphagous predators in field boundaries (Dennis & Fry, 1992). In addition, densities of general arthropods and polyphagous predators show similar patterns within a range

of grass plant structures (Luff, 1966a) and vegetation types (Lys, 1994; Thomas *et al.*, 1994).

It is generally accepted that individuals will show a preference for habitats that optimise their survival and fecundity (Orians, 1980). In practice however, sites selected for overwintering will reflect costs incurred in searching (e.g. energy depletion, increased risk of predation and the risk of sudden and adverse climatic changes) and the amount of information available to an individuals at the time of site selection (Orians & Wittenberger, 1991). For example, an individual may lack information on the habitat quality of one site relative to others within a field boundary, and the habitat quality may change temporally. For species migrating from the field, the potential to find optimal overwintering sites will be limited by their dispersal ability, the location of optimal sites in relation to the field boundary edge and impediments to movement caused by the physical structure of the field boundary vegetation. Species that fly to field boundaries are expected to show a more homogeneous overwintering distribution than ground-active species since movement through the boundary habitat is not impeded by vegetation structure (Riedel, 1995). Dense vegetation (Rivard, 1965; Klazenga & de Vries, 1994) and a deep litter layer (Greenslade, 1965) have been shown to impede carabid dispersal. Similarly, structural complexity at the ground layer has been shown to restrict the movement patterns of Coccinellidae (Grez & Villigran, 2000), whilst an increase in the physical complexity of ground vegetation (increasing in the order bare ground, crop stubble, barley crop and hedgerow) was found to reduce movement rates of *P. melanarius*, *P. madidus* and *H. rufipes* (Mauremooto *et al.*, 1995). Movement over bare ground was also influenced by the availability of cover, such that movement of *P. melanarius* was restricted when cover was absent (Brown, 2000). Additionally, the fractal geometry of the ground surface may be important in altering the effective distance dispersed by a ground active arthropod (Weins *et al.*, 1993; Mauremooto *et al.*, 1995; Thomas *et al.*, 1998). Smaller carabids may experience less resistance to movement caused by vegetation since they are able to move through smaller gaps (Powell *et al.*, 1985; Ekbom, 1994) but may have to disperse a greater effective distance than larger species.

The dispersal rate of beetles between fields is a critical parameter affecting the survival of metapopulations in farmland, especially where fields are frequently sprayed with insecticides (Sherratt & Jepson, 1993). Limited between-field movement can affect the refounding of local populations and consequently the provision of beneficial functions such as biocontrol. Furthermore, between-field movement of individuals will contribute to gene-flow between sub-populations. Studies examining the potential of epigaeic beetles to move across field boundaries have produced contrasting results. For example, grass and herbaceous margins represented linear features of variable permeability to carabids (Mader *et al.*, 1990; Duelli *et al.*, 1990; Kopp, 1998). Similarly, mark-release-recapture studies have found hedgerows to act as relatively impermeable barriers to between field movement of *P. melanarius* and *N. brevicollis* (Garcia *et al.*, 2000; Thomas *et al.*, 2001), or to have little restriction on between-field movement of *P. melanarius* and *P. madidus* (Holland *et al.*, in press). Comparison between these studies is limited by the absence of detailed descriptions of the microhabitat vegetation and structure of the field boundaries studied. For example, a dense hedgerow canopy may have a sparser hedge-base flora that is less restrictive to beetle movement compared to a hedgerow with a thin canopy. Additionally, factors such as hunger levels have been shown to influence movement rates and motivational states of beetles and may have differed between study sites (Wallin & Ekbom, 1994).

Studies of field boundary permeability have focussed on large to medium sized carabids, but small carabids e.g. *Bembidion* spp are likely to respond differently to vegetation structure, cover, microclimate and fractal geometry. In addition, studies have been conducted during the active breeding season when individuals tend to be active in fields. There may be significant population exchange between fields when species overwinter, aestivate or take refuge in field boundaries (Garcia *et al.*, 2000). Mixing of field populations over the winter would have important implications for gene flow, whilst individuals emerging into a different field after overwintering will enable locally extinct field populations to be refounded. Data on carabid and staphylinid movement through different field boundary types over winter could contribute valuable information for models of insect movement at the landscape scale (e.g. Corbett & Plant, 1993; Sherratt & Jepson, 1993; Vermeulen & Opsteeg, 1994).

The representation and spatial arrangement of microhabitat characteristics supporting high densities of overwintering Coleoptera will differ between field boundary types. Post and wire boundaries with a grassy margin will support a dense sward of sown grasses including favourable tussocky grasses such as *D. glomerata* and *H. lanatus*. Hedgerows tend to be raised above the field level and characteristically have mostly bare-ground and leaf litter underneath the canopy with some loose plant structures such as ivy. Ground flora at the canopy edges may be more dense and composed of taller grasses and herbaceous plants.

The work described in this chapter investigates the distributions of 'natural' and 'introduced' carabids and staphylinids within two boundary types. Using mark-release-recapture (MRR) techniques, marked beetles were introduced into field boundaries or order to investigate their release distribution in relation to their subsequent recapture distribution and that of naturally occurring populations. The distribution and preference of overwintering locations for introduced and natural populations of Carabidae and Staphylinidae within field boundaries was studied. Aggregations in beetle distributions and associations with abiotic variables were detected using novel statistical techniques (SADIE, spatial analysis by distance indices) to quantify spatial pattern (Perry *et al.*, 1999), and used to indicate habitat selection.

6.1.1 Aims

(i) To investigate active site selection by overwintering carabids and staphylinids within hedgerows and post and wire fences with grassy margins.

(ii) To determine to what extent spatial distributions differ between two field boundary types in relation to favoured microhabitats.

(iii) To assess the distances traversed by migrating individuals in each boundary type.

6.2 METHODS

6.2.1 Marking

For the purposes of mark-release-recapture studies a mark is required that can be applied easily to a sufficient number of individuals, last for the duration of the study, and have no effect on the behaviour or survival of marked individuals (Southwood & Henderson, 2000). In previous mark-release-recapture studies a range

of marking techniques have been used including paints, dyes, immunoglobulin, abraded and branded marks, radio isotopes and rare earth elements, and have been reviewed in Southwood & Henderson (2000) and Hagler & Jackson (2001). Beetles may be given a batch mark to identify the general origin of a group of individuals, or a unique identity code. Few techniques for marking beetles enable unique identification of individuals, especially for small species. Drills have been used to abrade coded areas of the pronotum and elytra on larger carabids (e.g. *Pterostichus melanarius*), and enabled unique identification of 1777 individuals (Thomas, 1995; Thomas *et al*, 1998). This technique has also been used to batch mark medium-sized carabids e.g. *N. brevicollis* (Garcia *et al.*, 2000), but would be unsuitable for small species. More commonly, beetles are marked using paints or dyes which provide an easy to apply and highly visible mark, though due to the waxy cuticle of the exoskeleton these marks can be temporary.

As part of this study a novel method was developed to mark carabids and other arthropods that possess a chitinised exoskeleton (Griffiths *et al.*, 2001). A Synrad Fenix Laser Marker (Synrad Inc, 6500 Harbour Heights Parkway Mukilteo, WA 98275, USA, http://www.synrad.com) was used to mark the elytra of a range of carabid species using a 25-Watt CO_2 laser and galvo-based marking head set with a 370mm lens at a speed of 380 mm.second[-1] and power settings appropriate to the species (5% - 20%). Beetles were restrained in position below the marking head using a 150 x 150 mm holding plate with a 10 x 6 grid of wells that were marginally larger than the beetles. The base of the wells was constructed from 1 mm wire mesh, allowing beetles to be held in place with suction (Hewlett, 1954) applied from a domestic vacuum cleaner connected to a small chamber attached to the holding plate. Prior to marking, beetles were sedated by chilling to ~4 °C (30min) then positioned in the wells (5 min for 60 beetles). The combination of chilling and suction prevented movement of the beetles and allowed accurate mass marking. Within each holding plate up to 60 beetles could be batch marked using an alphanumeric code that was positioned and formatted using Synrad Winmark software. Once restrained underneath the marking head beetles were rapidly marked at a rate of 20 second[-1]. The resulting code was etched onto the surface of the elytra but did not puncture the surface and could be read with the naked eye (digits had a text height of 1.5 mm).

A range of carabid species were marked experimentally including the large-sized *P. melanarius*, medium sized *P. cupreus* and *A. plebeja* and smaller *A. dorsale* and *B. lampros*. Large species were marked with a three-digit alphanumeric code, medium-sized beetles with a single digit code whilst the smallest species were spot marked.

To determine the effects of marking on individual beetles, cohorts of 30 marked and 30 unmarked beetles were observed over a 4-week period. Beetles were placed individually in 9-cm Petri dishes containing damp filter paper, and dishes were randomly arranged in a culture chamber. Beetles were fed a diet of *Lucilia caesar* (L.) maggots and cat food *ad libitum* and kept under a natural day-night regime in cool ambient conditions (19-21 °C). Food and filter papers were replaced on alternate days. After the four week trial no beetle had lost its mark and the codes remained clear on beetles alive after 3 months. Mortality in both cohorts was 6.6% or 2 individuals. No adverse effects on marked beetles were evident.

The laser technique was used to mark 296 *P. cupreus* for use in a MRR experiment to examine the movement of *P. cupreus* into a hedgerow field boundary overwinter. The 296 *P. cupreus* were collected from the Seale-Hayne farm in October 1999. Beetles were placed into a two-litre plastic container at maximum densities of 15 individuals/ container. The containers were three-quarters filled with a soil-compost mixture and covered with muslin. Two flat stones (approx. 5cm x 5cm x 1cm) were placed on the soil surface to provide cover. Beetles were fed a diet of *Lucilia caesar* (L.) maggots and cat food *ad libitum* and provided with moistened filter paper. Food and moistened filter papers were replaced every two days. Beetles were kept under a natural day-night regime in ambient conditions (2-10 °C). An elytron of each beetle was laser-marked with a single digit code in six cohorts ('C', 'M', 'S', 'n', 'o', 'x') on the 3rd November 2000. Beetles were observed for two further days prior to release into an outdoor arena on the 6th November 2000 (see Section 6.2.2 for details of release). In total, 280 marked individuals were released and sixteen beetles representing all cohorts were kept as a control group to monitor durability of marks and survival over winter. Control group individuals were kept in overwintering refugia under the same conditions as beetles prior to marking with the exception that food and moistened filter paper were replaced every three days. The

interval between changing food and filter paper was increased due to lack of feeding and general inactivity of beetles in the control group.

Methodology for laser-marking was not sufficiently developed to mass mark the small carabid *B. lampros* for use in MRR studies. Therefore this species was marked using a water based correction fluid ('Tippex') in white and green. Beetles were sedated by marking in a controlled temperature room maintained at 4 °C (Petersen et al., 1996; Southwood & Hendersn, 2000) and a small dot of Tippex was applied to one elytron with a no. 1 size artist's paint-brush. After marking, individuals were placed onto a clean dry surface until the paint had dried (5-10 seconds). For the trial, 1110 *B. lampros* were given a white Tippex mark and 350 individuals received a green Tippex mark (see Section 6.2.2 for details of *B. lampros* release into field boundaries). In addition, 80 *B. lampros* were marked (40 white and 40 green) and kept as a control group under standardised conditions (see above for *P. cupreus*) to observe durability of marks and overwintering survival. Loss of marked *B. lampros* through increased predation was not examined. *B. lampros* were marked between 3rd and 6th December and kept under observation until the 10th December when they were released.

6.2.2 Field boundary sites

A hedgerow and a post and wire (corresponding to H7 and PW6 in Chapter 2) field boundary bordering the same arable field and adjacent to different ley fields were selected for study. The post and wire fence has a 2.7 m wide sown grass margin on the arable side: 0.6m of the margin adjacent to the fence was long-established and the remainder was prepared by sowing with perennial rye grass (*L. perenne*) in spring. The grassy margin supported a mixture of cocksfoot (*D. glomerata*), yorkshire fog (*H. lanatus*), perennial rye grass and bents (*Agrostis* spp.), whilst close to the fence-line there were patches of cleavers (*G. aparine*) and nettles (*U. dioica*). Within the margin there was some dead plant stubble from summer herbaceous annuals and some bare ground. Vegetation density was greatest nearest the post and wire fence and decreased towards the arable field edge. The hedgerow had a dense canopy (8% gaps) of predominately hawthorn (*C. monogyna*), with some blackthorn (*P. spinosa*), hazel (*C. avellana*) and field maple (*A. campestre*). The canopy was 2.9m high by 3.0m wide and set on a 0.8m hedgebank. There was no ditch. A post and wire fence was

positioned on the arable side and associated with a 0.2m strip of grassy vegetation. The hedge-base was characterised by bare ground with some moss and leaf-litter cover and occasional lords and ladies (*A. maculatum*) and harts tongue fern (*A. scolopendrium*). At the canopy edges patches of nettles, cleavers, meadow grasses (*Poa* spp.) and perennial rye grass were found.

Five arenas were built, three into the hedgerow (numbered 1 to 3) and two in the post and wire boundary with grassy margin (numbered 4 and 5) (Figure 6.2.1). Four of the arenas (two in each boundary type) were 2 m by 3 m in length, one arena positioned in the hedgerow was 1.8 m by 4.2 m in length. The width of the latter arena was restricted by the position of woody shrubs but the length was extended to include a section of the ley field. All five arenas were positioned with the long side crossing the boundary and the short side running parallel to the adjacent fields. The arenas were constructed of a wooden frame (2 x 4cm wooden vertical and horizontal supports attached to fence posts at the four corners). Lay-flat polythene tubing (24 inch diameter) (Turner Whitehead Industries, Lincs.) was wrapped around the outside of the frame and dug 0.2 m into the ground. In the post and wire boundary the fence and entire width of the margin were enclosed in the two arenas (the lower two strands of fence wire were cut to allow the poly-tubing to pass through). The post and wire arenas extended 0.3m into the ley and arable fields on each side. In the hedgerow, the two smaller arenas extended to the edge of the canopy on both the ley and arable side (but did not include the post and wire fence on the outside of the hedgerow canopy adjacent to the arable field). The sides of the arenas followed the profile of the hedgerow bank. The larger arena extended to the edge of the canopy on the arable side (not including the post and wire fence) and extended 1.2 m into the ley field. The arenas were sub-divided into 0.04m^2 sampling units (0.2 m x 0.2 m) using string stretched across the top of the arenas and stapled to the wooden frame. The smaller arenas contained 150 sampling units, the larger arena 198 sampling units. Sampling units were labelled as rows A through to O (small arenas) or A to U (large arena) on the long side of the arenas and columns 1 through to 10 (small arenas) or 1 to 9 (large arena) on the short side of the arenas (Figure 6.2.2). Therefore, each sampling unit could be uniquely identified by arena, row and column. The microhabitat characteristics (including vegetation cover and type, leaf litter cover, stones, dead wood, bare earth and fence posts) were recorded per sampling unit within each arena

on the 30th and 31st January prior to destructive sampling. Minimum and maximum, air and soil temperature were recorded at eight locations (four sites in two profiles, $Temp_1$ and $Temp_2$) (see Figure 6.2.1) in each field boundary adjacent to the arenas. Temperatures were recorded on 18 occasions (every 2 to 3 days) from the 11th December 2000 until 2nd February 2001.
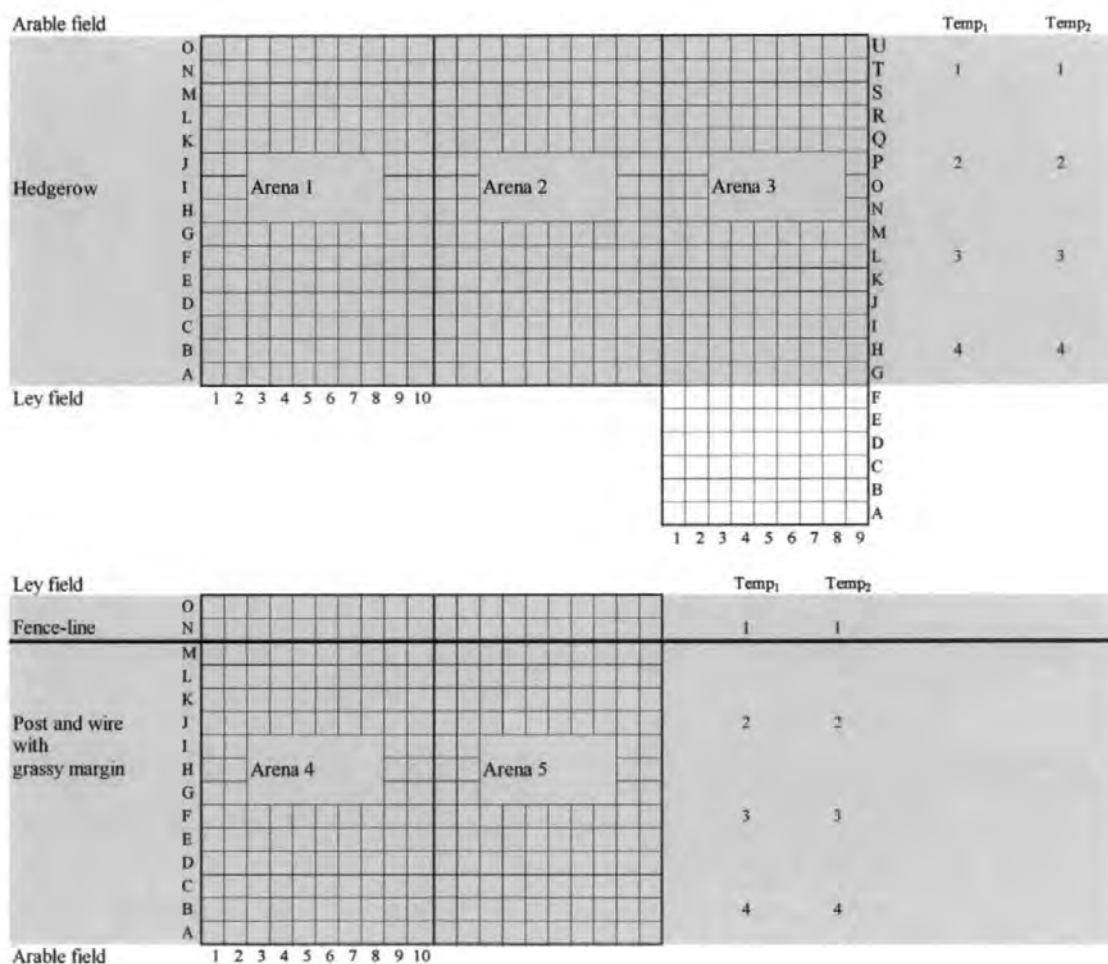
Figure 6.2.1 Plan of arenas 1, 2 and 3 in the hedgerow and arenas 4 and 5 in the post and wire with grassy margin, showing sampling units and the location of field boundary profile sites for measuring minimum and maximum soil and air temperature (°C) ($Temp_1$ and $Temp_2$).

175 individuals
B. lampros marked white

140 individuals
P. cupreus marked 'C', 'M' and 'S'

Arable field

Hedgerow

Arena 1: *B. lampros* (marked white) released in even distribution (n=350).

Arena 2: marked *B. lampros* released at ends (n=350).

Arena 3: marked *P. cupreus* released at ends (n=240).

Ley field

B. lampros marked green
175 individuals

P. cupreus marked 'n', 'o' and 'x'
140 individuals

175 individuals
B. lampros marked white

Ley field

Fence-line

Post and wire with grassy margin

Arena 4: marked *B. lampros* released at ends (n=350).

Arena 5: white-marked *B. lampros* released in even distribution (n=350).

Arable field

B. lampros marked green
175 individuals

Figure 6.2.2 Plan showing the release of marked *B. lampros* and *P. cupreus* at each arena.

6.2.3 Sampling

Marked beetles were released at equivalent densities in both field boundary types in two different patterns. Arena 1 (hedgerow) and Arena 5 (post and wire with grassy margin) were seeded with an 'even' distribution of marked *B. lampros*; in Arena 2 (hedgerow) and Arena 4 (post and wire with a grassy margin) marked *B. lampros* were released at each end adjacent to arable or ley fields; in Arena 3 marked *P. cupreus* were released at each end of the arena (Figure 6.2.2). In the even arenas (1 and 5) 380 *B. lampros* marked with white Tippex were released in an even distribution of 2.5 individuals.$0.04m^{-2}$ sampling unit (two or three marked individuals were released alternately in the centre of each sampling unit). In the end arenas (2 and 4) 175 *B. lampros* were released in row A (green Tippex) and row O (white Tippex) (n=350 per arena). Alternately 17 or 18 individuals were placed in the centre of each sampling unit in rows A and O. In Arena 2, row A was adjacent to the ley field, whilst in Arena 4 row A was adjacent to the arable field. Laser-marked *P. cupreus* (n=280) were released into Arena 3 in the hedgerow. A cohort of 140 individuals was released in row A (adjacent to ley edge) and row U (adjacent to arable field) by placing 15 or 16 laser-marked *P. cupreus* alternately in each sampling unit. The cohort released in row a were marked 'n', 'o' and 'x', while beetles released in row U were marked 'C', 'M' and 'S' (different marks within each cohort were not treated separately). Marked *P. cupreus* were released on the 12th November 2000, marked *B. lampros* were released on the 21st December 2000.

Destructive sampling took place between 5th and 9th February. This time was selected in order to examine the overwintering distribution of beetles during the harshest climatic conditions. Each sampling unit ($0.04m^2$) to a depth of 0.1 m was removed using spades and trowels and placed in a labelled, sealable plastic container together with leaf litter or ground vegetation associated with that sample. Sampling units were removed in the order A1 through to O10 or U9 (in small and large arenas respectively). All sampling units of a single arena were removed within four hours to minimise disturbance movement by overwintering beetles. A 15 gram soil sample was taken from each sample unit and placed in a separate labelled bag for measurement of gravimetric soil moisture. Samples were stored outdoors in shaded ambient conditions (2-6°C) prior to sorting. Soil, vegetation and litter of sampling units were sorted systematically for 20 minutes each on a large white tray. All Carabidae and

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Staphylinidae specimens found were removed by hand or pooter and placed in a labelled plastic bag for freezing and identification to species or genus. Discarded soil and vegetation was collected to return to the field boundary sites. All Carabidae specimens were identified to species with the exception of members of the genus *Agonum*, *Amara* and *Bembidion* (apart from *B. lampros*). Staphylinidae were identified to genus except for the more abundant *P. litoralis* and *T. rufipes*.

6.2.4 Analysis

The spatial distributions of beetles within arenas was analysed using SADIE (Spatial Analysis by Distance IndicEs) to determine whether beetles showed an aggregated (non-random) distribution (Perry *et al.*, 1999). SADIE uses spatially referenced count data to calculate the degree of clustering of high counts or 'patches' (using the index v_j and its probability P_j) and low counts or 'gaps' (using the index v_i and its probability P_i) (Perry *et al.*, 1999). If both indices have values of unity, the distribution of counts is spatially random according to the null hypothesis. If either index has a value above unity the data set has a non-random spatial pattern. The spatial distribution of patches and gaps are illustrated as two-dimensional contour plots (termed 'red-blue' plots), showing patches as red ($v_j > 1.5$) and gaps as blue ($v_i < -1.5$). In this study, contour plots were produced using the package Surfer for Windows Version 6.4 (Golden Software Inc., Colorado, USA) and the count values for each sampling unit were also shown. Association in spatial distribution between species or between species and gravimetric soil moisture may be determined by calculating the correlation coefficient X between the clustering indices of each data set (Perry & Dixon, 2002). The significance of the association for each sampling unit (X) was tested against values X_{rand} generated from a randomisation test that includes a Dutilleul (1993) procedure to provide a probability value P_D. Software for the spatial aggregation and association analysis with a full description of the methodology is available from Perry (2002).

To test for differences in temperature ($\log_{10} n+1$) between the profile locations (1-4) in each field boundary type a repeated measures general linear model (GLM) was conducted with profile locations as within-subject factors. Differences in mean soil moisture content (arcsine transformed) between the two field boundary types was tested with a one-way anova. All statistical testing was conducted using SPSS 11.5.1.

6.3 RESULTS

6.3.1 Marking

In the control groups for marked *B. lampros* and *P.cupreus*, no mortalities or adverse effects were observed. Individuals remained fairly inactive and burrowed into the soil-compost mix or underneath stones placed in overwintering refugia for shelter. Laser-marks on *P. cupreus* remained clear and readable with the naked eye at the end of the experimental period in February and also when individuals were released into the field in April. All *B. lampros* marked with white Tippex retained their mark but 36 (90%) specimens marked with green Tippex had lost their mark and the remaining 4 specimens were only partially marked. As a result, MRR studies utilised recaptures of laser-marked *P. cupreus* and white marked *B. lampros*, but disregarded green-marked *B. lampros* recaptures.

6.3.2 Sampling

Recapture rates of *B. lampros* released in an even distribution were 17.9% and 23.2% in Arenas 1 and 5 respectively (Table 6.3.1). For beetles released at the arena ends: 25.1% and 4% white marked *B. lampros* were recaptured in arenas 2 and 4 respectively, whilst 20.9% of marked *P. cupreus* were recaptured. SADIE aggregation and association analyses were conducted using recaptures of *B. lampros* released in an even distribution in arenas 1 and 5. However, SADIE is sensitive to low numbers (Thomas *et al.*, 2001) and insufficient recaptures were available for *B. lampros* and *P. cupreus* in arenas 2, 3 and 4 for analysis. Recaptures of *B. lampros* and *P. cupreus* in arenas 4 and 3 respectively, were sufficient to assess distance moved by individuals migrating from the field boundary edge.

Twenty-one species or genera of Carabidae and Staphylinidae with ≥ 5 individuals in a single arena were captured as a result of substrate sampling (Table 6.3.2). The most abundant Carabidae were *B. lampros, Metabletus obscuroguttatus* and *P. vernalis*, and the most abundant staphylinids were Aleocharinae spp., *P. litoralis, Stenus* spp., *Stilicus* spp. and *Tachyporus* spp.. SADIE aggregation and association were conducted with these taxa where sufficient numbers (≥ 100) were captured in an arena.

Species		B. lampros			P. cupreus
Arena	1	2	4	5	3
Released	380	175	175	380	240
Recaptured	68	7	44	88	49
% Recaptures	17.9	4.0	25.1	23.2	20.4

Table 6.3.1 Numbers of marked *B. lampros* and *P. cupreus* released and recaptured in each arena and % recaptures.

	Arena 1	Arena 2	Hedgerow Arena 3	Post and wire with grassy margin Arena 4	Arena 5
Carabidae					
Agonum spp.	5	3	11	22	17
Amara spp.	9	9	14	32	20
Badister bipustulatus	2	4	18	0	0
Bembidion lampros	379	209	332	245	364
Bembidion spp.	5	14	8	3	5
Demetrias atricapillus	14	20	22	14	35
Dystirius salinus	5	0	0	0	0
Metabletus obscuroguttatus	242	222	252	9	153
Pterostichus cupreus	20	24	31	3	2
P. strennus	39	6	16	8	14
P. vernalis	44	86	155	10	7
Trechus quadristriatus	24	14	15	7	13
Staphylinidae					
Aleocharinae spp.	1342	844	1861	125	471
Anotylus spp.	10	13	17	5	2
Paederus litoralis	25	30	44	13	156
Philonthus spp.	9	11	17	18	5
Stenus spp.	72	15	33	37	376
Stilicus spp.	45	2	9	44	44
Tachinus rufipes	35	22	58	32	21
Tachyporus spp.	90	57	142	228	269
Xantholinus spp.	45	26	59	64	72

Table 6.3.2 Total numbers of Carabidae and Staphylinidae taxa recorded within each arena (where the abundance of a taxon in any single arena ≥ 5).

6.3.3 Microhabitat of arenas

The spatial distribution of microhabitat characteristics in all five arenas is shown in Figure 6.3.1. Soil moisture (%) showed an aggregated distribution in arenas 1 to 4, but not in Arena 5 where soil moisture was generally homogenous (Table 6.3.3). The highly significant differentiation in soil moisture in Arena 3 was attributed to the inclusion of 0.6m of ley field that was considerably wetter than the main body of the hedgerow (Figure 6.3.2). Soil moisture was generally greatest at the boundary edges adjacent to the fields and therefore closer to the field level. Gaps representing areas of low soil moisture were positioned in a broad band across the middle of the arenas. These gaps corresponded to the raised bank in hedgerow arenas and the raised area near the fence line in the post and wire arenas. Overall, soil moisture was greatest in hedgerow arenas (30% ±0.25) compared to arenas in the post and wire with grassy margin (24% ±0.18) (F=356.4, df=1, 598, P<0.001).

Temperature differed measurably across the hedgerow profile, with minimum and maximum soil and air temperatures being greatest at site 4 (ley edge) and lowest at sites 1 or 2 (arable edge) (Table 6.3.4, Figure 6.3.3a and 6.3.3c). Variations in hedgerow soil temperature were greatest at site 1 (arable edge). In the post and wire with grassy margin profile, significant differences in minimum and maximum air temperature were observed, with sites 3 and 4 (arable edge) having highest temperatures (Figure 6.3.3b). Variations in soil temperature differed across all sites but were greatest at site 4 (arable edge) (Figure 6.3.3d).
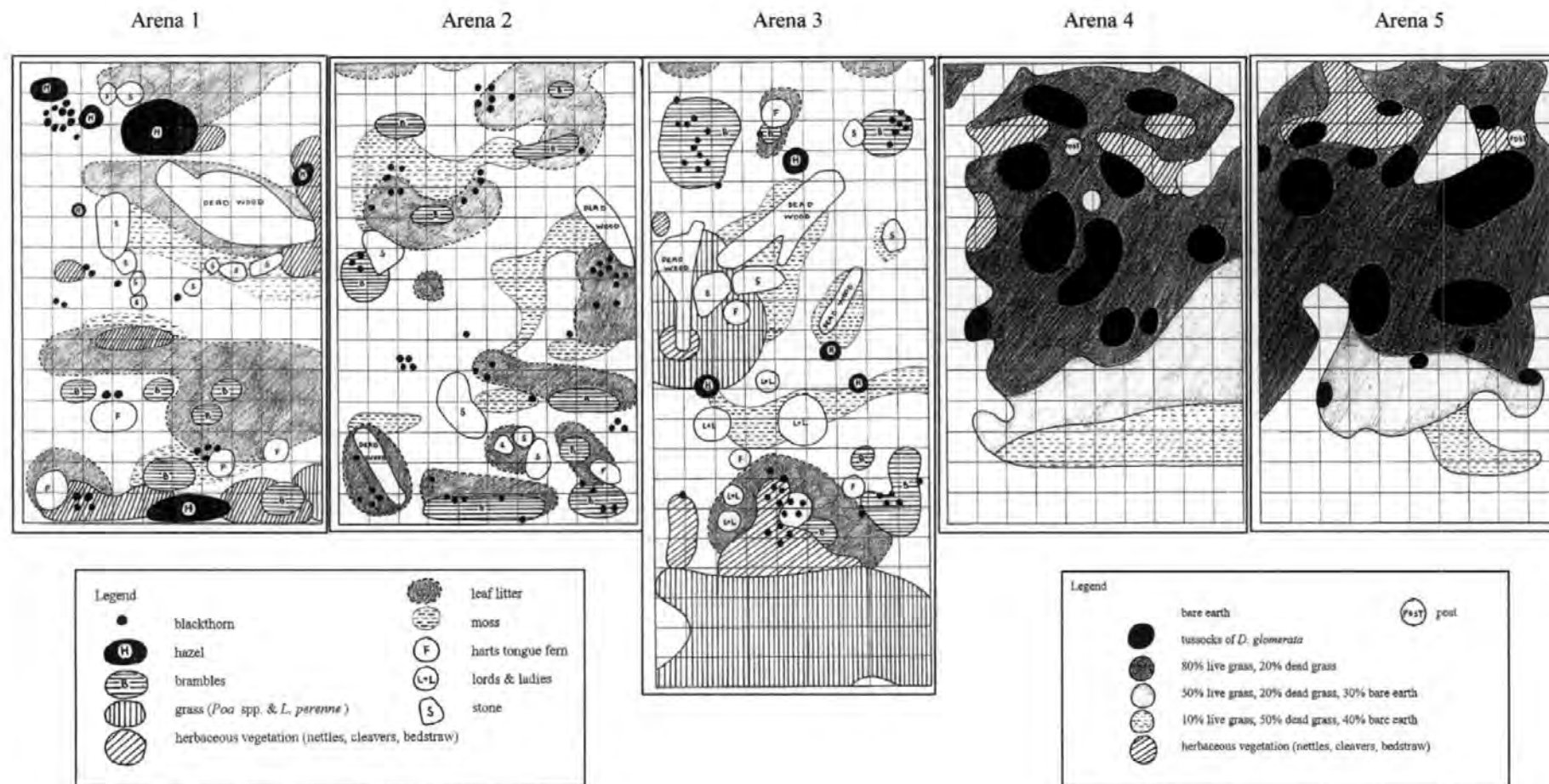
Figure 6.3.1 Habitat maps of Arenas 1 , 2 and 3 in a hedgerow boundary and 4 and 5 in a post and wire with grassy margin.

Arena 1   Arena 2   Arena 3   Arena 4   Arena 5

Legend

- blackthorn
- **H** hazel
- **B** brambles
- grass (*Poa* spp. & *L. perenne*)
- herbaceous vegetation (nettles, cleavers, bedstraw)

- leaf litter
- moss
- **F** harts tongue fern
- **L+L** lords & ladies
- **S** stone

Legend

- bare earth
- tussocks of *D. glomerata*
- 80% live grass, 20% dead grass
- 50% live grass, 20% dead grass, 30% bare earth
- 10% live grass, 50% dead grass, 40% bare earth
- herbaceous vegetation (nettles, cleavers, bedstraw)

- **POST** post

Soil moisture	I_a	P_a	V_i	P_i	V_j	P_j
Arena 1	1.715	0.002 **	1.650	0.004 **	-1.679	0.003 **
Arena 2	1.953	0.000 ***	1.821	0.001 ***	-1.733	0.002 **
Arena 3	3.956	0.000 ***	3.757	0.000 ***	-3.569	0.000 ***
Arena 4	1.578	0.006 **	1.596	0.004 **	-1.490	0.011 *
Arena 5	0.847	0.858	0.901	0.714	-0.853	0.904

Table 6.3.3 SADIE indices of overall aggregation (Ia), patches (Vi) and gaps (Vj) with probabilities (P) for soil moisture in each arena. Asterix indicate significance: * P<0.05, ** P<0.01, *** P<0.001.

Arena 1

```
33 33 23 34 36 35 31 33 33 32
32 37 29 34 36 33 34 30 32 23
31 27 34 29 27 31 25 28 27 27
31 30 32 18 31 30 25 29 27 22
29 31 30 36 24 26 22 26 25 25
28 27 33 31 27 28 26 26 31 31
28 26 33 20 26 28 28 19 27 26
27 32 32 28 30 27 27 24 29 25
27 29 29 32 27 27 22 21 27 25
24 26 31 27 32 24 34 30 27 30
29 27 23 23 19 30 27 30 27 23
33 31 27 26 28 28 18 27 27 20
31 31 27 26 29 29 26 27 31 29
24 32 30 31 30 23 29 34 32 29
27 35 37 36 33 30 31 31 31 38 32
```

Arena 2

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32 36 39 37 32 38 37 39 35 36
33 37 38 28 38 39 31 35 37 38
31 30 30 30 26 31 31 32 35 34
30 22 29 24 29 32 27 27 25 31
32 29 22 30 26 26 29 27 35 24
31 33 34 31 30 26 24 27 28 28
29 32 29 34 27 26 28 28 30 32
34 26 28 31 25 26 30 33 33 31
25 26 30 27 28 28 28 33 35 32
27 28 27 30 34 26 27 31 32 25
30 28 30 33 31 21 29 32 34 33
22 35 33 35 32 34 34 28 32 33
33 32 29 33 34 34 34 31 26 31
30 36 33 36 35 37 37 38 36 35
32 34 37 38 36 36 38 39 35 31
```

Arena 3

```
34 36 27 35 30 36 32 33 34
35 38 31 29 31 31 32 36 34
37 34 30 30 25 30 31 32 32
22 21 28 26 24 30 27 24 28
29 24 21 26 24 22 24 27 26
28 20 24 24 20 27 25 22 24
25 29 26 26 20 24 25 23 27
32 27 28 21 24 21 23 25 21
25 22 23 25 22 25 15 27 22
21 26 24 21 27 26 22 25 38
25 36 29 23 22 26 25 24 23
22 26 37 22 37 25 26 28 27
22 21 23 22 25 24 24 23 27
27 30 27 30 33 17 31 25 25
26 36 28 35 29 39 33 37 28
37 29 36 38 40 38 35 32 36
34 37 38 37 41 38 41 37 37
29 37 38 39 33 41 39 37 35
41 28 39 39 26 31 41 36 34
38 30 39 33 37 29 39 38 37
33 36 42 33 29 37 35 29 31
```

Arena 4

```
26 21 22 23 25 22 24 27 27 28
23 26 26 27 26 32 30 27 27 29
26 27 27 29 26 27 28 29 25 25
21 25 25 24 25 26 28 23 27 26
30 24 22 21 31 24 25 19 22 21
21 23 23 21 20 22 24 21 25 26
25 26 21 21 22 20 22 27 24 23
29 27 21 24 22 21 23 24 28 25
25 27 21 26 22 24 25 23 22 20
26 23 32 29 22 22 19 22 19 20
26 22 24 20 22 23 22 21 23 23
30 34 18 18 24 25 29 21 19 26
29 25 23 22 20 25 18 22 22 23
28 22 27 28 22 27 24 26 24 26
24 29 28 25 29 24 24 25 30 28
```

Arena 5

```
26 25 24 25 23 20 21 27 25 24
26 25 28 25 03 24 26 25 25 24
23 23 25 23 18 22 22 24 19 21
26 25 23 24 26 25 28 18 23 27
22 24 22 30 18 24 17 18 23 27
21 27 27 19 23 24 21 21 27 20
20 30 18 19 26 24 31 22 21 20
22 30 24 28 24 30 23 29 24 30
23 24 19 19 18 25 23 20 25 27
24 23 23 26 19 25 18 22 25 28
21 25 19 27 18 24 19 23 23 21
24 27 23 21 22 30 22 25 20 25
23 23 22 21 27 28 24 28 19 29
22 29 22 28 30 24 23 26 21 28
22 24 26 23 22 22 24 21 28 22
```

Figure 6.3.2 Red-blue plots of soil moisture spatial patterns in all five arenas (1, 2 and 3 in hedgerow; 4 and 5 in post and wire with grassy margin).

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	df	Hedgerow 3, 189		Post and wire with grassy margin 3, 189	
Air minimum	F	22.69		17.8	
	P	0.000	***	0.000	***
Air maximum	F	12.63		7.7	
	P	0.000	***	0.000	***
Variation in air temperature	F	5.93		2.56	
	P	0.001	**	0.056	
Soil minimum	F	23.92		1.35	
	P	0.000	***	0.260	
Soil maximum	F	17.69		2.86	
	P	0.000	***	0.060	
Variation in soil temperature	F	5.72		18.86	
	P	0.001	**	0.000	***

Table 6.3.4 Results of repeated measures GLM testing for differences in winter temperatures (°C) between profile sites (1-4) across each boundary type (hedgerow and post and wire with grassy margin). Asterix indicate significance: ** P<0.01 and *** P<0.001.

a) Hedgerow: air temperature
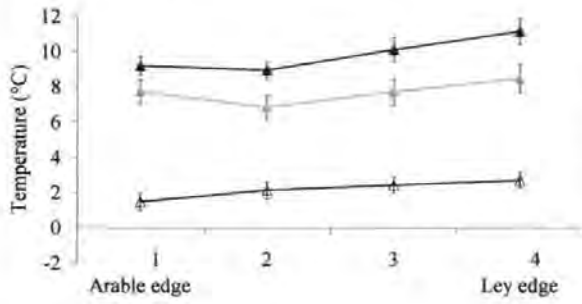
b) Post and wire with grassy margin: air temperature
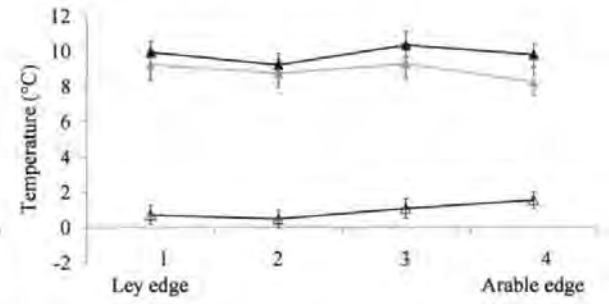
c) Hedgerow: soil temperature
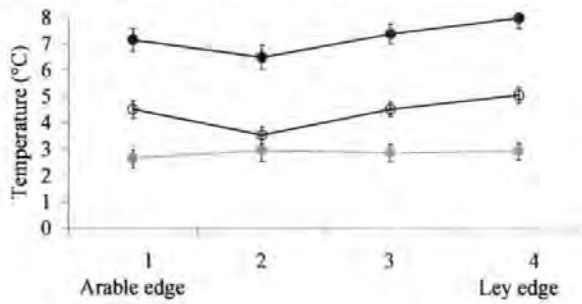
d) Post and wire with grassy margin: soil temperature
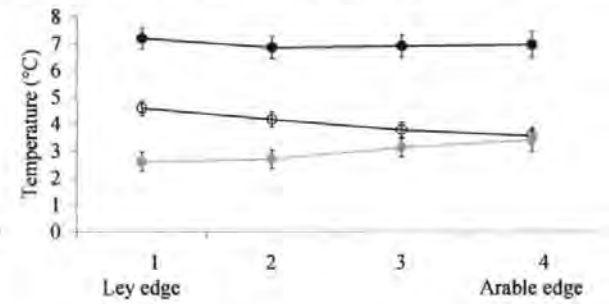
Figure 6.3.3 Winter temperature (°C, ±1 s.e.) profiles of a) Hedgerow: ground surface, b) Post and wire with grassy margin: ground surface, c) Hedgerow: soil and d) Post and wire with grassy margin: soil. Symbols represent: Δ = minimum air , ▲ = maximum air, ▲ variation in air temperature, ○ = minimum soil, ● = maximum soil, and ● variation in soil temperature.

6.3.4 Spatial distributions of overwintering species

(i) Marked populations

Marked *B. lampros* released in an even distribution into the post and wire with grassy margin (Arena 5) showed a strongly aggregated overwintering distribution on recapture (Table 6.3.5). Red-blue plots represent the spatial distribution as patches of high counts (red) and gaps of low counts (blue). Patches were generally located on the left of the arena and in the upper half close to the fence-line (Figure 6.3.4). There was no association between the initial even distribution of released *B. lampros* and the recaptured distribution. Strong associations were observed between the distributions of recaptured *B. lampros* and the distribution of the natural population. There were no associations between recaptured *B. lampros* and moisture in Arena 5. Distributions of patches and gaps of marked *B. lampros* showed similar patterns to the distributions of *D. glomerata* tussocks and bare earth respectively in Arena 5 (Figure 6.3.1).

B. lampros released in an even distribution in the hedgerow (Arena 1) showed a homogenous distribution on recapture (Table 6.3.5, Figure 6.3.4). However, no association was found between the initial distribution of released *B. lampros* and the recaptured distribution, whilst strong associations were observed with the distribution of the natural *B. lampros* population. There was no association between recaptured *B. lampros* and moisture (X=-0.063, P=0.77) in Arena 1.

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		Arena 1	Arena 5
a) Aggregation of recaptured *B. lampros*	I_a	0.941	2.062
	P_a	0.570	0.000 ***
	V_i	0.919	1.900
	P_i	0.644	0.000 ***
	V_j	-0.952	-2.033
	P_j	0.539	0.000 ***
b) Association between *B. lampros* recaptures and original even distribution	X	-0.051	-0.056
	P_D	0.733	0.753
c) Association between *B. lampros* recaptures and natural *B. lampros* distribution	X	0.355	0.624
	P_D	0.000 ***	0.000 ***
d) Association between *B. lampros* and soil moisture	X	-0.063	0.058
	P_D	0.770	0.247

Table 6.3.5 For recaptured marked *B. lampros* released in an even distribution in arenas 1 (hedgerow) and 5 (post and wire with grassy margin): a) SADIE indices of overall aggregation (Ia), patches (Vi) and gaps (Vj) with probabilities (P) and SADIE index of association (X) with probabilities (PD) between a) spatial patterns in recaptured *B. lampros* and original even distribution c) spatial patterns in recaptured *B. lampros* and naturally occurring distribution and d) spatial patterns in *B. lampros* and soil moisture. Asterix indicate significance: *** P<0.001.

Arena 1

0	1	0	1	0	0	0	2	1	0
0	0	1	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	1
0	0	2	0	0	0	0	1	0	0
0	0	0	0	0	1	1	0	0	0
0	2	0	0	0	0	2	0	1	2
1	0	1	1	0	0	1	1	1	6
7	0	0	0	1	0	0	0	0	0
0	0	0	0	1	1	0	0	0	0
0	0	2	0	4	1	0	0	0	1
0	1	0	0	0	0	1	2	1	0
1	0	0	0	0	0	0	1	0	0
0	0	0	0	2	0	1	0	1	1
1	1	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	1	2

Arena 5
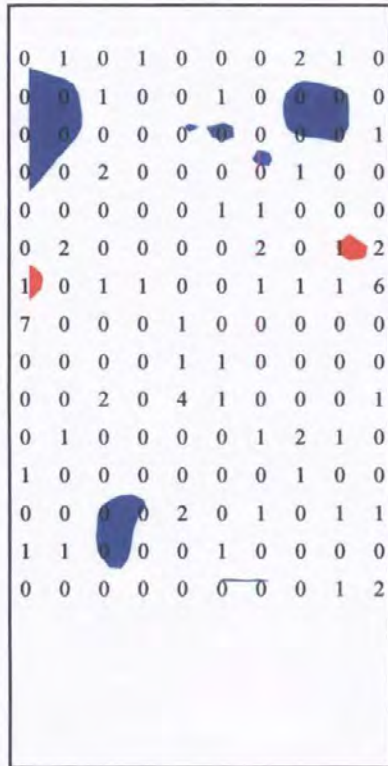
2	0	0	0	1	0	1	3	1	5
0	1	0	0	2	0	0	0	1	5
0	0	0	0	0	0	1	0	0	0
1	2	0	0	0	0	0	1	2	11
2	0	1	0	0	0	1	1	1	9
0	1	0	1	0	0	2	0	0	0
0	0	2	0	1	0	0	0	0	0
0	0	0	0	0	0	0	1	1	5
0	0	0	1	0	0	0	4	0	0
0	0	0	0	0	0	0	1	0	0
1	0	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	3	0
0	0	0	0	0	1	0	0	1	5

Figure 6.3.4 Red-blue plots of marked *B. lampros* released in an even distribution in arena 1 (hedgerow) and arena 5 (post and wire with grassy margin).

(ii) Natural populations

Natural populations of *B. lampros* showed strong clustering into patches and gaps in all arenas in both hedgerow and post and wire with grassy margin (Table 6.3.6). Aggregated distributions of *M. obscuroguttatus* were found in Arena 2 (hegderow) and Arena 5 (post and wire with grassy margin) but not in arenas 1 or 3. Aleocharinae spp. and *Tachyporus* spp. both showed highly aggregated spatial patterns in arenas 4 and 5 (post and wire with grassy margin), weaker aggregations in arenas 2 and 3 (hedgerow) and homogenous distributions in Arena 1 (hedgerow). *P. vernalis* showed a homogenous distribution in Arena 3 (hedgerow) whilst overwintering populations of *P. litoralis* and *Stenus* spp. showed strong clustering into patches and gaps in Arena 5. Total species richness was highly aggregated in arenas 2 to 5, but unclustered in Arena 1. The overwintering distributions of all species occurring naturally within the arenas show strong associations in all field boundary arenas (Table 6.3.7).

Within the hedgerow, gaps in the spatial patterns of *B. lampros, M. obscuroguttatus*, Aleocharinae spp. and *Tachyporus* spp. occurred in the upper part of the arenas (1-3), especially the top four rows adjacent to the arable field (Figures 6.3.5 to 6.3.8). Patches of high counts for these taxa were generally located in the middle and lower part of the arenas, corresponding to the hedge-bank and slope adjacent to the ley edge. The location of some patches coincides closely between taxa. For example, the lower left section of Arena 2 corresponding to the canopy edge supported a neighbourhood of high counts for *B. lampros, M. obscuroguttatus* and Aleocharinae spp. An area in lower middle section of Arena 3 also corresponding to the canopy edge, supported patches of all four taxa, whilst the field section included in Arena 3 (lower six rows) consistently showed gaps in the distribution of all four taxa.

Within the post and wire with grassy margin, patches of high counts for *B. lampros, M. obscuroguttatus*, Aleocharinae spp. and *Tachyporus* spp. occurred in the upper part of the arenas. This corresponded to the fence-line and mature section of grassy margin. The lower two-third or half of the post and wire arenas were characterised by gaps in the distribution of overwintering taxa.

There were few associations found between the overwintering distributions of naturally occurring taxa and soil moisture (Table 6.3.8). Weak association with soil moisture spatial patterns were found for *B. lampros* and *Tachyporus* spp. in Arena 4 and *Stenus* spp. in Arena 5. Patches of *B. lampros, Tachyporus* spp. and *Stenus* spp. coincided with areas of high soil moisture in these arenas. However, the soil moisture in Arena 5 did not show spatial aggregation. There appeared to be considerable correspondence between patches and gaps of *B. lampros, M. obscuroguttatus,* Aleocharinae spp. and *Tachyporus* spp and microhabitat characteristics of the arenas. Significant patches of *B. lampros* in Arena 1 were located in sampling units characterised by dense leaf litter, a dead wood stump with leaf-litter and herbaceous vegetation and a stone and blackthorn trunk surrounded by bare ground (Figure 6.3.1). Aleocharinae spp., *B. lampros* and *M. obscuroguttatus* were all found in high numbers in the bottom-left corner of Arena 2 characterised by the presence of a dead wood trunk surrounded by leaf-litter, some blackthorn trunks and mossy or bare ground. Other patches of Aleocharinae spp., *B. lampros, M. obscuroguttatus* and *Tachyporus* spp. were located in areas with mossy ground, a stone and leaf litter, blackthorn trunks and herbaceous vegetation. In Arena 3, one patch of *Tachyporus* spp. and *M. obscuroguttatus* (upper half-left) appeared to be strongly associated with an area containing dead wood logs and stones and surrounded by a mixture of mossy ground and herbaceous vegetation. A patch of Aleocharinae spp positioned just below was associated with an area of grassy vegetation. Aleocharinae spp. *M. obscuroguttatus* and *Tachyporus* spp. shared a patch of high counts (lower half-central) in an area characterised by a high density of blackthorn trunks, herbaceous vegetation and leaf litter. The main patch of *B. lampros* (positioned centrally in the arena) was located in an area of mossy and bare ground with occasional lords-and-ladies (*A. maculatum*) plants. In the post and wire arenas 4 and 5, patches of the four taxa were located in the upper parts of the arenas adjacent to the fence line characterised by a slightly raised bank supporting herbaceous vegetation and tussocks of *D. glomerata*. Several smaller patches positioned below the fence appeared to correspond to locations of tussocks of *D. glomerata*. The location of patches and gaps appeared to correspond to areas of mature and more recent margin habitat. The mature margin habitat had a dense grass cover and supported areas of tussocky grass and herbaceous vegetation. In contrast, the recently created margin had a high proportion of bare ground, thin grass cover and few tussocks of *D. glomerata*.

	I_a	P_a		V_i	P_i		V_j	P_j	
B. lampros									
Arena 1	1.574	0.007	**	1.398	0.021	*	-1.551	0.008	**
Arena 2	1.920	0.000	***	1.832	0.000	***	-1.837	0.001	**
Arena 3	1.689	0.012	*	2.007	0.001	***	-1.776	0.007	**
Arena 4	2.621	0.000	***	2.300	0.000	***	-2.571	0.000	***
Arena 5	2.738	0.000	***	3.057	0.000	***	-2.649	0.000	***
Metabletus spp.									
Arena 1	1.071	0.283		1.004	0.413		-1.058	0.300	
Arena 2	2.092	0.000	***	2.023	0.000	***	-2.037	0.000	***
Arena 3	1.307	0.099		1.360	0.077		-1.317	0.097	
Arena 5	2.276	0.000	***	2.204	0.000	***	-2.170	0.000	***
Aleocharinae spp.									
Arena 1	1.014	0.390		0.995	0.422		-1.020	0.359	
Arena 2	1.589	0.007	**	1.459	0.014	*	-1.491	0.014	*
Arena 3	1.571	0.024	*	1.683	0.009	**	-1.539	0.024	*
Arena 4	2.282	0.000	***	2.011	0.000	***	-2.294	0.000	***
Arena 5	2.915	0.000	***	2.901	0.000	***	-2.790	0.000	***
Tachyporus spp.									
Arena 1	1.101	0.226		1.183	0.113		-1.108	0.214	
Arena 2	1.364	0.039	*	1.221	0.091		-1.376	0.037	*
Arena 3	1.463	0.033	*	1.396	0.039	*	-1.500	0.027	*
Arena 4	2.972	0.000	***	2.647	0.000	***	-2.907	0.000	***
Arena 5	3.161	0.000	***	2.924	0.000	***	-3.050	0.000	***
P. vernalis									
Arena 3	1.283	0.119		1.254	0.110		-1.294	0.100	
P. litoralis									
Arena 5	2.180	0.000	***	2.047	0.000	***	-2.047	0.000	***
Stenus spp.									
Arena 5	2.633	0.000	***	2.819	0.000	***	-2.539	0.000	***
Species richness									
Arena 1	0.986	0.442		0.992	0.443		-0.949	0.571	
Arena 2	2.172	0.000	***	2.117	0.000	***	-2.126	0.000	***
Arena 3	1.806	0.005	**	1.477	0.030	*	-1.773	0.005	**
Arena 4	3.659	0.000	***	4.013	0.000	***	-3.671	0.000	***
Arena 5	4.182	0.000	***	3.952	0.000	***	-4.081	0.000	***

Table 6.3.5 SADIE indices of overall aggregation (Ia), patches (Vi) and gaps (Vj) with probabilities (P) for species or genus found in sufficient numbers and overall species

	X	P_D	X	P_D	X	P_D	X	P_D	X	P_D
Arena 1	*Metabletus* spp.		Aleocharinae spp.		*Tachyporus* spp.					
B. lampros	-0.07	0.790	0.20	0.014 *	0.20	0.012 *				
Metabletus spp.			0.45	0.000 ***	0.33	0.001 ***				
Aleocharinae spp.					0.36	0.000 ***				
Arena 2	*Metabletus* spp.		Aleocharinae spp.		*Tachyporus* spp.					
B. lampros	0.28	0.004 **	0.29	0.000 ***	0.36	0.000 ***				
Metabletus spp.			0.48	0.000 ***	0.28	0.001 ***				
Aleocharinae spp.					0.40	0.000 ***				
Arena 3	*Metabletus* spp.		Aleocharinae spp.		*Tachyporus* spp.		*P. vernalis*			
B. lampros	0.35	0.001 ***	0.16	0.053	0.24	0.001 ***	0.17	0.042 *		
Metabletus spp.			0.46	0.000 ***	0.48	0.000 ***	0.50	0.000 ***		
Aleocharinae spp.					0.36	0.000 ***	0.23	0.019 *		
							0.40	0.000 ***		
Arena 4			Aleocharinae spp.		*Tachyporus* spp.					
B. lampros			0.47	0.000 ***	0.59	0.000 ***				
Aleocharinae spp.					0.72	0.000 ***				
Arena 5	*Metabletus* spp.		Aleocharinae spp.		*Tachyporus* spp.		*P. litoralis*		*Stenus spp.*	
B. lampros	0.63	0.000 ***	0.62	0.000 ***	0.58	0.000 ***	0.65	0.000 ***	0.66	0.000 ***
Metabletus spp.			0.75	0.000 ***	0.67	0.000 ***	0.81	0.000 ***	0.78	0.000 ***
Aleocharinae spp.					0.66	0.000 ***	0.78	0.000 ***	0.66	0.000 ***
Tachyporus spp.							0.65	0.000 ***	0.67	0.000 ***
P. litoralis									0.84	0.000 ***

Table 6.3.7 SADIE association index with probability (P_D) between taxon distributions for each arena. Asterix indicate significance: * P<0.05, ** P<0.01, *** P<0.001.

	X	P_D
B. lampros		
Arena 1	-0.088	0.848
Arena 2	0.200	0.042
Arena 3	0.015	0.421
Arena 4	0.241	0.029 *
Arena 5	0.107	0.103
Metabletus spp.		
Arena 1	0.027	0.393
Arena 2	0.207	0.084
Arena 3	-0.168	0.967
Arena 5	-0.024	0.609
Aleocharinae spp.		
Arena 1	-0.148	0.940
Arena 2	0.054	0.300
Arena 3	-0.350	1.000
Arena 4	0.097	0.137
Arena 5	0.080	0.164
Tachyporus spp.		
Arena 1	-0.157	0.952
Arena 2	-0.073	0.819
Arena 3	0.269	1.000
Arena 4	0.146	0.049 *
Arena 5	-0.013	0.560
P. vernalis		
Arena 3	-0.006	0.519
P. litoralis		
Arena 5	0.077	0.176
Stenus spp.		
Arena 5	0.141	0.041 *

Table 6.3.8 SADIE association index (X) with probability (P) between moisture and naturally occurring taxon distributions for each arena. Asterix indicate significance: * $P<0.05$.

Arena 1

0	3	4	0	0	0	0	9	4	1
0	6	0	0	0	0	0	0	3	1
0	0	4	0	0	0	1	0	0	1
2	1	6	3	3	0	0	0	0	0
9	1	2	0	2	5	6	3	0	0
0	4	0	1	0	6	7	2	7	4
6	1	0	4	2	1	0	1	9	8
15	0	1	1	3	3	0	0	0	2
0	0	1	0	1	7	1	0	0	0
1	0	3	1	11	1	7	5	4	0
3	2	0	0	0	0	0	4	4	2
8	2	0	2	3	0	3	11	6	1
4	2	1	4	10	4	10	8	9	6
14	1	3	0	1	6	0	7	0	0
5	0	0	2	6	1	3	0	1	9

Arena 2

0	0	0	1	0	2	5	0	0	0
0	10	1	0	0	2	0	0	0	0
8	0	1	0	2	0	0	0	3	0
0	2	2	1	0	0	0	0	0	2
0	1	0	0	2	0	0	0	0	2
1	1	0	0	0	0	0	0	0	0
1	5	0	2	1	0	0	1	0	0
1	0	2	0	7	1	0	0	0	0
7	2	0	1	0	0	1	0	0	0
2	0	3	2	0	0	0	4	3	0
5	2	1	0	0	1	1	0	1	0
2	3	1	1	1	3	2	0	0	0
4	5	0	2	3	2	0	0	1	0
8	0	3	0	9	0	0	0	4	0
0	0	3	2	2	0	16	15	8	3

Arena 3

0	1	1	0	0	0	0	3	3	2
0	0	0	0	0	0	0	0	0	8
0	0	0	6	0	0	0	0	0	0
2	1	0	0	0	0	0	0	3	0
0	0	0	1	0	1	0	1	1
0	2	4	1	1	0	0	1	1
4	0	3	1	0	0	0	1	0
7	2	1	0	2	0	0	0	0
1	0	0	0	13	0	0	1	0
2	0	7	3	2	2	0	0	0
3	5	5	2	1	4	1	2	9
2	2	2	4	5	2	0	0	0
0	4	11	9	5	3	8	6	8
0	1	0	1	3	0	5	0	0
0	0	1	3	8	0	2	0	1
1	3	1	10	2	2	3	9	6
5	0	0	7	13	1	0	1	2
0	0	0	0	0	7	0	1	3
5	0	0	0	0	0	0	0	0
1	0	1	0	1	0	0	0	0
17	3	0	0	0	0	0	0	3

Arena 4

8	0	1	2	7	2	0	2	2	14
2	2	2	10	2	3	2	4	3	0
1	1	12	5	9	9	10	5	9	23
2	0	0	0	1	1	2	1	0	13
1	0	0	0	0	0	0	0	0	4
1	0	0	9	1	4	1	0	0	1
0	0	0	0	0	5	0	0	0	2
0	0	0	0	0	0	1	0	0	11
0	0	0	1	0	0	0	0	0	5
0	0	0	0	0	0	0	0	0	3
1	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	4
0	0	0	0	0	0	0	0	8
2	2	0	0	0	0	0	0	0	10
0	0	1	0	1	0	0	1	0	0

Arena 5

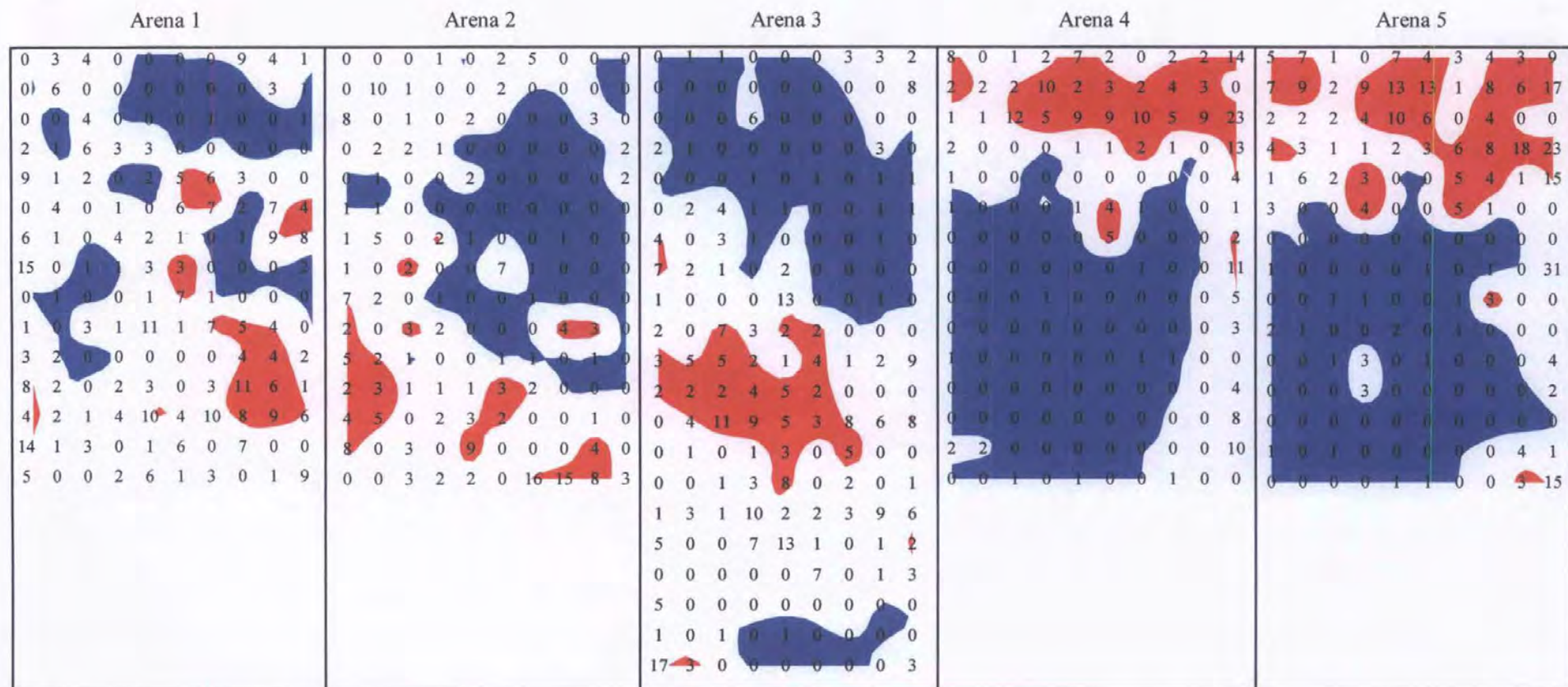|									
5	7	1	0	7	4	3	4	3	9
7	9	2	9	13	13	1	8	6	17
2	2	2	4	10	6	0	4	0	0
4	3	1	1	2	3	6	8	18	23
1	6	2	3	0	0	5	4	1	15
3	0	0	4	0	0	5	1	0	0
0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	1	0	31
0	0	1	1	0	0	1	3	0	0
2	1	0	2	0	1	0	0	0	0
0	1	3	0	0	0	0	0	0	4
0	0	3	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0
1	0	1	0	0	0	0	0	4	1
0	0	0	0	1	1	0	0	3	15

Figure 6.3.5 Red-blue plots showing the spatial patterns of *B. lampros* (natural population) overwintering in all five arenas (1, 2 and 3 in hedgerow; 4 and 5 in post and wire with grassy margin).
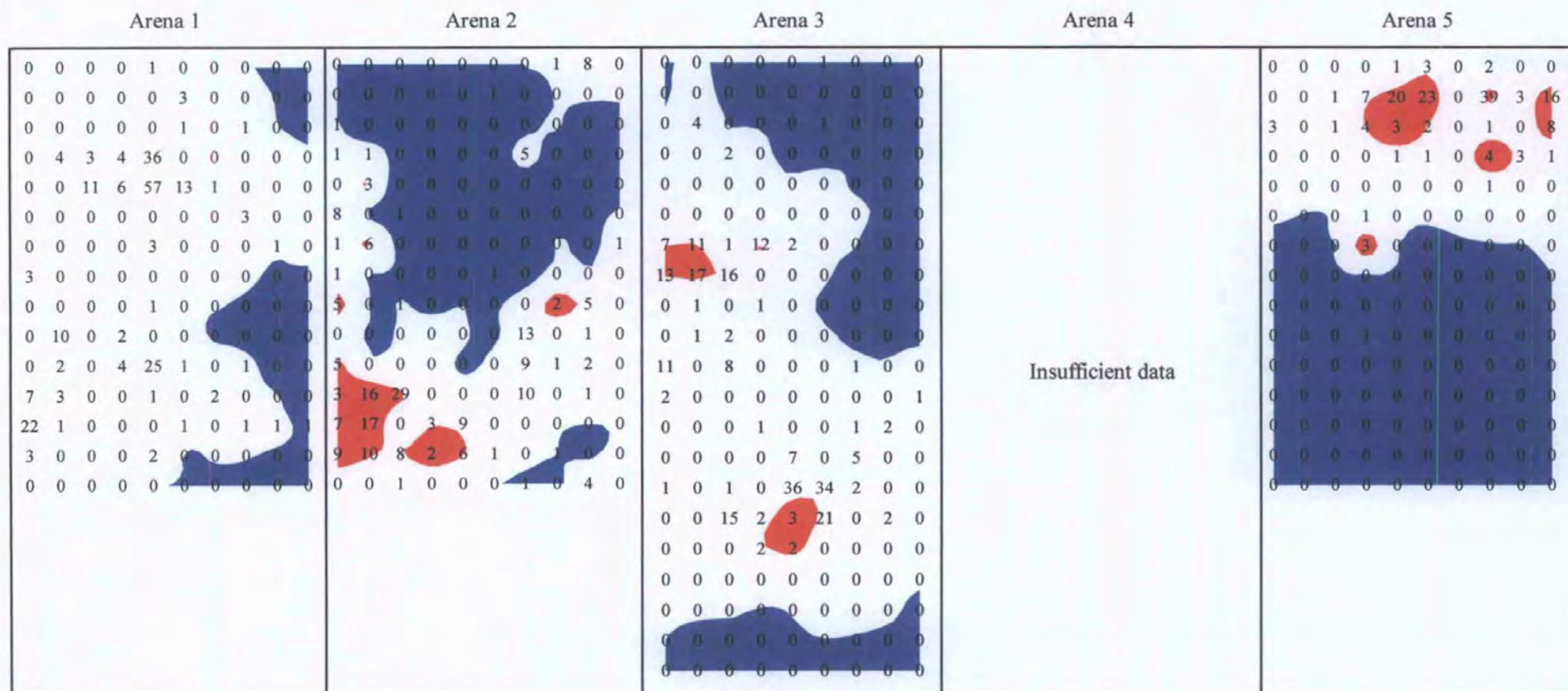
Figure 6.3.6 Red-blue plots showing the spatial patterns of *M. obscuroguttatus* overwintering in all five arenas (1, 2 and 3 in hedgerow; 4 and 5 in post and wire with grassy margin).
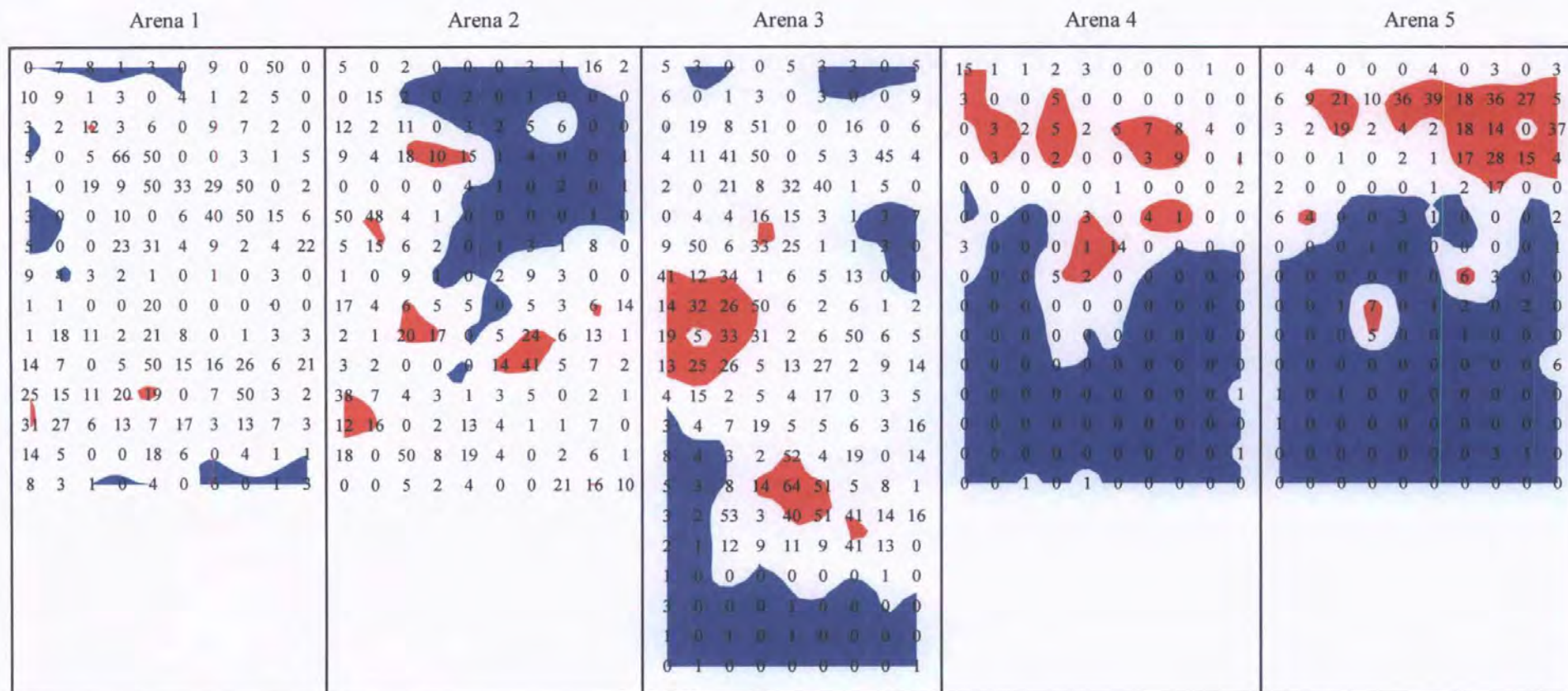
Arena 1   Arena 2   Arena 3   Arena 4   Arena 5

Arena 1

```
 0  7  8  1  3  0  9  0 50  0
10  9  1  3  0  4  1  2  5  0
 3  2 12  3  6  0  9  7  2  0
 5  0  5 66 50  0  0  3  1  5
 1  0 19  9 50 33 29 50  0  2
 3  0  0 10  0  6 40 50 15  6
 5  0  0 23 31  4  9  2  4 22
 9  8  3  2  1  0  1  0  3  0
 1  1  0  0 20  0  0  0  0  0
 1 18 11  2 21  8  0  1  3  3
14  7  0  5 50 15 16 26  6 21
25 15 11 20 19  0  7 50  3  2
31 27  6 13  7 17  3 13  7  3
14  5  0  0 18  6  0  4  1  1
 8  3  1  0  4  0  0  0  1  5
```

Arena 2

```
 5  0  2  0  0  0  3  1 16  2
 0 15  2  0  2  0  1  0  0  0
12  2 11  0  3  2  5  6  0  0
 9  4 18 10 15  1  4  0  0  1
 0  0  0  0  4  1  0  2  0  1
50 48  4  1  0  0  0  0  1  0
 5 15  6  2  0  1  3  1  8  0
 1  0  9  1  0  2  9  3  0  0
17  4  6  5  5  0  5  3  6 14
 2  1 20 17  0  5 24  6 13  1
 3  2  0  0  0 14 41  5  7  2
38  7  4  3  1  3  5  0  2  1
12 16  0  2 13  4  1  1  7  0
18  0 50  8 19  4  0  2  6  1
 0  0  5  2  4  0  0 21 16 10
```

Arena 3

```
 5  3  0  0  5  3  3  0  5
 6  0  1  3  0  3  0  0  9
 0 19  8 51  0  0 16  0  6
 4 11 41 50  0  5  3 45  4
 2  0 21  8 32 40  1  5  0
 0  4  4 16 15  3  1  3  7
 9 50  6 33 25  1  1  3  0
41 12 34  1  6  5 13  0  0
14 32 26 50  6  2  6  1  2
19  5 33 31  2  6 50  6  5
13 25 26  5 13 27  2  9 14
 4 15  2  5  4 17  0  3  5
 3  4  7 19  5  5  6  3 16
 8  4  3  2 52  4 19  0 14
 5  3  8 14 64 51  5  8  1
 3  2 53  3 40 51 41 14 16
 2  1 12  9 11  9 41 13  0
 1  0  0  0  0  0  0  1  0
 3  0  0  0  1  0  0  0  0
 1  0  1  0  1  0  0  0  0
 0  1  0  0  0  0  0  0  1
```

Arena 4

```
15  1  1  2  3  0  0  0  1  0
 3  0  0  5  0  0  0  0  0  0
 0  3  2  5  2  5  7  8  4  0
 0  3  0  2  0  0  3  9  0  1
 0  0  0  0  0  1  0  0  0  2
 0  0  0  0  3  0  4  1  0  0
 3  0  0  0  1 14  0  0  0  0
 0  0  0  5  2  0  0  0  0  0
 0  0  0  0  0  0  0  0  0  0
 0  0  0  0  0  0  0  0  0  0
 0  0  0  0  0  0  0  0  0  1
 0  0  0  0  0  0  0  0  0  0
 0  0  0  0  0  0  0  0  0  0
 0  0  0  0  0  0  0  0  0  1
 0  0  1  0  1  0  0  0  0  0
```

Arena 5

```
 0  4  0  0  0  4  0  3  0  3
 6  9 21 10 36 39 18 36 27  5
 3  2 19  2  4  2 18 14  0 37
 0  0  1  0  2  1 17 28 15  4
 2  0  0  0  0  1  2 17  0  0
 6  4  0  0  3  1  0  0  0  2
 0  0  0  1  0  0  0  0  0  1
 0  0  0  0  0  0  6  3  0  0
 0  0  1  7  0  1  2  0  2  0
 0  0  0  5  0  0  1  0  0  0
 0  0  0  0  0  0  0  0  0  6
 1  0  1  0  0  0  0  0  0  0
 1  0  0  0  0  0  0  0  0  0
 0  0  0  0  0  0  0  3  1  0
 0  0  0  0  0  0  0  0  0  0
```

Figure 6.3.7 Red-blue plots showing the spatial patterns of Aleocharinae spp. overwintering in all five arenas (1, 2 and 3 in hedgerow; 4 and 5 in post and wire with grassy margin).
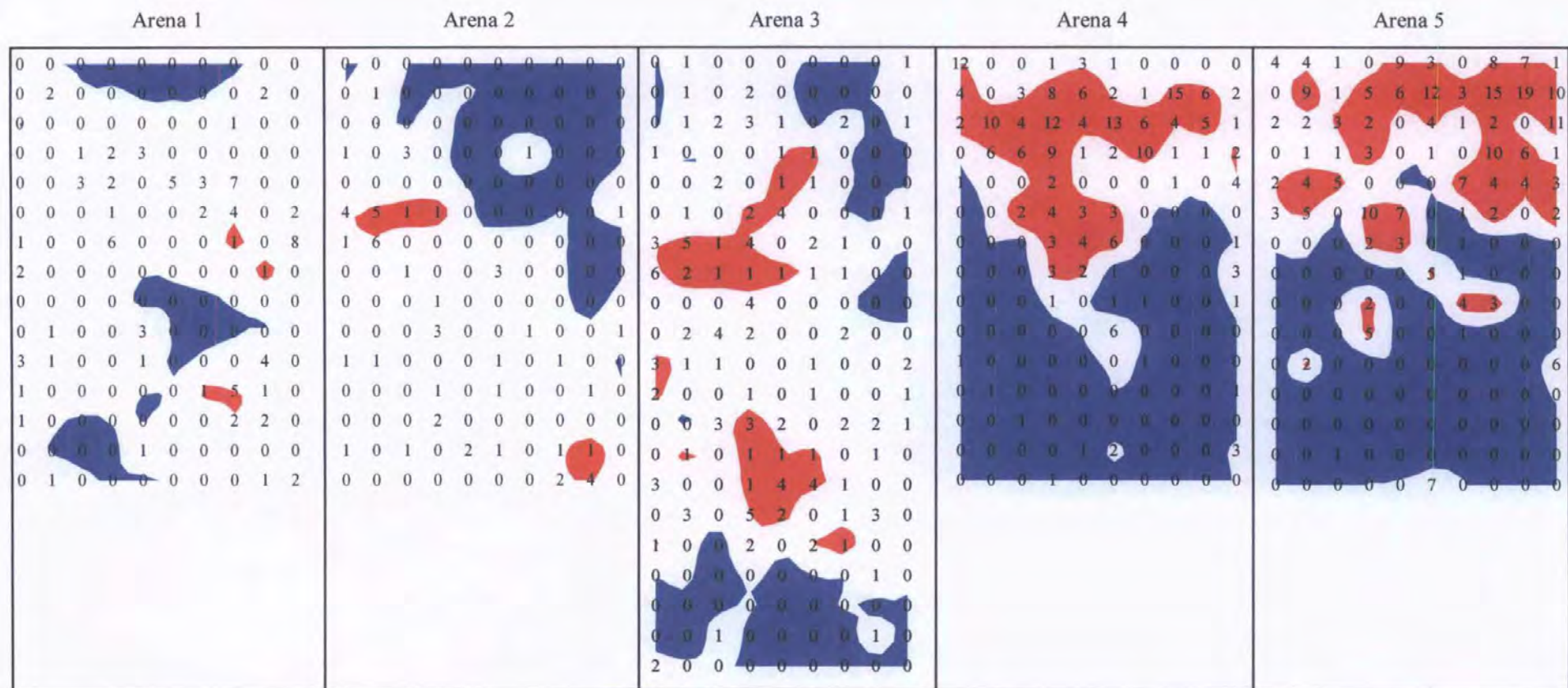
Figure 6.3.8 Red-blue plots showing the spatial patterns of *Tachyporus* spp. overwintering in all five arenas (1, 2 and 3 in hedgerow; 4 and 5 in post and wire with grassy margin).

6.3.5 Distance moved

In the post and wire boundary with grassy margin (Arena 4), a similar distribution with distance from the ley edge was shown by both recaptured *B. lampros* released at the ley edge and the natural population of *B. lampros* (Figure 6.3.9a). The majority of recaptures (85%) were close to the point of release (0.0-0.6 m from the ley edge). However a small proportion of marked *B. lampros* moved up to 2.2 m into the grassy boundary. The majority of the naturally migrating *B. lampros* population was not found at the arena edge but at 0.6 m into the boundary from the ley edge; this distance corresponded with the fence-line in the arena. Naturally migrating *B. lampros* were present in low levels throughout the hedgerow.

Most *P. cupreus* released at the arable edge remained within 0.4 m of the arable edge, though low numbers were found at 1.2m and 1.6m into the hedgerow and a single individual (4%) moved 2.8 m from the arable edge (Figure 6.3.9b). A high percentage (43.5%) of *P. cupreus* released at the ley edge were recaught 1.4 m into the hedgerow. This corresponded to the start of the bank slope just inside the canopy edge. Additionally, a considerable number (17%) moved 3.0m and one individual (4%) moved 4.2 m into the hedgerow from the ley edge, completely traversing the field boundary. Although naturally migrating *P. cupreus* were present in low levels throughout the hedgerow, most were found between 1.2m and 2.0m from the arable edge (2.6m and 3.4m from ley edge), a distance that corresponded with the top of the hedge bank.

a) *B. lampros* in arena 4

b) *P. cupreus* in arena 3
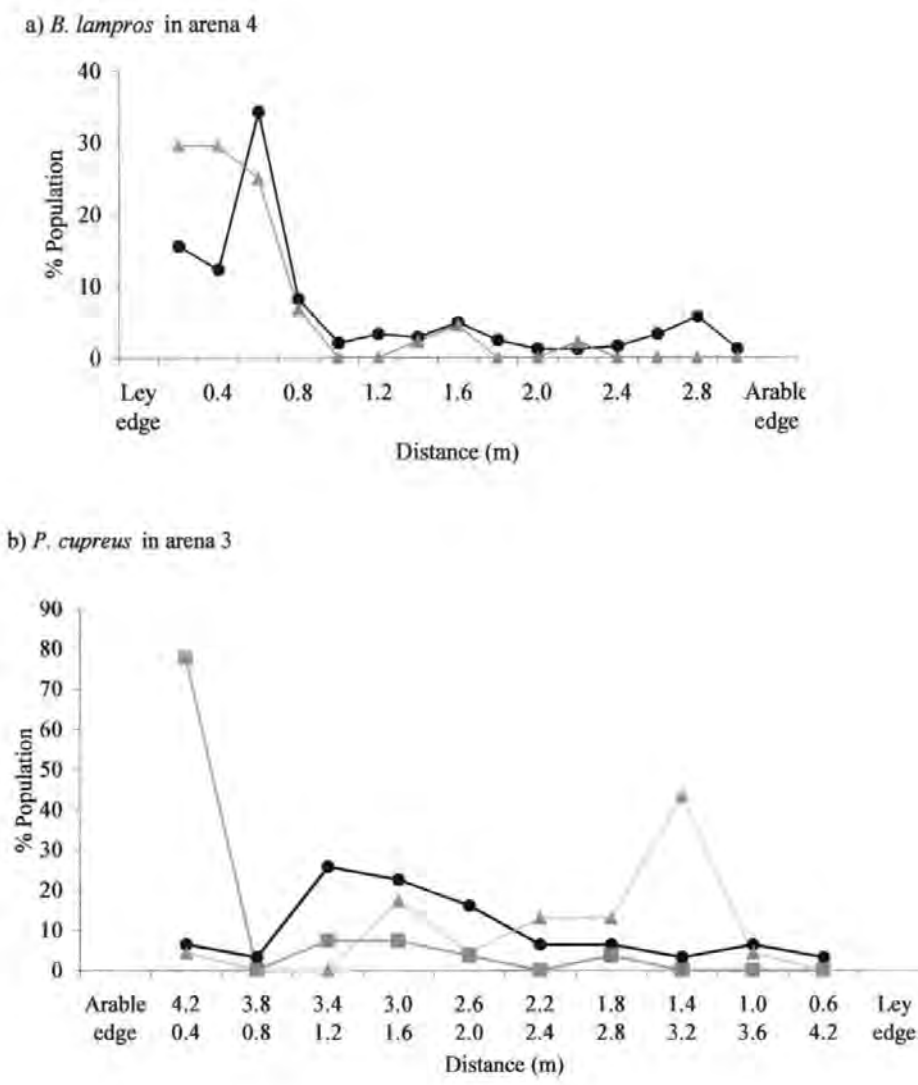
Figure 6.3.9 Distance moved (m) through a field boundary by marked and naturally migrating a) *B. lampros* in arena 4 (post and wire with grassy margin) and b) *P. cupreus* in arena 3 (hedgerow). Symbols represent: ● natural population, ▲ beetles released at ley edge, ■ beetles released at arable edge.

6.4 DISCUSSION

Active habitat selection was indicated by displacement of marked *B.lampros* from an even release distribution in both field boundary types, and subsequent recapture in an aggregated distribution in the post and wire with grassy margin. The preferred overwintering sites and distributions of recaptured *B. lampros* were highly similar to naturally occurring *B. lampros* that migrate from the field. This suggested that field-based *B. lampros* were able to locate optimal overwintering sites within field boundaries and that individuals were not limited by dispersal ability (Riedel, 1995), the costs of searching (Leather *et al.*, 1993) or physical impediments of ground vegetation (Greenslade, 1965; Rivard, 1965; Klazenga & de Vries, 1994). Additionally, differences in dispersal behaviour showed no apparent effect on the spatial distribution of overwintering species (Riedel, 1995). For example, members of the Aleocharinae, *Tachyporus* and *Stenus* genera typically disperse to field boundaries by flight (Coombes & Sotherton, 1986; Hunter *et al.*, 1991; Levesque & Levesque, 1995), whilst most *B. lampros* walk to field boundary overwintering habitat (Coombes & Sotherton, 1986). However, all carabids and staphylinids captured in sufficient numbers showed strong spatial association, indicating that broad overwintering habitat preferences were shared by species.

Within the hedgerow, overwintering beetles were found on top of the hedge-bank and the bank slope adjacent to the ley field. An area associated with both lower temperatures and soil moisture. In the post and wire with grassy margin, beetles were predominantly in the mature margin strip either side of the post and wire fence. An area associated with cooler air temperatures, lower variation in soil temperatures and suprisingly, higher soil moisture. Lower and more constant temperatures may be more favourable to overwintering survival and condition by maintaining cold-hardiness and reduced metabolic activity which could deplete energy reserves (Leather *et al.*, 1993; Petersen *et al.*, 1996). Consequently, species are likely to co-evolve a preference for, and ability to detect and select these favourable temperature conditions (Orians, 1980).

The distribution of overwintering beetles in the relatively drier areas of hedgerows supports evidence in the literature on the potentially adverse effects of high soil moisture (Sotherton, 1985; Leather *et al.*, 1993), although no clear

associations with soil moisture were found. In contrast, within the post and wire with grassy margin, some weak spatial associations between soil moisture and natural populations of *B. lampros*, *Stenus* spp. and *Tachyporus* spp. suggested that high soil moisture was actively selected. However, mean soil moisture was significantly greater in hedgerows compared to post and wire with grassy margin boundaries. Consequently, optimal soil moisture content may be between the mean values of 30% and 24% in hedgerows and post and wire with grassy margins respectively.

Areas of higher soil moisture in post and wire with grassy margin also supported other favourable microhabitat characteristics such as a dense and complex vegetation structure that is raised above the field level. Interactions between abiotic and biotic variables may subtly alter the favourability of overwintering sites (Paje & Mossakowski, 1984; Orians & Wittenberger, 1991; Martin, 2001). It would be interesting to examine the vertical stratification of beetles in tussock plants and other complex vegetation structures favoured by overwintering species, in relation to other abiotic variables such as soil moisture. The dense biomass of this plant structure may provide insulated overwintering conditions above the substrate level and thereby ameliorate the adverse effects of soil moisture.

When the post and wire with grassy margin was sampled, soil moisture was perceived to be greater in the recent margin and arable edge. This contrast between perception and actual values may result from the soil texture, which was finer grained and with little apparent organic debris in the recent margin. Use of the gravimetric method to measure soil moisture provided a crude measure of water content in the soil at the time of destructive sampling but may not reflect the soil moisture at the time of site selection or as 'experienced' by a beetle. For example, the method gave little indication of drainage rates, the presence of air pockets or channels through the soil, soil texture or the humidity, which could influence the suitability of a site for overwintering (Leather *et al.*, 1993). Humidity in particular is difficult to measure accurately in the field (Thomas *et al.*, 1992b). Future investigations into the influence of moisture in determining overwintering distributions of carabid and staphylinid species would benefit from semi-field or laboratory based choice trials.

Overwintering carabids and staphylinids showed preferences for certain microhabitat characteristics in each field boundary type, although these characteristics differed between the two boundaries. In the post and wire with grassy margin boundary, preferred overwintering sites were predominately located in the mature section of margin, though some *Tachyporus* spp. had colonised tussocks in the recent margin section. Patches of high counts were associated with high vegetation density, grass tussocks, herbaceous vegetation and proximity to the post and wire fence. Gaps in the overwintering distribution of carabids and staphylinids were associated with bare ground and sparse grass cover. Maturity strongly influenced the favourability of margin habitat to overwintering species. Recommendations for beetle-bank creation suggest that newly sown tussocky grasses take two to three years to mature into ideal overwintering habitat for beetles (DEFRA, 2003a). Therefore, the recent section of margin may eventually provide favoured overwintering sites for carabids and staphylinids. Differences in soil condition observed whilst sampling may also affect the developing plant community (Greig-Smith *et al.*, 1992). Increased aeration and organic matter content of the soil with the establishment and maturation of a permanent sward may improve the soil condition for overwintering carabids and staphylinids.

Within hedgerows, patches of high numbers of overwinters were associated with dead wood in particular, and also leaf-litter, areas of grassy and herbaceous vegetation, stones and the base of woody trunks. Preferences for these microhabitat characteristics during overwintering site selection reflects reports in the literature for high overwintering densities associated with these habitat features (e.g. Sotherton, 1985; Thomas *et al.*, 1992b; Dennis *et al.*, 1994; Maudsley *et al.*, 2002). Many of these preferred microhabitat characteristics could be augmented within field boundary habitats as part of habitat restoration schemes. However, some patches of *B. lampros* occurred in areas of bare ground on the hedge-bank slope, emphasising the importance of maintaining heterogeneity in microhabitats.

The spatial arrangement of overwintering beetles showed some differences between the two boundary types. Recaptured *B. lampros* showed no spatial aggregation within the hedgerow arena and aggregation indices for naturally occurring *B. lampros*, Aleocharinae spp., *Tachyporus* spp., *P. vernalis*, *P. litoralis*,

Stenus spp. and total species richness were generally weaker in hedgerow arenas compared to post and wire arenas. In contrast, all species showed highly aggregated distributions in the post and wire with grassy margin. The absence of aggregation indicated a random rather than a homogenous distribution (Perry *et al.*, 1999). Sampling units supporting high counts were more evenly dispersed throughout hedgerow arenas, whilst in the post and wire with grassy boundary high counts were clustered into neighbourhoods that contributed to the statistical generation of patches (Perry *et al.*, 1999). Differing distributions between the two boundary types may reflect spatial variation in overwintering resources. Preferred hedgerow microhabitat characteristics were more evenly dispersed throughout the boundary, whilst preferred characteristics of the post and wire with grassy margin showed strong spatial aggregation within the scale of the arena.

Within the preferred habitat adjacent to the post and wire fence, carabid and staphylinid species were closely packed. The vegetation structure in these areas was sufficiently complex to enable large numbers of overwintering species to co-exist. In tussocky grasses especially, the dense biomass of living and dead plant material provides multiple overwintering sites within the roots, at the base of the shoots and between the stems and leaves of the plant (Thomas *et al.*, 1991). In contrast, although many species share similar microhabitat preferences in hedgerows, few species co-habit exact overwintering locations. Subtle preferences in environmental gradients or interactions between species may determine precise locations of patches. For example, Dennis & Fry (1992) found that areas in field boundaries supporting highest polyphagous predator density also showed reduced diversity and concluded that optimal microclimatic conditions at a location may encourage large numbers of a single species to the exclusion of others.

Although preferred microhabitat characteristics in hedgerows supported high overwintering densities, several apparently similar microhabitats were unoccupied. Some carabid species show an 'aggregative' response; for example *A. dorsale, C. melanocephalus* and *P. niger* overwinter in large numbers under stones (Dennis & Fry, 1992). Additionally, the use of dry pitfall traps has been shown to increase captures due to the odours emitted by caught beetles attracting more individuals into the area, though it was uncertain whether this was an inter- or intra-specific response

(J. Holland, *pers comm.*). It is possible that early arriving overwinterering individuals attract subsequent individuals to aggregate in the same location. Alternatively, combinations of interacting abiotic and biotic variables may influence the favourability of apparently identical microhabitats (Paje & Mossakowski, 1984; Martin, 2001). Despite the convenience of assessing overwintering site selection based on visual microhabitat characteristics, the underlying importance of microclimatic variables needs to be considered.

B. lampros and *P. cupreus* were capable of traversing both post and wire with grassy margin boundaries and hedgerows respectively. Despite the complexity of the vegetation within the post and wire with grassy margin, 6.8% of recaptured *B. lampros* had moved more than halfway through the boundary. Movement through the boundary increases the likelihood that individuals will move into a different field after emergence from overwintering. For the medium sized *P. cupreus*, 16% of recaptures had moved more than halfway through the hedgerow boundary, although the proportions varied depending at which end the beetles were released (12% were released at the ley edge and 4% at the arable edge). One *P. cupreus* moved the entire hedgerow width from the ley edge. The distance moved appeared to reflect the distribution of favourable overwintering sites. For example, high suitability of habitat adjacent to the fence line may have resulted in the cessation of movement for the majority of the marked and natural *B. lampros* population in the post and wire with grassy margin.

Introduced *P. cupreus* and to a lesser degree *B. lampros* appeared to show lower dispersal from the boundary edge than their conterparts migrating naturally from the field. For example, a large proportion of *P. cupreus* released at the ley edge, overwintered at the edge of the hedgerow canopy and ley field, a site also favoured by several other species (e.g. *B. lampros, M. obscuroguttatus,* Aleocharinae spp. and *Tachyporus* spp.). Additionally, the majority of marked *P. cupreus* released at the arable edge were also recaptured at the arable edge. In contrast, most naturally occurring *P. cupreus* aggregated on the hedge-bank. The motivational state (e.g. hunger level) of Carabidae is known to influence their movement behaviour (Wallin & Ekbom, 1994) and may have reduced the dispersal distances of individuals fed *ad libitum* prior to release.

Further investigation is required to confirm into which adjacent field individuals emigrate, on emergence from overwintering. Movement through the field boundary by overwintering beetles suggests that individuals entering a boundary from one field may emerge into the adjacent field in springtime. The extent to which individuals cross between fields, and whether populations show a net migration towards one field, may depend on the spatial arrangement of favoured overwintering sites. Although field boundaries may act as effective barriers to between field movement during the active reproductive period of open-habitat species (Mauremooto et al., 1995; Garcia et al., 2000; Brown, 2000; Thomas et al., 2001), the use of field boundaries as sites for overwintering, aestivation or refuge may enable between field mixing of sub-populations. Such mixing will maintain gene flow, enable refounding of locally extinct sub-populations and contribute to the long-term persistence of meta-populations within farmland (Den Boer, 1990; Opdam, 1990). As a consequence, the potential of polyphagous predators to control arable crop pests across farmland may be maintained.

Laser-marking provided an efficient and effective technique to permanently mass-mark carabids and other arthropods with a chitinised body surface. Further development of the laser-marking and beetle holding techniques are likely to yield methods for individual coding of medium and small sized carabids, in addition to the large carabids already marked with unique codes. White Tippex for batch marking adhered well to the waxy cuticle and withstood burrowing over the winter period. Both marking techniques could be used for mark-release-recapture studies conducted at any stage of the adult life history. The laser mark is subtle and unlikely to increase the risk of predation, however care should be taken with the highly visible white Tippex if used during the active life-stage of an adult.

CHAPTER SEVEN: DISCUSSION

Field boundaries are the principal source of semi-natural habitat in lowland farmland and form a dominant feature of the farmed landscape. Changes in habitat characteristics, management and network density of field boundaries have occurred through changes in farming practice, resulting from an intensification of agricultural production. This study examined the potential of different field boundary types to contribute to the enhancement of biodiversity and promotion of sustainable agriculture, through augmentation of polyphagous predator populations.

In this study, field boundaries common to lowland farmland and categorised according to nationally applicable definitions (Haines-Young *et al.*, 2000) represented ecologically differing habitats at the farm-scale. The key differences between field boundary types were due to the woody abundance and frequency of young and mature emergent trees. Variations in associated herbaceous assemblages reflected these structural characteristics rather than differences in adjacent land-use, contrary to studies conducted at a regional scale (Cummins & French, 2001; Marshall & Moonen, 2002). The observed differences in field boundary characteristics will have implications for a wide range of farmland fauna including invertebrates, birds and small mammals (Parish *et al.*, 1994, 1995; Barr *et al.*, 1995; Flowerdew, 1997; Maudsley, 2000). Within this study, woody abundance and frequency of emergent trees were determining habitat factors in the density, richness and composition of epigeal overwintering arthropods.

In general, hedgerows had the highest representation of carabid and staphylinid taxa, supported a more diverse coleopteran fauna and provided a refuge to carabid species with poor dispersal powers. Degraded hedgerow boundaries supported the most diverse and equitable carabid community, whilst limited management probably enabled them to act as a refuge for carabid species with poor dispersal power to a greater extent that hedgerows. The grassy and natural regeneration vegetation associated with post and wire boundaries supported high densities of all taxonomic levels and was the most productive habitat for the emergence of overwintering polyphagous predators.

Furthermore, examination of the contribution of different field boundary types to full representation of arthropod biodiversity at the farm-scale demonstrated that all types contributed unique species of Carabidae and Staphylinidae. Consequently, a subset of all field boundary types was required for complete species representation at the farm-scale. This subset was in direct proportion to the field boundary types studied and was typical of that found generally in lowland farmland (Haines-Young *et al.*, 2000). Additionally, each of the three field boundary types defined in this study (hedgerow, post and wire and degraded) appeared to be equally important in the representation of whole-farm biodiversity as the complementary selection procedure did not select a single boundary type preferentially. This study provides empirical evidence to demonstrate that maximising or maintaining the heterogeneity of field boundary habitats represented at the farm-scale is likely to be the best strategy for continued full representation of arthropod biodiversity in farmland even though features such as post and wire fencelines are often considered to be of 'inferior' ecological value. The maintenance of arthropod biodiversity will have positive implications for the persistence of farmland wildlife through trophic interactions. Additionally, examination of ideal reserve selection for wildlife conservation at regional scales has indicated that by targeting habitat heterogeneity, it is more likely that cross-taxon biodiversity (e.g. plants, birds and mammals) may be maintained (Lombard, 1995).

These results may have implications for current perceptions regarding habitat quality and best practice for field boundary management. Within this study, each field boundary type contributed species-rich and species-poor assemblages, yet within the Countryside Survey 2000 they are ranked in order of perceived ecological value: hedgerows > degraded hedgerows > fences (Haines-Young *et al.*, 2000). This valuing system may be based on the potential of boundaries to support 'flagship' species of birds and mammals. However, degraded hedgerows are generally expected to support fewer invertebrate species than hedgerows due to reduced structural complexity (Forman & Baudry, 1984). The structural complexity of woody boundaries may have contributed to more equitable communities, but the determinants of arthropod assemblages are not always self-evident. Within field boundaries, current and historical management, land-use, and landscape structure in addition to habitat

structure and botanical composition will determine arthropod assemblages locally. Without detailed taxonomic surveys, the biodiversity value of a specific linear feature is difficult to quantify. Recent attempts have been made to develop knowledge-based habitat models to predict the occurrence of species and the ecological effects of land management (Petit *et al.*, 2003). However, such measures may be severely limited if the arthropod diversity of sites confounds perceived expectations. In addition, the implementation of such models to inform land management practices may result in loss of the biodiversity that land managers are attempting to conserve. Further research to establish the relative importance of different habitat, landscape and historical factors influencing arthropod biodiversity locally would aid decision-making regarding management options.

Current agri-environment schemes recognise the importance of field boundary management to enhance the conservation value of hedgerows and field margins (DEFRA, 2003a). Additionally, the importance of heterogeneity of management techniques, timing and intensity is increasingly recognised (Maudsley *et al.*, 2002). However, agri-environment schemes do not explicitly recognise the importance of field boundary habitat heterogeneity as a potential tool to enhance farmland conservation. Agri-environment schemes in The Netherlands have recently been critisised for failing to enhance farmland diversity of birds and plants, although species richness of hoverflies and bees did show modest increases in fields adopting management agreements (Kleijn *et al.*, 2001). Observed patterns of arthropod community structure and composition suggest that post and wire boundary habitat may perform a beneficial role in the development of sustainable agriculture. Despite the widespread use of fences in farmland, this boundary type does not feature within agri-environment schemes in the U.K. In addition, recommendations for the management of degraded hedgerows focus on habitat restoration. Such disturbance may result in the local extinction of species, which are then unable to recolonise due to poor dispersal powers and the fragmented nature of their populations in farmland (Den Boer, 1990). Whilst in many instances the use of restoration and habitat manipulation may contribute in the long-term to the wildlife value of a boundary (Maudsley *et al.*, 2002), care should be taken that this is not at a cost to rare species assemblages.

Carabidae were found to be the most sensitive indicators of differences in field boundary characteristics, supporting the role of this beetle family as an indicator of habitat type and change (Luff *et al.*, 1992; Kremen *et al.*, 1993). Landscape and network variables were equally, if not more, important than habitat factors in explaining variation in arthropod assemblages measured at Family or Order level of taxonomic resolution. In addition, field boundary characteristics only partially explained differences in Staphylinidae composition between field boundaries. Many of the staphylinid species captured migrate to field boundaries from fields by flight, possibly from several fields away. Therefore it is likely that these organisms will be more susceptible to variables operating at a multi-field scale. Patterns observed in the higher arthropod, coleopteran and staphylinid communities reinforce the need to examine the causative factors influencing arthropod biodiversity at a farm or landscape scale. The dominant carabid species were similar between field boundary types, but differences were observed both in the community structure and composition of rarer species. Stenotopic habitat preferences and poor dispersal ability may have contributed equally to the observed differences in carabid assemblages between field boundary types. The relative abundance of species with poor dispersal power in degraded field boundaries suggests sensitivity to disturbance, whilst the reduced physiological condition of woodland species indicates that even hedgerow habitat may be sub-optimal. The combined repercussions of homogenisation of the landscape and high disturbance in modern farming systems contribute to a trend of increasing dominance of arthropod assemblages by species that are eurytopic and with high dispersal powers.

Within this study considerable advances have been made in understanding the habitat preferences of Coleoptera, Carabidae and Staphylinidae overwintering as adults in field boundaries. Certain habitat features such as the base of post and wire fences, tree trunks, banks, margins and rocks have been identified as supporting high overwintering densities of these taxa regardless of field boundary type. In addition, environmental variables associated with these habitat features have been recorded, quantified and associated with community density patterns. Carabidae and Staphylinidae actively selected microhabitats in early winter and preferred sites with dense vegetation (particularly mature tussocky grass), leaf-litter and dead wood. The combination of location within a boundary and microhabitat characteristics, provided

optimal soil moisture and temperature regimes for overwintering. Optimal soil moisture content appeared to lie between 24% and 30%, though substrate moisture preferences detected under experimental conditions are necessary to support this observation. Lower and less varied temperature regimes appeared to be most favourable, and support similar findings produced under laboratory controlled conditions in the literature (Petersen, et al., 1996). Broad microclimatic preferences were shared amongst taxa, but particularly within the less structurally complex hedge-base, inter-specific interactions may have resulted in segregation of species patches (Loreau, 1984). These data may be used to determine the habitat preferences of particular species as well as functional groups such as polyphagous predators, closed-habitat species and low-powered dispersers. Preferred habitat features and microhabitat characteristics may then be created in new linear features or incorporated into pre-existing field boundaries to enhance conservation and biological control.

The physiological condition of overwintering carabid beetles was generally high and consequently it was concluded that that starvation-induced mortality was low. Mark-release-recapture studies suggested that individuals actively selected overwintering sites. Additionally, the spatial distribution of carabids and staphylinids suggested that neither dispersal ability nor habitat structure impeded individuals from locating suitable overwintering sites. It was concluded that individuals were able to search for and locate suitable overwintering microhabitats regardless of field boundary type. Hence, heterogeneous distributions of overwintering arthropods in field boundaries are probably the result of differential microhabitat selection rather than differential survival. Generally, overwintering survival does not appear to be a regulating factor in the population dynamics of carabid and staphylinid polyphagous predators overwintering as adults in field boundaries. Consequently a range of field boundary types may be used to augment natural enemy populations in farmland. Furthermore, a range of different habitats may ensure a more stable supply of polyphagous predators over time.

The mark-release-recapture component of this study demonstrated considerable movement of overwintering individuals through field boundaries, with subsequent mixing of populations migrating from different fields. This has implications for the persistence of open-habitat populations in farmland, and the

provision of beneficial agronomic services. However, to incorporate the permeability of field boundaries into landscape models of insect movement, transmission rates and distances moved by organisms need to be quantified in relation to habitat structure, the spatial distribution of preferred overwintering microhabitats, and the motivational state of individuals.

This study has demonstrated that field boundaries and adjacent margins differ in their associated community structure, spatial distribution and physiological condition of overwintering arthropods and polyphagous predators. In addition, the findings of this study have indicated the need to understand the behavioural mechanisms controlling the seasonal migration of carabid and staphylinid polyphagous predators between field and field boundary. The potential for field boundaries to support populations of polyphagous predators in farmland may be determined not by their habitat quality overwinter, but through differential selection of field boundary types (from adjacent fields) prior to overwintering, and differential dispersal (to adjacent fields) in spring. Seasonal migration is considered to be influenced by prey availability and a seasonal change in photophily (Thiele, 1977). A autumnal decrease in photophily may encourage field-active individuals to orientate towards large silhouettes such as those created by hedgerows and degraded boundaries, rather than post and wire fences, resulting in a differential selection of woody boundary types for overwintering. In spring, migration into fields may be driven by poor food availability in field boundaries in combination with an increase in photophily. It has been recognised that polyphagous predators are most effective if populations are dispersed and active in fields at the time of aphid colonisation (Corbett & Plant, 1993). Consequently, the provision of good quality field boundary habitat must be considered in relation to the spring dispersal of predators into the field prior to pest establishment. Field boundary habitat providing high prey availability in spring, such as tussocky grasses, may deter individuals from migrating into the field resulting in a potential build up of pest populations. Given the widespread recommendations for farmers to sow tussocky grasses in field margins and beetle banks, the potential influence of field boundary vegetation on spring migration of polyphagous predators requires further investigation. Conversely, given the temporal fluctuations in insect abundance (e.g. Scott & Anderson, 2003), habitats that act as a

refuge for alternative prey may provide resources to maintain polyphagous predator populations in years when food availability is low.

The presence of additional margins adjacent to pre-existing boundaries may contribute to enhanced overwintering condition of some polyphagous predators (e.g. *P. cupreus*) and may positively influence the post-overwintering condition of others (e.g. *B. lampros*). The latter may be particularly important as post overwintering mortality is frequently high in early spring (Riedel & Steenberg, 1998; Petersen *et al.*, 1996). Consequently, this study supports the creation of field margin habitat as a 'stand alone' feature, or adjacent to pre-existing field boundaries, to augment polyphagous predator populations. Additionally, several habitat features have been identified as supporting high overwintering densities or characteristic arthropod compositions. These features may be targeted as part of habitat creation or manipulation techniques to enhance polyphagous predator populations and/or arthropod biodiversity. However, the results of this study at a farm-scale advocate a precautionary approach to the management and manipulation of pre-existing field boundary habitat. Habitat augmentation rather than replacement may be most beneficial to the maintenance of arthropod biodiversity at the farm-scale.

Overall, this study has contributed useful information regarding the overwintering ecology of species selected for study and has identified some key areas where future work would be of value in order to develop biodiversity and conservation biological control strategies.

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APPENDIX ONE: PUBLICATION

SHORT COMMUNICATION

Laser marking the carabid *Pterostichus melanarius* for mark–release–recapture

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Key words. Carabid, laser marking, mark, *Pterostichus melanarius*, recapture, release.

Introduction

Marking, releasing, and recapturing insects in traps are used widely to estimate dispersal distances, habitat preferences, and population density. The limiting factor in using this technique is often the difficulty of marking large numbers of individuals (Dent & Walton, 1997), especially when candidate species such as the beneficial predatory beetle *Pterostichus melanarius* (Ill.) may number 140 000 per hectare (Purvis & Fadl, 1996). Associated statistical procedures are well developed (Schwarz & Seber, 1999) but cannot compensate for low recapture rates.

Current marking techniques include paints, dyes, immunoglobulin, abraded and branded marks, radio isotopes, and rare earth elements, and have been reviewed by Southwood and Henderson (2000) and Hagler and Jackson (2001). Some of these methods are impermanent while others are potentially toxic, time consuming and difficult to apply (causing handling mortality). Techniques such as the use of immunoglobulin allow batch marking but do not provide unique codings to allow identification of individuals. This study introduces a rapid technique to mark insects individually with a unique identity number using a laser.

Materials and methods

The Synrad Fenix Laser Marker (Synrad Inc., 6500 Harbour Heights Parkway, Mukilteo, WA 98275, U.S.A., http://www.synrad.com), used widely within the engineering sector, was employed to mark elytra of the carabid beetle *P. melanarius* (≈ 12 mm in length). The Fenix system utilises a 25-W CO_2 laser and galvo-based marking head (set in this case at 20% power with a 370-mm lens and a speed of 380 mm s^{-1}). The marking head is located directly above the object(s) to be

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marked and the format and position of laser etching are controlled by WinMark software (Version 2.0). The system has a maximum field range of 18×18 positions over a 220×220-mm area with a maximum laser incidence angle of 19°. Maximum marking speed is 180 characters per second (2 mm character height) with a positional accuracy of 0.05 mm. The choice of lens (80–370 mm), power setting (15–50%), and speed (300–1000 mm s^{-1}) were selected by a process of trial and error (10 attempts over 3 h) to obtain a clearly visible etched mark that did not puncture the surface of the elytron.

Beetles were restrained in position below the marking head using a 150×150-mm holding plate with a 10×6 grid of 5-mm deep wells. The wells (in this case 8×12 mm) were marginally larger than the beetles being marked. Marking alignment was achieved using Win-Mark Pro to set a grid of marks with the same spacing as the wells on the holding plate; the holding plate itself was aligned below the marking head (with an offset of 2 mm). Alignment accuracy was tested by trial marking using 8×12-mm strips of paper placed within the holding plate wells.

The base of each well was constructed from 1-mm wire mesh, allowing the beetles to be held in place by applying suction (Hewlett, 1954) using a domestic vacuum cleaner connected to a small chamber ($150 \times 150 \times 60$ mm) below the holding plate. Prior to marking, beetles were sedated by chilling to ≈ 4 °C (30 min) then positioned in the wells (5 min for 60 beetles). Chilling and suction prevented movement of the beetles, allowing accurate mass marking. Once the beetles were positioned, the laser marker was activated using WinMark Pro software.

To determine the effects of marking on individual beetles, cohorts of 30 marked and 30 unmarked individuals were observed over a 4-week period. Beetles were placed individually in 9-cm Petri dishes containing damp filter paper, and arranged randomly in a culture chamber. Beetles were fed a diet of *Lucilia caesar* (L.) maggots and cat food *ad libitum* and kept under a natural day/night regime in cool ambient

Fig. 1. Laser-marked *Pterostichus melanarius* using a three-digit code with a text height of 1.5 mm. The code is sufficiently distinct to be read either with the naked eye or using a hand lens. The electron-micrograph shows indentation on the surface of the elytron made by the marking procedure.

conditions (19–21 °C); food and filter papers were replaced on alternate days.

Results and discussion

Using the laser, a three-digit code with a text height of 1.5 mm was etched on an elytron of each beetle (Fig. 1). Once the beetles were retained within the holding plate, they were marked rapidly at a rate of $20 \, \text{s}^{-1}$. The exact position of the mark varied slightly (but insignificantly) due to variation in the exact orientation of beetles held within the wells. The mark was considered permanent as it was etched directly onto the surface of the elytron; after the 4-week trial, no individual had lost its mark, and the codes were still clearly evident on live beetles retained for 3 months. Mortality was identical in marked and unmarked cohorts, in both cases being two out of 30 (6.6%). No adverse effects on marked beetles were evident.

The marking technique appears harmless to *P. melanarius* and is likely to be harmless for other arthropods with hard wing cases or other exposed areas of heavily sclerotised or calcified exoskeleton. It is clearly important that the position of the mark should avoid areas where soft body tissue may suffer injury. The technique could be adapted for other species but settings would need to be optimised. In further trials, the smaller carabid *Bembidion lampros* (Herbst) was spot marked successfully while intermediate-sized beetles such as *Amara plebeja* (Gyllenhal) were marked with single digit codes. The equipment is sufficiently portable that it could be adapted for field use, although to date it has been used only in the laboratory. The complete marking system (including software) costs about £15 000, depending on specification.

Laser marking offers an opportunity to mark permanently, rapidly, uniquely, and *en masse*. This will enable more accurate estimation of population and dispersal parameters in mark–release–recapture studies.

Acknowledgement

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