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Role of aspect in terrestrial and intertidal distributional patterns, and ecological processes

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Role of aspect in terrestrial and intertidal distributional patterns, and ecological processes

by

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To my dad, who loved nature as much as I do

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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 without prior agreement of the Doctoral College Quality Sub-Committee.

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Abstract

Role of aspect in terrestrial and intertidal distributional patterns, and ecological processes – Axelle Amstutz.

Understanding better the impact of climate and changing environmental conditions on species and ecosystems has become one of the pressing research priorities. In addition, a need for more realistic field-based climate change experiments and focus on community and ecosystem functioning has grown in the last decade. The main aim of this PhD work was to study the effect of mainly temperature variation on species and ecosystems, by studying small-scale aspect (slope orientation) on both intertidal gullies and hedgerows/road verges in SW England. Such paralleled studies between terrestrial and marine ecosystem are sparse. I especially investigated (1) abiotic variations, (2) species distribution and richness, (3) species physiology (osmotic regulation) and phenology (gonad development), (4) leaf-litter decomposition as a key ecological process, and (5) comparison of conspecific species with different biogeographic origins, all between north- and south-facing aspects in both ecosystems. In both the intertidal and terrestrial ecosystems, south-facing slopes were much warmer (annual mean) and experienced more hot extreme events (more intense and frequent) than the opposite north-facing slopes; which corrobotate some future predictions by the IPCC. In addition, south-facing terrestrial slopes were significantly drier than the north-facing ones. Abundance and richness was greater on cooler north- than south-facing aspect on the rocky shore at all studied levels of organisation. Osmotic regulation did not seem to explain distributional change between two closely related limpet species, suggesting that other ecosphysiological or behavioural thermoregulation are factors involved. There was no variation with aspect in soil mesofauna, little variation in decomposition process, while greater differences were detected in terrestrial plants at most levels of organisation, except at the community level. This work showed that intertidal gullies and road verges are good systems to study the impact of temperature variations on ecosystem patterns and processes, and that aspect seem to buffer temperature extremes, offering refugia for cold-adapted and moist-tolerant species on the cooler and moister habitats (e.g. north-facing aspect). Aspect influenced species distribution at different levels (community, taxonomic, functional, species, and biogeographic origins), and differences between north- and south-facing aspects were more marked, however, on the intertidal than on land. In the future, slope aspect could be at interest for the conservation and management sector as a way to locally buffer global warming.

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Chapter 1: General introduction

1.1 Climate change patterns and future predictions

It is now unequivocal, that the planet is experiencing a warming of its global climate with an average global temperature increase of 0.85°C (0.65 to 1.06°C) since the late 19th century. (IPCC, 2013)(Figure 1.1). Although the climate has been relatively stable over the last thousand years (i.e., ±0.5°C air temperature variation, and ±4 ppm atmospheric CO_2) (Ridgwell and Valdes, 2009), IPCC reports (2007, 2013) as well as numerous studies (e.g. Scheffers et al., 2016) provide convincing evidence that the recent and present warming is faster than what could be expected under 'natural' processes and that anthropogenic activities are causing it. Thus, climate change is often referred in the literature as 'anthropogenic climate change' (ACC) (e.g., Midgley et al., 2002; Thomas, 2010).

While there remains some uncertainties regarding the impact of ACC on earth's climate systems, impacts are already apparent and changes projected by models indicate major repercussions for natural environments (Murphy et al., 2009; Defra, 2019). It is likely that by the end of the 21st century, the global surface temperature will exceed 1.5 °C or 2°C depending on the greenhouse gas emission scenario (IPCC, 2013). Because the greenhouse effect also modifies moisture, light, gas composition and wind speed (Kennedy, 1995) other key meteorological factors are predicted to change over time, and unbalancing the global water cycle (IPCC, 2013). Drought and rainfall events are expected to last longer, and in some places, summer to be hotter as well as winter being colder.

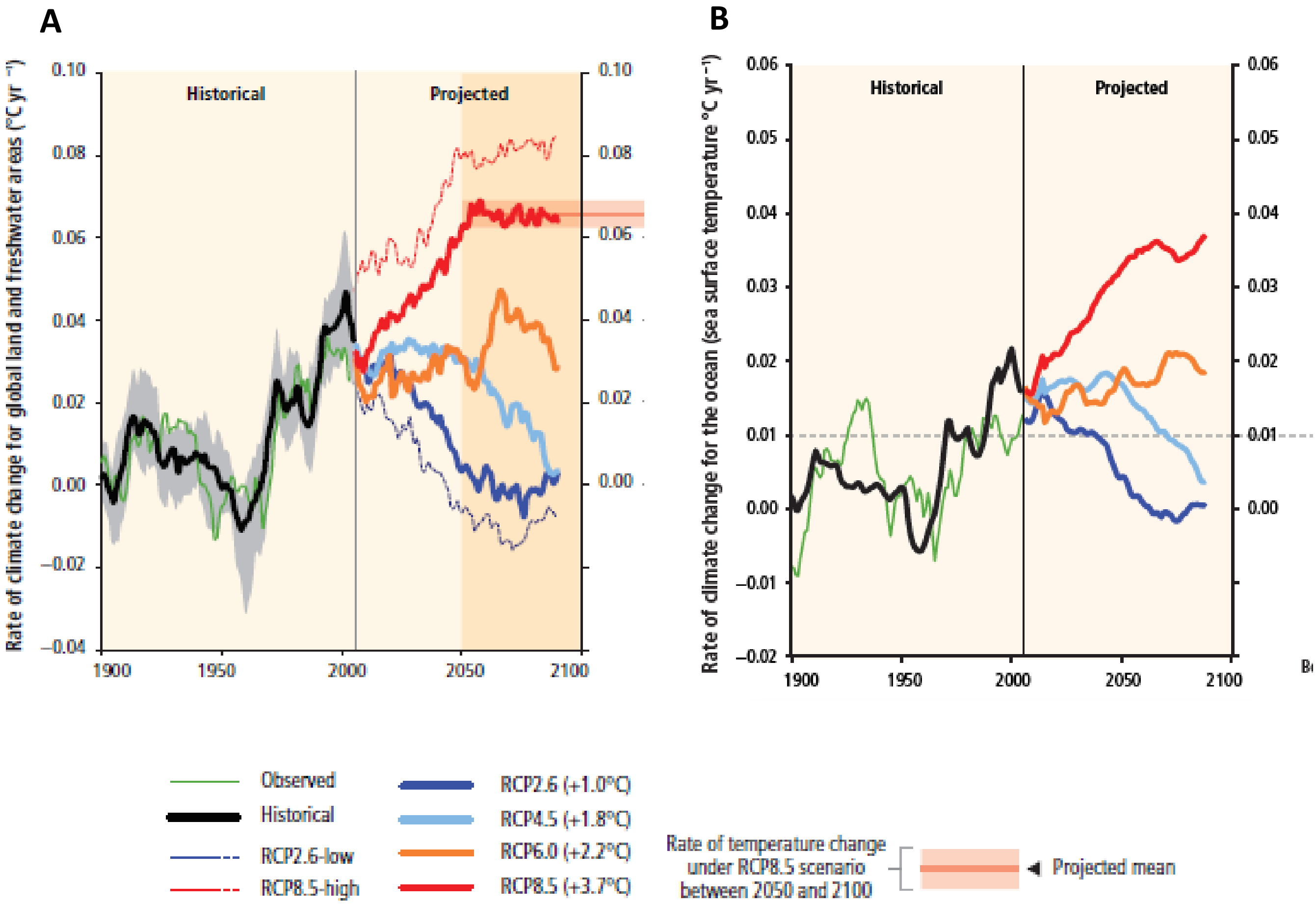

Figure 1.1: Rate of climate change for **A.** land and **B.** ocean (sea surface temperature (SST) °C yr^{-1}) according to the different scenarios (i.e. RCP2.6, RCP4.5, RCP6.0, RCP8.5). Observed rates of climate change are derived from CRUTEM4 (**A**) and HadISST1.1 (**B**) climate data analysis. Grey shading indicates model uncertainty. Future projections based on the four Representative Concentration Pathway (RCP) emissions scenarios are averages of CMIP5 climate models. Figures from IPCC (2014).

The oceans will also continue to warm, with a predicted increase from 0.3°C to 2°C at a depth of about 1000 m by the end of the 21st century, shrinking continuously the Arctic sea ice (IPCC, 2013). In addition, as extreme climatic events will be more frequent (IPCC, 2019); flooding risks will increase (IPCC, 2013) as a result of increase of waves height and velocity (Helmuth et al., 2010a), and heat waves are predicted to become more common. During the period 1881 to the present, the top ten warmest years postdate 2002 in the UK (Met Office, 2019a). Extreme summers could even become more common by mid-century (with probabilities of the order of 50% depending on the emissions scenario followed) (Met Office, 2019a and 2019b). In the UK, the rate of recent warming has been above the global average (1°C since pre-industrial period) (Met Office, 2019a). The United Kingdom Climate Impacts Programme (UKCIP) developed a set of ACC scenarios that predict a temperature rise between 0.9°C and 5.4°C in summer and 0.7°C to 4.2°C in winter, by the 2070s in the high emission scenario (Met Office, 2019b). Seasonal weather patterns will also change. Winters are predicted to be wetter, while summers will become drier (IPCC, 2012; Met Office, 2019). By 2050, typical spring temperatures are expected to advance by one to three weeks and onset of winter might be delayed by a similar period (DEFRA, 2009).

These rapid environmental changes have already started to impact species and ecosystems (Chown et al., 2010; Letcher, 2016; Scheffers et al., 2016). Understanding the mechanisms underpinning species and ecosystem responses (i.e. patterns of stress, mortality, and reproduction) to the ACC is a vital pre-requisite for mechanistic ecological forecasting, and to anticipate and predict its cascading effects on ecosystems (Classen et al., 2005; Parmesan and Hanley, 2015).

1.2 Impacts of ACC on ecosystems and species

1.2.1 Physiological responses

Temperature is often described as the most limiting factor in plant and animal fitness and survival, but linked changes in desiccation (Hamilton, 2017; Suykerbuyk et al.,2018) as well as drought stress (Fathi and Tari, 2016; Sourour et al., 2017) and ocean acidification (Boyd et al., 2018) are also important environmental factors affecting organismal ecophysiology in plants and marine organisms, respectively. Temperature controls the rates of chemical and biochemical reactions, and these constraints lead to thermal sensitivity of function at cellular, systemic, and organismal levels (Angilletta 2009). In plants, temperature affects rates of most biotic processes, including phenology, growth, carbon fixation, and respiration, and is therefore a a major determinant in their biogeography. Combined, these interactions impact growth, species composition, and susceptibility to disturbance (Chuanyan et al., 2005). Even small temporal and spatial variations in body temperature affect individual performance (i.e. capacity to function, usually expressed as a rate or probability) in nature (Dowd et al., 2015). The responses of organismal performance to temperature gradients are unique to each species, and can be characterised by several parameters (Figure 1.2): (1) the thermal optimum (T_{opt}); (2) the thermal breadth (or performance breadth); (3) the thermal limits, referred as the critical thermal minimum (CT_{min}); the critical thermal maximum (CT_{max}); and the maximal performance (P_{max}) (Angilletta, 2009). Some traits of interest, such as growth rate, change repeatedly in response to temperature (labile traits) and can be determined according to the range of temperatures experienced (i.e. environmental or body temperature) (Figure 1.3) (Angilletta, 2009).

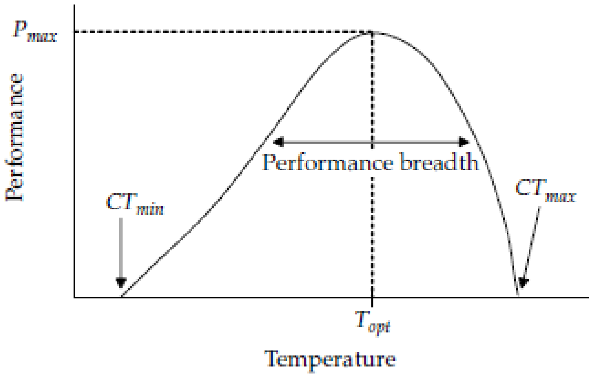

Figure 1.2: A hypothetical performance curve showing the stereotypical optimum at an intermediate temperature, with thermal optimum (T_{opt}), performance breadth, critical thermal limits (CT_{min} and CT_{max}), and maximal performance (P_{max}). (Angilletta 2009)

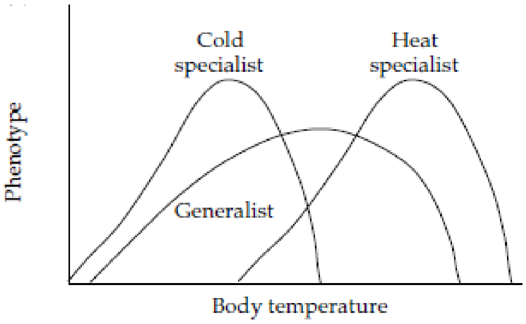

Figure 1.3: Thermal reaction norms characterize many different kinds of traits. Example of labile trait, where instantaneous (or short-term) fluctuations in body temperature affects the phenotype. (Angilletta 2009)

In general, most warm-adapted (e.g. tropical) species live closer to their thermal tolerance limits and have lower abilities to increase heat tolerance through acclimation than more cold-adapted (temperate) species (Somero et al., 2005). Therefore, tropical and subtropical species are more likely to suffer from severe ecophysiological responses linked to ACC (Letcher, 2016).

Analogous to thermal tolerance, terrestrial and marine species distributions can also be related to their lowest precipitation level and desiccation pressure. Crimmins et al. (2011) for example, demonstrated that some tree range shifts were driven by water balance more than temperature. Both Letcher (2016) and Parmesan and Hanley (2015) reviewed the impact of drought and dry soil condition on plant growth, reporting a consistent trend towards a reduction of growth and increase in mortality.

Although many studies have addressed the impact of experimental warming and/or elevated CO_2 or light on the physiology of plant (tundra plants: Arft, et al., 1999; lichens: Buffoni et al., 2002; trees: Danby and Hik, 2007; crops: Kakani, et al., 2003; algae: Häder, et al., 2001 and Wahidin et al., 2013) or animal species (sea cucumber: Dong et al., 2008; marine molluscs: Dong and Gray, 2011; Miller et al., 2015; Tagliaolo and McQuaid, 2016) in order to predict and understand what will be the real impact of ACC on organisms; observed physiological responses to increasing temperature due to ACC are rare, as difficult to detect. However, there is more evidence linked to ocean acidification (coral reef: Kaniewska et al., 2012; fish: Cattano et al., 2018; phytoplankton: Meyer and Riebesell, 2015). In intertidal gastropods, field-based investigations such as heart rates and body temperature have provided organismal-level response to changes within a local environment, which can be modelled for prediction of future species distributions in responses to changing climate (Letcher, 2016).

Some intertidal gastropods such as the Indo-Pacific *Echinolittorina malaccana* cope with desiccation by reducing or even stopping their metabolic activity, often combined to a rapid induction of an isolation (behavioural) response (withdrawal into the shell and aperture closure) (Marshall et al., 2013).

1.2.2 Behavioural responses

The buffering influence of behavioural thermoregulation is particularly important in ectotherms as a response to climate warming, and is often missing from models predicting the impact of ACC on species (Kearney et al., 2009; Ng et al., 2017). These behaviours can be of two degrees, and Ng et al. (2017) referred to them as *flight* response and *fight* response. The flight response consists in the organisms choosing micro-habitats that permit the escape of extreme conditions and maintance of physiological functions. For example, the selection of cooler micro-environments has been widely reported in intertidal ecosystems (e.g. molluscs: Dillon et al., 2010; Chapperon and Seuront, 2011; Marshall et al. 2013) while selection of warmer micro-habitats is more common with terrestrial ectotherms (e.g. snakes: Cox et al., 2019). In fight response, organisms modifying their own environments minimize extreme temperatures, and examples on intertidal organisms are various. During low tide, marine gastropods can retract their foot in their shell (Vermeij, 1971; Miller and Denny, 2011) and some can stay attached to their hot substrate by a layer of mucus only. Under hot conditions – especially in the tropics or under extreme hot temperatures, limpets are known to behaviourally thermoregulate their body by lifting their shell from the rock allowing cooling using the 'mushrooming' behaviour (Williams and Morritt, 1995; Williams et al., 2005). This behaviour can however, also increase desiccation rate and water loss (Lowell, 1984).

Numerous experimental studies have examined the behavioural responses of plants and animals under warming, drought or desiccation pressure, or higher light intensity; but only few studies have reported clear behavioural patterns linked to ACC. For instance, the marine gastropod *Nerita atramentosa* tends to aggregate on boulders, in South Australia, in order to reduce both desiccation and heat stress (Chapperon et al., 2013). A multifunctional behavioural trait was found in the crab *Scopimera intermedia*, sponging (water uptake from sediments) was found to reduce body temperature of about 1.3°C (Hui et al., 2018).

1.2.3 Phenological responses

Phenology is the study of the cycling of biological events throughout the year (Bradley et al., 1999), e.g. flowering, fruiting, migration, or reproduction. Many meta-analyses have reported shifts in the timing of those seasonal events (Parmesan and Yohe, 2003; Parmesan, 2006; Poloczanska et al., 2013; Ge et al., 2015), and in their review, Parmesan and Hanley, (2015) noted that the phenological patterns of responses to ACC reported from five major global meta-analyses, had a less than one in a billion chance of occurring at random. The majority of studies have documented ongoing advances in phenology (i.e. Bradley et al., 1999) which is often widely associated with spring warming (Bradley et al., 1999; Parmesan and Yohe, 2003; Poloczanska et al., 2013). There is however, emerging evidence that some species can respond to climatic events from other seasons (Parmesan and Hanley, 2015) such as the winter vernalization for some terrestrial plants (Cook et al., 2012). Such complex responses, which could easily go unnoticed, suggest that the proportion of species sensitive to ACC is likely underestimated (Parmesan and Hanley, 2015). Some studies have demonstrated delays (Barbraud and Weimerskirch, 2006) or absence of drift in response to ACC (Bradley et al., 1999; Lane et al., 2012). This has led ecologists to raise the question about phenological adaptability and its importance in species survival during extended ACC.

Whilst, there is overwhelming evidence of the phenological responses to ACC for terrestrial species, especially plants (Bradley et al., 1999, Parmesan and Hanley, 2015), insects (Robinet and Roques, 2010; Forrest, 2016), and birds (Bradley et al., 1999; Brabraud and Weimerskird, 2006), much less is known about the responses of aquatic species. The meta-analysis of Poloczanska et al. (2013) revealed that phenology of marine species (from phytoplankton to marine reptiles and mammals) had an earlier onset, with for example, over the last 50 years, spring events shifted for many species with an advancement of 4.4 ±0.7 days per decade and summer events by 4.4 ±1.1 days per decade.

Evidences in delays, avancements, and asynchronies in reproductive phenology (e.g. in corals, Shlesinger and Loya, 2019) linked to ACC, are growing. Each species may respond differently to another. For instance, Moore at al. (2011) looked at the reproductive phenology of two con-specific intertidal limpets in SW England; *Patella depressa*, a ‘southern’ or Lusitanian species (i.e. having a warm water centre of distribution); and *Patella vulgata*, a ‘northern’ of boreal species (i.e. having a cool water centre of distribution). Over 50 years, *P. depressa* advanced (average 10.2 days) and extended its reproductive season. In contrast, *P. vulgata* experienced a delay in the timing of its reproductive development, and reduction of gonad maturity success leading to more frequent reproductive failure years. Plankton and other marine organisms, which are dependent on temperature to stimulate their physiological developments or larval release, have shifted their seasonal cycle in response to ACC (Beaugrand, et al., 2003; Edwards and Richardson, 2004; Moore et al., 2011; Asch, 2014). Some planktons (diatoms) have, however, shown little change in the timing of their spring blooms, which might suggest they are more dependent on day length or light intensity rather than temperature (Edwards and Richardson, 2004). Many fish species also have their time of spawing and larval emergence temperature-dependant. For example, the Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* have to delay their migration or halt during the summer when water temperature becomes to high (Jonsson and Jonsson, 2009; Baisez et al., 2011), and higher mortality rate was found in stranglers *S. salar* (Baisez et al., 2011). Water flow is also known to influence the accessibility of rivers for returning adults salmonids to their spawning sites (Jonsson and Jonsson, 2009). Therefore, the predicted wetter and milder (leading to decreasing of ice cover) winters in the Atlantic regions (IPCC, 2013) will also have an implication in the salmonids migration.

Some global warming-induced phenological shifts may lead to an increase in asynchrony between interacting trophic levels, such as prey-predator or insect-host relationship (e.g., Weiss et al., 1988; Mysterud et al., 2001; Beaugrand et al., 2003; Edwards and Richardson, 2004; Parmesan, 2007). Hipfner (2008), for instance, demonstrated that along the western coast of Canada, there was less temporal overlap between the copepod *Neocalanus cristatus* and the zooplanktivorous seabird *Ptychoramphus aleuticus* in warm years, during the nesting-provisioning period of that bird. The copepod became scarce two to three weeks earlier, and was less prevalent overall in warmer years. This had a negative impact on *P. aleuticus*'s offspring survival and body mass. In the North Sea, plankton fluctuations (abundance, body size and delay in the timing of occurrence) have been unfavourable to the survival of cod larvae/junevile (e.i. poor recruitment), relying a lot on this source of food (Beaugrand et al., 2003). In addition, the failure of one species (e.g. increase of mortality due to trophic mismatch, or spawning or recruitment failure) might be advantageous for another one from the same trophic level and living in the same niche, which could therefore become more abundant and take over that niche.

1.2.4 Biogeography and range shifts

Climate is the major influence on the geographical distributions of species (Suggitt et al., 2015). Physiological tolerances, and in particular thermal adaptation, play an important role in regional-scale biogeographic (latitudinal) distributions, but also in local scale vertical distributions along subtidal-to-intertidal gradients in coastal ecosystems, or elevation in montane environments (Somero et al., 2005). Such patterns underscore the importance of physiological responses to climate as a primary mechanism for establishment of range boundaries; cold intolerance limits poleward range (i.e. leading range edge), while heat intolerance limits equatorial range (i.e. trailing range edge) (Wethey, 2002). It is important to note however, that biotic/ecological interactions also play a significant role in defining range boundaries. For example, both Wethey (1983) and Connell (1961) demonstrated that competition with a dominant species of barnacle (*Semibalanus balanoides*) had a direct impact in shaping the northern range limits of the co-ocurring *Chthamalus stellatus*.

Range extensions at the leading edge are predicted to advance by virtue of an organism's ability to colonize suitable habitat. Indeed, warming is expected to increase organismal performance, survivorship and fecundity of species restricted at their leading edge by their cold tolerance, and will ultimately result in population increase (Pörtner and Farrell, 2008). Range extension can happen with change in other abiotic parameters, such as precipitation and soil moisture on land (Bonebrake and Mastrandrea, 2010; Chen et al., 2011) or can results from indirect processes, such as arrival of a critical habitat-forming species facilitating colonization (Yamano et al., 2011)

Range contractions by contrast, may occur at the trailing range limit when population decline from areas of a species' historical range (Helmuth et al., 2006a) and where climate becomes unsuitable (Letcher, 2016). Lethal or sub-lethal effect of high temperature in population at their trailing edge, when physiological thresholds are exceeded as environmental temperature increases is well-documented (e.g., Beuekma et al., 2009; Jones et al., 2010; Smale and Wernberg, 2013). However, to date there is considerably less evidence for climate driven range contraction than expansion (Davies et al., 2006; Parmesan and Yohe, 2003; Sunday et al., 2012). Data selection results might lead to an over-estimate of range expension and an under-estimation of range contaction (Thomas et al., 2006; Thomas, 2010). Range extensions, often associated to warming climate at high latitudes, tend to be easier to detect compared to range contractions at lower latitudes (Wilson et al., 2004; Hampe and Petit, 2005; Thomas et al., 2006). Indeed, range contractions starting with populations fragmentation, can be harder to identify when the last population in a defined region has fully disappeared, especially when distribution are mapped on a coarse-resolution grid (Thomas et al., 2006). It is also more difficult to attribute to climate change any range contraction (Thomas et al., 2006). It has also been suggested that range contraction takes longer to occur compared to range extension. For example, high propagule production and ecological generalism (i.e. broad diet and habitat) can increase invasiveness at extension (leading) edge (Kolar and Lodge, 2001), while it can also delay extinctions at contraction (trailing) edge by increasing the persistence species (Purvis et al. 2000). It is also reasonable to think that there is a sampling bias, as many more research institutes are on temperate/ higher latitudes than in (sub-) tropical/lower latitudes, which might have led to inconsistency in sampling effort with greater sampling at leading than trailing edges.

Severe range contraction occurs on range-restricted organisms, such as polar and mountaintop species, which are the first groups in which entire species have gone extinct due to recent ACC (Parmesan, 2006). The geographic ranges of many terrestrial species have shifted poleward and toward higher altitudes (Parmesan, 2006; Wilson et al., 2007; Parmesan and Hanley, 2015), as well as to greater depth for marine species under climate change (Jones et al., 2009; Poloczanska et al., 2013; Fosseheim et al., 2015). Range shifts are not homogenous and differ between species (Figure 1.4). Marine organisms for example, have a faster expansion rate than terrestrial animals and plants, due to their high rates of propagule production and enhanced dispersal abilities (Figure 1.4; Parmesan and Yohe, 2003;

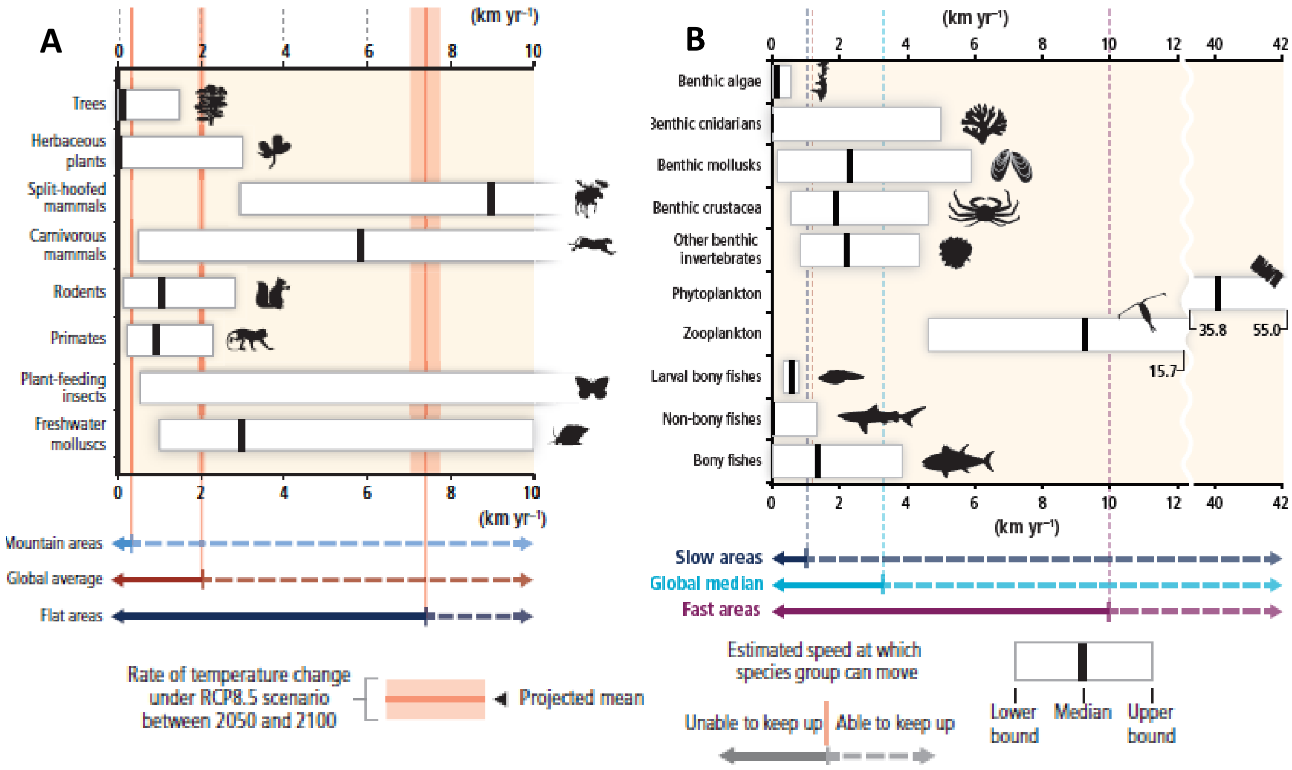

Figure 1.4: Rates of displacement of several **A.** terrestrial and freshwater species groups (including passive and active dispersal rates for upstream movement) in the absence of human intervention, and **B.** marine taxonomic groups based on observations over 1900-2010. Pink bands illustrate the interpretation of this figure according to the RCP8.5 scenario. Rates of displacement are given with an estimate of the median (black bars) and range (boxes = approximately 95% of observations or models). Estimate of median displacement rate for several groups exceed the highest rates on the axis. Figures from IPCC (2014).

Poloczanska et al., 2013). 75% of 129 coastal marine species have undergone poleward shifts in their geographic distribution globally, at an average rate of 19 km/year (Sorte et al., 2010).

The predicted increase in frequency and intensity of extreme climatic events might also play an important role in dictating patterns of species range expansion and contraction. More common heatwave events have for example caused catastrophic mortalities (e.g., Garrabou et al., 2009) or range retraction (e.g., Smale and Wernberg, 2013) of marine species, while the extreme cold winter of 1962/63 in Britain, reduced the northern range limit of many intertidal species by hundreds of kilometres (Crisp, 1964a) and for up to 40 years before recovery (Firth et al. 2015). Similarly, an extreme cold event in 2001 caused large-scale mortality and die-back in Scots pine (*Pinus sylvestris*) close to its low latitude range limit in Spain (Camarero et al., 2015). Those rare extreme events are believed to have the potential to limit species' range boundaries locations as they often exceed the thermal tolerances of species (Sunday et al., 2012).

Several reviews and meta-analyses have summarized ACC-linked species range shifts over recent decades (Parmesan and Yohe, 2003; Sunday et al., 2012; Poloczanska et al. 2013; Parmesan and Hanley, 2015), with as predicted, a general trend for poleward and upward (altitude) range shift. However, some counter-intuitive distributional changes could be driven by climatic factors other than temperature. Parmesan and Hanley (2015) for example, reported several instances where downward (downhill) shifts were associated with changes in precipitation and water availability. However, temperature is still predicted to be the most important factor shaping the distribution of most species, as the oak *Quercus labata* which is expected to constrict its range around water bodies and finally disappear when exceeding threshold of maximum temperature in the area (McLaughlin and Zavaleta, 2012).

In their meta-analysis, Poloczanska et al. (2013) reported that marine species have expanded on average 72.0 ± 13:5 km per decade, with the fastest expansions in highly mobile or dispersive pelagic organisms (phytoplankton, 469.9 ± 115.3 km per decade; bony fish, 227.5 ± 76.9 km per decade ; invertebrate zooplankton, 142 ± 27.8 km per decade). Trailing-edge range contractions by contrast, were significantly slower than expansion, with an average of 15.4 ± 8.7 km per decade. IPCC (2014) reported a much greater range shift of marine species (benthic, pelagic and demersal) and communities (i.e., up to a thousand kilometres), although range shifts are not uniform across taxonomic groups, or ocean regions. In some cases, species with warmer thermal tolerance windows are predicted to replace congeners; this is the case with the boreal barnacle *Semibalanus balanoides* and the limpet *Patella vulgata,* which have declined in abundance around the coastline of Britain and northern Europe and are being slowly replaced by *Chthamalus spp.*, and *Patella depressa* respectively (Letcher, 2016).

1.2.5 Biodiversity

ACC is increasing shift of species distribution and has already started impacting the composition of ecological assemblages (Wilson et al., 2007; Parmesan and Hanley, 2015; Letcher, 2016). Species richness is increasing with incoming southern and low elevation species to northern and higher altitude zones, respectively, where local species have not left (see Whalter et al., 2009). It is already apparent that temperature variation (both warming and cooling) has facilitated changes in marine biodiversity both on ecological and evolutionary timescales (Letcher, 2016). As the ocean warms, the tropics lose diversity; temperate regions show species turn over and sometimes increase in net diversity, whereas, so far, polar environments mostly show decline in cryophilic species and invasion of subpolar ones (Letcher, 2016). Several models have predicted major consequences of climate change for biodiversity; such as extinction of many plants and animals, and a large-scale dieback of tropical rain forests (Thomas et al., 2004; Willis and Bhagwat, 2009). Many previous studies have not considered the acclimation capacity of organisms, and their coarse spatial scales are insufficient to capture topographic or 'microclimatic buffering' (Willis and Bhagwat, 2009; Lavergne et al., 2010). However, models that are more sophisticated have recently started taking into account, as spatial solution, topography, biophysical feature (e.g., vegetation cover) and behaviour in order to obtain more accurate predictions in species thermal niche and distribution (Lembrechts et al., 2018a; Barton et al., 2019).

Although human land use remains currently the main driver of terrestrial species extinction and habitat loss, ACC is predicted to become equally or even more important in the next few decades (Millennium Ecosystem Assessment, 2005; Dawson et al., 2011). Indeed, its impact on biodiversity (i.e. loss of biodiversity and increase of risk extinction) is increasing very rapidly, more than with over-exploitation or habitat change (Millennium Ecosystem Assessment, 2005).

1.2.6 Adaptation and acclimation

One way organisms cope with environmental change is to acclimatise via phenotypic plasticity; i.e. an individual's (genotype's) ability to express different phenotypes depending on ambient environmental conditions (Nicotra et al., 2010; van Asch et al., 2012; Parmesan and Hanley, 2015), e.g. changes in phenology (natural timing events). Uncommon in terrestrial ectotherms (Dillon et al., 2010), several intertidal species adaptively depress metabolism independent of temperature in order to conserve energy reserves when resting (or aestivating) under fluctuating high aerial temperature (Marshall et al., 2013). An example of phenotypic plasticity within the rocky shore can be found amongst limpets. Indeed, they have been reported to have the ability to change their shell morphology across natural thermal gradients (Harley et al., 2009); specifically that: (1) taller limpets' shell remain cooler by reduced conduction (i.e. conduction proportional to foot surface area, which in turn is proportional to the length and width of the shell) and facilitating convective cooling when catching fast wind); and (2) that additional features such as bumps and ridges increasing shell surface area, increase the rate at which excess heat is lost *via* convection (Vermeij, 1973; Johnson II, 1975). More recently, Harley et al. (2009) rigorously tested the actual thermal significance of morphological variation in limpets, by mimicking their body temperature. They confirmed these early hypotheses but argue that those morphologically thermal advantages could increase mortality *via* fish and bird predation, as well as wave force.

The capacity for phenotypic modification, while it may play some roles (e.g. Anderson et al., 2012; Nicotra et al., 2010; Thuiller et al., 2008) is not thought to be sufficient to allow species to adapt to a new set of environmental circumstances, and so genetic changes (adaptations) are necessary (Hoffmann and Sgro, 2011; Asch et al., 2012; Merilä and Hendry, 2014). However, evidence of adaptive evolution linked to ACC in the wild represents a major and ongoing challenge (Merilä and Hendry, 2014).

1.2.7 Genetic and evolutionary responses

Genetic adaptation is crucial to prevent population extinction (Hoffmann and Sgrò, 2011), but examples where climate change results in genetic changes in wild populations are few (Merilä and Hendry, 2014; Muñoz et al., 2015). Van Asch et al. (2012) report through long-term observational data and experiments that climate-linked changes in the egg hatching date of the winter moth (*Operophtera brumata*) has a genetic underpinning. A single amino acid replacement is sufficient to produce a novel protein, better fitted to the new thermal range (Somero, 2010) and this has already been suggested to be highly correlated with biogeographic and vertical distribution (Crummett and Eernisse, 2007; Dong and Somero, 2010). Such variation will be important in governing range shifts in response to ACC. For instance, Buckley et al. (2011) used an amplified fragment length polymorphism (AFLP)-based genome scan to test for evolutionary change during the range expansion of the butterfly *Aricia agestis*. These authors suggested that the allele frequency variation found between candidates from long-established and recently colonized sites would have triggered an adaptation to new habitats at its range margin, allowing the poleward range expansion of this species in the UK. In certain cases, genomic vulnerability can accurately forecast which population may be at risk of declining with new ACC conditions. For example, Bay et al. (2018) compared the genomic basis of climate adaptation of the yellow warbler, a wide spread bird in North America, occupying a various range of habitats. By comparing the DNA of various populations, the authors found that the most vulnerable populations (e.g. population with greatest shift in allele frequencies to keep pace with ACC) were located in a region already affected by droughts over the last decade, which coincided with recent decline of the same population. This result suggests that the failure to adapt may have already negatively influenced populations.

Genetic diversity may also have the potential to protect communities from environmental variability (Lavergne et al., 2010). For instance, the genetic diversity of the eelgrass *Zostera marina* positively affects seagrass meadow resilience to global warming, enhancing ecosystem recovery (Ehlers et al., 2008). Similarly, Guo et al. (2018) have shown that low genetic diversity in a mangrove suffered from much greater destruction from flooding events, suggesting that low genetic diversity populations would be positively correlated with declines linked to sea level rise. However, similar experiments have yet to be conducted with more complex ecological systems to better evaluate how genetic diversity and species evolution impact ecosystem functioning, especially in non-equilibrium conditions caused by strong climate forcing (Lavergne et al., 2010).

1.3 Methods for climate change studies

1.3.1. Experimental climate manipulation

Global-change variables are difficult to manipulate, especially *in situ*, due to their temporal and spatial scale of interaction with local biota (Helmuth et al., 2006a; Wernberg et al., 2012). But, since global warming became a general concern, scientists have combined field and 'laboratory' experiments by using passive and active warming methods, in order to look at plant responses to a warming climate. Passive warming, is a method that actually slows down relative heat loss. This approach has inherent methodological issues (Aronson and McNulty, 2009). Passive night-time warming, can for example, involve an infrared (IR) reflective shade (curtain) covering the soil, but limit completely external precipitation. The system is also ineffective when there is little or no sunshine. A second example, the field chambers, including greenhouses, tents, and open-top chambers (OTC) (Arft et al., 1999). The use of greenhouses as a warming tool was criticised by Kennedy (1995) as they also form a barrier to precipitation and gas exchange and alter the intensity and distribution of incident radiation. OTCs were used intensively in the 1980s and 1990s, mostly for polar and altitudinal studies, and appeared to simulate more realistic warming summer scenarios compared to the closed and ventilated chambers (Bokhost et al., 2011). This relatively cheap method also allows warming during both day and night; however, temperature cannot be controlled precisely and varies greatly. Similarly, the amount of light and precipitation entering the OTC can vary (Bokhost et al., 2011), according to size, shape, and opening diameter (Marion et al., 1997). Although passive warming systems are adequate for fieldwork in remote areas without access to electricity, they are ineffective when challenged by extreme climatic events (Arft et al., 1999). Although OTCs are probably the most used warming method, they have not always successfully changed abiotic parameters (Musil et al., 2009).

Active warming methods apply an external source of heat to the soil and vegetation. Although those techniques provide direct temperature control, they are costly, demand constant management, and are impracticable in remote areas (Aronson and McNulty, 2009). The most common active warming systems are heating cables and infra-red (IR) lamps. Overhead IR lamps/heaters requiring high-energy flow (Bokhorst et al., 2008) and active management to maintain a constant temperature (Aronson and McNulty, 2009). Canopy height and dense ground cover can also inhibit soil surface warming. Heating cables can be placed above (Grime et al., 2008) or buried in (Schindlbacher et al., 2011) the soil. In both cases, flora and fauna can be highly impacted and disturbed by the direct heat conductance, but the main advantage of this method is the ability to keep the soil in an almost constant temperature.

Due to the biophysical properties of the water, the logistic and cost of underwater environment access intensify the difficulties in undergoing warming manipulation experiment in the marine environment (Wernberg et al., 2012). Manipulation of the substrate temperature on the rocky shore has been recently done by using black and white plates from the same material, in order to look at barnacle recruitment and grazer abundance (Kordas et al., 2015; Lathlean et al., 2017). Mesocosms, experimental enclosures from one to several thousands of litres, in which multiple physical and chemical parameters can be manipulated, are becoming increasingly popular in climate-change research in aquatic ecosystems, as they bridge gaps between small-scale, less realistic microcosm experiments, and large-scale, more complex, natural systems (Stewart et al., 2013; Falkenberg et al., 2016; Guy-Haim et al., 2017).

1.3.2 Natural laboratories

Laboratory experiments often look at individual species responses according to a highly controlled, but limited number of abiotic parameters, which decrease their realism (Wernberg et al., 2012; Parmesan and Hanley, 2015). There is no doubt that these experiments provide valuable information, but the lack of inclusion of biotic interactions, equally important as abiotic factors, can lead to incorrect predictions. Field research focuses more on species interactions within more natural ecosystems, taking into account natural variation in abiotic and biotic factors. Nevertheless, field experiments often fail to manipulate a realistic range of climate-linked scenarios as they rarely look at multi-factor changes in parameters linked to ACC.

Most community-level studies on the impact of ACC-linked warming on ecosystem interactions and processes have focussed on (mainly terrestrial) plants. To date, very few marine and intertidal field-based experiments have considered the impact of climate change on a whole ecosystem, due to the difficulties in controlling the climate change factors *in situ*. Other approaches requiring no abiotic manipulations at all can be, however, a good alternative. Wernberg et al. (2012) described three of them, the ‘opportunistic and natural experiments’, the ‘comparative experiments, and the ‘mensurative experiments’. The ‘opportunistic and natural experiments’, can rarely been planned and are therefore not a reliable tool to climate change studies. For example, Schiel et al. (2004) have surveyed the intertidal and subtidal environments before and after the implantation of a power-generating station, which resulted in a 3.5°C increase of the seawater of the local bay. In contrast, the ‘comparative experiments’, where identical manipulations or samplings are carried out in different places and characterised by a different climate are especially useful. For example, Wernberg et al. (2010) took advantage of over a latitudinal gradient in the SW Australia where a large temperature gradient (2-4°C) was associated with a small variation in light, nutrient level, grazing pressure. Consequently, these authors were able to study the performance of kelp species in a warming ocean climate. Fernández (2016) investigated the multidecadal change in the distributional limit of cold and warm temperate seaweed on the northern coast of Spain. The change in sea surface temperature, due to upwelling, was used as the main explanation of changes in biogeography and assemblage composition. A number of authors have tested the effect of temperature on intertidal patterns by sampling around the Icelandic coast, where warmer Atlantic water and cooler Arctic influences create a temperature gradient of 5°C (Ingólfsson, 1996; Espinosa and Guerra-García, 2005). Finally, ‘mensurative experiments’ *in situ* provide only variable(s) or treatment(s), which vary in space or time. Hall-Spencer et al. (2008), for example, studied the effect of the ocean acidification on the benthic ecosystems, at shallow local sites where volcanic CO_2 vents lowered the local seawater pH.

Observations and experiments conducted within sites that offer north- and south-facing aspects might also offer a solution to this lack of *in situ* studies. Although climate factors like temperature, humidity and soil moisture vary with aspect, other anthropogenic stressors (e.g. elevated CO_2, N-deposition) and impacts (grazing, disturbance) are likely to be held relatively constant over a short geographical range. A further advantage is that the impact of ACC-relevant temperature scenarios on species ecophysiology and community interactions can be investigated without the need to use any of the manipulative methods described in the above section 1.4.1. In addition, a combination of experimental sites that utilise local variation in aspect can in theory, extend across broad latitudinal ranges to determine how a series of climate scenarios affects species performance and ecosystem processes.

1.4 Aspect

1.4.1 Aspect and microclimate

Slope inclination and orientation (aspect) modify the amount of solar radiation received by the surface; up to 700 Wm^{-2} more on south- than north-facing slopes during a clear summer day in England (Bennie et al., 2008), and in combination with differences in wind direction (Cantlon, 1953) and speed (McCutchan and Fox 1996), determine local microclimate (Geiger, 1995). The amount of incident radiant energy is probably the most important abiotic parameter in species responses to climatic conditions, as it directly affects the ambient temperature (Davies et al., 2006), moisture (i.e. in terrestrial ecosystems, Begun et al., 2010), and desiccation (i.e. in intertidal ecosystem). This is why, when attempting to predict species distribution under ACC scenarios, one major approach is to model slope and aspect in terms of solar radiation measurements (Bennie et al., 2008).

In their review, Guan et al. (2013) considered studies where slopes and aspect were used as a tool in models to predict air temperature on land, as terrain slope and aspect contributed significantly to interpreting the minimal (T_{min}) and maximal (T_{max}) temperatures. In the mid-latitudes of the Northern Hemisphere, northward (pole)-facing slopes are consistently colder than the southern (equator)-facing slopes at the same elevation, and this temperature difference is less pronounced in locations closer to the equator. Rorison et al. (1986) for instance, reported a 2.5-3°C annual mean temperature difference between adjacent north-and south-facing slopes in British calcareous grassland. Moderate topographic variation could also produce significant gradients in soil moisture (Chen et al., 1993; Chu et al., 2016) and near surface air (Bennie et al., 2008) and soil temperature (Cantlon, 1953; Begun et al., 2010) between north- and south-facing aspects. Soil moisture (Begun et al., 2010; Chu et al., 2016), pH (Rech et al., 2001; Sariyildiz et al., 2005; Sidari et al., 2008), litter decomposition processes (Mudrick et al., 1994; Sidari et al., 2008; Begun et al., 2010; Chu et al., 2016), and texture (Sidari et al., 2008; Måren et al., 2015) also vary according to aspect and slope angle (Cantlon, 1953; Carter and Ciolkosz, 1991), with a direct impact on soil fauna as well as plants.

Local variation in aspect and slope in land can create temperature differences higher than those associated with regional variation in elevation and latitude (Figure 1.5; Natural England Report, 2014). Ectotherms are sensitive to climatic factors such as solar radiation, substratum and air temperatures, as those climatic factors drive their own body temperature (Denny and Gaines, 2007). Using robolimpets as a surrogate for limpet body temperature on rocky shores, Seabra et al. (2015) even demonstrated that thermal differences between sun-exposed and shaded micro-habitats were higher than those experienced among seasons, latitudes, and shore levels.

Topography and slopes influence greatly the amount and time organisms and their environment are exposed to solar radiation (Bennie et al., 2008), and thus local temperatures (Geiger, 1995), desiccation and moisture level. Ultraviolet-B (UV-B) radiation (280-320 nm) is a natural environmental stimulus for plants (Biever and Gadner, 2016). An increase of UV-B impacts plant reproduction by producing smaller flowers with shorter reproductive organs, a reduction in the amount and quality of pollen (Koti et al., 2004), and both reduced germination (Feng et al., 2000) and plant growth (Feng et al., 2003; Bernal et al., 2015). These changes have been associated with diminished photosynthetic and transpiration rates, water use efficiency, and changes in pigment concentration (Feng et al., 2003). UV-B radiation enhancement in algae has been associated with chemical composition change, believed to be a screen against harmful UV radiations (Pavia et al., 1997) that cause damage to cellular DNA (Biever and Gardner, 2016).

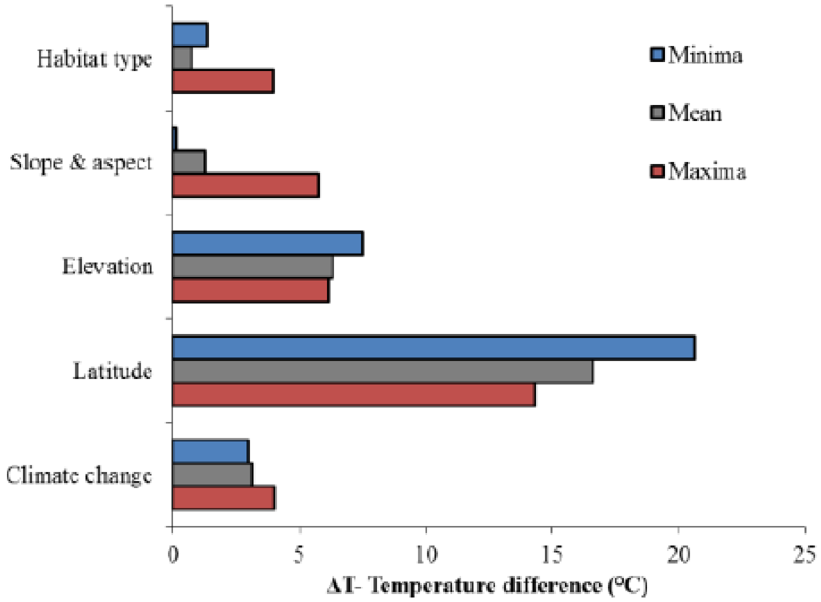

Figure. 1.5: The degree of variability in mean (grey), minimum (blue) and maximum (red) temperatures that habitat type (open and closed habitats), slope & aspect (north- and south- facing slopes), elevation and latitude provide. These temperature differences were compared with climate change predictions derived from ensemble mean projections conducted at 50 km resolution by the Prudence project, for 2100 relative to 2000 levels. Figure gathered and published by Natural England Report (2014).

Although many experiments have examined the impact of light exposure on terrestrial plants (reviewed by Bornman and Teramura, 1993; Caldwell et al., 1998), seaweeds and plankton (reviewed by Häder et al., 2003), few have considered animal responses. Shade is an important factor dictating the recruitment of many intertidal invertebrates and has a direct impact on patterns of within-shore species distribution (Blockey and Chapman, 2006). Exposure to UV-B for example, has a negative impact on molluscan embryo mortality (Przeslawski et al., 2004), energy balance (i.e. slower accumulation of body mass: Pulgar et al., 2017; increase of prey detection and capture time: Valiñas and Helbling, 2016), and for fish, respiratory frequency (Valiñas and Helbling, 2016), and active shelter selection (Pulgar et al., 2017). Interestingly, on land, UV-B exerts a positive influence on caterpillar growth rate (McCloud and Berebaum, 1999).

Trophic interactions are also impacted by UV-B-induced changes. Herbivory can increase (Ballaré et al., 2011; Pavia et al, 1997) when plant chemical composition alters as result of changes in incident UV radiations (but see McCloud and Berebaum, 1999), although, impacts depend on the identity of the herbivore and its adaptation to both the enhanced ambient UV radiations, and tolerance to chemical defences in the primary producers (McCloud and Berebaum, 1999). Similarly, the changes in leaf secondary metabolite profiles induced by light exposure can for some plant species, be transferred to the litter, affecting decomposition, carbon dynamics and as a result, the microbial soil community (Ballaré et al., 2011; Jones et al., 2016).

1.4.2 Facilitation of range shifts and refugia

In marine and intertidal environments, artificial structures such as seawalls and sea defences offer many more vertical surfaces than most surrounding natural habitats. The construction of these structures has however, been closely associated with the spread of non-native species (Bracewell et al., 2012) and, in particular, may represent stepping-stones for Lusitanian (southern distribution) warm water species trying to expand their range poleward. Alternatively, pole-facing slopes (and for natural shores, their more complex topography) may provide refugia for boreal (northern-distribution) cold water species to persist in suitable microclimates, where regional climatic conditions become less suitable (Bennie et al., 2008; Lima et al., 2016).

The term ‘refugia’ was first introduced to refer to locations where species survived the last glacial period, and is now increasingly used to refer to areas that should be conserved to limit the impacts of rising global temperatures in the 21st century (Aschcroft, 2010). Lusitanian species usually contract their distributions to refugia during glacial periods, while boreal species would usually restrict to refugia during interglacial periods (Stewart et al., 2010). Therefore, in the context of the ongoing ACC, boreal species, or species that prefer cooler conditions are of most immediate concern as they are currently restricted to interglacial refugia and face increased threat with further rising in global temperature (Ashcroft, 2010). Over the last decades, different definitions of ‘refugia’ have evolved, depending on the area of research (ecology, paleontology, genetic, etc.), and the type of refugia we are referring to: glacial or inter-glacial. In this thesis, I will use the definition given by Keppel et al. (2012), where refugia are defined as habitats allowing organisms to persist in and potentially expand from under changing environmental conditions; they are known to have facilitated the persistence of components of biodiversity over millennia and under climate change. On land, this is the case of the butterfly *Heseria comma* which has used south-facing slopes in Britain, to allow colonisation of new habitat patches on their northern margin limit over at least a period of 20 years (Thomas et al., 2001).

Species reaching the end of their distributional range will tend to find themselves on slopes facing the centre of their range (Huggett, 2004). In other words, in the Northern hemisphere, south-facing slopes tend to be more suitable habitats for species with a southern distribution, and north-facing slopes for species with a northern distribution (Stoutjesdijk and Barkman, 2014). For example, the wild strawberry (*Fragaria vesca*), commonly found in low level areas and gentle slopes in temperate Europe, at its leading range edge (poleward) in northern Norway tends to be restricted to south-facing, while at its trailing range edge (equatorial) in the Mediterranean lowlands, it occurs mainly on north-facing slopes (Stoutjesdijk and Barkman, 2014).

1.4.3 Observed distribution patterns according to aspect

Slope orientation strongly influences meso- (tens to hundreds of kilometres) to micro-climatic (less than 0.1 km) conditions by changing many environmental factors. As such, it is a potential cause of biodiversity change (i.e., loss of species and invasion of new ones, Åström et al., 2007). Biotic factors such as food availability, competition and predation can however, also play an important role in species abundance and distribution patterns. A marked contrast between vegetation types occurring on the equator-facing and polar-facing slopes has been observed in most continents and terrestrial ecosystems (see next paragraph). In order to avoid confusion with studies undertaken in the Southern hemisphere, the terms 'polar-facing' (p-f) and equatorial-facing' (e-f) will be used thereafter instead of 'north-facing' and 'south-facing', respectively.

In general, because of drier (xeric) and warmer nature, e-f slopes allow greater abundance and / or species richness of xeromorphic species (adapted to environments with little liquid water such as a desert or an ice- or snow-covered region). This general pattern has been shown for shrubs (Badano et al., 2005; Måren et al., 2015), evergreen species (Armesto and Martínez, 1978), cacti (Badano et al., 2005), and herbaceous species (Andrés et al., 1996). Other plant taxonomic and functional groups, such as trees (Cantlon, 1953; Badano et al., 2005), bryophytes (Cantlon, 1953; Åström et al., 2007), ferns and sedges (Cantlon, 1953), and mature plants are more common on the cooler and moister p-f slopes. Seedling recruitment may also be higher on these slopes (Cantlon, 1953; Måren et al., 2015). Although there are some notable departures from these general patterns, this may reflect local variation in land use practices (Bochet and Garcia-Fayos, 2004; Bennie et al., 2006) and regional climate (Cantlon, 1953; Andrés et al., 1996). Lichens are probably the group displaying the biggest variation of distribution according to aspect (Watson, 1960; Chu et al., 2000; Hauck et al., 2007). This might be due to the level of adaptation to light, temperature and water stress of their symbiont, which can change from one species to another. For example, Hauck et al. (2007) found that chlorolichens, lichens being equipped of a protection against high solar irradiation, were present on both p- and e-f surfaces, while the species without this adaptation were restricted to the cooler and moister aspect. Although soil fauna abundance and diversity is affected by slope aspect (Mudrick et al., 1994; Sidari et al., 2008; Begum et al., 2010; Chu et al., 2016;), such variations have also been explained by the above vegetation type, as well as the soil chemistry (Chu et al., 2016).

The comparison of e- and p-f slope has been actively studied at Lower Nahal Oren, Mount Carmel in Israel, since 1991, start of the 'Evolution Canyon' project, initially designed in the attempt to analyse genotype and phenotype divergences of organisms in response to sharp abiotic and biotic factors over a small geographic distance (Nevo, 1995). This location consists of a microsite displaying the biotic meeting of three continents: xeric elements from Africa and Asia, primarily on the e-f slope, and European element on the p-f one (Nevo, 1995). Although both slopes are separated by only 200 m (at bottom) and 500 m (at top) (Figure 1.6; Nevo, 1995), the e-f slope received up to 800% more solar radiation than the p-f one, and therefore experienced greater temperature and drought (Nevo, 2012). The drier e-f slope is dominated by grass and African-Asia biota, while more European woody plants, water-dependent cryptogamic plants and fungi dominate the shadier and humid p-f one (Figure 1.6). Major plant and animal taxa are also greatly impacted by aspect. (Nevo, 1995). Figure 1.7

illustrates taxa with higher (underlined in blue), similar (underlined in green) and lower (underlined in red) species richness on the p-f than e-f slope.

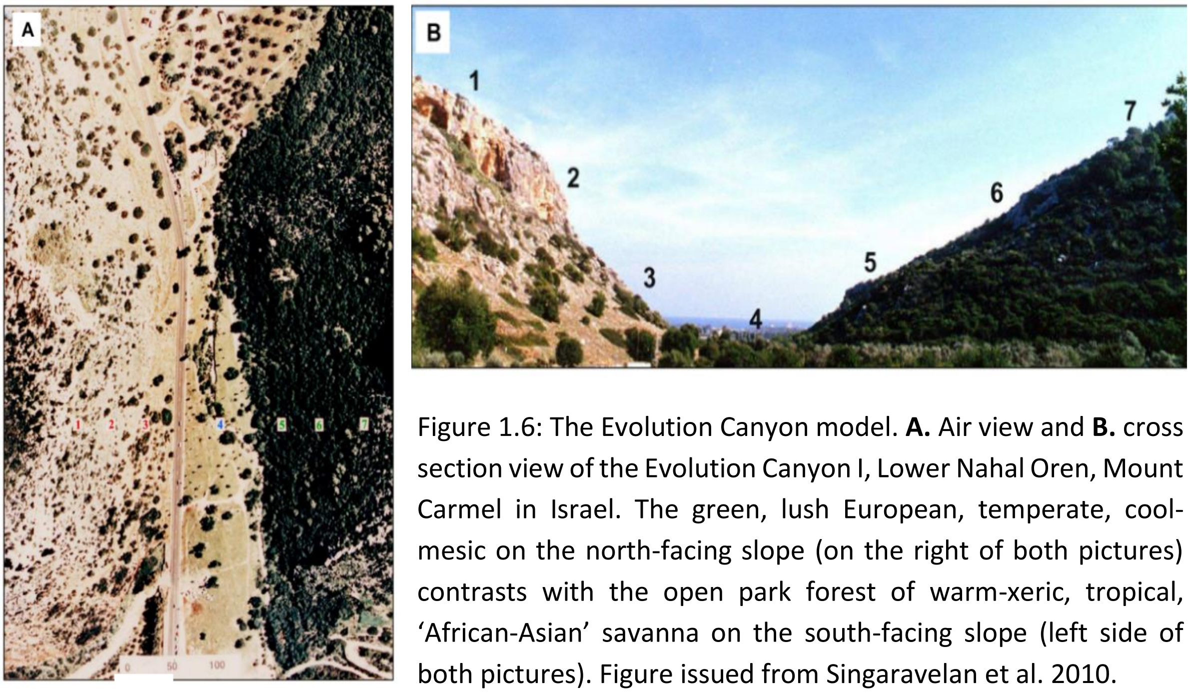

Figure 1.6: The Evolution Canyon model. **A.** Air view and **B.** cross section view of the Evolution Canyon I, Lower Nahal Oren, Mount Carmel in Israel. The green, lush European, temperate, cool-mesic on the north-facing slope (on the right of both pictures) contrasts with the open park forest of warm-xeric, tropical, 'African-Asian' savanna on the south-facing slope (left side of both pictures). Figure issued from Singaravelan et al. 2010.

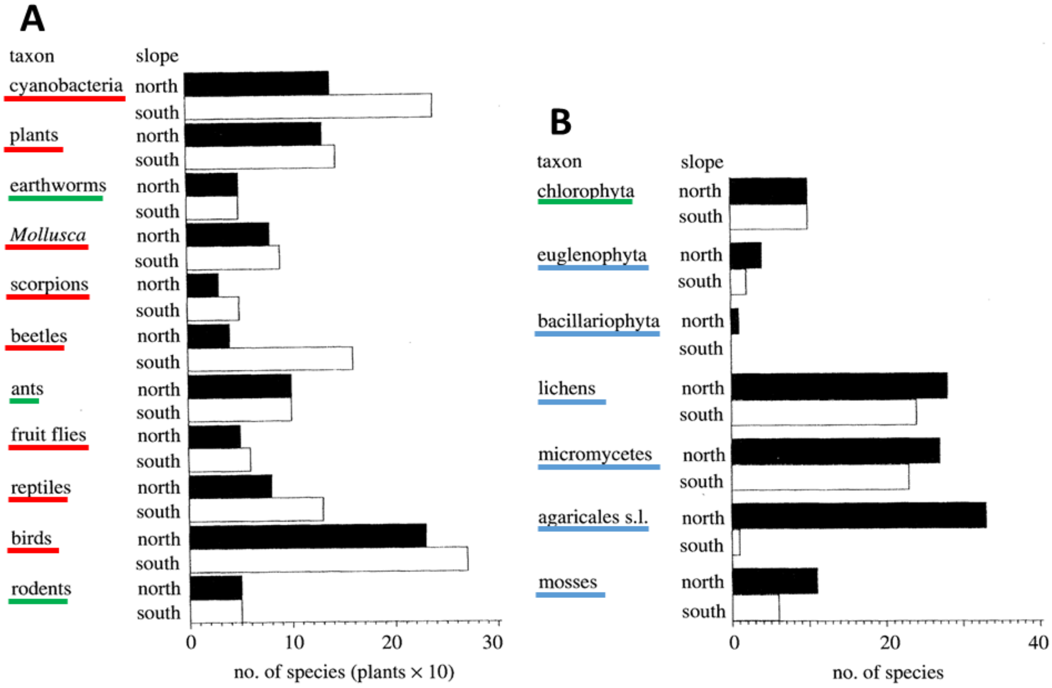

Figure 1.7: Species richness of major plant and animal taxa **A.** cyanobacteria, angiosperm plants and animals, and **B.** cryptogamic plants and fungi, on opposite north- (black) and south-facing (white) slopes at 'Evolution Canyon' in Israel. The polar-facing (black) and equatorial-facing (white) slopes represent, respectively, the estimates of the 'European' and 'African-Asia' biota. Taxa names were underlined in blue, green, or red when species richness was, respectively, higher, similar, or lower on the north- than south-facing slope (Figure from Nevo, 1995)

In mountainous systems, along an altitudinal gradient, similar plant communities can be found at different elevations according to which aspect they are growing on (Mark et al., 2001; Stoutjedijk and Barkman, 2014). For instance, spectacular vegetation differences were found between the p- and e- f aspect of a 50 cm wide ridge on an 800 m high Lägern mountain, near Baden in the Swiss Jura (Stoutjedijk and Barkman, 2014). The cold p-f aspect supported beech (*Fagus sylvatica*) forest with sub-alpine plants such as alpine penny-cress (*Thlaspi alpestre*) and green spleenwort (*Asplenium viride*). The flora of the warmer e-f slope by contrast was dominated by oak (*Quercus pubescens*) woodland and included southern elements such as pale-flowered orchid (*Orchis pallens*), wonder violet (*Viola mirabilis*) and bastard balm (*Melittis melissophylum*). Most notably, the contrast on either side of the ridge was equivalent to an altitudinal difference of 1 km, and a latitudinal difference of 1,000 km (Stoutjedijk and Barkman, 2014).

Aspect-linked variation in plant distribution and abundance patterns are well known, but less attention has focussed on terrestrial animals and marine organisms, probably due to the complexity of studying mobile organisms and the accessibility of some sites (i.e., rocky shores). Looking at sessile intertidal organisms, Wethey (1983) noticed that the zonational distribution of barnacles, on the east coast of North America, was impacted by slope and aspect on the shore. *Chthamalus* zone was narrower on vertical surfaces compared to horizontal ones or gentle slopes. Its zonation was also wider on the e-f than p-f surfaces. Looking at the entire intertidal community, Firth et al. (2016) reported greater taxon richness and abundance of all taxa on the mid-shore, but gastropods and filter feeders on the high shore were more abundant on p-f than e-f surfaces in both natural and artificial habitats.

Boreal and ubiquitous groups also exhibited a general preference for p- rather than e-facing surfaces.

The segregation of organisms at smaller spatial scales (micro-climate and micro-habitat), such as slope aspect, often enables coexistence at larger spatial scales, thus enhancing biodiversity at any given scale (Firth and Crowe, 2010). It is important therefore, to note that any difference in distribution pattern is not necessary related to the surrounding microclimate. Different theories would suggest that this is a result of environmental tolerance (Nakamura, 1976), interspecific competition for common resource (Schoener, 1974; Wethey, 1983), differential predation (Underwood and Jernakoff, 1981), or habitat heterogeneity (Schroder and Rosenzweig, 1975).

1.4.4 Ecological processes and aspect

Although field observations have focussed on the aspect-related distribution pattern of plants, and to lesser extent animals, less attention has been drawn towards the physiological mechanisms and ecological interactions, which might also underpin this variation. Some authors (Yom-Tom, 1972; Davies et al., 2006; Cadenas et al., 2007) showed that the aspect-linked variations of some terrestrial animals' abundance and diversity were solely temperature dependant, but others explained variations in terms of food availability (Oosenbrug and Theberge, 1980), predator pressure (Yom-Tom, 1972), or shelter availability (Yom-Tom, 1972). With aspect-related variations in species distribution patterns, ecological processes such as predation, grazing, decomposition, competition, are also predicted to vary.

In Polar Regions for example, changes in grazing activity, quality of the forage (higher quality on p-f slopes at higher altitudes), and timing of snow melt that extended the period of access to newly emergent plants with higher digestibility were associated with aspect. (Mysterud et al., 2001). In addition, those authors demonstrated that the body weight of red deer was correlated with the diversity of aspects. In intertidal ecosystems, grazing activity of marine gastropods also varies with aspect. Using wax discs, Firth et al. (2016) estimated grazing intensity of limpets on a British rocky shore, and found a significantly greater grazing activity on the e- than p-f surfaces. There is clear evidence that grazing activity is positively related with the variable topography, offering a shift in plant abundance, diversity and quality, and phenology.

1.4.5 Physiology, phenology and aspect

Using chlorophyll fluorescence in leaves as indicator of physiological status, Bellot et al. (2003) demonstrated that three woody species (*Quercus coccifera*, *Pistacia lentiscus* and *Pinus halepensis*) from a semi-arid Mediterranean shrubland in SE Spain were less stressed on p-f slopes than on e-f slopes. In Norway, the crude protein content of graminoids and herbs is highest in spring, after the snowmelt, and exponentially decreases in time during the summer (Albon and Langvatn, 1992). Slope aspect may play an important role in plant development and quality. Mysterud et al. (2001) suggested that delayed snowmelt and lower temperature on p-f slopes, tend to retard plant development, and enhance their digestibility with higher protein content.

Although phenological responses vary between species in the same location (Cantlon, 1953; Weiss et al., 1988; Mudrick et al., 1994), a general trend has been observed in relation to aspect. Earlier dormancy break (e.g. first buds and stems, Cantlon, 1953), enhanced flowering in late summer (Cantlon, 1953), faster spring growth (Endresz et al., 2005), greater annual growth (lichens: Armstron and Smith, 1993; trees: Cantlon, 1953), susceptibility to drought (leaf fall: Cantlon, 1953; shoot die back: Endresz et al., 2005), are reported on e-f slopes. The general pattern of enhanced growth on e-f slopes may result from higher light radiation and therefore elevated photosynthesis. During the winter, it appears that p-f slopes can become less favourable to organisms (e.g. too cold and more frost-days). For instance, in a north-eastern American mountain, several perennial plants such as *Galium trifolium* and *Solidago caesia*, produce new leaves and stems on e-f slopes, while grasses and sedges show leaf elongation throughout the winter (Cantlon, 1953).

For animals, body temperature of intertidal and terrestrial invertebrates is generally higher on e-f slopes or sun-exposed habitats, with concomitant impacts on ecological processes (Weiss et al., 1988; Seabra et al., 2011). Ecological processes are however, not only driven by climatic and physiological tolerances. Yom-Tom (1972) demonstrated for example that the reproduction of two desert snails was also dependant on adult population density. With almost double the population on p-f slopes, adults had higher fecundity on the e-f slope. However, eggs and juvenile mortality was much higher on those slopes, likely due the high temperatures experienced.

Decomposition is a key ecological process as it is central to terrestrial ecosystem functioning by mineralizing nutrients from plant material, and by providing organic and inorganic elements to roots and other organisms (Mudrick et al., 1994; Newsham et al., 1999). Decomposition is significantly more rapid on p-f slopes (Mudrick et al., 1994; Sariyildiz et al., 2005), probably due to the greater moisture. Mudrick et al. (1994) report that in the Appalachian forest (east USA), the decomposition of the leaves from the yellow-poplar, a tree species dominating p-f slopes, was highest during the 11 months of the survey in the p-f slopes. By contrast, the chestnut oak, a species dominating e-f slopes, had the lowest leaf decomposition of the three species studied, and did not show significant difference with aspect (Mudrick et al., 1994).

1.5 Study rationales and aims

The overarching aim of this thesis is to determine how aspect, or slope orientation, affects species distribution patterns and ecological processes in both terrestrial and intertidal habitats. In the current urgency to better understand the importance of climate on species biology, physiology and interactions, there is a growing need for experiments taking into account natural variation in both abiotic and biotic factors (Wernberg et al., 2012; De Frenne et al., 2013). Slope aspect is widely used as a model system to investigate the effet of temperature (and moisture) on species distribution. Despite their scale, mountains are the most studied system when investigating aspect, but this should be taken with caution. Indeed, when comparing within the same mountain, slopes separated from hundreds of meters, would likely show environmental (e.g. geology), weather (e.g. rainfall) and land use variations, due to their large scale, which may be difficult to differentiate from aspect variations. To date, only few studies tested the impact of aspect, at very small scales, on communities instead of selected species, and this is especially the case in intertidal ecosystems. To cover the knowledge gaps cited above, I first undertook detailed spatio-temporal surveys in order to have a broader picture of the impact of aspect on species distribution and richness (at community, taxonomic and functional groups, biogeography origin, and species levels) on both terrestrial and intertidal ecosystems. Then, components of physiology in marine molluscs, as well as a key ecological processes were investigated according to aspect.

In Chapter 2, I first determined the temperature difference according to aspect (north- and south- facing) on the rocky shore, and then investigated the relative abundance and richness of intertidal organisms according to aspect. This detailed spatio-temporal survey is important in the way that it can inform us on variations from species to communities, mainly due to direct and indirect effects of temperature at a very small-scale. In Chapter 3, I tested whether potential variations in phenology (e.g. gonad development) and physiology (e.g. osmotic regulation) of the limpets between aspects could explain their different distribution on both north- and south-facing substrata demonstrated in the previous chapter. First, I investigated inter-species variations according to aspect. Indeed, as the Lusitanian limpet *P. depressa* was more abundant that the boreal *P. vulgata*, especially on the south-facing aspect where its abundance was two-fold, I expected *P. depressa* to experience less osmotic stress than its congener which could give an advantage in colonising the warmer south-facing substrata. In parallel to Chapter 2, Chapter 4 examines the distribution of terrestrial plants on hedgerows. Hedgerows are important because of their landscape, archaeological, conservation, cultural and agricultural significance (Bickmore, 2002). Despite their high diversity and their ideal structure forming a tall wall of vegetation, only a handful of studies looked at the impact of aspect on those habitats (e.g. Downeswell, 1987; Merckx and Berwaerts, 2010). Species distribution patterns are likely not only to reflect inherent ecophysiological limitations but also be a consequence of ecological interactions. On land, due to the constant inter-connection between the above and belowground habitats, I decided in Chapter 5, to survey distribution patterns in soil mesofauna and investigate litter decomposition, key ecological process, according to aspect. This thesis ends with a general conclusion and reflection as the final chapter (Chapter 6).

Chapter 2: Impact of aspect on distribution pattern and biodiversity in the intertidal

2.1. Introduction

As reviewed in Chapter 1, many ecosystems are being impacted by rising temperatures and more frequent extreme climatic events linked to antropogenic climate change (ACC). For example, extreme cold snaps or heatwave events are known to cause mass mortality in terrestrial (Healey, 1967; Morignat et al., 2014) and marine (Crisp, 1964b; Tsuchiya, 1983; Garrabou et al., 2009; Reusch et al., 2005; Firth et al., 2011) systems, which can sometimes facilitate biological invasion (Steiner et al., 2010). Thermal tolerance and acclimation to climate and extreme climatic conditions determine the range distributions of species (Wethey, 2002). Species survival relies on how organisms track climate shifts and their ability to adapt to and/or disperse into newly suitable habitats (Loarie et al., 2009; Urban, 2015). The first study to show that climate change-induces range shifts (Parmesan, 1996) demonstrated that populations of Edith's checkerspot butterfly (*Euphydryas editha*) extended northwards, at their leading edge, and that extinction rate (decreasing with altitude) was linked to climate. Since then, refugia (i.e. habitats allowing organisms to persist in and potentially expand from under changing environmental conditions) drew increased attention, and studies on those thermal refuges have proliferated, especially in terrestrial ecosystems (Keppel et al., 2012; Morelli et al., 2016). Range contraction at trailing range edges occur when physiological thresholds are exceeded as environmental temperature increases (e.g. Wethey et al., 2011). In the case of extremely cold winters, where species do not have time to acclimate or find refuge, mass mortality is often unavoidable. As a result of the severely cold winter 1962-63 for example, Europe's coasts suffered extensive mortality of several ecologically dominant "ecosystem engineer" species such as limpet *Patella vulgata*, the reef building polychaete *Sabellaria alveolata*, and mussel *Mytilus edulis* (Crisp, 1964a). Such local or regional extinction could have a dramatic impact on the whole intertidal community assemblage and community functioning. Disappearance of local species, as well as ongoing warming, can also favour non-native species extension or invasion (e.g. Steiner et al., 2010), which, in turn, could also change population dynamics (Pessarrodona et al., 2018).

Extreme events are particularly stressful for sessile organisms or with limited mobility (Mislan and Wethey, 2015). The problem is greater in intertidal habitats where marine animals and algae, already live at their physiological thermal limits (Helmuth et al., 2006a, 2010; Hofmann and Todgham, 2010; Somero, 2010; Chapperon et al., 2017) and are exposed to drastic changes twice-daily in physico-chemical conditions, and especially when low tides occur during the hottest (or coldest) part of the day. By consequence, intertidal organisms have long been considered as indicators of climate change (see Southward et al., 1995; Hawkins et al., 2009; Mieszkowska et al., 2014; for reviews). The responses of marine and coastal organisms to the physical and chemical stressors associated with anthropogenic climate change (ACC) are particularly well studied across a range of levels. These include (i) molecular and cellular processes (leading to acclimation and evolution); (ii) organismal responses (physiology, phenology and behaviour); (iii) population change (demography, reproduction, and competition) and (iv) community level (species interactions) (see reviews by Harley et al., 2006; Kordas et al., 2011; Harvey et al., 2014). Marine ectotherms are known to have their thermal tolerance windows roughly matching ambient temperature variability (Poloczanska et al., 2016). Temperature has a fundamental effect on biological processes simply by its influence on molecular kinetic energy and transcriptional changes, critical in thermal acclimation (Somero, 2005, 2010). This would interact together with levels (i) to (iv) listed above, and impact species biogeography. Shifts in range distribution are probably the most observed responses to ACC in the marine environment over recent decades (reviewed by Poloczanska et al., 2013; Brown et al., 2016). Species distribution shifts are impacting ecological assemblages, and in particular, species abundance and biodiversity (Letcher, 2016; Hawkins et al., 2008), as well as ecosystem functioning (Pessarrodona et al., 2018). For example, an expected increase in grazer diversity with ACC might result in reduced primary production, decreasing the export of macroalgal detritus into coastal ecosystems (Hawkins et al., 2008). In addition, changes in phenology (timing of biological events such as breeding, migration) can have cascade effects within the food web, resulting in mismatch between prey-predator blooms (Philippart et al., 2003; Edwards and Richardson, 2004; Durant et al., 2007).

The biological importance and impact of rising temperatures differ however, between and even within intertidal species (Harley et al., 2006). Lusitanian (warm-water adapted) and boreal (cold-water adapted) species for example, react differently to thermal stresses associated with ACC (Firth et al., 2009; Somero, 2010). Warm-adapted species are most susceptible to local extinctions near their thermal maxima at their trailing range edge where their abilities to increase thermal tolerance through acclimation are limited (Somero, 2010). Similarly, cold-water species are more vulnerable to thermal minima reached at their leading range edge. Therefore, populations at range margins are assumed to be more stressed and sensitive to climate than those at the centre of range distribution, where individual fitness is highest and populations often have their highest density (Guo et al., 2005). However, Helmuth et al. (2002) demonstrated that temperature can be relatively constant over a species distribution (14° latitudinal range), and that synchrony of low tide with hottest air temperatures and wave actions had an important role in driving geographic patterns. Therefore, populations at range margins are not always guaranteed to be the most sensitive to ACC (Helmuth et al., 2002).

The British Isles are ideal location to study the response of biogeographic ranges of marine and intertidal organisms. This region supports many intertidal species with overlapping distributional limits; i.e. where boreal cold-water species with trailing range limits overlap with the leading range limit boundary of Lusitanian warm-water species (Forbes, 1858; Figure 2.1). Several Lusitanian species for example, have their northern limit in Wales, or their eastern limit in the English Channel along the south coast of England. This represents an excellent test system for investigating the impacts of ACC and extreme climate events on the structure and functioning of intertidal organisms (e.g. Hiscock et al., 2004; Mieszkowska et al., 2005; Mieszkowska et al., 2006; Firth et al., 2009; Oróstica Vega, 2018). Thanks to valuable long-term observations on sessile or sedentary rocky shore species (Southward and Crisp, 1954; Southward, 1967; Southward et al., 1995) it has been possible to detect the movement of several species as a consequence of ACC. The Lusitanian reef-forming polychaete *Sabellaria alveolata* has for example, recolonised locations from which it had previously disappeared as a result of very cold winters (Firth et al., 2015). The intertidal gastropods *Phorcus lineatus* (formerly *Osilinus lineatus)* and *Steromphala umbilicalis* (formerly *Gibbula umbilicalis*), both Lusitanian, have undergone north and north-eastern range extensions (Mieszkowska, et al., 2006). In addition to comparing shifts in species biogeography, historical field-based observations also allow us to model physiology, behaviour and geneticss of those same species and thus infer the likely future impact of ACC on species distributions (Hawkins et al., 2016b).

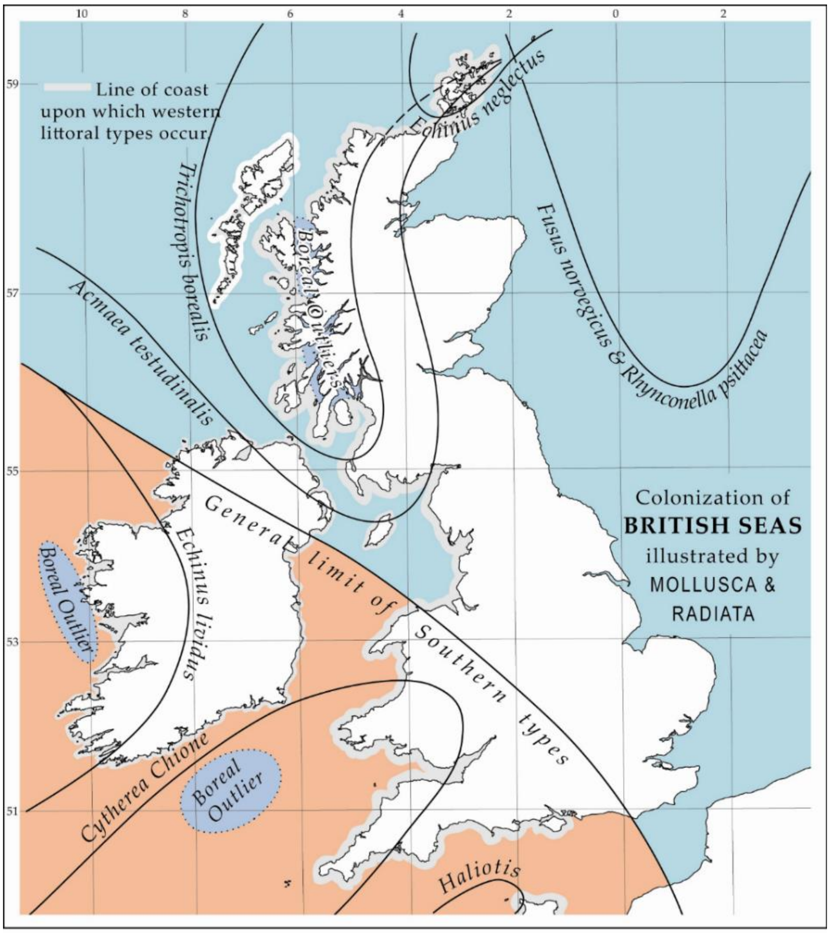

Figure 2.1: The biogeographical characteristics of the coast of the British Isles, including the range limits of some species. Figure adapted from Hiscock et al. (2004) and originally drawn by Forbes (1858). Anglesey is absent from the map as it was in the original publication. Note that many species names have changed since the original map was drawn.

In tandem with regional-scale latitudinal variation, the topography and configuration of individual shores can provide insights into how and why species distributions vary in response to the environment. Aspect may be important. At a regional scale for example, due to warm Atlantic influence from the S and SW, and the Arctic influence from the N and NE, the seawaters around Iceland experience a 5°C temperate gradient from the north to south coast (Espinosa and Guerra-García, 2005). This high temperature gradient across a relatively short North/South orientation, allowed several scientist to investigate the effect of temperature on intertidal patterns (Espinosa and Guerra-García, 2005; Ingólfsson, 1996). A general decrease of species richness and diversity towards the north was assumed to be linked to the temperature difference (Espinosa and Guerra-García, 2005), and a decrease in barnacles and mussels towards the south was associated to higher population of the predators *Carcinus maenas* and *Nucella lapillus*, both relatively southern species[1] (Ingólfsson, 1996). In both studies, a significant relationship was found between algal composition and macrofauna, suggesting that "bottom-up" regulation might be greater than "top-down" one (Ingólfsson, 1996).

At more local scales, rock surfaces on north (pole)-and south (equator)-facing slopes are also likely to vary greatly in terms of environmental conditions. In a study of 13 different locations along the Iberian Atlantic coast, Seabra et al. (2015) for example demonstrated that thermal differences between sun-exposed and shaded micro-habitats on rocky shores were higher than those experienced among seasons, latitudes, and shore levels. Pole-facing surfaces can be 10-15°C cooler than adjacent unshaded ones (Denny and Gaines, 2007) and crevices 12°C cooler than adjacent sun-exposed rock (Gray and Hodson, 2003). Such differences may place tremendous stress on intertidal organisms. In Australia for example, daily maximal body temperatures of the whelk *Dicathais orbita* was on average 3.18°C cooler in shallow rock pools than on horizontal rock (Lathlean et al., 2015).

With such locally variable environmental and organismal temperature differences, community structure and functioning might be expected to differ even at a small scale depending on aspect. Although the impact of aspect on species distributions is relatively well understood for terrestrial ecosystems, (e.g. Cantlon, 1953; Nevo, 1995; Åström et al., 2007; Ameztegui et al 2012; Gilliam et al., 2014; Chu et al., 2016), remarkably few studies however, consider the impact of aspect on local scale variation in species distribution and abundance

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[1] In Iceland, *Nucella lapillus* is considered a Lusitanian (warm water) species, while it is often referred as a boreal (cold water) species in more southerly locations in Europe.

in the rocky intertidal. Most of them moreover, focus on one taxa or taxonomic group only (e.g. barnacles, Wethey, 1983; lichens, Chu et al., 2000).

However, Firth et al. (2016) sampled entire intertidal communities in the UK and reported a general trend towards greater taxon richness and abundance on north- than south-facing substrata in both natural rocky shores and seawalls habitats. Species richness of filter feeders and gastropods were significantly higher on north- than south-facing substrata in high-shore. Both ubiquitous and boreal cold-water (e.g. the marine grazers *Patella vulgata* and *Littorina spp.*, and predator *Nucella lapillus*[2]*)* species were more abundant on north-facing substrata. Limpets are keystone grazers of the intertidal, *Patella depressa* and *P. vulgata* are both very common species in the mid-shore in Britain, with a Lusitanian and boreal distribution, respectively. Having its northern range limit in Wales (Hawkins, 2012), it was maybe not surprising that Firth et al. (2016) found *P. depressa* most frequently associated with the south-facing substrata in the SW of England. This is analogous to the butterfly *Hesperia comma* which was restricted to south- and south-west facing slopes at its northern geographical range, in southern England (Thomas et al., 2001). In addition to improving our understanding of species distribution in a climate change world, Firth et al. (2016), with their study of the rocky shore aspect, also highlighted the importance in understanding the potential effects on ecological processes. Those authors found that grazing activity was three times greater on south- than north-facing aspects. Limpet grazing was significantly greater on south- than the north-facing substrata, and even when corrected for the exact number of limpets present, grazing remained over twice as intense on the southern aspect. The described variations in intertidal community assemblages and grazing activity with aspect can however, only be assumed to be linked with temperature variation between aspects as the authors did not

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[2] In the UK, the marine gastropod *Nucella lapillus* is considered a boreal (cold water) species

measure temperature in their study. The study by Firth et al (2016) also focussed on a comparison of natural versus artificial surfaces and consequently, the sample size for north and south-facing natural sites was limited in number and sample season, while the second part of study conducted exclusively in natural rock gullies describes only variation in limpet abundance at a single site.

The aim of this Chapter is to investigate in how intertidal communities vary according to local changes in aspect across several shores and with season (summer *versus* winter). In addition, I consider different levels (community, functional, taxonomic and biogeographic groups, and species) and how temperature variation within those microclimates might also explain observed variation in species distribution. Given the geographic location in southwest England, species included boreal, Lusitanian and ubiquitous (widespread) species. Specifically I tested the following hypotheses:

(1) Temperature (averages and extremes) vary according to aspect, with higher temperature on south-facing aspect;

(2) Community assemblages, species richness and relative abundance (taxonomic and functional) varies with aspect;

(3) By virtue of expected higher temperatures, south facing slopes will support a greater proportion of Lusitanian compared to boreal or ubiquitous taxa (and with more boreal on north-facing);

2.2. Materials and methods

2.2.1 Model system

Four natural rocky shores located in the Southwest Peninsula of England were sampled: Bude, (N 50° 50' 12''W 4° 33' 25'') and Croyde (51°08’02’’N, 04°14’38’’W) on the N coast of Devon and Cornwall respectively. Bantham (50° 16' 37''N, 3° 53' 5''W) and South Milton Sands (N 50° 15' 14''W 3° 51' 43'') on the S coast of Devon (Figure 2.2A). Those four very exposed to moderately exposed rocky shores have similar biotope, described by Connor et al. (2003) as 'LR.HLR.MusB: mussel and/or barnacle communities', where eulittoral boulders are dominated by mussels *Mytilus edulis*, barnacles *Chthamalus spp.* and or *Semibalanus balanoides* and limpets *Patella spp*. Red algae as well as the red coralline algae often occupy damp cracks and crevices of rocks, which are also refuge for small molluscs (e.g., mussels, winkles and whelks). The lichen *Lichina pygmaea* may also be predominant, especially in the south of Britain.

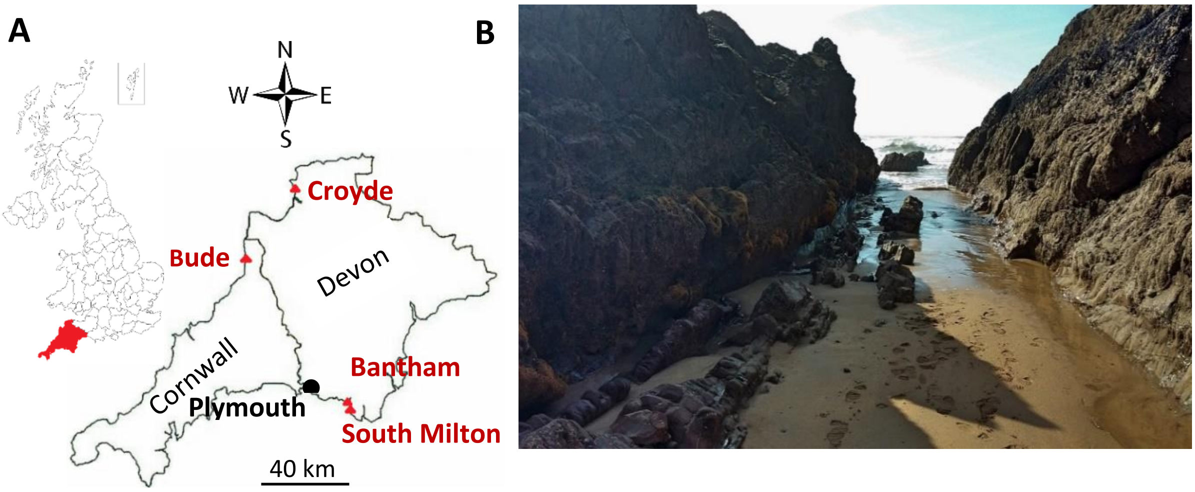

Figure 2.2: **A.** Location of the four natural rocky shores studied in the south west of England, UK. Bude and Croyde are on the west coast of England, while Bantham and South Milton Sands are on the south coast but still facing west. **B.** Tall vertical rocky gullies in Bude, England, perpendicular to the beach, offering a north- and south-facing aspect. Note the difference in shading between north-facing (shaded) and south-facing (sun-exposed) rock faces. Photograph taken on 30/03/2016 at 3:40 pm.

Local geology may influence local distribution and determine the broad character of the population (Lewis, 1964). Therefore, it is important to note that Croyde and Bude are on the same coast and strata, both sites consist of inter-bedded shales and sandstones, varying in age (Upper Devonian and Carboniferous, respectively) (British Geological Survey, 2017). Rock formations at Bantham and South Milton Sands were of similar age and composition (i.e. Devonian Meadfoot group – slate, siltstone and sandstone) (British Geological Survey, 2017). Connor et al. (2003) even described a variant of the LR.HLR.MusB biotope in locations with soft rocks (e.g. shales), such as both study sites on the south coast, where limpets dominate due to the absence or scarce abundance of barnacles.

The Atlantic north coast, as on the N coast of the SW Penincula of England, tends to be windier (in frequency and strength), and the seawater cooler than on the south coast, which is more protected by the English Channel (Plymouth Coastal Observatory). For example, in Perranporth (50°20.77’N, 05°09.71’W) on the north coast, the average air temperature and average wind speed from 2011 to 2017 were 11.3°C and 6.9 m/s respectively. The maximum wind speed recorded in 2018 was 32.7 m/s; and the minimum and maximum air temperature recorded on the same year was of -4.5°C and 25.5°C, respectively (Plymouth Coastal Observatory, 2019a). On the other hand, in Looe (50°20.70’N, 04°27.17’W) on the south coast, the average air temperature and average wind speed on the coast from 2010 to 2017 was of 14.7°C and 5.0 m/s, respectively. The maximum wind speed recorded in 2018 was 22.8 m/s; and the minimum and maximum air temperature recorded that same year was of -1.6°C and 30.1°C, respectively (Plymouth Coastal Observatory, 2019b).

Biological communities were compared at two spatial scales: small (metres apart within shores), and medium (~100 km apart between coasts). All locations were deliberately selected because shores were west-facing and with shales folded such that strata are tilted 80-90° (i.e. vertical dip) running perpendicular to the shoreline. Erosion of those sedimentary rocks has, thus, created several 1-5 m high, almost vertical gullies, offering at mid-shore height, paired north- and south-facing aspects separated by only a few metres (see pictures 2.2B). As this survey was conducted in the Northern Hemisphere, ‘south-facing’ will refer as the equator-facing, and the ‘north-facing’ as the polar-facing slopes. As wave-exposure is one driver shaping biogeography of intertidal organisms (Underwood and Jernakoff, 1984; Helmuth et al., 2006b; Wernberg and Connell, 2008), all the selected gullies were parallel to each other and perpendicular to the sea, so that wave action was similar across aspects and gullies.

Rocky shores are complex ecosystems with rocks from different textures and materials, slopes angles, aspect, presence of rock pooles and crevices. However, in this study, only one microhabitat will be sampled: vertical substrata. Vertical substrata are often thought to be harsh environment on the shore, as with little protection from various abiotic factors. However, when comparing vertical *versus* horizontal substrata in the NW Mediterranean rocky shores, Benedetti-Cecchi et al. (2000) found that limpet activity was similar on both inclinations, and that physical conditions were not found as stressful for macroalgae on vertical substrata as initially supposed. Instead, greater variations occurred from shore to shore. Featureless vertical habitats are known to support reduced local biodiversity (Chapman and Blockley, 2009), but greater diversity is still found on vertical substrata in natural rocky shores compared to artificial structures (e.g., seawalls) (Firth et al., 2016).

2.2.2 Field survey

Temperatures on north- and south-facing substrata

In line with the need for more local-scale studies for better species distribution predictions (Elith and Leathwick, 2009), there has been in the last decade a rapid expansion of the use of data loggers to record small scale environmental or organismal (through loggers mimicking body temperature) temperature variation in the rocky intertidal (see Judge et al., 2018 for review). Here, data loggers (iButtons DS 1921G#F5, Maxim Integrated, San Jose, CA, USA) were also deployed at the mid shore level (i.e. within the barnacle zone), to record (hourly for a full year) temperature variation on both the north- and south-facing sides of gullies. Prior to deployment, data loggers were waterproofed with plastic tool dip (Plasti Dip, Plasti Dip International, Blaine, MN, USA) following the method used by Roznik and Alford (2012) who reported that this significantly reduced failure probability and data loss. Although the accuracy of the temperature readings may be affected, this difference is lower than the manufacturer-specified accuracy of 1.0°C (Roznik and Alford, 2012). Data loggers were attached to a vertical rock surface with a marine epoxy (Veneziani Subcoat S (A + B), Nautimarket s. r. l., Carlino, Italy). Both the coated iButtons and the blue epoxy were sprayed with a waterproof matt grey paint to provide camouflage as much as possible and keep similar albedo of the natural rock. Three data loggers were attached on each side of two gullies per site (3 x 2 (aspect) x 2 (gullies) x 4 (sites); a total of 48 loggers). Deployment started in September 2016 for a full year of recording. However, due to a high number of data logger loss, from February, recording was suspended in all sites and resumed in June 2017 with new iButtons. This gap of five months in the dataset was filled by re-deploying new data loggers during the same period the following year in 2018.

Mean temperatures, as well as extremes (>30°C, >40°C, <0°C and <-10°C), were examined on both aspects. Data were obtained during low tide (LW, low water) and high tide (HW, high water) but in order to guarantee that extracted temperatures recorded during emersion and immersion, a window of 1 hour either side of the HW and LW, was selected. HW and LW were obtained using the Belfield software Tide Plotter (Version 5.8, Belfield software Ltd, 1997-2017, Portions Crown Copyright). It is, however, important to note that some (hot) extreme temperatures might be missed, if recorded by the data logger outside this 2-hour window during LW.

Biological sampling

All locations were sampled at LW, spring tides between June 2016 and January 2017. At each location, four gullies (figure 2.1B) were selected on condition that they offered north- and south-facing sides with surfaces as vertical as possible. Twelve 0.50 x 0.50 m quadrats were randomly positioned at similar shore height to the data loggers along each of the four gullies, such that samples on north- and south-facing slopes were opposite each other (i.e. six matched pairs of north/south quadrats positioned at the same relative shore height along each gully). This yielded a total of 192 quadrats across all four locations. All quadrats were placed on vertical, flat surfaces, avoiding crevices, pools and other microhabitat that may have affected surface area and topographic complexity within the quadrat. Any featureless vertical artificial structures have a reduced local intertidal biodiversity (Chapman and Blockey, 2009), therefore a similar pattern can already be expected on the selected and comparable micro-habitat on natural rocky shores.

In each quadrat, the following response variables were recorded (i) overall percentage cover of sessile organisms (lichens, algae barnacles, mussels, sponges and *Sabellaria* aggregations), (ii) abundance (per m^2) of mobile organisms (molluscs, crustaceans, worms, and anemones). The same survey was undertaken during both the summer and winter. Quadrats during the second sampling season (winter) were placed in the exact same place as during the first sampling season (summer), when possible.

In order to estimate barnacle diversity and abundance, four sub-samples per quadrat were collected using smaller quadrats (0.03 x 0.03 m). They were photographed and all barnacles later identified and counted using imageJ (Version 1.50, National Institute of Health, Bethesda, MD, USA). *Semibalanus balanoides* and both species of *Chthamalus* are the commonest intertidal barnacle species of the British Isles (Southward and Crisp, 1954) and in this biotope (Connor et al., 2003). As their breeding and settlement period occurs in spring (Jenkins et al., 2000) and in summer (Burrow et al., 1992) respectively in SW England; analyses of the pictures were only undertaken for the winter survey. By doing so, the whole settlement period was over and successful new recruiters large enough to be identified.

Statistical analyses

Daily means and daily average maxima and minima of the temperature were tested according to aspect with a one-way ANOVA (Analysis of Variance). Daily means were calculated and tested in the same way for each season, as well as low and high tide. Due to gaps in the dataset, for the season-breakdown analysis, selected periods during the winter (i.e. 01/01 to 28/02), spring (i.e. 24/05 to 20/06), summer (i.e. 27/06 to 9/08) and autumn (i.e. 01/10 to 30/11), were chosen in order to exclude any seasonal gaps, however, this was not possible to achieve for the summer in Croyde and Winter in Bude.

A four-factor design was employed using distinct categories: Substrata (fixed, two levels – 'north-' and 'south-facing'), Coast (fixed and orthogonal, two levels – 'north' and 'south'), Season (fixed and orthogonal, two levels – 'summer' and 'winter'), Site (random, four locations listed above, and nested within Coast). To examine the overall similarity of the communities according to these factors, a non-metric Multidimensional Scaling (nMDS) was undertaken using the Bray-Curtis index of similarity on 4th-root transformed abundance data of all taxa, to 'down-weight' the influence of abundant taxa and account for high numbers of zeros (Clarke et al., 2014). Differences in intertidal community structure and composition were investigated with Permutational Multivariate Analysis of Variance (PERMANOVA). The contributions of individual taxa to dissimilarities between the two aspects were determined using Similarity Percentage Analysis (SIMPER). All multivariate analyses were carried out using the PRIMER 7 (Plymouth Routines in Multivariate Ecological Research) package and the PERMONOVA add-on. All taxa were subsequently partitioned into functional or taxonomic groups (lichens, primary producers, grazers, carnivores, and filter feeders) to examine the species richness according to aspect and to perform an ANOVA with the following factors: Season, Aspect, Coast, Site. Abundance was examined with specific focus on taxa or taxonomic groups. Prior to all ANOVA, data was checked for normality and homogeneity of variances; no further transformations were required. All ANOVA were performed on the software MINITAB version17.

2.3. Results

2.3.1 Temperature variation and aspect

Annual mean temperatures on south-facing aspects (13.4°C ± 0.1) were just under 1°C warmer than on the north-facing ones (12.6°C ± 0.2) across sites (Table 2.1). Average and extreme temperatures varied with aspect across all sites (Tables 2.1, 2.2 and 2.3). Mean temperature variation according to aspect oscillated between 0.6°C and 1.0°C within all seasons, with 0.6°C difference in spring, 0.9°C in summer and winter, and 1.0°C in autumn, across all sites.

Average temperatures differed with aspect for all sites (Table 2.1). Aspect effect on mean temperature variation was more consistent over the sites in summer, followed by autumn. Site comparison within the different seasons was difficult to achieve due to data gaps for some sites (e.g. Bude and Croyde, in winter and summer respectively) (Table 2.1 and Figures 2.3 and 2.4). The effect of aspect on the substrata temperature was unsurprisingly greater when exposed to the air during LW (Table 2.2). At low tide, annual mean temperatures were 1.6°C (or 1.2°C when considering daily mean temperature only) warmer on the south- than

Table 2.1: Daily mean temperature (± SE) recorded during periods of the winter (01/01 to 28/02), spring (24/05 to 20/06), summer (27/06 to 9/08) and autumn (01/10 to 30/11), excluding gaps in the data, on north and south facing gullies, on the mid-intertial of four locations of the SW Peninsula of England – Bantham and SMS (South Milton Sands) on the south coast, and Croyde and Bude, on the north coast. North- and south-facing temperature were recorded on the same gully. Due to gaps in the data set, mean for some seasons/aspect was not possible to do and the empty cells were grayed. Significant difference in temperature (p< 0.05) between aspect is in bold.

		Winter		Spring		Summer		Autumn		All seasons	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing
South coast	Bantham	7.6 ± 0.30	8.2 ± 0.30	15.9 ± 0.16	16.0 ± 0.20	**17.0 ± 0.18**	**18.0 ± 0.26**	**11.6 ± 0.27**	**12.6 ± 0.36**	12.2 ± 0.30	13.0 ± 0.31
		$F_{1,117}$ = 2.06 , p = 0.154		$F_{1,54}$ = 0.02 , p = 0.886		**$F_{1,86}$ = 8.92 , p = 0.004**		**$F_{1,120}$ = 4.78 , p = 0.031**		$F_{1,382}$ = 2.73 , p = 0.099	
	SMS	**6.9 ± 0.33**	**8.8 ± 0.22**	16.8 ± 0.23	17.0 ± 0.28	**16.6 ± 0.03**	**17.8 ± 0.21**	**11.9 ± 0.35**	**13.2 ± 0.33**	**12.2 ± 0.32**	**13.5 ± 0.30**
		$F_{1,114}$ = 20.62 , p = 0.000		$F_{1,54}$ = 0.28 , p = 0.602		**$F_{1,86}$ = 30.59 , p = 0.000**		**$F_{1,120}$ = 6.72 , p = 0.011**		**$F_{1,380}$ = 8.33 , p = 0.004**	
North coast	Bude		8.0 ± 0.20	**15.2 ± 0.10**	**15.3 ± 0.16**	**17.0 ± 0.11**	**17.6 ± 0.15**	13.0 ± 0.26	13.1 ± 0.18	15.0 ± 0.07	15.1 ± 0.02
				$F_{1,54}$ = 0.55 , p = 0.460		**$F_{1,86}$ = 9.09 , p = 0.003**		$F_{1,100}$ = 0.48 , p = 0.490		$F_{1,244}$ = 0.13 , p = 0.720	
	Croyde	7.4 ± 0.15	7.8 ± 0.19	15.6 ± 0.11	16.7 ± 0.23			**12.0 ± 0.21**	**13.0 ± 0.29**	10.9 ± 0.28	11.7 ± 0.32
		$F_{1,111}$ = 2.30 , p = 0.132		**$F_{1,54}$ = 20.77 , p = 0.000**				**$F_{1,121}$ = 8.19 , p = 0.005**		$F_{1,289}$ = 2.92 , p = 0.089	
	All sites	**7.3 ± 0.16**	**8.2 ± 0.14**	**16.0 ± 0.09**	**16.4 ± 0.12**	**16.9 ± 0.08**	**17.8 ± 0.12**	**11.9 ± 0.14**	**12.9 ± 0.15**	**12.6 ± 0.16**	**13.4 ± 0.15**
		$F_{1,345}$ = 18.87 , p = 0.000		**$F_{1,278}$ = 5.17 , p = 0.024**		**$F_{1,262}$ = 40.89 , p = 0.000**		**$F_{1,448}$ = 22.18 , p = 0.000**		**$F_{1,1339}$ = 12.75 , p = 0.000**	

north-facing substrata, while on average, no temperature difference was found according to aspect at high tide (HW).

Table 2.2: Daily mean temperatures (± SE) recorded during low tide (LW) and high tide (HW) on north- and south- facing gullies, of the mid-intertial of four locations of the SW Peninsula of England. Recording started in September 2016 and ended in August 2017. Note that due to loss of loggers beteween February and June 2017, values were supplemented with data collected for the same period in 2018. North- and south-facing temperatures were recorded on the same gullies. Significant difference in temperature ($p < 0.05$) between aspect is denoted by bold font.

Coast	**Location**	**LW** North-facing	**LW** South-facing	**HW** North-facing	**HW** South-facing
South	Bantham	12.3 ± 0.07	12.8 ± 0.08	12.8 ± 0.2	12.9 ± 0.2
		$F_{(1,630)} = 14.63$, $p = 0.000$		$F_{(1,448)} = 0.14$, $p = 0.704$	
	South Milton Sands	12.1 ± 0.08	12.8 ± 0.08	13.2 ± 0.3	13.7 ± 0.3
		$F_{1,653} = 20.86$, $p = 0.000$		$F_{1,448} = 2.05$, $p = 0.153$	
North	Bude	12.8 ± 0.06	13.5 ± 0.07	13.2 ± 0.3	13.5 ± 0.2
		$F_{1,540} = 0.23$, $p = 0.635$		$F_{1,437} = 0.52$, $p = 0.469$	
	Croyde	10.8 ± 0.05	12.8 ± 0.07	13.3 ± 0.3	13.4 ± 0.3
		$F_{1,537} = 20.79$, $p = 0.000$		$F_{1,386} = 0.21$, $p = 0.646$	
	All sites	11.8 ± 0.1	13.0 ± 0.1	13.2 ± 0.1	13.3 ± 0.1
		$F_{1,2366} = 42.11$, $p = 0.000$		$F_{1,1725} = 0.65$, $p = 0.421$	

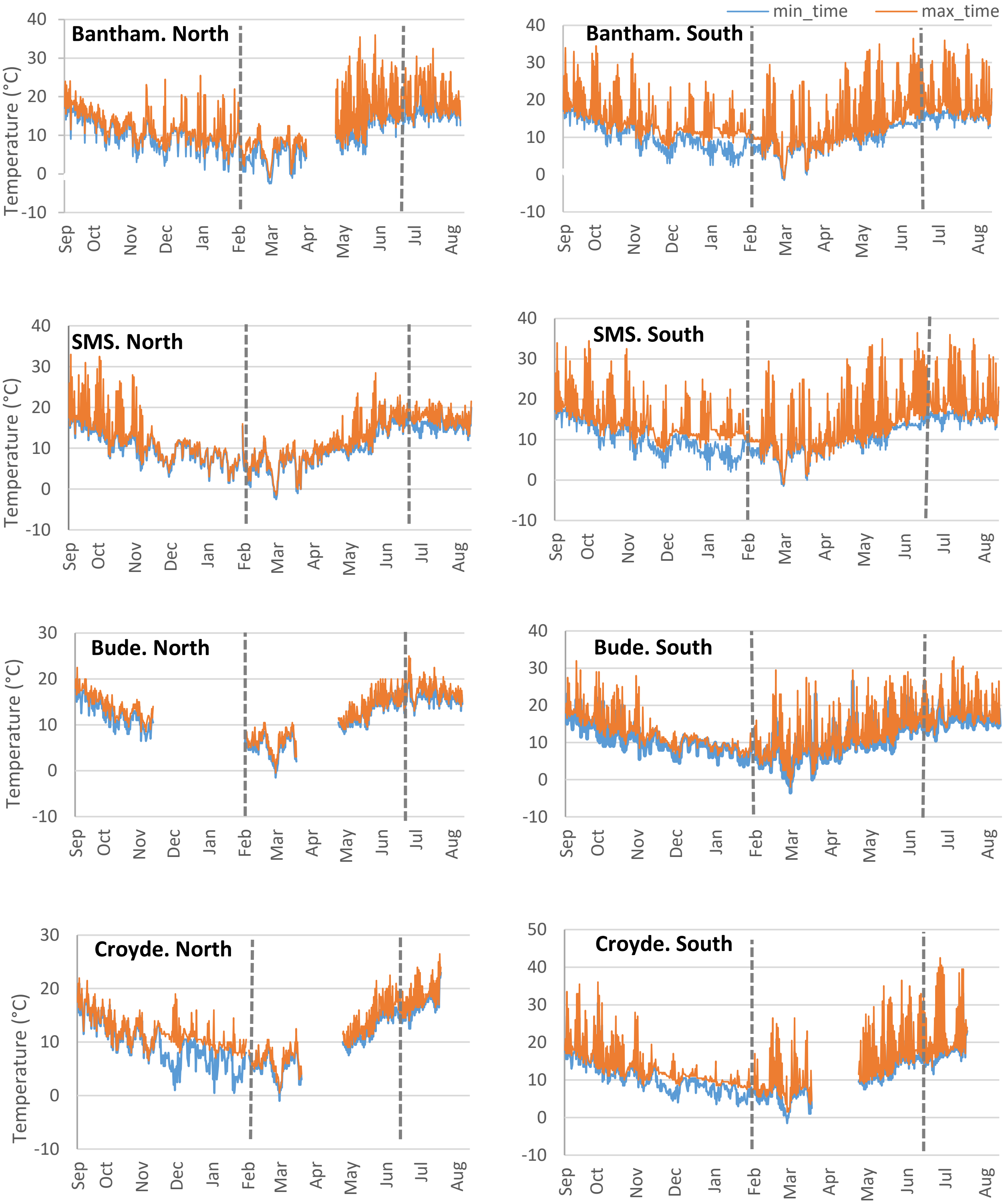

Figure 2.3: Mid-intertidal maximum (in red) and minimum (in blue) temperatures during the low tides on north- and south-facing substrata from four different sites in SW England (Bantham; South Milton Sands, SMS; Bude; and Croyde). The maximum and minimum temperatures are the extremes taken within a 2-hour window during each low tide every day. Start of the recording was in September 2016 and ended in August 2017. Please note that due to loss of loggers between Feb-Jun 2017 (between the hatched lines), the values were supplemented with data collected for the same period in 2018. The data were inserted here to maintain an “easy to view” consistent seasonal comparison. The gaps in the dataset represent time periods where lost data loggers have not been replaced.

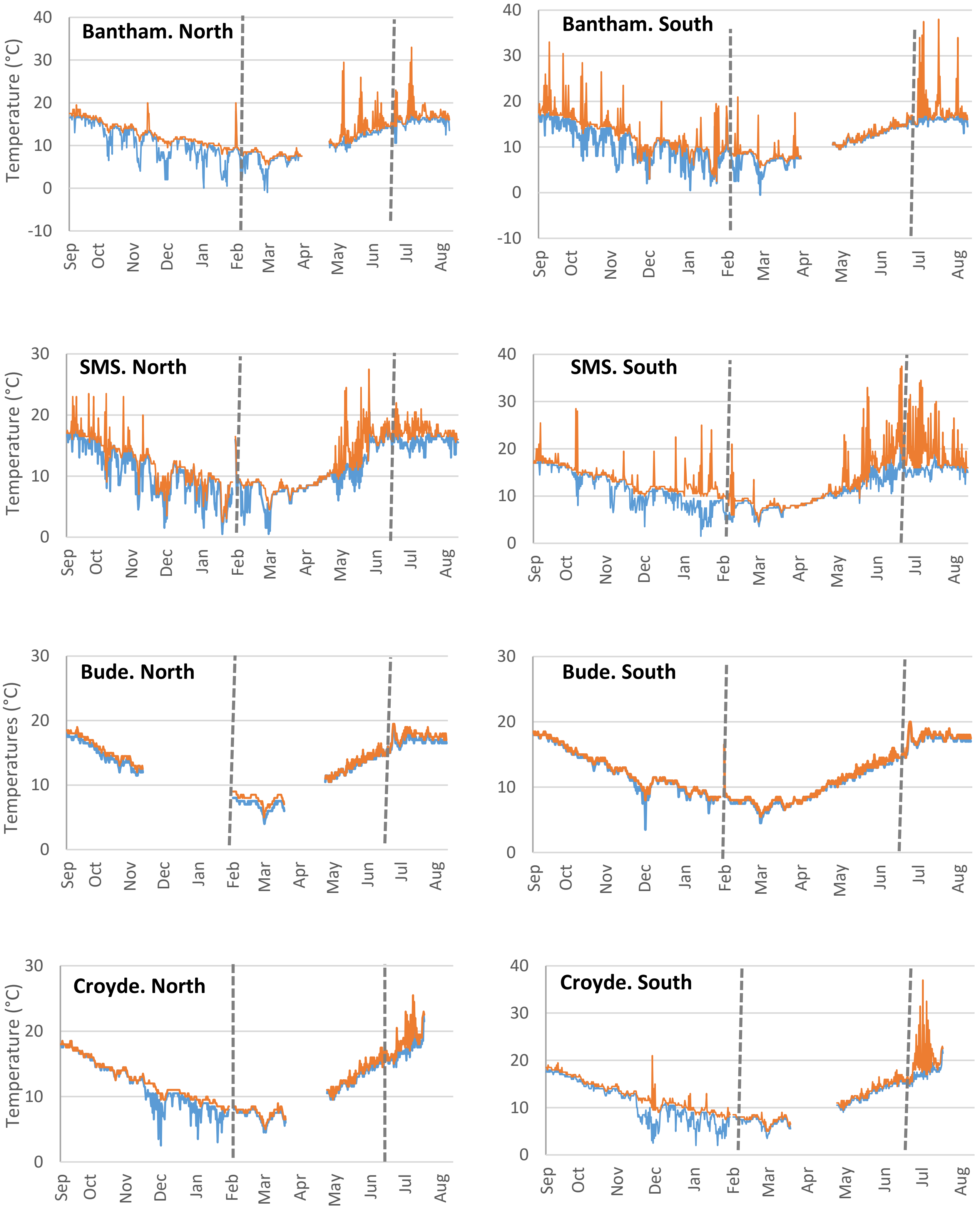

Figure 2.4: Mid-intertidal maximum (in red) and minimum (in blue) temperatures during the high tides on north- and south-facing substrata from four different sites in SW England (Bantham; South Milton Sands; SMS, Bude; and Croyde). The maximum and minimum temperatures are the extremes taken within a 2-hour window during each high tide every day. Start of the recording was in September 2016 and ended in August 2017. Please note that due to loss of loggers between Feb-Jun 2017 (between the hatched lines), the values were supplemented with data collected for the same period in 2018. The data were inserted here to maintain an "easy to view" consistent seasonal comparison. The gaps in the dataset represent time periods where lost data loggers have not been replaced.

Aspect-linked variation in temperature extremes was much greater for absolute and average maximum- compared to minimum-temperatures, particularly at LW (Table 2.3; Figures 2.3 and 2.4). Average maxima were 4.2°C warmer on south- than north-facing substratum, with site variation (3.8°C, 5.6°C, 2.3°C and 5.2°C differences, in Bantham, South Milton Sands, Bude and Croyde, respectively). Although gaps in the data set, not been filled by data logger replacement (e.g., in Croyde during the summer and Bude during the end of autumn/winter, see Figure 2.3 and 2.4) might have influenced means among sites on each aspect, the annual mean (excluding aspect) of study sites (or the nearest meteorological recording point) from the same coast are still very similar. Annual mean of South Milton and Bigbury on Sea (next to Bantham), Bude and Croyde are 10.2°C, 10.4°C, 10.7°C and 11°C respectively (climate-data.org).

Extremes were not always recorded on the same hour or even same day across sites (Table 2.3). For instance, the highest temperature recorded on south-facing substratum (Croyde, June 2017) was 5°C higher than the maximum on north-facing one (Bantham, July 2017), while there was only a 0.5°C difference in extreme minima (Table 2.3). Maximum temperatures on the south-facing substrata were observed between late mornings to mid-afternoons, while maxima on north-facing ones were achieved later in the afternoon.

Therefore, at the same time of the day, organisms living on both aspects of the same gully experienced very large temperature differences, with one significantly greater than the other. For the upper value recorded at Croyde for example (42.5°C), the corresponding temperature on the north-facing aspect from the same gully was only 22.5°C. Minimum temperatures for both aspects were recorded during early morning or during the night and unsurprisingly given the buffering provided by seawater, temperate maxima and minima occurred during LW (Figure 2.3 and 2.4). The amplitude of extreme temperature variation was lower while loggers were submerged during HW compared to LW, especially on the north coast. During LW, loggers frequently recorded temperatures exceeding 30°C on both aspects, especially at the south coast sites.

Even though the highest temperature was recorded on the north coast (42.5°C in Croyde, on south-facing aspect on the 27/06/17 at 14:20, see Table 2.3), on average, more extreme summer temperatures were recorded on the south- compared to the north-coast (Table 2.4A). Temperatures above 30°C, recorded during daytime LW, were counted 41 times on north-facing gullies and 158 occasions on the south-facing gullies on the south coast, in contrast to zero occurrence on north-facing gullies and 95 times on south-facing gullies of the north coast. Although there was no aspect-variation in the number of temperatures recorded below zero degree, data allowed to demonstrate that the south coast was hit by more cold temperatures (<0°C) than the north one (about 35 records on the south coast against 9 on the north one; Table 2.4B). No temperature below -10°C was recorded, and very few extremely hot temperatures above 40°C was recorded but on south-facing substrata only (Table 2.4).

Table 2.3: Extreme temperatures recorded over a 12-month period with the associated recording date and time, and daily average minima and maxima (± SE) also over a year-long period. All recordings were collected from the mid-intertidal shore at four sites in the SW Peninsula of England – Bantham and South Milton Sands (SMS) on the south coast, and Bude and Croyde on the north coast. Averages with * should be taken with caution as there are gaps in the data in winter or summer which would therefore influence the average minima and maxima, respectively. Significant difference in temperature ($p < 0.05$) between aspect is in bold.

		Minimum temperature		Maximum temperature		Daily average minima		Daily average maxima	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing
South coast	Bantham	-3°C 28/02/18 00:18 1/03/18 01:18	-2.5°C 27/02/18 07:18 01/03/18 02:18	37.5°C 5/07/17 19:20	42°C 6/07/17 12:20	8.3 ± 0.3	8.7 ± 0.2	**17.5 ± 0.4**	**21.3 ± 0.5**
						$F_{1,230} = 0.18$, $p = 0.67$		**$F_{1,230} = 96.44$, $p = 0.0$**	
	SMS	-3°C 01/03/18 01:18	-2°C 01/03/18 02:18	34°C 14/09/16 14:40	37.5°C 11/06/18 12:17 20/06/18 14:17	9.3 ± 0.2	9.1 ± 0.2	**15.8 ± 0.3**	**21.4 ± 0.4**
						$F_{1,254} = 0.51$, $p = 0.47$		**$F_{1,254} = 15.66$, $p = 0.0$**	
North coast	Bude	-1.5°C 01/03/18 00:18	-3.5°C 01/03/18 01:18	26.5°C 25/06/17 15:20	33°C 06/07/17 12:20 14/09/16 12:40	10.9 ± 0.3 *	9.4 ± 0.2	**15.3 ± 0.3**	**17.6 ± 0.3**
						$F_{1,440} = 0.43$, $p = 0.51$		**$F_{1,440} = 96.74$, $p = 0.0$**	
	Croyde	-1°C 01/03/18 00:18	-1.5 27/02/18 01:18 & 22:18	26.5°C 17/07/17 17:20	42.5°C 27/06/17 14:20	9.2 ± 0.3	9.5 ± 0.3	**14.5 ± 0.3 ***	**19.7 ± 0.5 ***
						$F_{1,222} = 0.08$, $p = 0.77$		**$F_{1,222} = 58.48$, $p = 0.0$**	
	All sites					9.3 ± 0.1	9.2 ± 0.1	**15.8 ± 0.2**	**20.0 ± 0.2**
						$F_{1,1152} = 0.06$, $p = 0.80$		**$F_{1,1152} = 224.49$, $p = 0.0$**	

Table 2.4: Total numbers of **A**. hot extreme temperatures above 30°C ad 40°C and **B.** cold extreme ones below 0°C and -10°C recorded (hourly) over 12 months on both north- (blue) and south-facing (red) aspects. All recordings were collected from the mid-intertidal shore at four sites in the SW Peninsula of England – Bantham and South Milton Sands (SMS) on the south coast, and Bude and Croyde on the north coast.

A	Number of hot extreme events (>30°C) recorded in 12 months		Number of hot extreme events (>40°C) recorded in 12 months	
	North-facing	South-facing	North-facing	South-facing
Bantham	24	93	0	6
SMS	17	65	0	0
Bude	0	5	0	0
Croyde	0	90	0	0
Mean all sites (± SE)	10 ±6	63 ±20	0	1.5 ±1.5
B	Number of cold extreme events (<0°C) recorded in 12 months		Number of cold extreme events (<-10°C) recorded in 12 months	
	North-facing	South-facing	North-facing	South-facing
Bantham	37	41	0	0
SMS	40	23	0	0
Bude	5	18	0	0
Croyde	5	9	0	0
Mean all sites (± SE)	22 ±10	23 ±7	0	0

2.3.2. How aspect affects intertidal communities

Community composition on north-facing substrata was significantly different than on the south-facing aspects (Figure 2.5, Table 2.5, main effect of 'Aspect'). On the MDS plot – where similarity of community composition is denoted by proximity of symbols – clear differentiation can be seen between communities from north- (blue) and south-facing (red) aspects. The overall intertidal community assemblage across the four sites had a dissimilarity of 39% associated with aspect, with 14 species (or groups of species) contributing most to this dissimilarity (Table 2.6). The lichen *Lichina pygmaea*, barnacles, fucoids, the mussel *Mytilus edulis,* and the anemone *Actinia equina* were all more abundant on south-facing slopes. The lichen *Verrucaria mucosa*, the encrusting coralline *Lithophyllum incrustans*, the alga *Osmunda pinnatifida*, the polychaete *Sabellaria alveolata*, the limpets *Patella vulgata*, *Patella depressa* (and unidentified juvenile limpets), and the gastropod *Littorina saxalitis* were more common on north-facing aspects. *L. pygmaea*, contributed the most (3% aspect-related variation) to overall community dissimilarity (Table 2.6).

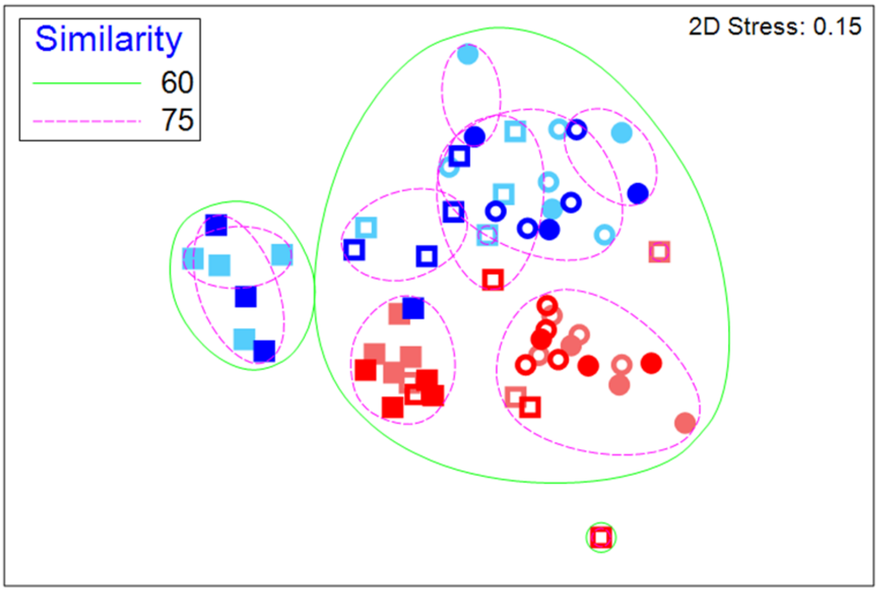

Figure 2.5: Non-metric MDS ordination of Bray-Curtis resemblances between multivariate community compositions according to aspect (north/south orientation) for a total of 174 quadrats sampled from four sites across two coasts of the SW Peninsula of England over two seasons. Each symbol represents the intertidal community on one side of one gully (aspect) at one location during either the summer (lighter colour, e.g. light blue and light red) or winter (darker colour, e.g. dark blue and dark red) sampling. The north coast, represented by the square symbol, includes the sites Croyde (□) and Bude (■), while the south coast of the SW England, represented by a circle symbol, includes the sites South Milton Sands (○) and Bantham (●). The colour indicates the aspect, with blue, the north- and red, the south-facing.

There was also a significant main effect of the factor 'Site', although all interaction terms were non-significant (Figure 2.5 and Table 2.5, see main effect 'Site'). The MDS plot (Figure 2.5) shows that intertidal communities are different from one site to another (each site – represented by a distinct symbol – tends to be grouped). In addition, the assemblage community on the northern aspect at Bude was considerably different from any other assemblage (less than 60% similarity), and was probably driving most of this ‘site’-effect (Figure 2.5). Even though Bude and Croyde (N coast), and Bantham and South Milton Sands (south coast) tended to be more similar to each other, the main factor ‘Coast’ was not significant (Figure 2.5, Table 2.5 (t = 1.06, p = 0.30). In fact, communities at Bude and Croyde were more different from each other (t = 3.04, p = 0.01) than the south-coast sites. This difference might be driven by a greater number of species recorded in Bude compared to Croyde (e.g. *Sabellaria alveolata*, *Onchidella celtica*, *Acanthochitona fascicularis*, and unidentified algae).

Table 2.5: PERMANOVA results for the intertidal community composition from four locations in the SW Peninsula of England (Bantham and South Milton Sands, on the south coast; and Bude and Croyde, on the north coast; see Figure 2.2) at two sampling seasons (winter and summer), on north- and south-facing substrata. PERMANOVA main factors are Season (Se), Coast (Co), Aspect (As), Site nested in Coast (Si(Co)), with their related interaction terms. Significant (p<0.05) values are denoted by bold type.

Source	df	MS	Pseudo-F	p-value
Season	1	994.51	12.795	0.067
Coast	1	386.52	1.4246	0.186
Aspect	7	1738.4	10.321	**0.001**
Site(Coast)	2	416.71	2.0346	**0.024**
Se x Co	1	129.68	0.80727	0.488
Se x As	6	183.77	2.4298	0.137
Co x As	2	246.04	1.3553	0.371
Se x Si(Co)	2	59.153	0.28881	0.991
As x Si(Co)	2	161.81	0.79003	0.683
Se x Co x As	1	67.129	0.59327	0.642
Se x As x Si(Co)	2	76.225	0.37217	0.952
Residuals	31	204.81		

Table 2.6: SIMPER Results from the species, or group of species (e.g. all barnacles) ranked according to their contribution to the overall 38.6% dissimilarity associated with aspect, with respect to average abundance (Av. Abund), average dissimilarity (Av. Diss), quotient of dissimilarity and standard deviation (Diss/SD), % contribution to differences (Contrib %) and cumulative % contribution to differences (Cum %). Abundance highlighted in red and blue indicat the highest abundance of that species/group on the southern and northern aspect, respectively. Note that the difference in average abundance is not necessarily statistically different, but considered different enough to play an important role in community dissimilarity.

Species	N-facing Group Av. Abund	S-facing Group Av. Abund	Av. Diss	Diss/SD	Contrib %	Cum. %
Lichina pygmaea	0.07	**0.80**	3.08	1.1	7.98	7.98
Verrucaria mucosa	**0.88**	0.24	3.05	1.38	7.9	15.88
Lithophyllum incrustans	**0.83**	0.20	2.63	1.64	6.82	22.7
Osmundea pinnatifida	**0.67**	0.06	2.33	1.6	6.05	28.74
All barnacles	2.32	**2.62**	2.33	1.31	6.04	34.78
Fucus sp.	0.34	**0.64**	2.14	1.31	5.56	40.34
Mytilus edulis	0.37	**0.41**	2.06	1.01	5.33	45.67
Patella vulgata	**1.98**	1.68	1.95	1.35	5.06	50.73
Sabellaria alveolata	**0.51**	0.07	1.91	0.64	4.94	55.67
Unidentified juvenile *Patella sp.*	**1.42**	1.24	1.88	1.1	4.88	60.55
Littorina saxalitis	**0.34**	0.24	1.62	0.96	4.2	64.75
Patella depressa	**2.12**	1.93	1.58	1.35	4.1	68.85
Actinia equina	0.23	**0.30**	1.4	1.04	3.63	72.48

In total, 45 species were recorded (including seven unidentified species) across all locations and aspects. Species richness was higher on north- than south-facing substrata (ANOVA $F_{1,302}$ = 44.69, *p* = 0.02; Figure 2.6A, Table 2.5, main effect ‘Aspect’). During the summer survey, a total of 45 species (mean = 10.7 ±0.4 per quadrat) recorded on north-facing slopes, against 30 on south-facing (mean = 7 ±0.2 per quadrat). Slightly fewer species, however not significant (Table 2.5), were sampled during the winter survey, with 42 species on the north- (mean =

9.4 ±0.2 per quadrat) against 24 species (mean = 7 ±0.2 per quadrat) on the south-facing substrata.

2.3.3. Aspect related variation in species richness and abundance of functional and taxonomic groups

Species richness of primary producers, and grazers was greater on north- than south-facing substrata (averaged of both sampling seasons), while lichens, carnivores, and filter feeder did not show any variation with aspect (Table 2.7 main effect 'Aspect'). For both sampling seasons, primary producers contributed most to the overall species richness, followed by grazers, filter feeders, lichens (Figure 2.6). Lichens are not strictly a functional group but due to the important of some species, such as *L. pygmaea*, as source of food (e.g., for limpets) and shelter (e.g., for *Littorina saxalitis*), therefore were kept as an entire group. As the carnivores

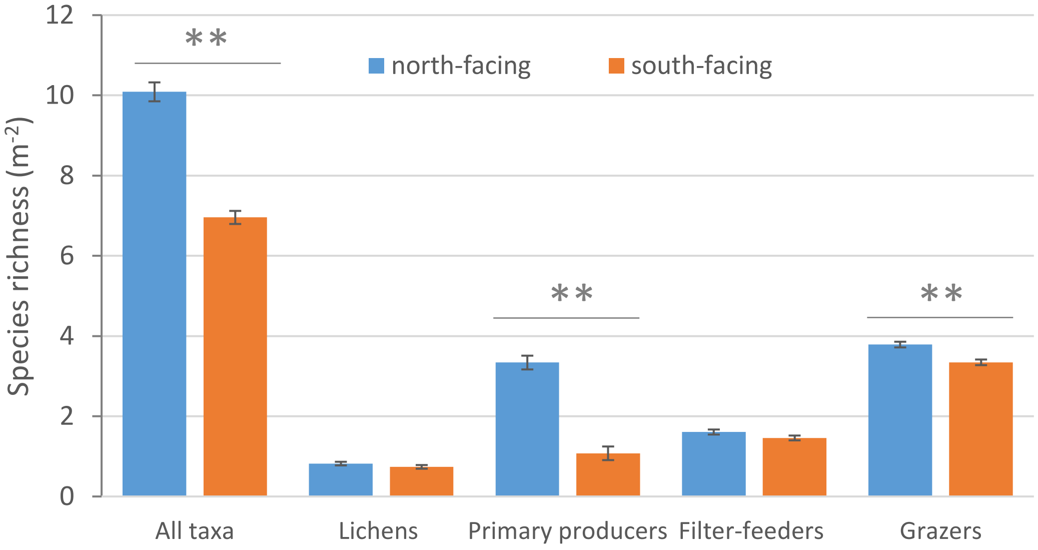

Figure 2.6: Mean species richness of all taxa and the major functional groups (e.g. Lichens, primary producers, filter feeders and grazer) according to aspect (blue, north-facing; and red, south-facing). This graph represents the average of the species richness recorded during the summer and winter, across four different locations in the SW of England. ** significant with *p*<0.01; and no significant difference (*p*>0.05) are left blank.

Table 2.7: ANOVA results of the effect of Coast (north and south coasts of the SW peninsula of England), Site (Bude and Croyde on the north coast, Bantham and South Milton Sands on the south coast), Aspect (north- and south-facing), and Season (summer and winter) on the species richness of organisms from functional groups (e.g. lichens, primary producers, grazers, carnivores and filter feeders) in the mid shore rocky intertidal. Bold text indicates significant outcomes from ANOVA. Se, Season; Co, Coast; Si(Co), Site(Coast); As, Aspect.

Source	d.f.	All taxa			Lichens			Primary Producers		
		m.s	*F*	*P*	m.s	*F*	*P*	m.s	*F*	*P*
Season	1	30.2	11.09	0.079	6.8	2.98	0.227	0.05	0.02	0.905
Coast	1	120.9	0.75	0.477	22.1	3.17	0.217	10.9	0.17	0.723
Site(Coast)	2	160.9	11.09	0.156	6.9	2.39	0.248	65.9	5.39	0.169
Aspect	1	**864.2**	**48.09**	**0.02**	0.7	0.76	0.474	**456.2**	**36.88**	**0.026**
Se*Co	1	4.7	1.74	0.317	0.6	0.27	0.655	13.4	4.53	0.167
Se*As	1	**42.7**	**6.92**	**0.009**	**1.5**	**4.98**	**0.026**	4.3	1.4	0.238
Se*Si(Co)	2	2.7	0.44	0.644	**2.2**	**7.57**	**0.001**	2.9	0.96	0.384
Co*As	1	10.9	0.61	0.517	1.2	1.24	0.381	5.7	0.47	0.564
Si(Co)*As	2	17.9	2.91	0.056	**0.9**	**3.13**	**0.045**	**12.3**	**4.01**	**0.019**
Error	353	6.17			0.30			1.63		
Total	365									

Source	d.f.	Carnivores			Grazers			Filter feeder		
		m.s	*F*	*P*	m s	*F*	*P*	m.s	*F*	*P*
Season	1	5.0	8.44	0.100	0.2	0.06	0.826	1.3	3.20	0.215
Coast	1	103.6	3.29	0.211	8.6	0.60	0.518	83.9	6.31	0.129
Site(Coast)	2	31.5	39.33	0.129	14.3	6.46	0.172	13.3	16.17	0.060
Aspect	1	7.4	7.20	0.115	**16.7**	**37.54**	**0.025**	1.8	2.49	0.255
Se*Co	1	3.7	6.24	0.129	4.5	1.86	0.306	1.9	4.70	0.162
Se*As	1	0.02	0.02	0.883	**9.0**	**13.42**	**0.000**	0.08	0.25	0.617
Se*Si(Co)	2	0.6	0.73	0.484	**2.4**	**3.64**	**0.027**	0.4	1.33	0.265
Co*As	1	0.02	0.02	0.897	1.0	2.30	0.269	0.5	0.68	0.498
Si(Co)*As	2	1.0	1.26	0.286	0.4	0.66	0.515	0.7	2.33	0.099
Error	353	0.81			0.59			0.30		
Total	365									

functional group was dominated by only one species, the Dog Whelk *Nucella lapillus,* more abundant on north-facing aspects, however not significant ($F_{1,61}$ = 3.76, *p* = 0.057), I did not consider this functional group in further analysis.

Richness of filter feeders was similar on both aspects, and across all sites and coasts. Eight species of filter feeders were recorded (dominated by various barnacles), but it is interesting to note that compared to the north coast, both south coast sites (Bantham and South Milton Sands) were almost devoid of mussels (Appendix 1 & 2). After barnacles, the next most abundant filter feeders was the reef-forming worm *Sabellaria alveolata*, especially common at Bude. For homogeneity between seasons, the barnacles were kept as a single group, as barnacles were identified to species only for the winter survey. Although the four-factor design ANOVA did not allow to detect any aspect-related varaiation in the abundance of barnacles, *Chthalamus spp.* had its abundance significantly higher on the south-facing substrata ($F_{1,163}$ = 23.44, p = 0.000). Relative abundance of *Semibalanus balanoides* and juveniles, or dead barnacles did not vary with aspect. There was however, a surprising significant local variation (i.e. site) in the abundance of barnacle species (Table 2.8).

Table 2.8: Variation in average barnacle abundance (ANOVA) according to the influence of 'Coast' and 'Site' (e.g. Bude and Croyde on the north coast, Bantham and south Milton Sands on the south coast of the SW peninsula of England), 'Aspect' (north- and south-facing), and the interaction terms. Bold text indicates significant outcomes from ANOVA. Results in bod red reflect significant abundance on south- than north-facing substrata. As, Aspect; Co, Coast; Si(Co), Site(Coast).

		Adults						Juveniles					
Source	d.f.	*Chthalamus sp.*			*S. balanoides*			*Chthalamus sp.*			*S. balanoides*		
		m.s	*F*	*P*	m.s	*F*	*P*	m.s	*F*	*P*	m.s	*F*	*P*
Aspect	1	2030	2.44	0.257	101.4	2.35	0.261	65.2	0.81	0.461	3.78	0.05	0.851
Coast	1	1091	3.21	0.212	**10385**	**22.2**	**0.042**	1343	4.19	0.177	2888	6.3	0.129
Site(Co)	2	348	0.41	0.711	484	11.0	0.083	331.2	4.02	0.199	475.4	5.6	0.153
As * Co	1	559	0.67	0.498	171	3.96	0.180	62.8	0.78	0.468	122.9	1.5	0.346
As * Si	2	**858**	**6.82**	**0.001**	43.9	1.79	0.170	**82.4**	**4.09**	**0.02**	**85.5**	**3.7**	**0.026**
Error	157	126			24.5			20.2			23		
Total	164												

Although primary producers, as an entire group, were more species-rich on north- compared to south-facing substrata (Figure 2.6, Table 2.7, main effect 'Aspect'), the different taxonomic group of the primary producers varied differently. Chlorophyta and Rhodophyta were also more abundant on north-facing substrata during summer and winter. Rhodophyta for instance, were 6 times and 11 times more abundant on the north- than south-facing substrata during summer and winter, respectively (Figure 2.7). There was near complete absence of Chlorophyta on south-facing substrata for both seasons with low (1-2% cover) but still significantly higher abundance on the opposite aspect (Figure 2.7). Because Rhodophyta were the most diverse (16 species against 5 for both Chlorophyta and Phaeophyta) and abundant group, it was probably driving most observed aspect-linked and seasonal variation.

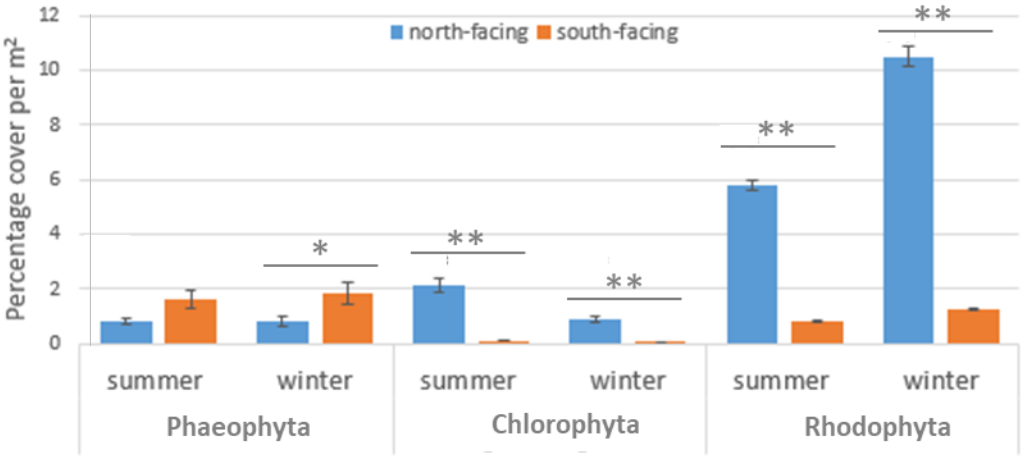

Figure 2.7: Percentage cover of the different algal groups (e.g. Phaeophyta, Chlorophyta, and Chlorophyta) according to aspect (blue, north-facing, and red, south-facing) during two sampling seasons (summer and winter), from four different locations in the SW of England. * significant with *p*<0.05; and ** significant with *p*<0.01; and no significant difference (*p*>0.05) are left blank.

The functional group 'grazers' did not have a significant effect on any other main factors than 'Aspect' with prevalence to north- than south-facing substrata (Table 2.7; Figure 2.6). This group included 10 species, dominated by limpets with an average abundance of 127.7 ±3.5 *Patella depressa* and 73.1 ±2.1 *P. vulgata* m^{-2}, followed by the lined topshell, *Phorcus lineatus* with 1.6 ±0.3 m^{-2}.

2.3.4. Biogeographic origin and aspect

Although ubiquitous species were more frequently encountered on north- than south-facing substrata, neither boreal nor Lusitanian species richness varied with aspect (Figure 2.8A). Taxonomic groups (gastropods, barnacles and limpets) that had both boreal and Lusitanian representatives were selected for comparison of how aspect affected their abundance. Lusitanian topshells (*S. umbilicalis* and *Phorcus lineatus*), the Lusitanian limpet (*P. depressa*) and the boreal limpet (*P. vulgata*) were all significantly more abundant on north- than south-facing substrata (Figure 2.8D and 2.8B). The abundance of Lusitanian barnacles *Chthamalus spp.* (*C. montagui* and *C. stellatus*) was however, greater on south- than north-facing substrata, but other boreal species, the barnacle *S. balanoides* and the littorinids (*Littorina littorea* and *Littorina saxatilis*) did not vary with aspect (Figure 2.8C and 2.8D).

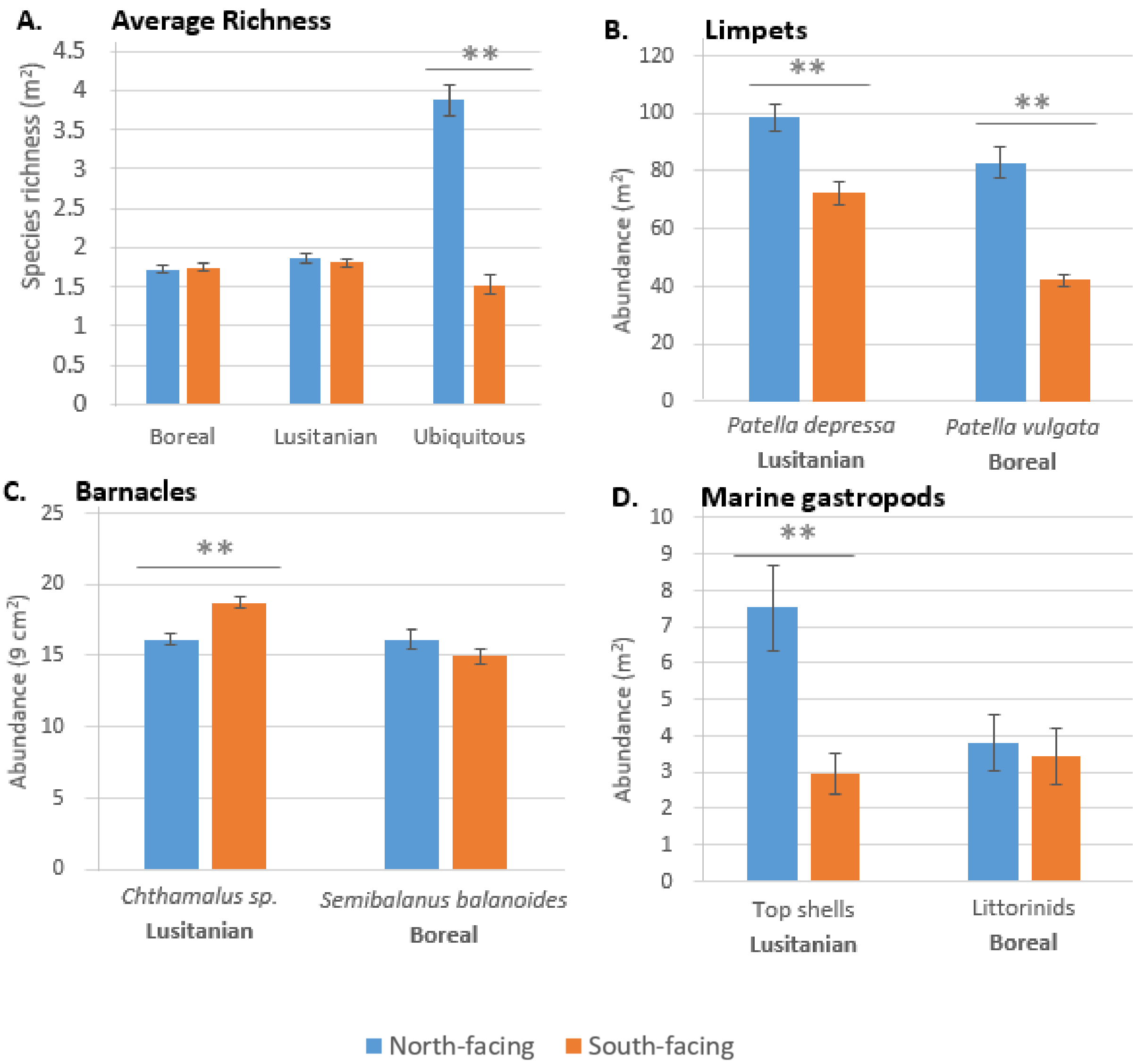

Figure 2.8: **A.** Mean species richness of the different biogeographic origin species (the Boreal cold-water, Lusitanian warm-water, and the widespread Ubiquitous species). Average abundance of key boreal/Lusitanian pairs of **B.** limpets (*Patella depressa*, Lusitanian; and *Patella vulgata*, boreal species), **C.** barnacles (with *Chthamaus sp.*, Lusitanian; and *Semibalanus balanoides*, boreal species) and **D.** marine snails (with Topshells, Lusitanian; and the *Littorinids*, boreal species. The average abundance and species richness were sampled in mid-intertidal shore during summer and winter, on two different aspects (north-facing in blue, and south-facing in red), from four different locations in the SW of England. Note that the barnacles' abundance was sampled in the winter only. As *Chthamalus montagui* and *Chthamalus stellatus* had similar patterns and abundance, both species were averaged as *Chthamalus sp.* ** significant with p<0.01; and no significant difference (p>0.05) are left blank.

2.4. Discussion

The aim of this study was to determine how variations in average and extreme temperatures on north- and south-facing aspects influence species richness and abundance of intertidal species at different levels (community; functional, taxonomical, and biogeographical groups; and species levels) and different scales (spatio-temporal). Two of my three hypotheses were supported. First, average mean and extreme temperatures did vary according to aspect across all locations and seasons. Second, and presumably related to temperature variation, species richness and abundance of several taxonomic/functional groups and species was influenced by aspect. Despite the striking temperature differences between north- and south-facing slopes however, neither Lusitanian or boreal species were consistently more abundant on the warmer south-facing, or cooler north-facing substrata. Consequently, I found little support for the third hypothesis, although at an individual level, biogeographical origin seemed to have been an important factor driving abundance.

An annual average difference of 1°C (when including all data, or 0.8°C when including selected periods in all seasons, excluding gaps) was found between south- and north-facing substrata across all sites. At low tide, this temperature difference was even 1.6°C, while aspect variations were minimal during low tide, likely due to the buffering effect of the seawater. The annual average difference according to aspect aligns closely with the 0.85°C global combined land and ocean warming (0.65 to 1.06 °C) since the late 19th century; and the 1.6°C difference experienced during aerial exposure aligns with the 1.5°C projected warming by the end of the 21st century under intermediate to high greenhouse gas emission scenarios (RCP4.5 to RCP8.5) (IPCC, 2013, 2018). This study also provides evidence that south-facing intertidal substrata experience significantly more frequent (almost 8 times more) high extremes temperature than opposite north-facing substrata, although cold extreme temperatures did not vary with aspect.

Extreme events, such as heat waves are predicted to increase in intensity, duration and frequency (4 to 10 times more common, depending on the emission scenario) (IPCC, 2012). Using 10 combined climate models estimating global mean surface air and sea temperatures based on historical simulations, a recent study has even predicted anomalously warm 5 consecutive years (2018-2022) (Sévellec and Drijfhout, 2018), which was confirmed for summer 2018 and 2019 by record-breaking heat waves in Europe. My results also suggest that both direct exposure to sunlight radiation, and timing of low tide play a key role on the temperature difference with aspect (e.g. when low tide falls around noon, when the sun is at its highest position in the sky). Helmuth et al. (2002), similarly, demonstrated that on a warmer coastline (California), intertidal mussels would experience less thermal stress than individuals from a cooler shore further north (Washington), simply because low tide in California in the same season fell in the middle of the night. Therefore, the role of aspect on the rocky shore would directly be influenced by regional or local climate, weather, and tidal range. For instance, in my study, exposure to the Atlantic Ocean influence on the north coast of SW England tended to decrease average and extreme temperatures compared to the south coast.

At low tide, body temperature of intertidal species is controlled by climatic factors such as solar radiation, air and rock temperatures (Denny and Gaines, 2007). My data show that at low tide in the SW Peninsula of England, organisms on south-facing substrata would likely be exposed to greater thermal stress (with variation depending on the season; Geiger, 1995; Stoutjesdijk and Barkman, 2014) than organisms on the opposite north-facing substrata, which experience maximum temperature towards the end of the low tide. On the shore, some animals can behaviourally modify their exposure to extreme temperatures by selecting favourable microclimates, or by directly escaping the changing environment (migration, or range extension / contraction) (Chapperon and Seuront, 2011; Wiliams et al., 2016). Denny et al. (2011) demonstrated the importance of habitat heterogeneity to reduce the relative importance of extremes. They found that within-site (336 m long) temperature variation could exceed variation among sites along 14° of latitude (1660 km of Pacific shoreline). The results from my study, also highlight the importance of microclimate created by aspect to act as a buffer and refugia against the effect of ACC. Denny et al. (2011) stressed however, that, even though thermal tolerance on organisms (even from same species) is closely linked to the amplitude of the buffering effect, local variation in microclimate (e.g. aspect and topography) has received little attention from a physiology point of view. In the next chapter, I explore how osmotic physiology varies according to aspect.

In the British Isles, and depending on relative shore exposure, barnacles, mussels or fucoids are often the dominating sessile organisms in the mid-intertidal zone (eulittoral) (Lewis, 1964). Given that site selection and survey design attempted to control for variation in shore exposure, aspect-specific variation in incident radiation and therefore temperature is the most important determinant of most species distribution. In my study, species richness and relative abundance for several species varied with aspect, at different levels (community, functional groups, taxonomic groups, geographical origin). Aspect impacted greatly the intertidal community assemblage, with greater species richness on the north- than south-facing substrata, in concordance with Firth et al. (2016). However, in their study (looking at both natural rocky shores and sea walls), aspect did not affect the species richness of the key functional groups, whereas, I found that species richness of primary producers and grazers were significantly higher on the north- than south-facing substrata during both seasons. My results corroborate Firth et al. (2016) who showed that aspect was impacting abundance of several taxa or groups of taxa, such as gastropods (*P. vulgata*, *N. lapillus*, *Littorina spp*.) and algae, however, different species than in my study, such as *Hildenbrandia rubra* (Guiry and Guiry, 2019), likely due to the different location, rocky shore type and habitat sampled.

Different algal groups responded differently to aspect in terms of their abundance. Chlorophyta and Rhodophyta, for example, were more prevalent on the north-facing substrata during both seasons, avoiding likely higher thermal and desiccation stress, which could be experienced on south-facing substrata. At the species level, the Rhodophyta, *Osmundea pinnitifida*, and *Lithophyllum incrustans*, as well as the Chlorophyta *Cladophora spp*. were significantly more abundant on north-facing substrata. The fact that *L. incrustans* and *Cladophora spp*. tend to better tolerate temperature fluctuations than desiccation stress (Hiscock, 2003; Budd, 2007), would explain their predominance on the north-facing aspect. Although *O. pinnitifida* does seem to be resilient to light and temperature variation (Tillin, 2016; Gonçalves, 2018), it, however, tends to settle on shores where fucoid canopies are reduced or even absent. Fucoids (Phaeophyta) were more abundant on the south-facing substrata, with a significant difference for the winter only. *Fucus serratus*, were the major representative of this group. Due to their ability to deal with a high desiccation rate (up to 90% of its water content lost in 2 hours) and fast recovery from emersion (Schagerl, 2011), *F. serratus*, have therefore an advantage to settle more on warmer substrata, but with less competition for space and supposedly less grazing pressure, which would have potentially favoured settlement of *O. pinnitifida* on the opposite aspect.

Marine gastropods living on the intertidal are exposed daily to extreme desiccation stress during each low tide (Lewis, 1964). As my year-long survey of relative temperature data show, south-facing substrata can easily reach much higher extreme temperatures than on the north-facing substrata, causing direct ecophysiological stress and constraining many species to seek refuge during low tides (Gray and Hodgson, 2003; Monaco et al., 2016). In addition, however, trophic interactions could influence aspect-driven variation in species distribution. The higher species richness and overall algal cover on the north-facing aspects could have been linked to increased abundance of many grazers such as *S. umbilicalis*, *O. celtica*, and the keystone species of limpet *P. vulgata* and *P. depressa*, on the north-facing aspects. Limpet grazing has both direct and indirect impacts on fucoid settlement (Hawkins, 1992) and keeping a balance between the important limpet-barnacle-fucoid interactions that characterise the mid-shore rocky intertidal around the British Isles (Hawkins and Hartnoll, 1983). My study showed greater abundance of limpets on the north- compared to south-facing substrata. In contrast, barnacles were significantly more abundant on south- than north-facing substrata, and fucoids had a similar trend (however not significant). Although grazing activity was not measured in this study, it is likely that higher abundance of fucoids on the south- than north-facing substrata could be linked to less grazing pressure. Fucoids are predicted to decline, shift poleward and a few species might even become extinct from the southern coasts of Europe with ACC (Hawkins et al., 2008; Jueterbock et al., 2013). The high desiccation tolerance (e.g. *Fucus spiralis,* Schagerl, 2011), as well as beneficial roles of desiccation on algal physiology (e.g. desiccation increases thermal-tolerance and protects from heat-induced mortality; Hunt and Denny, 2008) might be under-estimated. This group of algae might therefore perform better than models predict in response to ACC.

In turn, *N. lapillus*, also more common on north-facing slopes, is known to seek refuge when unfavourable conditions (Hughes and Burrows, 1991), and has experienced for example, a masse mortality in 1995 likely linked to the warm late spring-early summer that year (Gibbs et al., 1999). Therefore, *N. lapillus* would tend to find refuge on the north-facing substrata, for themselves and its eggs (about 9 times more eggs on north- than south-facing substrata), which are sensitive to desiccation, and probably light exposure too (Przeslawski et al., 2004). In addition, *N. lapillus* predates principally mussels and barnacles (Hughes and Burrows, 1991) as well as other marine gastropods (Moore, 1936), and is known to have the ability to select its prey (Hughes and Dunkin, 1984; Hughes and Burrow, 1991). Under favourable conditions, dogwhelks tend, for example, to avoid smaller prey to maximize their energy (Hughes and Burrow, 1991); and bigger dogwhelks (and therefore more experienced ones) tend to predate bigger mussels (Hughes and Dunkin, 1984). Although the size of *N. lapillus* and its prey were not investigated according to aspect in this study, the prevalence of the former on the north-facing substrata could be also linked to greater diversity and abundance of bigger prey (more mussels and limpets on the north- to south-facing slopes) on the same aspect. In localities where mussels are present, barnacles may be partially or completely excluded from their diet (Moore, 1936). This could perhaps explain partially the much greater abundance of *N. lapillus* in Bude compared to the other studied rocky shores, as *Mytilus edulis* were present almost only in that location.

It is reasonable to suggest that relative differences in distribution patterns and abundance of primary producers, grazers and predators, in addition to being driven by the variations in mean and extreme temperatures, are also a facet of interactions between trophic groups. As the major species interactions (e.g. predation, competition, facilitation etc.) structuring ecological communities are climate-dependent (Gilman et al., 2010), there is growing concern that ACC might affect greatly those interactions (Gestoso et al., 2015). However, potential changes might be able to be detected first by comparing population dynamics and interaction at much smaller scale, between north- and south-facing substrata.

Corroborating Firth et al. (2016), I failed to find any aspect-linked variation in lichens species richness. However, aspect did have a significant impact on the abundance of several species. The boreal *Verrucaria mucosa* was more abundant on the north- than south-facing substrata, while the Lusitanian, light-demanding (Lewis, 1964) species *Lichina pygmaea* had the opposite pattern, supporting previous findings where *L. pygmaea* was especially found on south-facing (Southward and Crisp, 1954; Ballantine 1961; Connor et al., 2003), or on sunny (Connor et al., 2003) substrata. The small bush-like *L. pygmaea* competes for space with the barnacles, act as shelter for many tiny organisms (Kronberg, 1988; Connor et al., 2003), settling ground for some algae (e.g., *Pelvetia canaliculata*, Lorenzen, 2007) and even limpet food. Therefore, change in this lichen species could in the long-term influence the functioning of the mid-shore intertidal ecosystems. In the context of global warming, *L. pygmaea* might succeed better than other species and an increase in their abundance could favour settlement of many other organisms.

As engineer species, the sand reef-forming *Sabellaria alveolata*, and the bed-forming mussels *Mytilus* create a diversity of microhabitats, increase space to be newly colonized. They also accumulate faeces and pseudo-faeces, important food sources to other organisms, therefore increase diversity, and may control ecosystem processes (Iwasaki, 1995; Enderlein and Wahl, 2004; Dubois et al., 2006; Desroy et al., 2011). The presence of both species, mainly on north-facing substrata in Bude, might explain why species like the Celtic sea slug *Onchidella celtica*, the chiton *Acanthochitona fascicularis*, the worms *Eulalia viridis* and *Lineus ruber*, and several unidentified algae were only present there. Due to the inconsistency of both those filterfeeders presence across site, statistic analyses failed to evidence significant effect of the main factor aspect. However, where common, both species showed prevalence on the cooler and moister northern aspect. This reinforces the importance of microhabitats, and microclimates (e.g. provided by aspect) in preserving key species which may otherwise suffer greatly from extreme temperatures and ACC. Overall, barnacles, very common filterfeeders in the mid-intertidal, had greater abundance on the south- than north-facing slopes, which could be explained by their rather high thermal tolerance (Southwards, 1958) and by taking advantages of less competition for space and potentially less predation pressure on the southern aspect.

Despite clear temperature differences between north- and south-facing aspects, there were no consistent patterns in the relative distribution of boreal (cold-adapted) or Lusitanian (warm-adapted) species. Indeed, where variation was apparent, patterns were often surprising. Lusitanian topshells (*Steromphala umbilicalis* and *Phorcus lineatus*) and the limpet *P. depressa,* were for example, more abundant on the cooler north- than south-facing substrata. Lusitanian barnacles *Chthamalus spp*., known for their higher tolerance to elevated temperature and desiccation than their competitor *Semibalanus balanoides* (Southward, 1958; Boaden and Seed, 1985) were, however, significantly more abundant on south-facing substrata. Although no difference was found in the abundance of barnacle juveniles, further studies could investigate the difference in settlement and recruitment rate according to aspect, which could eventually reflect a different mortality rate of those key species according to microclimate. Littorinids (*Littorina littorea* and *Littorina saxalitis*), despite their boreal distribution are adapted to prolonged desiccation (Southward, 1958; McMahon, 1990), which may allow them to extend their distribution equally on both aspects, even to very wide range of habitats, especially at shore heights beyond the range of other intertidal organisms (Lewis, 1964; Mill and Grahame, 1990). For ‘Ubiquitous’ species, richness was more than twofold greater on north-facing substrata and aspect-related variations in these species that seem to be driving the community-level patterns described above.

Intertidal organisms on south-facing or unshaded substrata are at greater risks of desiccation and heat stress, and therefore mortality (Seabra, 2011). My study, for instance, demonstrated that temperature on south-facing substrata could reach at least 42.5°C, which is above the heat coma point of many intertidal molluscs (Southwards, 1958) identified in this survey. If south-facing substrata are already too hot for many intertidal organisms, in the context of ACC, where heat waves are predicted to be intensified (IPCC, 2012), the effect of shade on the cooler north-facing aspect may provide refuge for numerous species intolerant or event tolerant to high thermal and desiccation stress, whatever their biogeographical origin.

Like the boreal-distribution limpet *P. vulgata,* the Lusitanian *P. depressa* was more abundant on north- facing slopes and was also the most common of the two limpet species. Even though, those two closely-related species have different biogeographical origins, they occupy similar niches (Hawkins et al., 2009), exploit similar food resources (Thomson et al., 2000) and have similar thermal tolerance (e.g. lethal point 50% of 43.3°C and 42.8°C for *P. depressa* and *P. vulgata* respectively; Southward, 1958). Nonetheless, body temperature affects almost every facet of organismal physiology (Denny and Gaines, 2007), and thus, have a potential to affect processes such as survival, growth and reproduction. Both limpet species differ at least in their reproduction, (investigated in the following chapter) with *P. depressa* reproducing during the summer and *P. vulgata* over the autumn/winter. Any potential microclimate-induced (e.g., aspect) variation in their reproduction success (i.e. greater success on north-facing substrata) could have contributed to the greater abundance of both limpets on the cooler north-facing substrata.

In Britain, both the Lusitanian barnacles *Chthamalus spp*. and the limpet *P. depressa* are predicted to replace the boreal *S. balanoides* and *P. vulgata*, respectively (Hawkins et al., 2016; Letcher, 2016). With global warming, north-facing or any shaded, cooler substrata may become of major importance for these boreal species as they may provide refugia for more 'cold water' adapted organisms to persist in suitable microclimates, where regional climatic conditions become less suitable for them (Bennie et al., 2008; Lima et al., 2016). As for the less inhabited south-facing or any sun-exposed warmer substrata, they may act as stepping-stones for some species with greater tolerance to high temperature extending their range poleward. It is reasonable to think that this process is currently being illustrated in the SW Peninsula with the Lusitanian barnacle *Chthamalus spp* and limpet *P. depressa*. For example, Firth et al. (2016) published that in Croyde, SW England, in 2005 *P. depressa* was three times more abundant on the south- than north-facing substrata. Comparison with the data I collected in the exact same location in 2016, might suggests that *P. depressa* seemed to have switched its prevalence on north-facing substrata, as well as increased its abundance on both aspects in 13 years.

2.5. Conclusion

This study shows how aspect is an important factor influencing local patterns of species distribution and abundance in the rocky intertidal. Overall, many species sensitive to desiccation and thermal stress were more dominant on the north-facing substrata. In addition to an annual mean LW temperature over 1.6°C higher, as the maximum temperature recorded on south-facing aspects (up to 42°C) approaches the upper thermal tolerance of many intertidal species (Southward, 1958) encountered in this survey, it is not surprising that several species were absent or at lower abundance on south-facing-facing aspects. On that basis, the use of north- and south-facing substrata in temperate rocky shores seems to be a good tool to study the potential effect of a temperature on organisms and ecological patterns and processes. This could be especially true when low tides fall into warmest time of the day in order to capture greater temperature differences. In addition, very short-term environmental variability, such as extreme events, is on a time scale far too rapid for adaptation through evolution to occur for most organisms (Burggren, 2018), therefore any shaded and cooler microhabitats (e.g. north-facing substrata, crevices, etc.) would have a great importance as buffer or refuge. Moreover, looking at small-scale distributional patterns would eventually allow us to spot range shifts linked to ACC (e.g. extension or retraction, and local extirpation), especially at range limits such the British Isles in the case of several marine species, which would not be able to be detected at a larger scale yet. When not in an overlap of biogeographic ranges, changes in distributional patterns of marine and intertidal species might be first detected at regional (e.g. (Ingólfsson, 1996; Espinosa and Guerra-García, 2005) or latitudinal scale. However, it is important to keep in mind that thermal stress and tolerance of species might not always vary with latitudinal gradient (e.g. Helmuth et al., 2002; Lee and Boulding, 2010). As ACC is expected to impose increasing thermal stress on intertidal organisms, understanding the mechanisms by which body temperatures affect those processes is of primordial importance, as they would translate into major potential changes of biogeographic patterns (Hofmann and Todgham, 2010). In the next chapter, I investigate osmotic stress according to aspect on limpets, key grazers of the North East Atlantic.

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Chapter 3: Implications of aspect and environmental conditions in limpets physiological variations

3.1 Introduction

Understanding phenotypic responses of organisms to environmental variation is an ongoing goal for ecologists (see reviews Pigliucci, 2001; DeWitt and Scheiner, 2004). In particular, temperature is likely to be the most important ecophysiological variable affecting the performance of ectotherms (Angilletta et al., 2002; Angilletta, 2009), by influencing their biochemical reaction rates and metabolism (Clarke, 2003). Decades of laboratory-based research have demonstrated that increasing temperature strongly affects biochemical and physiological rates of organisms, such as their survival, growth and reproduction. Daily variations in temperature may differ between microhabitat, meaning that individuals from the same species can respond differently to temperature (Sinclair et al., 2006). In Chapter 2, I showed that mid-shore intertidal south-facing substrata were on average about 1°C to 1.5°C (when considering LW data only) warmer than the opposite north-facing ones, and that hot extreme events were more frequent and intense on the south-facing substrata. Temperatures above 30°C were about 8 times more frequent on south- than north-facing intertidal substrata, and temperatures above 40°C were restricted to the southern aspect only.

Distribution of many sessile organisms may be limited by environmental factors, and especially by thermal stress experienced during aerial exposure at low tide (Connell, 1961; Wethey, 1983; Helmuth and Hofmann, 2001). In Chapter 2, the distributional differences found in the warm-water Lusitanian limpet, *Patella depressa* and the cold-water boreal limpet, *Patella vulgata*, in SW England, were mainly assumed to be linked to temperature differences between aspects. Both species were significantly more abundant on the cooler north-facing substrata, although *P. depressa* was more abundant than *P. vulgata* on both aspects, but especially on the southern one (i.e. two-fold). Thirteen years prior to my survey, *P. vulgata*'s abundance was not affected by aspect, and *P. depressa* was three time more abundant on south- than north-facing in SW England (however data for only one site: Croyde) (Firth et al., 2016). Many closely related species, such as *P. depressa* and *P. vulgata*, are morphologically similar but physiologically distinct which may result in different but overlapping range distributions. For example, among a blue mussel complex comprising three sister species (*Mytilus trossulus*, boreal distribution; *M. edulis*, cold-temperate and *M. galloprovincialis,* warm-temperate), *M. galloprovincialis* had the highest scope for growth (SFG, energy available for growth and reproduction) at higher temperatures (Fly and Hillbish, 2012). This may reflect an energetic advantage associated with its dominance in warmer regions, while no evidence for a SFG adaptation was found at lowest temperature for the boreal *M. trossulus* (Fly and Hillbish, 2012). The limpets *P. depressa* and *P. vulgata* have similar upper lethal temperature limits (e.g. 50% lethal point of 43.3°C and 42.8°C respectively; see Evans, 1948; Southward, 1958), thus they may not have markedly different SFG with respect to temperature. Nonetheless, their differential biogeographical origins may still result in some variations in other facets of their physiology.

The physiological performance of limpet, such as, cardiac activity, upper thermal tolerance limit (by heat coma temperatures, HCT), cellular stress responses (by heat-shock protein expression), have been widely studied. Increasing environmental temperature and exposure to aerial condition resulted for example in an increase of heart rate (Santini et al., 2000; Dong and Williams, 2011), change in aerial respiration rate (Branch, 1979; Tagliarolo et al., 2013), or in an increase of salinity (e.g., in rock pools) that led to a rise in limpets' osmolality and mortality (Firth and Williams, 2009). Rainfall however, seemed to counter balance the effect of high temperature (Firth and Williams, 2009). In addition, the benefit of the mushrooming behaviour to thermoregulate their body temperature is well described (e.g. Williams et al., 2005). Thermal tolerance has commonly been tested *via* heat-shock protein expression. Those proteins are known to respond to a wide range of physical and metabolic stress (e.g. thermal and oxidative stress) and are rapidly synthesised after being exposed to one of these stresses, which will subsequently prevent protein denaturation and aggregation (Oksala et al., 2014). Species from warmer or more stressful environment (e.g. high intertidal shore) tend to induce stress protein (e.g. Hsp60, hsp70) allowing them to increase heat shock tolerance (Sanders et al, 1991; Dong and Williams, 2011; Prusina et al., 2014).

The upper shore limit of the limpet distribution is thought to be restricted mainly by desiccating conditions, temperature variations and osmotic stress (Vermeij, 1971; Branch, 1981; Alistair, 1995). Therefore, osmotic status, or differences in haemolymph (extracellular) osmolality, has been used to investigate the effect of various climatic and weather conditions on limpet physiology and behaviour. These stressors include heat stress (Williams et al., 2011), heavy rainfall (e.g. monsoon) (Denny and Blanchette, 2000; Morritt et al., 2007; Williams et al., 2011), salinity variation (Firth et al., 2009), and freezing stress (Hawes et al., 2010).

In marine molluscs, the colourless haemolymph, fulfils similar functions to both blood and interstitial fluids found in mammals and constitutes about 30-80% of the soft parts (Burton, 1983). Limpets are surrounded in their shell by exosomatic fluid (also referred to as pallial, extraviseral, or mantle water) which is derived originally from seawater trapped within the shell, on the foot and around the nuchal cavity, immediately above their head. Marine molluscs are osmoconformers, i.e. they do not regulate their extracellular osmolality and so their body fluids are in equilibrium with the seawater in which they live (Denny and Gaines, 2007). Therefore, a 'normal' osmolality of a marine mollusc is about 1000 mOsmol.kg^{-1}, similar to full-strength seawater osmolality (Denny and Gaines, 2007), although haemolymph of marine molluscs tends to be slightly hyperosmotic (Burton, 1983). Salinity is an important abiotic factor to an osmoconformer, as any change in salinity produces water movement into and out of cells (Denny and Gaines, 2007). Due to their lack of regulatory abilities, species-specific difference in osmolality must also often be associated with morphological differences in shell or body architecture (Davies, 1969; Vermeij, 1973). For example, bigger limpets may retain more water than smaller ones (e.g. shell length; Morritt et al., 2007) and taller limpets may desiccate at a slower rate than flatter ones (Vermeji, 1973) especially animals with smaller circumference and lower tissue surface area from which water can be lost (Davies, 1969). *Patella vulgata* with its more conical shell than *P. depressa*, could therefore have an advantage and might be less susceptible to desiccation stress.

Two major types of salinity stress may affect marine molluscs during low tide. First, there is ***hypersaline stress***, resulting from desiccation. Here, water leaves the cells and extracellular space, which results in intra cellular crowding, causing cell death in extreme cases. Second, ***hyposaline stress*** due to rainfall or freshwater run off resulting in the dilution of the haemolymph, which in turn will cause cells to swell and burst (Denny and Gaines, 2007).

Low tide during a hot sunny day will increase desiccation stress. Loss of water by evaporation, from both haemolymph and pallial water will concentrate all solutes and thus, result in an increase in the osmotic pressure of these fluids, which drives water to leave the cells (Burton, 1983). Due to its direct contact with the environment (e.g. substratum), pallial water would be predicted to increase first. As only a thin membrane separates the haemolymph and pallial water (Davis and Fleur, 1903), equilibrium between both fluids will eventually take place and the osmotic pressure of the haemolymph will start to increase. When clamped tight onto the substratum, temperature within the shell would increase and stimulate increased metabolism, resulting in the production of metabolites and end products such as organic acids. It will also change the ion balance, and increase CO_2,retention,which in turn would lead to respiratory and metabolic acidosis (i.e. pH decrease in fluids inside the shell and body) (Marshall and McQuaid, 1992; Williams and McMahon, 1998).

Heavy rainfall during low tide has a major impact on haemolymph osmolality via dilution by addition of fresh water, and even dislodgement threat in the case of heavy rainfall (Morritt et al., 2007). The only defence limpets can mount to defend their internal osmotic balance is a behavioural one. They can clamp tightly to the rock in order to reduce contact of their soft tissues with freshwater (Morritt et al., 2007). However, this clamping behaviour may induce a physico-chemical stress with high production of metabolites such as alanine and aspartate (Santini et al., 2001), and associated increase in haemolymph concentration causing ionic and acid base disturbance, and ultimately, a potential increase in pallial water concentration (Morritt et al., 2007). Furthermore, increased relative humidity during rainfall may allow respiratory gas exchange without desiccation, but only if the limpets are not firmly clamped on to their scar. Thus, maintaining aerial gas exchange necessitates a trade-off between maintaining access to the air and the threat of pallial water (and so haemolymph) dilution by contact with freshwater.

Most studies looking at limpet osmolality investigate one climatic condition and for a single species only. In this experiment, I investigate the combined effect of aspect and various climatic conditions on the extracellular osmolality of two species of limpets (*P. vulgata* and *P. depressa*). The aim is to test how aspect, and therefore temperature variation and desiccation stress, influences the physiology of these congeneric limpets, given their different biogeographical origin, and observed aspect-linked differences in abundance on the rocky shore (see Chapter 2). This was achieved by investigating how the osmolality of the haemolymph and pallial water in both species differs with aspect, under four different weather conditions (full sun, partially overcast, windy, and rainy). The following specific hypotheses were investigated:

(1) The Lusitanian *P. depressa* will exhibit different stress responses to the boreal *P. vulgata* depending on aspect and the nature of the weather stress experienced.

(2) Limpet stress response varies with aspect and weather conditions, specifically:

2a - In full sun and partially overcast weather, hypersaline stress (i.e. increased haemolymph and pallial water osmolality) will be higher on warmer south-facing substrata.

2b - During windy conditions, desiccation stress (i.e. increased haemolymph and pallial water osmolality), will depend more on wind direction than aspect.

2c - Heavy rain will cause hyposaline stress (i.e. reduced haemolymph and pallial water osmolality) but with no variation between aspect.

3.2. Material and methods

3.2.1 Field sampling and laboratory analysis

At each of four natural rocky shores, located in the SW Peninsula of England (See Figure 2.2), two gullies were selected based on the vertical dip of the rock strata and their paired north- and south-facing aspects, separated by only few meters and sampling areas chosen to be as flat and vertical as possible, avoiding any microhabitats. From each gully side, ten *Patella depressa* and ten *Patella vulgata* were carefully (and without damage) removed using an oyster knife during spring tide during the summer. Each site was sampled once over one or two days, in 2017 or 2018. Limpet size is an important factor in thermoregulation (Lowell, 1984); smaller limpets tend to have higher body temperatures (Davies, 1970) and lose relatively more water and, consequently, have higher haemolymph osmolality (Williams et al., 2005). In addition, as body size can influence the volume of pallial water (Vermeij, 1973) only limpets from the same size range (20-35 mm length shell) were removed. Both haemolymph and pallial water were sampled using a plastic syringe (vol. = 1 ml) fitted with a 22 g needle as follows:

Upon removal, the limpet was immediately turned ventral side up and the remaining pallial water collected using the syringe, and then transferred to a centrifuge tube (Eppedorf, vol. = 1.5 ml). Once all of the pallial water had been removed, haemolymph was collected from the same individual using another syringe, by direct puncture of the pallial vein (Williams et al., 2005), and the resultant sample transferred to a centrifuge tube. All micro-centrifuge tubes were transferred to a cool box containing ice blocks, to keep the samples cool until they could be returned to the laboratory up to 4 hours after harvest. This sampling generated 640 samples (n= 10 x 2 (fluid type) x 2 (species of limpet) x 2 (aspects: North/South facing) x 2 (gullies per site) x 4 (sites)).

Field sampling was undertaken during various weather conditions, which could potentially have differential impacts on individuals. Accounting for the potential rapid change of weather within the same sampling day, the weather condition, in which each sample was collected, was carefully noted. Although weather conditions are complex and do not always display a single environmental condition, sampling conditions were categorised as 'full sun', 'partially overcast', 'overcast', or 'rainy', depending on the dominant weather condition at the time. Data analyses were performed for each weather condition separately.

To limit complexity in the data, the stressor wind was not investigated. However, on the shore, wind can decrease temperature (Landsberg, 1947; Gallien, 1985; Williams and Morritt, 1995), and depending on its direction and speed, it can also either increase or decrease wave action and alter the splash of intertidal organisms during emersion (O'Gower and Meyer, 1965). Increased air movement is positively correlated with evaporative cooling (Denny et al., 2011) and evaporative water loss of marine animals during low tide (Gallien, 1985). Therefore, increased wind speed may leads to higher desiccation (Iacarella and Helmuth, 2012), which could result in reduced activity (Courtney, 1972) and, in more extreme cases, detachment of intertidal organisms from the rock surface (Courtney, 1972).

It was not possible to standardise collection times because of the time taken to sample so many individuals. When limpets are immersed, water loss will increase with time, at least in hot conditions (Williams et al., 2005). Therefore, limpets sampled at the end of the spring tide would have spent about four hours out of water (and would be more stressed) than those sampled earlier that day at the beginning of low tide. However, to account for this possible confounding fact, or sampling followed exactly the same protocol at each field site, to establish some consistency across all sites, aspects and weather.

A preliminary study on *P. vulgata* showed that freezing samples for one week significantly increased the haemolymph osmolality ($F_{1,13}$ = 8.66, p = 0.012; based on 7 individuals) but not the pallial water ($F_{1,16}$ = 0.29, p = 0.273; based on 10 individuals). Indeed, haemolymph osmolality was 923 ±4 mOsm.kg^{-1} and 951 ±9 mOsm.kg^{-1} before and after freezing, respectively, while the pallial water osmolality was 1007 ±35 mOsm.kg^{-1} and 1065 ±37 mOsm.kg^{-1} before and after freezing, respectively. Therefore, haemolymph and pallial water samples collected in the field were not frozen, but analysed on the same day of collection. When it was not possible to process all the samples on the same day, the untreated samples were placed in a fridge (~ 5°C) and analysed the next day at the latest, which did not affect the results. Although osmolality in pallial water and haemolymph can be positively correlated (i.e. following similar osmotic trends) (Williams et al., 2005; Morritt et al., 2007), which would be predicted in animals with limited osmoregulatory capacity, here both fluids have been analysed separately as they are physiologically different.

The osmolality of (8µl) haemolymph and pallial water samples was measured (where possible in duplicate) with a Vapour Pressure Osmometer (5600, Wescor, USA) and expressed in milliosmoles per kilogram (mOsm.kg^{-1}). The amount of stress was estimated by comparing the osmolality obtained in both fluids and under the different variables, with the inshore seawater osmolality (about 1000 mOsmol.kg^{-1}; Denny and Gaines, 2007), which corresponds to the expected osmolality during limpet immersion at high tide. A gradient of 1 mOsmol.kg^{-1}, although only 0.1% of total osmolality, represents a significant driving force for osmosis (i.e. water movement across cellular membranes) (Burton 1983). Consequently, anything above a 0.1% osmotic difference with the inshore seawater osmolality should in theory be considered as osmotic stress, with a positive value referring to desiccation stress (water loss) and any negative value referring to dilution stress (water addition). However, due to potential natural and intra-specific variations; I refer in my study to 'significant' stress when the stress reaches more than 5% difference with the inshore seawater osmolality.

3.2.2. Statistical analyses

One-way ANOVA was used to compare both fluids (separately) between each species, with aspect (north- and south-facing) in order to check for inter-specific differences, and then under the different weather conditions ('full sun', 'partially overcast', 'overcast, and 'rainy') in order to check the implication of aspect under different weather. In this study, as weather conditions tended to change from one site to another (because collected during a different day), sites were not considered as factor but as replicates. All the ANOVA analyses were performed with Minitab version 17.

3.3. Results

3.3.1. Biogeographic origin, osmolality and aspect

When not accounting for the different weather conditions, overall osmolality of both haemolymph and pallial water did not differ between species ($F_{1,348}$ = 0.452, p = 0.452 and $F_{1,345}$ = 0.05, p = 0.823; respectively; Figure 3.1). Osmolality of haemolymph did vary with aspect ($F_{1,354}$ = 5.01, p = 0.026) but not pallial water ($F_{1,354}$ = 1.75, p = 0.187). For both limpet species there was an overall trend of hypo-osmolality (Figure 3.1), on north-facing substrata, and hyper-osmolality on south-facing ones, however, not significant. Surprisingly however, *P. depressa* tended to show higher osmotic stress on south-facing substrata than its congener, although this was not significant. In addition, and unlike *P. vulgata*, osmotic stress (haemolymph only) in *P. depressa* varied with aspect being greater on south-facing substrata ($F_{1,179}$ = 6.06, p = 0.015; Figure 3.1).

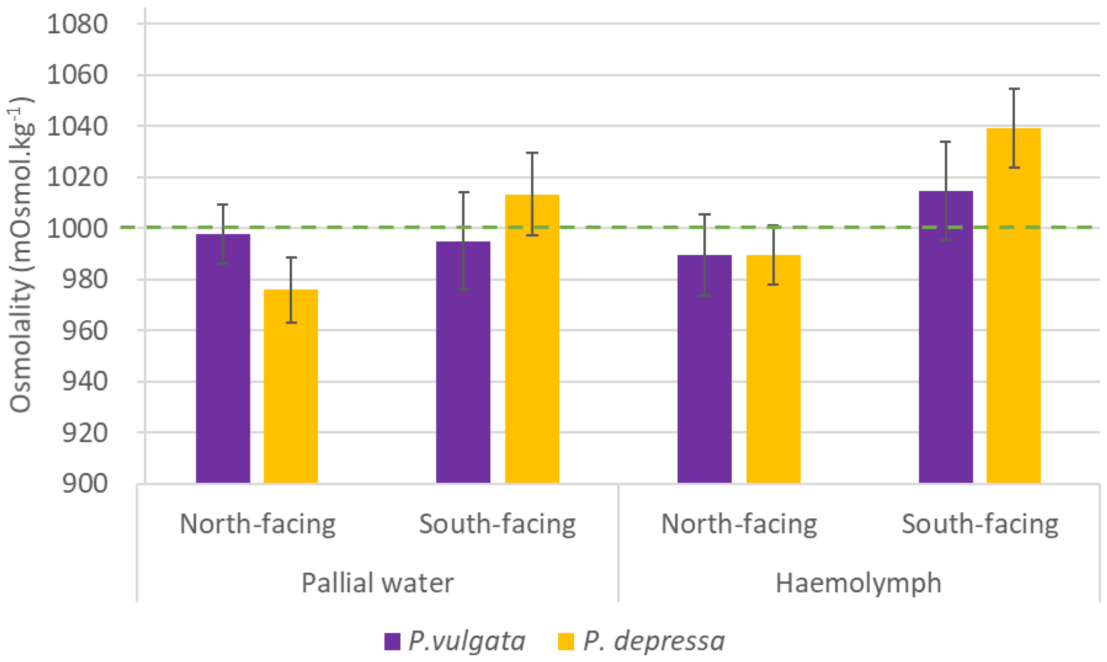

Figure 3.1: The influence of slope aspect on mean osmolality (± SE) of haemolymph and pallial water from two different limpet species*,* the boreal *Patella vulgata* (violet), and the Lusitanian *Patella depressa* (yellow)(at $p < 0.05$). Limpets were sampled during the summers 2017 and 2018 from four shores located in SW England. The dotted green line represents the inshore seawater osmolality (1000 mOsmol.kg^{-1}), i.e. the 'normal' osmolality that any osmocomformer species, like limpets, have when immersed in seawater (Denny and Gaines, 2007).

3.3.2. Aspect, weather conditions and osmolality variation

Despite the apparent lack of aspect or species-specific differences in overall osmolality (for all weather conditions combined) of both fluids, analysis of data according to the different weather conditions ('rainy', 'overcast', 'partially overcast', 'full sun'), revealed some significant differences (Table 3.1).

Osmolality regulation of *P. vulgata* and *P. depressa* significantly differed only on north-facing aspect, and especially in the haemolymph. *P. vulgata* had greater (indication of desiccation/hypersaline stress) and lower (indication of dilution/ hyposaline stress) haemolymph concentration than *P. depressa*, in full sun and rainy conditions, respectively.

Table 3.1 The influence of slope aspect on mean osmolality (mean ± SE) of haemolymph and pallial water from two different limpet species, the boreal *Patella vulgata*, and the Lusitanian *Patella depressa*, under different weather conditions. Limpets were sampled during the summers 2017 and 2018 from four shores located in SW England. Significant difference in osmolality ($p< 0.05$) between species is in bold with * or ** for significance at $p< 0.05$ or $p< 0.01$, respectively.

Weather Conditions	**Aspect**	**Haemolymph (mOsmol.kg^{-1})**		**Pallial water (mOsmol.kg^{-1})**	
		Patella vulgata	*Patella depressa*	*Patella vulgata*	*Patella depressa*
Rainy	North-facing	**827.8 ±30.3**	**920.9 ±18.4**	891.9 ±25.4	921.6 ±18.5
		$F_{1,37} = 7.06$, $p = 0.012$ *		$F_{1,36} = 0.88$, $p = 0.355$	
	South-facing	580.9 ±62.2	707.2 ±40.5	641.1 ±29	686.5 ±47.8
		$F_{1,18} = 2.90$, $p = 0.106$		$F_{1,18} = 0.66$, $p = 0.428$	
Overcast	North-facing	998.0 ±34.9	1038.7 ±10.8	992.5 ±9.7	997.5 ±13.8
		$F_{1,39} = 1.30$, $p = 0.262$		$F_{1,39} = 0.09$, $p = 0.767$	
	South-facing	1029.4 ±15.5	1040.0 ±12.4	998.9 ±14.1	1001.0 ±17.5
		$F_{1,38} = 0.29$, $p = 0.596$		$F_{1,37} = 0.01$, $p = 0.926$	
Partially overcast	North-facing	**1016.6 ±13.3**	**957.4 ±18.4**	**1000.4 ±10.5**	**942.0 ±14.5**
		$F_{1,77} = 6.85$, $p = 0.011$ *		**$F_{1,78} = 10.61$, $p = 0.002$** **	
	South-facing	1050.9 ±9.1	1068.61 ±7.3	1027.1 ±6.5	1043.9 ±6.0
		$F_{1,95} = 2.20$, $p = 0.141$		$F_{1,93} = 0.36$, $p = 0.066$	
Full sun	North-facing	**1187.7 ±6.2**	**1163.2 ±7.5**	1197.7 ±11.5	1183.2 ±13.9
		$F_{1,18} = 6.30$, $p = 0.022$ *		$F_{1,18} = 0.65$, $p = 0.430$	
	South-facing	1251.6 ±17.0	1220.2 ±18.0	1228.8 ±13.7	1213.5 ±26.4
		$F_{1,18} = 1.59$, $p = 0.223$		$F_{1,18} = 0.27$, $p = 0.612$	

During partially overcast condition, *P. vulgata* had significantly lower haemolymph and pallial water concentration than *P. depressa* on north-facing aspects.

Due to the overall similarity in osmolality of *P. vulgata* and *P. depressa*, and the very few inter-specific differences identified so far, results for both species were pooled for further analysis (i.e. Figure 3.2 forward). Taking the two species pooled together, both pallial water ($F_{1,349}$ = 160.91, p = 0.000) and haemolymph ($F_{1,352}$ = 136.75, p = 0.000) osmolalities differed under the different weather conditions and aspect.

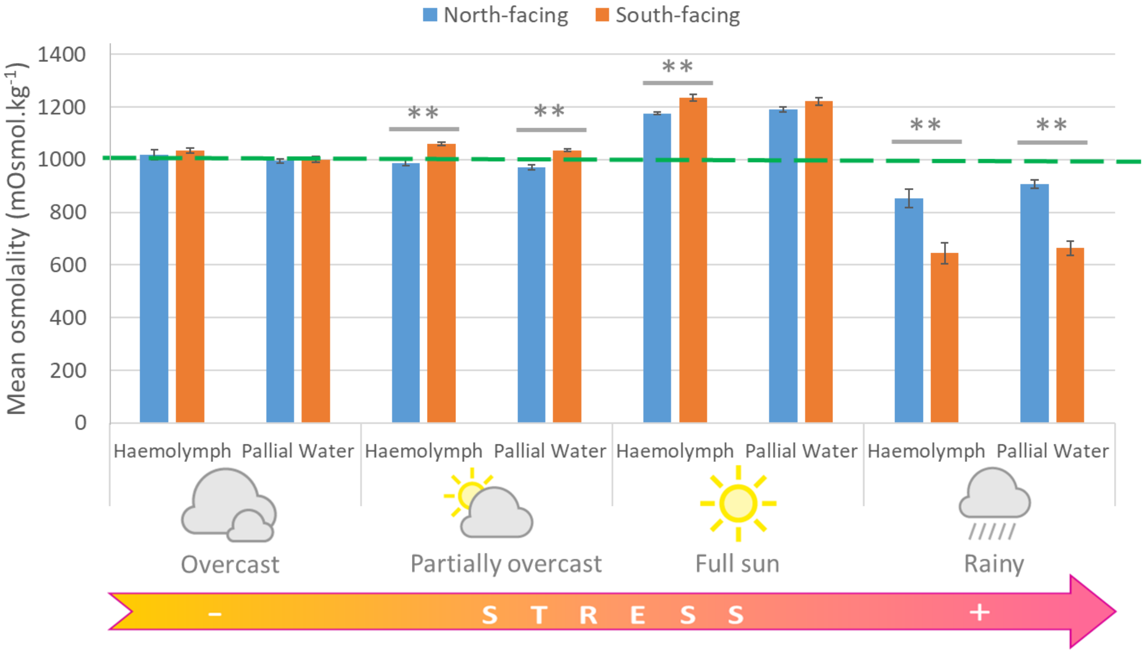

Figure 3.2: Mean osmolality (± SE) of haemolymph and pallial water from two different species of limpets, *Patella vulgata* and *Patella depressa* (however, here pooled together as no significant inter-specific differences), sampled in the SW of England during summers 2017 and 2018, under four different climatic conditions (full sun, partially overcast, overcast and rainy), and over two aspects (blue, north-facing; and red, south-facing). The dashed green line represents the inshore seawater osmolality (1000 mOsmol.kg^{-1}), which is also the 'normal' osmolality that a limpet, or any other osmocomformer, would have when immersed in seawater (Denny and Gaines, 2007). **, significant at $p < 0.01$ between aspect.

Overcast days were the least stressful for limpets, with no difference in osmolality according to aspect. Haemolymph and pallial water osmolalities were unchanged from the inshore seawater osmolality (1000 mOsmol.kg^{-1}) (Denny and Gaines, 2007), which roughly corresponds to the osmolality limpets should have while immersed in seawater during high tide.

Partially overcast days were the second least stressful weather condition. Haemolymph and pallial concentration were on overall similar to the inshore seawater osmolality, with a difference with it up to 6%, which is just above the set 5% of osmolality change indicating threshold of significant ecophysiological stress (see in Material and method section for further details). There was a significant difference in osmolality in both the haemolymph ($F_{1,174}$ = 34.04 , *p* = 0.000) and pallial water ($F_{1,173}$ = 41.49 , *p* = 0.000) according to aspect, with greater osmolality on the south- than north-facing substrata (1060.2 ±6 against 987.4 ±11.7 mOsmol.kg^{-1} for the haemolymph, and 1035.8 ±3.6 against 971.2 ±9.5 mOsmol.kg^{-1} for the pallial water).

During full sun days, there was significant differences in aspect in the osmolality of haemolymph only ($F_{1,38}$ = 19.24 , *p* = 0.000), with greater osmolality on south- than north-facing substrata (1235.9 ±12.9 mOsmol.kg^{-1} and 1175.5 ±5.6 mOsmol.kg^{-1}, respectively) reflecting desiccation. Given the stipulation that osmotic stress occurs at osmolality 5% above or below the presumed 'normal' osmolality for any osmoconformer in contact with seawater at 1000 mOsmol.kg^{-1} (Denny and Gaines, 2007), full sun days are considered to be significant events for both aspects. Although significant aspect-related variation in osmolality was only found in haemolymph, the level of desiccation in the pallial water was still on average similar to the one experienced in the haemolymph, ranging from +17% to +24% compared to the inshore seawater on south- and north-facing substrata.

During rainy days, aspect was affecting osmolality of haemolymph ($F_{1,37}$ = 15.88 , *p*= 0.000) and pallial water ($F_{1,37}$ = 27.81 , *p* = 0.000), with much lower concentration on the south- than north-facing substrata, indicating greater dilution (hyposaline stress) on that aspect. Both fluids behaved similarly on both aspect (Figure 3.2). Rainy condition was recorded in this experiment as being the most stressful weather condition with up to 34-35% osmotic stress (compared to the inshore osmolality) on the south-facing substrata for both fluids.

3.4. Discussion

Patella vulgata displayed greater osmotic stress than *Patella depressa* during only rainy and full sun situations (See Table 3.1) and only in its haemolymph, while *P. depressa* was more stressed than its congener, in both its fluids but on northern aspect only. Consequently, there was little support for the hypothesis 1 that the congeners would show variation in stress responses associated with their different biogeographic origin. When species were combined, I also found physiological variation in limpet osmolality according to aspect under different weather conditions, supporting hypothesis 2. Greater desiccation was apparent in limpets' haemolymph on south- than north-facing substrata during partially overcast and full sun conditions, while greater dilution happened in limpets' pallial water on north-facing substrata during overcast days and in both fluids from the south-facing substrata during rainy condition. Osmotic stress measured during overcast and partially overcast conditions could be considered non-significant assuming the '5% departure from' inshore seawater osmolality criteria. Overall, rainy condition was the most stressful weather condition for limpets, followed by full sun.

Although several studies have investigated differences in the thermal tolerance and/or physiological traits of closely-related species from different biogeographic origins, they compare species from different tidal heights and/or distinct latitudinal ranges (e.g. Stillman and Somero, 2000; Sorte and Hofmann, 2005; Fly and Hillbish, 2012). This can lead to asynchrony between timing and amplitude of the tidal environment between sampling sites. Not only does that potentially confound conclusions it also limits potential comparison with the current study. In general however, warm-water species have better thermotolerance than congeners from colder regions (Sorte and Hofmann, 2005; Fly and Hillbish, 2012). In some cases however, since warm-adapted species may live closer to their upper thermal limits, they would have less ability to increase heat tolerance through acclimation than cold-adapted species (Somero, 2005), and this is more true for species on their south range (trailing edge) (e.g. Sorte and Hofmann, 2004).

The range limit of the Lusitanian *P. depressa* are extending northwards (Mieszkowska et al., 2006; Firth et al., 2009; Hawkins et al., 2009), moving into the traditional range of the boreal *P. vulgata,* which naturally extends to Norway. As my study was performed (in SW England) relatively close to *P. depressa'*s northern limit (Wales), it would be reasonable to think that individuals close to their northern range limit (leading edges) should be less threatened by increased temperature than the ones along the trailing edges of its southerly distribution. Indeed, populations near their trailing edges may live closer to their upper thermal limits and would therefore have less ability to increase heat tolerance through acclimation than individuals from more northern latitudes, like in SW England. *P. depressa* was expected, in this experiment, to exhibit less desiccation stress than its boreal congener *P. vulgata* on both aspects, and even more on the warmer south-facing substrata. Overall, however, both species had similar osmolality and osmotic stress across both aspects and weather conditions, refuting the first hypothesis.

Patella vulgata only experienced more stress than *P. depressa* during rainy (lower osmolality = higher dilution stress) and full sun conditions (higher osmolality = higher desiccation stress) in its haemolymph, on north-facing substrata only.

Rainfall decreases the salinity of limpet internal fluids with likely impact on internal oxygen concentrations (Firth and Williams, 2009). In addition, when clamped to the rock surface for a prolonged time, limpets can experience anoxia, which tend to reduce muscle tension, and this is especially known for *P. vulgata*'s foot muscle (Grenon and Walker, 1981). This reduction in foot muscle tension would prevent efficient adhesion to the substratum and increase hypo-osmotic stress (dilution) under rainy conditions. Therefore, the greater haemolymph dilution of *P. vulgata* compared to *P. depressa* during rain, found in this chapter, could be explained by the fact that this former species is potentially more susceptible to both anoxia and reduced foot muscle tension than its congener.

Although greater desiccation stress experienced by *P. vulgata* compared to *P. depressa* was only found on one aspect in full sun condition, this greater hyper-osmotic stress could still suggest two conclusions. First, the fact that *P. depressa*'s upper thermal limit is 0.5°C greater than *P. vulgata* (43.3°C for *P. depressa* and 42.8°C for *P. vulgata*; Evans, 1948) and can survive for longer under hot aerial conditions (3.5-3.75 h for *P. depressa* and 2.75-3 h for *P. vulgata* under 40°C exposure; Evans, 1948), could give the former a physiological advantage in extreme hot days. Second, several authors have argued that shell shape and colour influence thermoregulation (Davies, 1969; Vermeij, 1971, 1973; Lowell, 1984; Nuñez et al., 2018), and shell shape variation in limpets has even suggested to be adaptational response to desiccation (Lowell, 1984; Nuñez et al., 2018). *P. vulgata* has a lighter coloured, more conical shell (leading to greater extraviseral space, which could result in reduced desiccation; Marshall and McQuaid, 1992) which could limit both water loss and hyper-osmotic stress. Therefore, results of my experiment suggest two points. First, this previous theory does not fully explain inter-specific variation. Or, second, although *P. vulgata* had a shape and colour shell advantage over *P. depressa*, this latter would have exceeded the former. Due to its more southerly distribution, *P. depressa* might be a better performer and might be more heat and desiccation tolerant than *P. vulgata,* which has a more northerly distribution. In this case, *P. vulgata* would lose advantage over its congener. Although this was not investigated in this study, both limpet species may also prefer slightly different micro-habitats. It is, however, difficult to explain why this osmotic inter-specific variations happened on the north-facing substrata only, where overall temperature and hot extreme events were less frequent than on the south-facing substata.

Despite the few inter-specific variations, overall osmolality of *P. depressa* and *P. vulgata* did not differ from each other (first hypothesis refuted). This suggests that either biogeographical origin of closely related species or potential variation in limpet shell architecture and colour do not always influence their physiology and performance, or might even counter balance each other. It is important to keep in mind my study was performed during summer only, and species performance is not homogenous over time. Jansen et al. (2007) demonstrated that among congeneric mussels, the warm-water *Mytilus galloprovincialis* was more sensitive to cold shock than the cool-water species *M. edulis*. Similarly, both *Patella* species might differ in their performance under cold weather conditions; this could be tested by repeating this experiment over the winter.

As demonstrated in Chapter 2, south-facing substrata are significantly warmer than north-facing ones and endure more extreme hot temperatures, therefore, it is not surprising that aspect would have impacted limpet osmolality, under different weather conditions (hypothesis 2 supported). During both full sun, and partially overcast days, an aspect effect emerged, with significantly higher osmolality of the haemolymph on south- than north-facing substrata. Rock surface temperature is strongly related to thermal and desiccation stress experienced by invertebrates (Marshall et al., 2010). Therefore, during extreme heat, south-facing substrata would warm up more than the opposite north-facing ones, and limpets from south-facing aspect would therefore suffer greater desiccation stress. Even though temperature is considered as probably the most important abiotic factor impacting intertidal species during aerial exposure (Somero, 2005; Sorte and Hofmann, 2005), my results also support the observation that rainfall can even be more stressful for limpets. Rain was indeed the most stressful weather condition out of the four studied in this study, with an average decrease of osmolality (compared to inshore seawater osmolality) of 22.7%.

In temperate climates, rain tends to decrease air temperature and increase relative humidity, which might encourage limpets to move and graze on the rock surface. Dilution in that case is unavoidable. Moreover, Morritt et al. (2007) suggested that swelling of limpet tissues, especially at the mantle edge, would affect the capacity to clamp back to the rock and form a tight seal. This could also be a (combined) reason explaining why rain tends to be more stressful than desiccation on both *P. depressa* and *P. vulgata*. Results also showed a significant effect of aspect, with a decrease of 34.6% and 54% of limpets' osmolality (both fluids combined as not significantly different) on south- and north-facing substrata, respectively, compared to the inshore seawater osmolality. A south-southwest coastal wind (Channel Coastal Observatory, 2019) was recorded during collection of the samples. Thus, it is reasonable to suggest that the rain was not falling fully vertically but at a certain angle from S-SW to N-NE, following the wind direction. In that case, more rain would have been running down on the vertical south-facing substrata, explaining the higher hypo-osmotic stress on that aspect, while north-facing substrata would have been slightly more protected from both wind and rain. Chew et al. (1999) already suggested that the marine molluscs *Onchidium tumidum*[3] was better able to cope with hyper-osmotic stress (linked to desiccation) than hypo-osmotic one. Therefore, following this, another explanation, albeit very speculative, is that limpets *P. depressa* and *P. vulgata* living on much warmer south-facing substrata might tend to put more effort and energy in developing a better acclimation and resistance to hyper-osmotic stress than limpets on cooler north-facing substrata, and would thus cope less efficiently with hypo-osmotic stress.

Hoffman and Blows (1994) thought that comparing closely related species with different distributions could allow identifying traits responsible for species' distribution. My study failed to provide concrete physiological difference (based on osmolality) between two closely related species with different distributional ranges that were expected to react differently to temperature. Morritt et al. (2007) investigated the difference in physiological stress experienced by the limpet *Cellana grata* on vertical *vs.* horizontal substrata. Two methods were tested: osmolality of pallial water and haemolymph, and cardiac activity, under the same situation. A significant effect of the substratum orientation (vertical *vs*. horizontal) was found with cardiac activity only, but not with the osmolality of the limpets. This could suggest that physiological response to any stress might not be detectable via all physiological tests, and therefore all organs of the animal. Physiological differences between *P. depressa* and *P. vulgata* on both north- and south-facing substrata should be investigated further using other techniques.

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[3] Note that the correct spelling used by the authors should have been *Onchidium tumidum* and not *Onchidium tumidium,* and the current accepted name is now *Paromoionchis tumidus.*

Chapter 4: Distribution patterns of terrestrial plants according to aspect in hedgerows

4.1. Introduction

Weather and climate are very important factors dictating the distribution and functioning of living organisms (Stoutjesdijk and Barkman, 2014; Suggitt et al., 2014; Parmesan and Hanley 2015). Although vegetation, soil and fauna are interrelated in a complex manner, climate is key to understanding the distribution of plants. In addition, topographic factors such as altitude, aspect and slope inclination greatly affect animals and plants (Huggett, 2004). As illustrated in Chapter 1 (Figure 1.5), however, aspect, or slope orientation, can create temperature variation above that experienced at different elevations or latitudes. Slope inclination and orientation modify the amount of solar radiation received by a surface. During a clear summer day for example, a British south-facing grassland slope received up to 700 Wm^{-2} more than the opposite north-facing one (Bennie et al., 2008). The amount of incident radiant energy is probably the most important factor directly affecting the ambient temperature (Davies et al., 2006). In Chapter 2, I demonstrated that in the rocky intertidal, the south-facing substrata had significantly greater daily mean average (during aerial exposure, LW) and frequency of hot extreme temperatures than on north-facing ones. On land, Rorison et al. (1986) reported that in some British grasslands, south-facing slopes had an annual mean temperature 2.5-3°C greater than north-facing ones. In Canadian prairie, even gentle south-facing slopes (13-18°) have increased average air and soil temperatures by up to 1°C and 3.6°C respectively, compared to the opposite north-facing ones (Ayyad and Dix, 1964).

As reviewed in Chapter 1, in addition to changes in temperature, complex topography, such as aspect, can also affect soil moisture, impacting directly soil fauna and plants and undoubtedly influencing local variation in plant species distribution patterns and community structure. Such variation has long fascinated plant biologists, especially in mountain ecosystems. In Mediterranean mountains over the world (e.g., in Texas see Cottle 1932; in Israel see Kutiel 1992; in Australia see Bale et al., 1998; and in Chile see Badano et al., 2005) cooler pole-facing slopes tend to form dense forests and/or shrublands characterised mainly by evergreen, scleromorphic, hygrophilous, or mesomorphic species. Tall grasses (Cottle, 1932), mosses and liverworts (Åström et al., 2007), ferns and sedges (Bale et al., 1998) also tend to dominate the lower layer of pole-facing slopes of Mediterranean and temperate-climate mountains. On the other hand, the warmer and drier equator-facing slopes of Mediterranean mountains tend to be characterised by more fragmented/open forests (Bale et al., 1998), or are dominated by shorter xeric vegetation (Cottle, 1932; Badano et al., 2005). The open canopy provides opportunity for shorter grasses, herbaceous plants and hardy ferns (Cottle, 1932; Kutiel, 1992; Bale et al., 1998). Equator-facing slopes, suffer from greater species loss in response to clear-cutting forest (Åström et al 2007) and due to their drier soil and more flammable vegetation, are also more prone to fire (Huggett, 2003; Lafon, 2019). Cantlon (1953) reported differences for tree, shrub, herb, and bryophyte layers between pole- and equator-facing slopes in North America and interestingly, noted how the differences in herbaceous layer were greater than those in tree composition. This degree of difference was the result of the presence of certain species restricted to one aspect, and to the large difference in species abundance between aspects.

Despite the focus on mountains as a model for the influence of aspect on vegetation, these studies often fail to account for different land uses, soil properties (Yimer et al., 2006; Sidari et al., 2008; Begun et al., 2010), and local climate (e.g., see rain shadow effect, Galewksy, 2009; Sklenář and Lægaard, 2018) which can vary, independently from aspect. As aspect has often been associated as a natural tool to study the impact of temperature variations, especially in plants distribution, minizing other environmental or anthropogenic variations is therefore essential. One way of limiting combinaison of factors is to downscale the choice of study sites.

As seen in Chapter 1, rapid environmental changes linked to ACC have already started to impact species and ecosystems globally. Among terrestrial ecosystems, the most common responses to climate change are phenological shifts (e.g. flowering, fruiting, bird migration, animal reproduction etc.) and change in species range distribution (Letcher, 2016). Shift of species distribution, essentially poleward and towards higher latitudes (Parmesan and Hanley, 2015) are also linked to change in biodiversity (Parmesan and Yohe, 2003; Walther et al., 2009; Storlie et al. 2014). As we are facing one of the greatest challenges in modern science in predicting how ACC will affect species (Schwenk et al., 2009), robust models are more needed than ever. Potter et al. (2013) stressed the need to downscale grid length in species distribution models, in order to improve our understanding and lead to better predictions. In addition, due to its temperature- and moisture-related variations in species distribution, slope aspects (e.g., north- and south-facing) have already been suggested as a model system that could inform us on potential future variations associated with ACC (Nevo, 2012). Therefore, this chapter will aim to investigate the effect of slope aspect on vegetation at a small-scale (smaller than mountain), on hedgerows, very common and important habitat in the British Isles, offering tall and vertical hedges, which could remind the shape of the intertidal gullies sampled in Chapter 2.

By virtue of their structure (i.e. narrow and tall), hedgerows, according to their orientation, likely display very strong microclimatic variations. Even though the base is the dampest part of hedgerows (Hooper et al., 1976), exposure to full sun can encourage much drier and hotter conditions (Huggett, 2014). Shaded sides can be 0.5 – 2.0°C cooler, and with higher relative humidity than a sunny one (Pollard et al., 1974). Therefore, there is a growing interest in the impact of aspect on the floristic components of the hedgerow banks (Pollard et al., 1974), plant phenology (Khemira et al. 1993) and animal activity (Proesmans et al., 2018). However, detailed systematic study according to aspect are yet rare, and to my knowledge, no study has been providing accessible abundance data of plant species, family and other taxonomic or functional groups of hedgerow vegetation according to north/south facing. Indeed, many authors would just state a trend or focus on selected species. For example, Dowdeswell (1987) only reported that the south-facing herbaceous layer of hedgerows in England were more 'luxuriant' and diverse than north-facing ones, with meadowsweet (*Filipendula ulmaria*) dominant in south-facing aspects but absent on the grass and rush-dominated north-facing hedgerow margins.

Vegetation distribution is controlled by many direct and indirect factors. First, plants vary greatly in their ability to tolerate extreme heat or cold (Huggett, 2004) and temperature often dictates distributional boundaries (Stoutjesdijk and Barkman, 2014). Species reaching the limit of their distributional range tend to find themselves on slopes facing the centre of their range (Huggett, 2004). In other words, in the Northern hemisphere, species with a southern distribution reaching their northern range limit (leading edge) might find south-facing slopes more suitable; while species with northern distribution might be found more abundant on the north-facing slopes near their southern range limit (trailing edge) (Stoutjesdijk, and Barkman, 2014). Second, plants have different ecological requirements (e.g., soil moisture content, temperature, light exposure etc.) which mean, they would respond to distinct microclimate (Classen et al., 2005) and habitats (DEFRA, 2007). In addition, in any given habitat, plants, animals and soil are interconnected and influence each other. Linkage between roots, biological turn over (through biomass consumption and decomposition, humus formation, and partial reuse of mineralized components) and nutrient cycling contribute to the integration of plant communities (van der Maarel, 2005). Plant species richness and distribution are also controlled by belowground soil-dwelling invertebrates *via* predation on dormant seeds, mortality after germination or during seedling establishment (Brown and Gange, 1989). Aboveground herbivory, especially on seedlings (Hanley et al., 1995; 1996) is also critical for plant settlement and survival, and therefore distribution patterns. Although this chapter covers only the plant survey on hedgerows, the role of decomposition (and by inference nutrient cycling) as well as soil mesofauna distribution and richness is investigated in Chapter 5.

Here, the influence of aspect on plant species abundance and richness were investigated at a local-scale using British hedgerows as a model system. Moreover, despite the well-known patchiness and mosaic patterns of plants distribution (van der Maarel, 2005); most aspect-related plant surveys considered only very few, or even a single study site, thus limiting inference regarding local or regional distribution patterns. To mitigate this limitation several sites were sampled to address the following questions:

(1) Does plant richness vary with aspect?

(2) Do species with different ecological requirements prefer north- or south-facing aspects?

(3) Is there any evidence that geographical origin of species affects their distribution on either aspect? For example, are thermophilic species more common on south- than north-facing aspects and *vice versa* for cold-adapted species?

4.2. Material and methods

4.2.1. Hedgerows as a model system

Hedgerows are strips of woodland edge habitat bordering agro-ecosystems and transport networks. Although there have been major losses over recent decades, the total extent of hedgerows in Britain was estimated in 2008 at about 477,000 km (Carey et al., 2008) with limited losses since then. By virtue of their regional extent, age, structural heterogeneity, and linearity, they represent vitally important conservation habitat in the degraded rural and urban landscape of the British Isles (Dover, 2019). Hedgerows have been part of the British landscape for at least a thousand years, but most were planted between 1750 and 1850 following a series of Enclosure Acts where the British Parliament empowered enclosure of open fields and common land by rich landowners (Jennings, 1978). The earliest were created about 5,000 years ago by forest clearance in order to form fields, but subsequently, additional hedges were planted by farmers to create barriers or shelter crop plants (Jennings, 1978). Many hedges in SW England are more than 800 years old (Hooper et al., 1976) and the number of woody plant species present in each hedgerow may be a good indicator of their age (Chapman, 1994). Hedgerows are often compared to woodland habitat or woodland corridor, accommodating some rare woodland species of high ecological values. However, several authors, (see French and Cummins, 2001), have debated this status and an extensive hedgerow survey in Britain, only 12% fitted their 'woodland class'.

Hedgerows are formed of two parts (Figure 4.1A), the *hedge,* self-supporting woody vegetation usually forming a boundary or barrier, and the *hedge-bottom* or *hedge bank,* usually an earthy bank which is mainly covered by a graminoid and herbaceous ground flora

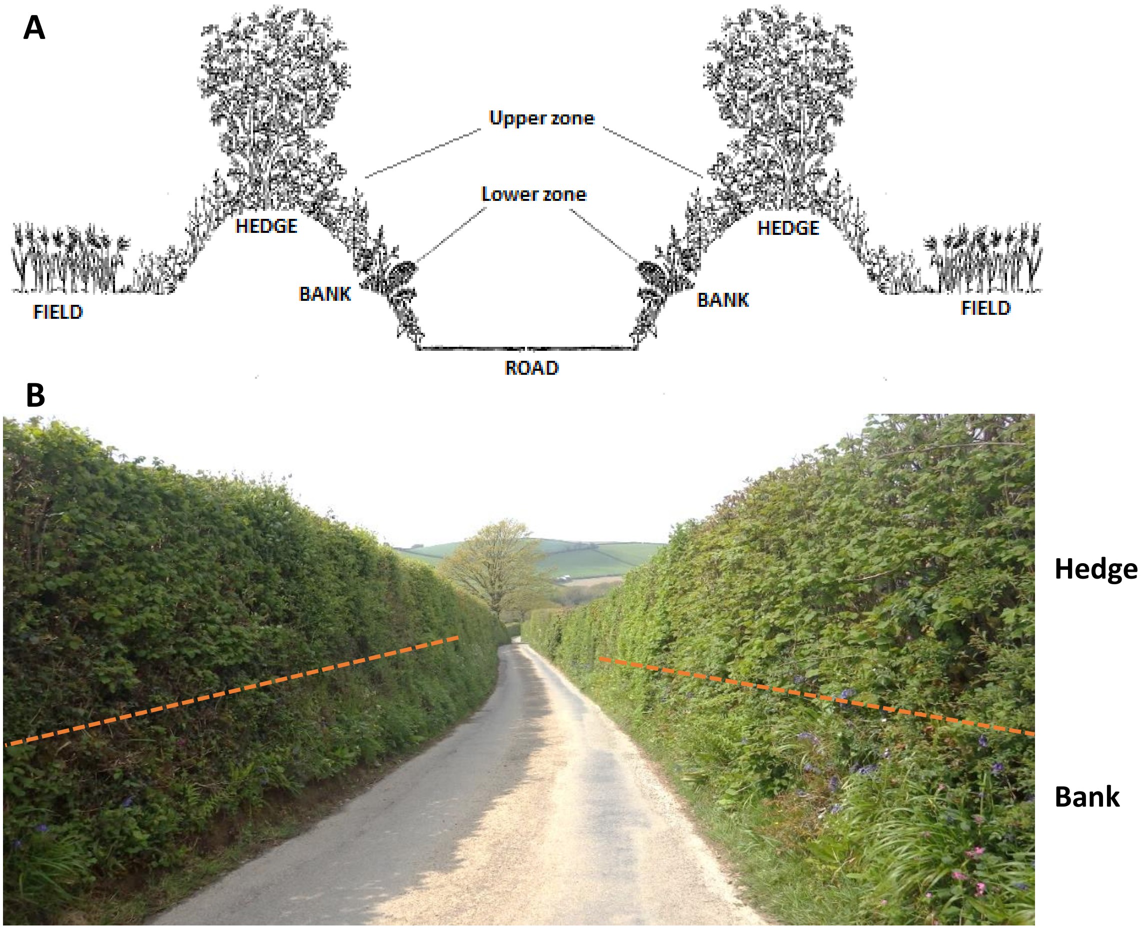


Figure 4.1: **A.** Description of the type of hedgerows sampled on both side of a countryside road (Redrawn from figure Dowdeswell, 1987 pp 45). **B.** Picture of hedgerows (with hedge and hedge bank) of Creacombe site, displaying north (shaded) and south (sunny)-facing hedgerows (taken on the 4th of May 2017 at 13:30). The plant survey was done on the upper zone of the hedge bank.

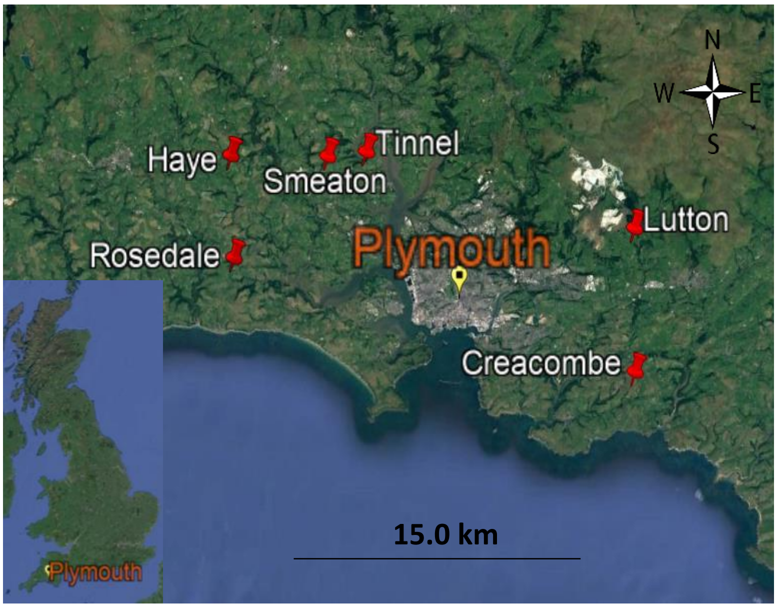
(including ferns and bryophytes). Due to the importance of historical, management and ecological effects between those two parts of the hedgerow, hedges and hedge-bottoms are treated as ecologically independent units (French and Cummins, 2001).

Most hedgerow trees are deciduous (Wilson, 1979), and the relative contribution of each species varies regionally across the UK (Chapman 1994). In SW England, the most common hedgerow species are *Fraxinus excelsior* (ash), *Fagus sylvatica* (beech), *Prunus spinosa* (blackthorn or sloe), *Rosa canina* (dogrose), *Crataegus monogyna* (hawthorn*), Coryllus avellana* (Hazel), *Quercus robur* (English oak) (Bickmore, 2002; Hodgson, 2010). British hedgerows support about 500-600 vascular species, although only half this number occurs frequently (Pollard et al., 1974) and no plant is restricted to this habitat; i.e. species found in hedgerows are normally from nearby habitats (past or present).

Flowering plant composition is thought to be a good indicator of hedge age and conservation status. For example, the Wood anemone (*Anemone nemorosa*), and Primrose (*Primula vulgaris*), Dogswood mercury (*Mercurialis perennis*), Yellow archangel (*Lamiastrum* ancient hedge (Chapman, 1994).

4.2.2. Study sites

Hedgerows are varied (e.g. founded on banks or stonewalls, with a ditch, stream, or field margin at their base) and so I sampled only hedgerows planted onto an earth bank (also called ‘turf hedge’ or ‘Devon hedge’ in SW England; Menneer, 1994) with absence of ditch, stream and grassland strip on the sampled side of the hedgerow. Six countryside roads (Figure 4.2) with structurally similar adjacent hedgerows on both roadsides located in SW England (Figure 4.1 and Table 4.1) were sampled. All locations were sites on west-east running roads in order to provide adjacent north- and south-facing hedgerows and situated away from houses, trees, or any feature, causing additional shade, variation in plant propagule supply, or disturbance. In addition, because the ground flora composition of hedgerows in SW England varies between road- and field-facing margins, due to agro-chemical use (see Grove et al., 2007; Hanley & Wilkins, 2015), surveys weres carried out on the road-facing side of the hedgerow only. As this survey was conducted in the Northern Hemisphere, hereafter south-facing hedgerows are referred to as ‘equator-facing’, and north-facing as ‘polar-facing’.



Location	Latitude and Longitude
Tinnel	50°27’10.35’’N 4°13’59.27’’W
Smeaton	50°26’58.10’’N 4°16’1.69’’W
Rosedale	50°23’36.97’’N 4°21’21.45’’W
Haye	50°27’70.22’’N 4°21’39.97’’W
Lutton	50°19’53.32’’N 3°58’44.04’’W
Creacombe	50°24’36.53’’N 3°58’45.71’’W

Figure 4.2: Location of the six countryside roads (lanes) with their latitude and longitude coordinates studied in the surroundings of Plymouth, in the SW of England, UK. All hedgerows on both sides of the countryside roads were identical in type (hedge planted on an earth bank, with absence of a ditch), and similar hight.

Table 4.1: Height of the hedges and hedgerow bank, and major shrubs and trees species forming the hedges in each studied sites (see locations in Figure 4.2). S, referes to 'south-facing', and N, to 'north-facing' hedgerow. Note that due to the vegetation overgrowing the hedge, the height of this one is only approximative, as delimitation between bank and hedge would not always be distinct.

Sites and aspect	height (cm) hedge	bank	Main hedge-forming woody plant
Tinnel S	125	90	*Betula pendula*; *Betula pubescens*; *Prunus spinosa*
Tinnel N	110	120	*Betula pendula*; *Betula pubescens*
Smeaton S	100	110	*Fraxinus excelsior*; *Quercus robur*
Smeaton N	80	110	*Acer campestre*; *Corylus avellana*; *Quercus robur*
Rosedale S	100	110	*Corylus avellana*; *Ligustrum vulgare*
Rosedale N	90	140	*Corylus avellana*; *Prunus spinosa*
Haye S	70	150	*Quercus robur; Prunus spinosa*
Haye N	100	150	*Prunus spinosa*
Lutton S	120	120	*Corylus avellana*; *Fraxinus excelsior*
Lutton N	80	140	*Corylus avellana*;
Creacombe S	80	150	*Fraxinus excelsior; Rosa sp.*
Creacombe N	50	200	*Fraxinus excelsior*

4.2.3. Field surveys

4.2.3.1. Hedgerow plants sampling

All locations were sampled during spring 2017 and 2018. Each location (e.g. countryside road) was selected on condition that they offered hedgerow vegetation composition and structure on north- and south-facing aspects as similar as possible. Plants were surveyed on the upper zone of the bottom/bank of the hedgerow, the dampest and more fertile part of the hedgerow (Menneer, 1994). Diversity and species richness of the woody hedge does not tend to affect species richness of the hedgerow bank, but the height of both ot either the hedge and the hedgerow bank can (Mercer et al., 1999). By consequence, paired north- and south-facing hedgerows were selected on condition they had similar hedge and hedgerow bank height. Ten 0.50 x 050 m quadrats were randomly positioned along a 150m long transect at a consistent height within the upper zone of the hedge bank (Figure 4.1A), and such that samples on north- and south-facing hedgerows faced each other (i.e. 5 matched positions at the same relative height). This yielded 60 quadrats across all locations. All quadrats were placed on flat and vertical surfaces to minimise any localised variation in topography and micro-habitat.

4.2.3.2. Species richness of hedgerow vegetation

In addition to estimating relative (percentage) cover of all component fern, herb and woody species, the overall contribution of ‘mosses’ and ‘graminoids’ within each quadrat was determined. Later flowering of grass, and sedge species, often coinciding with hedgerow maintenance, limited identification consequently, they were not identified to species, but assigned instead to a single group ‘graminoids’. Similarly, due to the difficulties associated with identification, mosses were kept in a single group. Both percentage cover and species richness were calculated according to aspect at taxonomic level, and abundance of common species were also compared with aspect.

4.2.3.3. Autoecology and habitat indictors

Ellenberg (1979) defined a set of indicator values for European vascular plants that assign a score for habitat characteristics of each plant species, according to their preferences for light, temperature, ‘continentality’, nutrients, soil moisture, pH, and salinity. These ‘Ellenberg’s values’ have been widely used, and especially to explain the cause of vegetation change. Hill et al. (1999) published Ellenberg’s indicator values for the entire native British and Irish flora, based on Ellenberg (1979) work but excluded the Ellenberg indicators ‘temperature’ and ‘continentality’ as neither were satisfactory in an oceanic climate as in Britain. The considered indicators, used in this survey are the following: Light (**L**), Moisture (**F**), Reaction (**R**), and Nitrogen (**N**), and described in Appendix 4. Due to the location of the sampled sites, far enough from the coast the indicator related to the tolerance to salinity was discarded in this survey.

- **L**: Indicates the shade or sun tolerance of a plant. Scale from 1 (plant restricted to deep shade) to 9 (plant demands full sun).
- **F**: Indicates moisture or drought tolerance. Scale from 1 (extreme dryness, restricted to soils that often dry out for some time) to 12 (submerged plant, permanently or almost constantly under water).
- **R**: Indicates soil or water pH level. Scale from 1 (extreme acidity, never found on weakly acid or basic soil) to 9 (basic reaction, always found on calcareous or other higher pH soils.
- **N**: Indicates soil fertility level. Scale from 1 (extremely infertile sites) to 9 (extremely rich situations, such as cattle resting places or near polluted rivers).

Each species was assigned a value for each indicator (after Hill et al. (1999)), to score their autoecology attributes (for full list see Appendix 5).

4.2.3.4. Biogeographical origin of hedgerow plants

Grime et al. (1988) assessed the biogeography of European plants in Northern Europe, using geographical and ecophysiological datasets. The plant distribution classification generated by those authors was used here to examine a potential relationship between the biogeographical origin of species and their distribution according to aspect on hedgerow banks. This classification consists of distributions restricted mainly by latitudes (southern and northern distribution), or longitudes (west, i.e. more oceanic distribution, or east, more continental distribution). The different classes are:

- **S**: Largely restricted to southern areas and absent from parts of both northern Britain and Scandinavia
- **s**: Similar as S but distributed throughout either northern Britain or Scandinavia
- **N**: Species largely restricted to northern areas
- **W**: Largely restricted to NW Europe with distribution centred on the Atlantic seaboard
- **w**: Similar as W but extending to a considerable extent into central regions
- **E**: More widespread in NE and NW Europe
- **U**: ubiquitous species without well-marked geographical restriction in N Europe

4.2.4. Statistical analysis

To examine the overall similarity of the plant communities according to aspect, a *non-metric Multidimensional Scaling* (nMDS) was performed using the Bray-Curtis index of similarity on 4^{th}-root transformed cover data, to down-weight the influence of abundant species and high presence of zeros (Clarke et al., 2014). Differences in plant community structure and composition were investigated using *permutational multivariate analysis of variance* (PERMANOVA). A two-factor design was employed using distinct categories: 'Aspect' (fixed, two levels – north- and south-facing) and 'Site' (random, six sites '). All multivariate analyses were carried out using the PRIMER 7 (Plymouth Routines in Multivariate Ecological Research) package and the PERMANOVA add-on.

Variations in, (1) species richness of the functional groups (ferns, herbs, shrubs, graminoids, and mosses), (2) abundance of some selected taxa or taxonomic groups, and (3) species richness of biogeographical origin groups (S, s, N, W, w, E, U) were tested against the factor 'Aspect' using a one-way *Analysis of Variance* (ANOVA). All ANOVA were performed using MINITAB (v 17).

4.3. Results

4.3.1. Variations in plant community composition

In total, 91 plant species were recorded across all locations and aspects, including 66 herbs, 15 shrubs, and 10 ferns (see Appendix 3 for full species list). Aspect had little effect on relative species numbers (70 species (groups) on north-facing hedgerows; 73 on south-facing), however not significant ($F_{1,56} = 3.36$, $p = 0.072$), but 22 species were restricted to north-facing hedgerows and 24 to south-facing hedgerows. Although this doubtless contributed to between-'site' differences (Table 4.2), PERMANOVA results failed to show any variation in plant community composition associated with aspect (Table 4.2).

Table 4.2: PERMANOVA results for the plant community (including, herbs, ferns, mosses, graminoids, and shrubs) sampled in hedgerow banks from six different locations in the SW England, according to the main factors 'Aspect' (north-and south-facing hedgerow), and 'Site' (see details of sites in Table 4.1) and the interaction term 'Aspect x Site'. The survey was carried out in spring 2017 and 2018, with a total of 60 quadrats (5 quadrats on each aspect of each site). NS, no significant difference ($p>0.05$); and ** significant with $p\leq0.01$.

Souce	df	MS	Pseudo-F	p-value	
Aspect	1	4337.5	1.5483	0.198	NS
Site	5	6278.8	4.8558	0.001	**
Aspect x Site	5	2810.1	2.1733	0.001	**
Residuals	46	1293			

There was however, a significant ‘Site’ x ‘Aspect’ interaction; pairwise tests showed that on north-facing hedgerows, the community structure at Tinnel and Smeaton, Tinnel and Rosedale, and Rosedale and Haye did not vary. Floral composition at all other north-facing sites differed with location. For south-facing hedgerows, community structure varied between all sites, except Tinnel and Smeaton, which were strongly similar. The MDS plot (Figure 4.3) also illustrates well the site variation and ‘Aspect’ x ‘Site’ interaction between plant communities (each quadrat’s community represented by a circle). The distance between circles shows similarity between plant communities (e.g. very close circles will tend to be very similar). Closed and open circles, representing respectively, north- and south-facing plant community from one quadrat, did not cluster in two groups, as it would have been the case if plant communities varied with aspect. Instead, both close and open circles tended to cluster

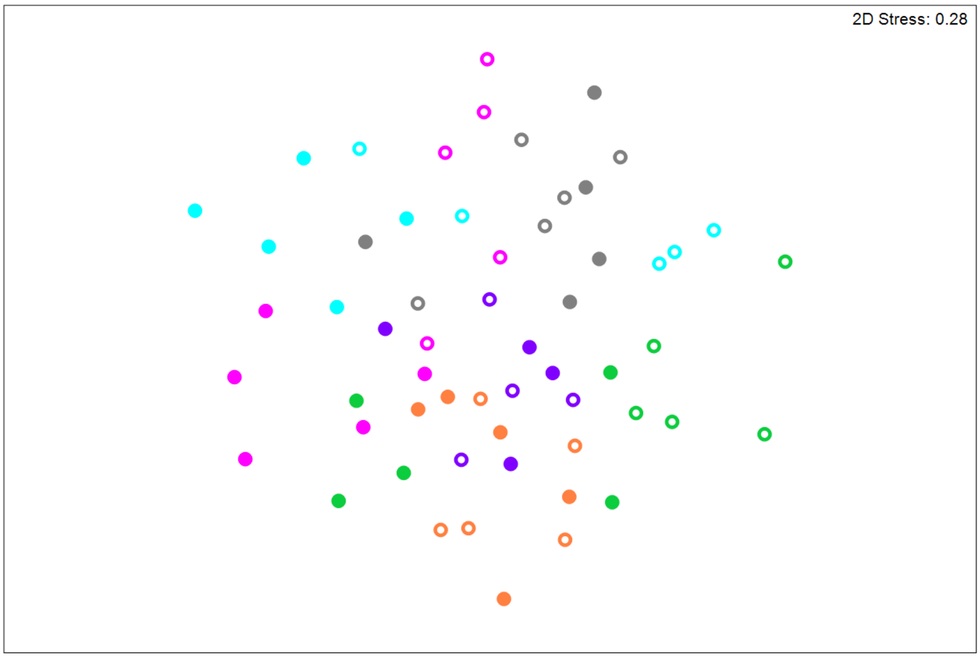


Figure 4.3: Non-metric MDS ordination of Bray-Curtis resemblances between multivariate community compositions for a total of 60 quadrats sampled from six sites across the SW England peninsula. Each site is represented by a colour (Tinnel, violet; Smeaton, orange; Rosedale, green; Haye, pink; Lutton, turquoise; and Creacombe, grey). North- and south-facing slopes are represented by full and empty circles, respectively. Each circle represent the whole plant community in one quadrat.

by colour (where each colour represents a different site), demonstrating that plant communities significantly differed with the locations. Although the PERMANOVA did not show significant variation between north- and south- facing hedgerow vegetation, this does not preclude species- or species group-specific variation. nMDS showed that overall plant community assemblage across the six sites had a dissimilarity according to aspect 59.6%.

4.3.2. Variations in a plant taxonomic level and aspect

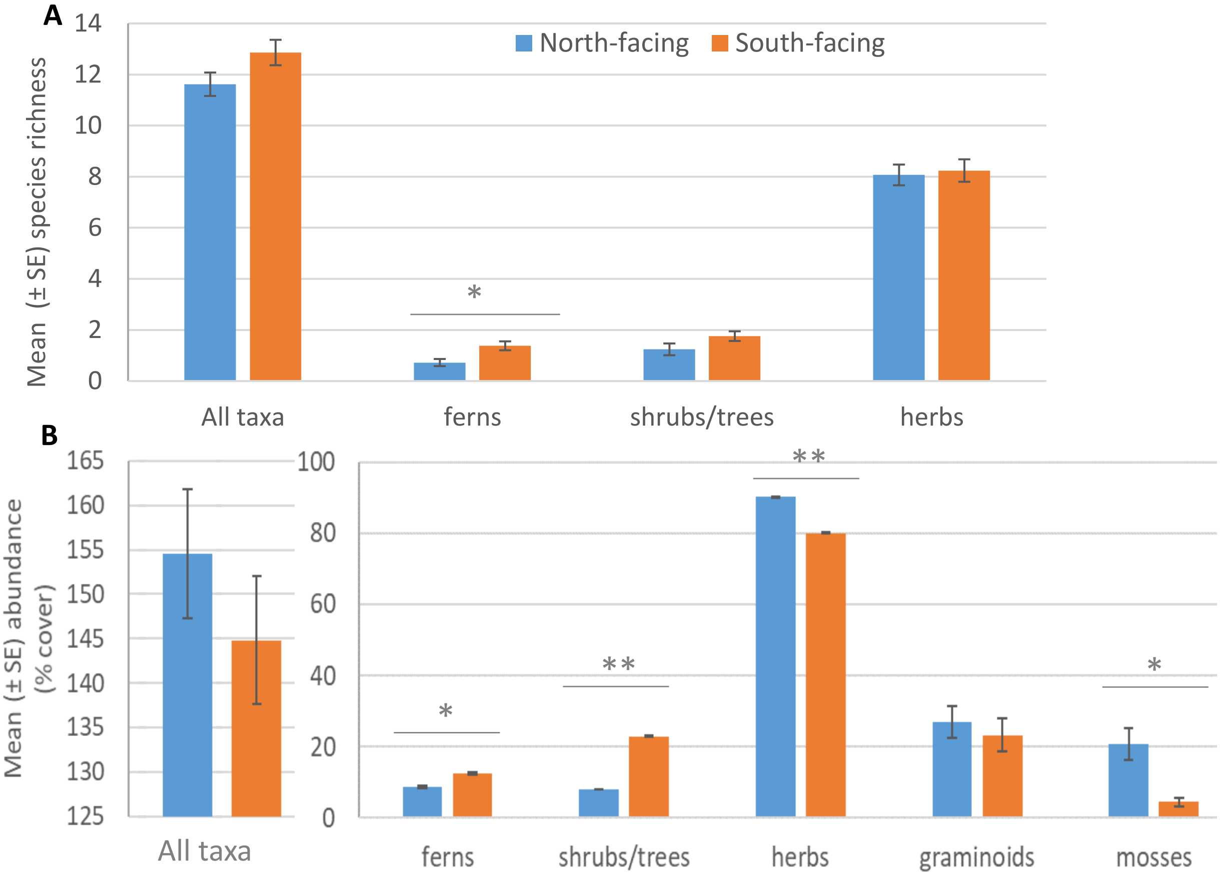


Figure 4.4: One-way ANOVA results of **A.** Mean species richness and **B.** mean percentage cover of the main plants groups according to aspect (blue, north-facing; and red, south-facing) recorded on hedgerows banks across six different locations in the SW England. * significant with *p* ≤0.05; ** significant with *p* ≤0.01; and no significant difference (*p*>0.05) are left blank.

At the taxonomic group level, average species richness of shrubs and herbs did not vary with aspect. For ferns however, average species richness was significantly higher on south-facing hedgerows (Figure 4.4A). The overall abundance of major plant groups was more influenced by aspect (Figure 4.4B). Ferns and shrubs were significantly more abundant on south-facing hedgerows, while herbs and mosses followed the opposite pattern. The abundance of graminoids did not vary with aspect. In overall, among the whole plant community, herbs were the most abundant, followed by graminoids, shrubs, mosses and then ferns.

4.3.3. Variations in plant species level and aspect

Although more than 90 species were recorded, most were limited to only one or two sites, and/or present at very low abundance. Consequently, only species found in at least three of the six sampled sites are considered for further analysis including 16 (of 66) herbs, 6 (of 10) ferns, and 5 (of 15) shrubs (species in bold in Appendix 3).

The most common herbs accounted for about 56% of the total percentage cover of the plant community on both north- and south-facing hedgerow banks. Among them, *Geranium lucidum* (shining crane's Bill) and *Rumex acetosa* (common sorrel), were the only two species showing any significant variation, both with higher abundance on north- than south-facing hedgerows (Figure 4.5A). Several other species showed some (non-significant) preference for south-facing hedgerows; *Hedera helix* (ivy), the most abundant herb recorded in this survey, as well as the very common *Galium mollugo* (hedge bedstraw), and *Hyacinthoides non-scripta* (bluebell). It is interesting to note that congeners *Galium mollugo* and *G. aparine* (goosegrass or cleavers), showed opposite trends in terms of aspect, (although both not significant).

The most common shrubs (listed in Figure 4.5B), accounted for a smaller proportion of the total plant community (6.9% and 18.6% cover, on north- and south-facing hedgerows, respectively). Of these, *Rosa sp*. (most likely dominated by *Rosa canina*), *Corylus avellana* (hazel), *Prunus spinosa* (blackthorn), and *Quercus robur* (English oak) displayed higher abundance on south- facing hedgerows. Only *Rosa* and *Corylus* showed a significant variation however. *Rubus fruticosus* (bramble or blackberry), the most common shrub in this study, had almost equal abundance on both aspects. The overall higher abundance of four of the five most common shrub species on the south-facing aspect, likely explains the significant cover variation of the shrub group according to aspect.

Ferns accounted for 5.7% and 9.9% of total cover on north- and south-facing hedgerows, respectively, and although they were the only group displaying significant variation in species richness with aspect, no single species was significantly more abundant on either aspect (Figure 4.5C).

Asplenium adiantum nigrum (black spleenwort), *Asplenium trichomanes* (Maidenhair spleenwort), and *Pteridium aquilium* (bracken) were completely absent from north-facing hedgerows, but ANOVA failed to locate any significant variation probably due to overall low occurrence. Similar to the *Galium* species, the conspecific ferns *Dryopteris affinis* (scale male fern) and *D. filix-mas* (male fern) displayed opposite preferences for aspect. *D. affinis* tended to be more abundant on the north-facing hedgerows, while *D. filix-mas* more on the south-facing ones. *Phyllitis scolopendrium* (hart’s tongue), the most common fern in this survey, preferred south-facing hedgerow margins. The absence of some species from north-facing hedgerow, and the consistent variation in abundance of fern species with aspect, although not significant, might have both contributed to the significant variation of percentage cover of the fern taxonomic group according to aspect.

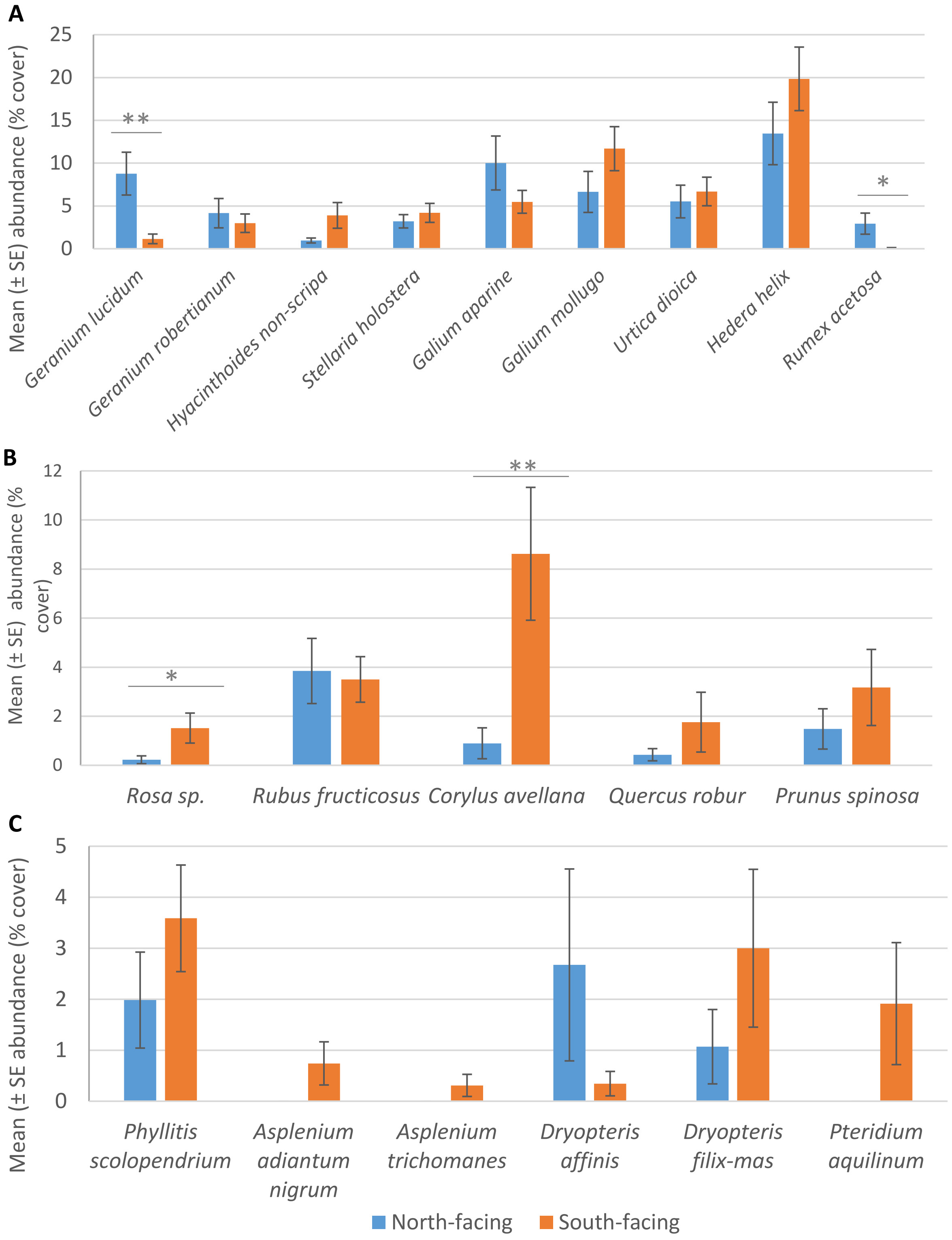


Figure 4.5: One-way ANOVA results of mean percentage cover of the most common and abundant **A.** herbs, **B.** shrubs, and **C.** ferns, according to aspect (blue, north-facing; and red, south-facing) recorded on hedgerows banks across six different locations in the SW England. * significant with *p* ≤0.05; ** significant with *p* ≤0.01; and no significant differences (*p* >0.05) are left blank.

4.3.4. Autoecology and habitat indicators

Ellenberg values for all plant species did not vary significantly with aspect (Table 4.3). Means generated for light (L), moisture (F), soil fertility (N) and soil/water pH (R) values correspond to a plant community dominated by semi-shade, moisture-dependent plants - on intermediate to rich fertility, (weakly) acid soils to weakly basic soil (see Appendix 5 for full explanation of the indicators value and Appendix 6 for values of each species). There was however, a significant site effect on the habitat indicators F ($F_{5,52}$ = 2.78, $p = 0.027$), N ($F_{5,52}$ = 4.45, $p = 0.002$)and R ($F_{5,52}$ = 2.53, $p = 0.040$).

Table 4.3: Mean of Ellenberg values for light (L), moisture (F), nitrogen indicator of soil fertility (N), reaction (R) indicator of soil or water pH; of all vascular plant species (ferns, herbs and shrubs/trees species) recorded on both north- and south-facing hedgerow banks from six different locations in the SW of England. NS, for Non-Significant difference with p <0.05 between aspects.

	Light (L)	Moisture (F)	Nitrogen	Reaction (R)
North-facing	5.76 ± 0.13	5.29 ± 0.06	6.47 ± 0.27	6.30 ± 0.06
South-facing	5.56 ± 0.11	5.25 ± 0.06	6.02 ± 0.20	6.37 ± 0.06
	NS	NS	NS	NS

4.3.5. Biogeographic origins of plants and aspect

Among the different biogeographical groups described by Grime et al. (1988), southern plants '**s**' (largely restricted to southern areas in Europe with presence up to northern Britain and/or Scandinavia) contributed most to species numbers on both aspects. These were followed by the 'ubiquitous' group and then southern plants '**S**' (largely restricted to southern areas in Europe with absence from northern Britain and Scandinavia). There were significantly more '**S**' species on south-facing hedgerow banks ($F_{1,56}$ = 7.66, $p = 0.008$), typified by the shrubs

Corylus avellana and *Rosa sp.* The south-western distribution '**Sw**' species group was also significantly more abundant on the north- than south-facing hedgerows ($F_{1,56}$ = 4.49, p = 0.036), including the herbs *Primula vulgaris* and *Geranium lucidum*, plants typically found in semi-shaded moist habitats. The other groups, '**sW**', '**SW**', '**sw**' and '**ws**' were present at very low proportions on both sides of hedgerows and did not vary with aspect.

Among the several species restricted to one aspect, 15 of 17 (88%) and 9 out 16 (56%) respectively were recorded only on south- and north-facing hedgerows, and had a southern or south-western distribution. However, due to very low abundance and/or sighting frequency, ANOVA failed to show any significant variation in abundance with aspect.

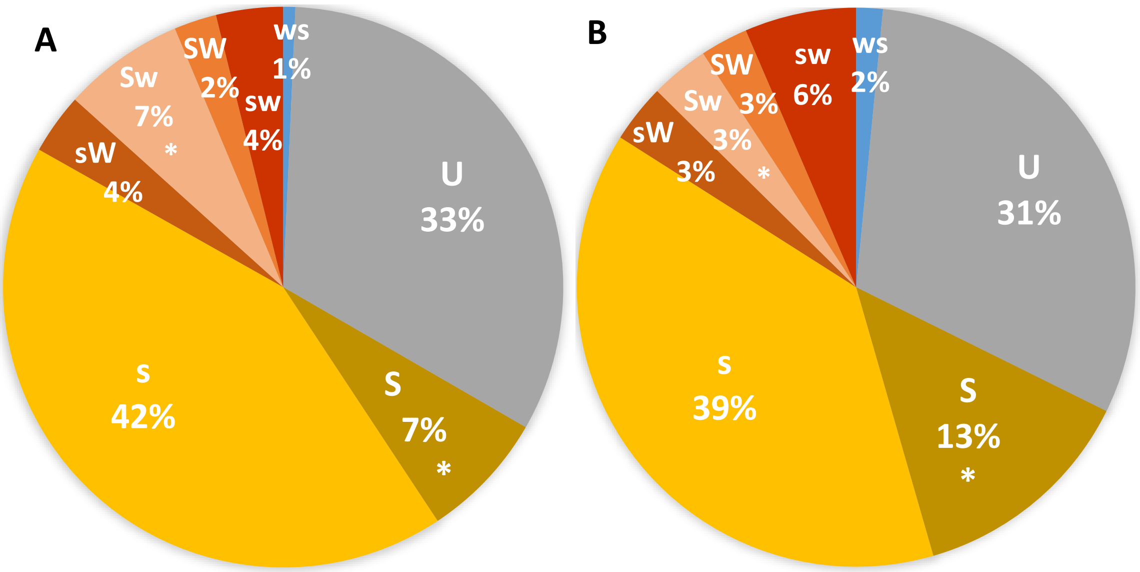


Figure 4.6: Proportion of plants species richness sampled on **A.** north-facing and **B.** south-facing of hedgerow banks, from six different locations in the SW England, according to their biogeographical origin. The classification used is from Grime et al. (1988), who split species in the following main categories: **S**, largely restricted to southern areas and absent from parts of both northern Britain and Scandinavia; **s**, similar as S but distributed throughout either northern Britain or Scandinavia; **W**, largely restricted to NW Europe with distribution centred on the Atlantic seaboard; **w**, similar as W but extending into central regions; and **U**, **s**pecies without well-marked geographical restriction in N Europe. For the combined categories such as sW, Sw, sw, and ws, if there is a dominant distribution from either south or west, the respective letter is in capital. * shows significant difference between aspect.

4.4. Discussion

Contrary to most studies investigating the impact of aspect on plant communities and diversity, my study failed to show any significant variation with aspect on the plant community assemblage, which could be reflected by the plants from both aspects having overall similar ecological requirements (expressed with Ellenberg's indicators). Nonetheless, there was evidence that aspect had some influence on the distribution of plants at different level: taxonomic, species and biogeographic origins.

The mosaic structure of hedgerow plant community assemblages was reflected with the wide spectrum of Ellenberg values obtained across all species. Although no significant difference was found between the habitat indicator values averages and aspect, results described the overall plant community as having prevailing semi-shade, moisture and with medium to low soil pH. Although plant community assemblages did not vary with aspect, a significant site effect accounted for plant community variations, presumably linked to agriculture and soil conditions. This was supported by the fact that, herbs were especially associated with rather rich, fertile soil, an observation that parallels McCollin et al. (2000) findings. Hanley and Wilkins (2015) showed that the arable crop type had not influence on both plant community facing the field and pollinator activity of bumblebees on hedgerows. However, Mercer et al. (1999) reported that both the type of land use adjacent the hedgerows and the hedgerow type had an effect on plant species richness and composition and that aspect did not. Although it is difficult to choose study sites with same distance from nearest forest, gardens, or wild flowers fields, or hedgerows formed from the exact same hedge species, this may have likely contributed to this strong site effect in the plant community assemblages sampled in hedgerow. In addition, the soil chemistry and underlying geology of each hedgerow were not investigated in this study; it is likely they played a role in the vegetation differences recorded over this survey.

Although a decline of herb species, and matched increase in graminoids was reported over a 20 year period for hedgerows in the UK (Carey et al., 2008), herbs were by far, the dominant plants (species richness and abundance) recorded in my survey (as (French and Cummins, 2001), accounting for 90% and 78% of mean cover on north- and south-facing margins respectively. Herbs and mosses were significantly more abundant on the north- than south-facing hedgerows, while it was the opposite for the ferns and shrubs. Mosses, because of their intolerance of desiccation, were even almost restricted to the north- rather than south-facing aspect (see also Cantlon, 1953; Forman and Baudry, 1984). Due to the low frequency and abundance of all plant species recorded in this survey, detailed analyses were difficult. For example, 16 (of 66) herbs, 6 (of 10) ferns, and five (of 15) shrubs were present in at least half the sampled sites. Aude et al. (2003) had to ignore 50% of recorded plants for similar issues, highlighting the need for significant replication when undertaking plant surveys of fragmented and variable habitats like hedgerows (Marshall and Moonen, 2002).

The most common shrub species recorded in the hedge-base (*Rosa* spp., *Rubus fruticosus*, *Corylus avellana*, *Quercus robur* and *Prunus spinosa*) are all very common hedgerow components in SW of England (Devon City Council & Devon hedge group, 1997; Dover, 2019). Light-tolerant trees and shrubs such as, *Rosa spp*. and *C. avellana* are more frequent in margin habitats such as hedgerows (Sarlöv Herlin and Fry, 2000), and here were more abundant on the south-facing hedgerows suggesting that light is more important than moisture in contributing to tree and shrub distribution. Among the common herbs, only two species

(*Geranium lucidum* and *Rumex acetosa*) had a significant prevalence for one aspect. Although associated with semi-shaded to well-lit places, their greater abundance on north-facing slopes can be associated with their requirement for damp soil (Appendix 6). In contrary to shrubs, soil moisture tends to be more important than light in the distribution of herbs in hedgerow, likely due to their greater sensitivity to wilt. A requirement for chilling to stimulate seed germination can also be an important factor influencing species distribution (Grime et al., 1988). A combination of these factors could explain why *G. aparine* had higher abundance on north-facing aspects in this study. In addition, plants such as *Hyacithoides non-scripta* require early season light, warm, and moist soil for development of young plants (Grime et al., 1988), which might explain its predominance on the south-facing aspects.

Although generally associated with forest/woodland habitat, ferns were the only taxonomic group with species richness significantly impacted by aspect, but abundance was counter-intuitively greater on south-facing hedgerow margins. This pattern was driven by several species restricted to the south-facing aspect only (*Asplenium adiantum nigrum*, *Asplenium trichomanes*, and *Pteridium aquilinum*). Ferns are often associated with humid habitat as water is an essential medium for their reproduction (de Gasper et al., 2015), however, some species, such as *Dryopteris filix-mas*, showed a clear preference for south-facing aspects, a pattern likely reflecting the fact that this species is relatively light-demanding (Biological Record Centre, 2008a). The most abundant fern species in this study, *Phyllitis scolopendrium*, was more common on south-facing aspects. Although this species is often associated with moist (Biological Record Centre, 2008b) and shaded to semi-shaded habitats (Appendix 4), *P. scolopendrium* could have benefit from its rather smaller size, (compared to other fern, herb and shrub species) to grow underneath dense foliage of woody species (*C. avellana*, *P.*

spinosa, *Q. robur*) dominating the hedge banks on south-facing aspects, which would have brought them the necessary shading. In addition, *P. scolopendrium* might have taken adventage of a potential lesser competition for space on the south-facing aspect on the lower vegetation layer underneath tall ferns and shrubs dominating this aspect. Indeed, this lower vegetation layer tended to be dominated on the north-facing aspect by mosses and small herbs species. *Dryopteris affinis*, a species known for its preference for shady, well-drained conditions, was more common on north-facing aspects. It is also worth bearing in mind that soil physio-chemistry is a crucial component to fern species composition (Tuomisto and Poulsen, 1996; Jones et al., 2011) and although not quantified here, aspect-related variation in soil may explain some observed patterns.

As discussed in Chapter 1 (see also Chapter 2), aspect may be important in influencing local patterns of distribution for species from different biographical origins, especially those at their range limits. For hedgerows in SW England, more plants with a ‘ubiquitous’ and NW European distribution, and moist/shade tolerant species might be predicted to favour north-facing slopes while species with higher thermal tolerance (i.e. southern distribution species) will prefer south-facing slopes. This study provides support for this hypothesis in that the species richness of extreme southern distribution **‘S’** (absent from northern Britain and Scandinavia) species was significantly greater on the south-facing hedgerows. Species richness of the south-western distribution ‘**Sw**’ group was significantly greater on the north- than south-facing hedgerows. This biogeographic group was dominated with the forest or shade-tolerant species *Arum maculatum*, *Geranium lucidum*, and *Primula vulgaris*, which likely found refuge on the north-facing hedgerow and therefore avoided settle to on the warmer and drier south-facing hedgerows (Pollard et al., 1974).

While nearby farming practices have some influence over the hedgerow community, species richness is greatly determined by management, pollinators, and spatial scale promoting dispersal (e.g., distance from the nearest woodland or wildflower meadow, allowing dispersal of a variety of plants) (Moonen and Marshall, 2001; Campagne et al., 2006). Hedge maintenance can increase diversity as it may allow better recruitment (Aude et al., 2003), but not always (e.g., no effect on woody species richness (Staley et al., 2013) and composition (Alignier, 2018)). In addition, a decline in intensity of field margin management, leading to the development of the tree layer, can result in an increase of shade-tolerant plant abundance (Alignier, 2018). This could homogenise the aspect-related microclimates. The height of woody hedgerow has already been suggested to be the reason for the absence of aspect-related variation in plant species composition (Le Coeur et al., 1999).

With ACC, increased temperature will likely favour hedge growth, necessitating greater management with potential impacts on woody plant diversity (Natural England and RSPB, 2014). If left unmanaged, the increased shading may cause a long-term change in flora (and fauna), and this microclimate may act as buffer, especially north-facing aspects may offer a refuge from hot and drier summers. In addition, a reduction in frost events likely to occur on the south-facing aspects, could influence fruiting in some hedgerow species and the formation of berries (Natural England and RSPB 2014). Aspect has often been associated with warmer and drier soil on south- than north-facing slopes (Cantlon, 1953; Griffiths et al., 2009; Chai et al., 2018), while other soil properties (e.g., pH, organic matter content, nutrients content) also varied but inconsistently. Those variations may influence fauna distribution and ecological processes, which in turn would also impact plant distribution. Some of which, will be investigated in the following chapter.

Chapter 5: Little implication of aspect on soil invertebrate abundance and litter decomposition

5.1. Introduction

Plant litter decomposition is an important ecosystem process in soil and nutrient cycling and global carbon storage in terrestrial ecosystems (Aerts, 1997); detrital food webs processing more carbon and energy than the ‘better-known’ grazer food webs (Berg and McClaugherty, 2014). Litter decomposition consists of physical, chemical (oxidation and condensation) and biological mechanisms transforming organic matter into increasingly stable forms (Berg and McClaugherty, 2014). Physical fragmentation of the litter can come from different cycles (e.g., wet-dry, shrink-swell, hot-cold; Miller et al., 2005), wind, and leaching (i.e., loss of nutrient and incompletely decomposed organic compounds transported out by water). In addition, biological mechanisms involve ingestion and digestion, as well as extracellular enzymatic activity.

Decomposition is important at biosphere and ecosystem levels (Berg and McClaugherty, 2014). First, it releases the so-called greenhouse gases (GHGs): carbon dioxide (CO_2) mainly via microbial respiration (Phillips and Nickerson, 2015), methane (CH_4) and nitrogen-based gases (Aerts, 1997; Aerts and de Caluwe, 1999). Therefore, factors increasing decomposition rate can potentially increase GHG release into the atmosphere. However, decomposition also allows, *via* formation of humus, storage of carbon and related stable organic compounds in soils, which is then not circulating in the atmosphere (Andreetta et al., 2011). Secondly, decomposition is important regarding nutrient cycling (availability of nutrients largely due to decay dynamic). Micro-organisms (bacteria and fungi) reduce and mineralize litter into basic inorganic molecules, such as ammonium, phosphate, CO_2 and water, which are then available for plants or micro-organisms (Aerts, 1997). Finally, decomposition changes some soil properties (e.g., nutrient-holding capacity and pH), diversity and stability of ecological communities (Berg and McClaugherty, 2014).

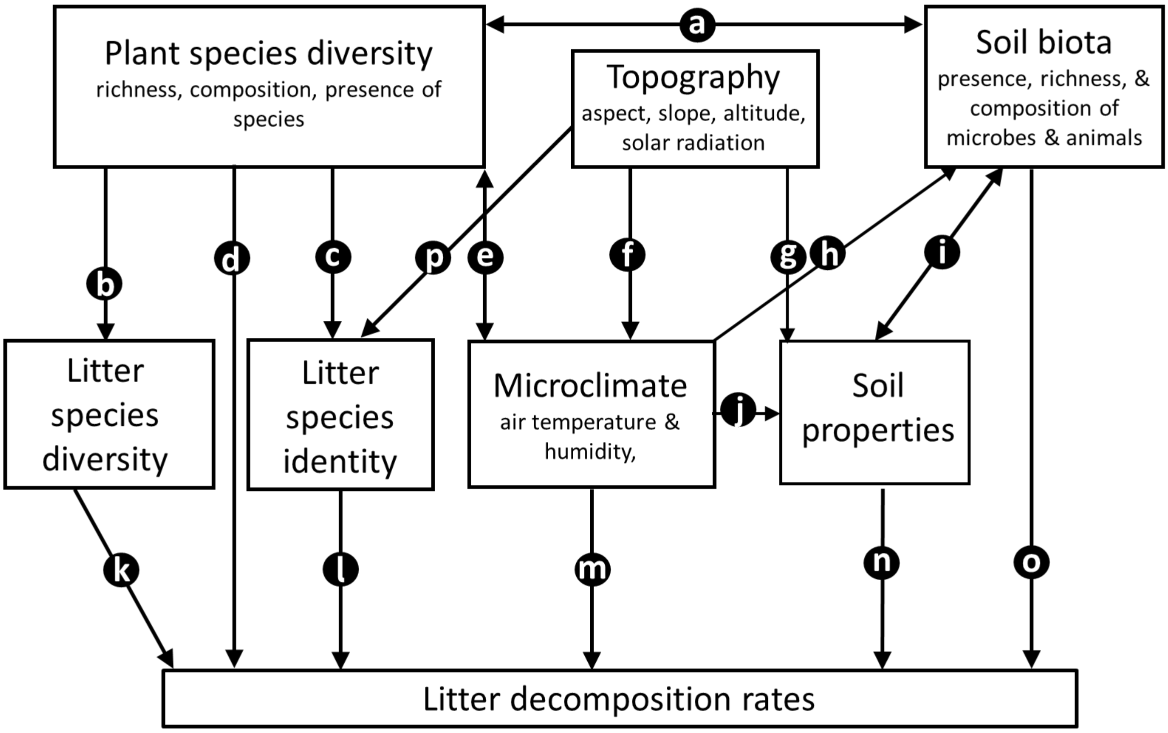


Figure 5.1: Diagram representing the direct and indirect interactions of abiotic (f-h, j, m-n, p) and biotic (a-e, k-l, o) variables influencing the litter decomposition rate. Factors m, j, n and o will be analysed in this chapter.

About 90% of net primary production enters soil systems through dead plants (litter) in grasslands, and through leaves, roots and wood in forest systems (Coleman et al., 2004). Litter decomposition rates depend on a range of interconnected abiotic (e.g. soil properties and solar variations) and biotic (e.g. litter plant species, and soil decomposers) factors, (Figure 5.1). Climate, litter quality and chemistry, soil organisms and nutrient availability, as well as site-specific factors, are the main factors influencing decomposition rate, (Swift et al., 1979; Lavelle et al., 1993; Aerts, 1997; Berg and McClaugherty, 2014).

Plant community composition, depends on climate (Figure 5.1e) and affects both the amount and composition of litter produced, as well as its chemical and morphological characteristics (Figure 5.1b and 5.1c; Scherer-Lorenzen et al., 2007; Hector et al., 2000; Berg and McClaugherty, 2014). Indeed, leaf chemical and morphological characteristics of different species, and the morphological and chemical properties of plant roots can have a positive or negative effect on soil decomposers (Figure 5.1a; e.g. Yang and Chen, 2009) and decomposition rates (Figure 5.1o; Cornelissen, 1996). For example, decomposition can increase or decrease depending on the number of plant species contained in litterbags (Figure 5.1k; e.g., Gartner and Cardon, 2004). In addition, the C:N ratio, and proportion of both lignin and secondary chemical compounds, influence decomposition rate (Figure 5.1l; e.g., lower C:N generally decompose faster; Bardgett, 2005; Aert, 1997). Aboveground plant species composition and/or richness can also affect decomposition (Figure 5.1d); higher plant species and functional group richness in grassland were, for example, linked to faster decomposition (Spehn et al., 2005; Scherer-Lorenzen, 2008). When investigating decomposition in forest systems, different decomposition rates have also been associated with different species composition (Albers et al., 2004).

Soil properties also influence soil biota and litter decomposition (Figure 5.1i and 5.1n). Organic matter is extremely effective at retaining water within the soil matrix, and is of particular importance for biota as it is the primary source of nutrients and C (Bardgett, 2005). Soil pH controls nutrient availability (N and P most limit primary productivity in natural and managed terrestrial ecosystems; Chapin et al., 2002), and impact directly biota abundance and diversity (e.g. earthworms, Edwards 2004; gastropods, dipteran larvae and predatory beetles, Kuperman, 1996). Consequently, decomposition tends to be faster in neutral than acidic soils (considering all other factors equal) (Bardgett, 2005).

Decomposer organisms are essential for the functioning of terrestrial ecosystems largely because they decompose dead organic material in soil, converting this into carbon dioxide and other soluble nutrients forms that provide resources for other biota and primary production (Wardle and Van der Putten, 2002; Gobat et al., 2004). Overall, earthworms, mites and collembola are major contributors to litter decomposition (Berg and McClaugherty, 2014). Macro-arthropods, such as dipteran larvae, millipedes and woodlice, and earthworms are considered primary decomposers as they start breaking down leaf litter by allowing access by other species such as springtails (Collembola) (Sutton, 1972; Oliver and Meechan, 1993; Gobat et al., 2004) and stimulating microbial activity (Hättenschwiler et al., 2005). Earthworms, via their numerous burrows (e.g. up to 400 500 meters of tunnels per 1m^2 grassland) allow important aeration, increase penetration and retention of water in soil (Edwards, 2004; Gobat et al., 2004). They also have a major role in the breakdown of organic matter, release and recycling of nutrients, and are great benefit to the soil as their casts (faecal material) are more microbially active than the surrounding soil and plant nutrients in a form that can be readily utilized (Bardgett, 2005). Through these interactions, earthworms are often key organisms in the overall decomposition process. Millipedes are also important detritivores, however, as they are not well equipped with specialized enzymes to enable them to digest the leaf material itself, as in the earthworms, they preferably feed on dead litter, which has already undergone some microbial decomposition (Blower, 1985). Then, smaller pieces of leaves cut by primary decomposers are reduced in size by springtails and other small animals such as mites and enchytraeids (potworms), before being buried by soil fauna and by leaching. Finally, abundant and diverse microorganisms participate to the further degradation and mineralization of complex organic substances into inorganic molecules such as ammonium, phosphate, carbon dioxide and water (Aerts, 1997). Bacteria can be found in soil at a density of hundreds to thousands in 1 g of soil, with an estimated 2 to 3 million species (Dejonghe et al., 2001) and slightly less for fungi species (Bridge and Spooner, 2001; Hawksworth, 2001). Although micro-arthropods generally exert positive effect on litter mass loss (See Hättenschwiler et al. (2005) and Kampichler and Bruckner (2009) for reviews), little is known about the relative roles of microbial and animal-decomposer diversity in decomposition processes, and, as consequence, are often excluded from decomposition experiments, especially at the large or global scale (Wall et al., 2008).

The last major factor affecting decomposition rate is climate. Decomposition tends to be faster in wet and hot places, such as the tropics, compared to temperate or xeric areas (Aerts, 1997; Takeda, 1998), conditions under which detritivores are more active (Thakur et al., 2018). In many biomes, the effect of soil fauna on litter decomposition is climate-dependent (Wall et al., 2008; García-Palacios et al., 2013). As current anthropogenic climate change (ACC) predictions are mostly forecasting global changes with warmer (and drier, for some regions) soil conditions (IPCC, 2014), soil biological processes and soil biota activity are likely to change too. Despite the crucial importance of litter decomposition and soil biota activity on terrestrial ecosystems, there is so far no consensus about how exactly ACC will alter the structure and functioning of soil communities and by extension the decomposition process (Yin et al., 2019a), and studies on the impact of ACC on those processes have only risen in the recent years. Thakur et al. (2018) found that combined warming (applied via infrared heater cables) and precipitation reduction decreased detritivore feeding activity during a four-year experiment in boreal forest in North America. On open habitats – grasslands and crops in Germany – the potential effect of ACC on soil fauna (Yin et al., 2019b) and decomposition rate (Yin et al., 2019a), was investigated using a structure similar to a tent reproducing future climatic conditions, reflecting increased daily mean air (0.55°C) and soil (0.50°C at 15 cm depth) temperatures, combined with an increase (~10%) and decrease (~20%) of rainfall during spring / autumn and summer, respectively. The authors found that both taxa and total abundance of meso- and macrofauna tended to be lower under the future climatic conditions, and that there was greater macrofauna taxa diversity and higher abundance in grasslands than croplands. In parallel, a decrease of litter decomposition rate was found in grassland but not in crops, under those future climatic conditions compared to the ambient one.

An alternative to warming systems, which can have several limitations such as, their high cost, maintenance effort, impossibility to operate under certain climatic conditions as well as in remote areas, is the use of the polar- and equator-facing slopes. As reviewed in Chapter 1 and demonstrated in Chapter 2, aspect (Figure 5.1f), as well as microclimates created by variation in canopy species (Figure 5.1e; Kim et al., 2011; Inkiläinen et al., 2013) can influence the duration and intensity of solar irradiation (Ishii and Higashi, 1997), the moisture content, temperature, rainfall reception (Griffiths et al., 2009) and evapotranspiration (Sariyildiz and Küçük, 2008), soil properties and aboveground vegetation.

Chapter 2 demonstrated that small-scale thermal variation had an important role in the variation in community assemblage composition on the rocky intertidal. Similarly, the microclimate related to terrestrial aspect is associated with differences in vegetation (see Chapter 4; and examples from mountains: Cantlon, 1953; Ameztegui et al., 2012; and grasslands: Watson, 1960; Bennie et al., 2006). In addition, aspect-linked variation in leaf chemistry (Figure 5.1p; Sariyildiz et al., 2005), and soil properties (Figure 5.1g; Bardgett, 2005; Sidari et al., 2008; Chu et al., 2016; Chai et al., 2018) are also apparent. Indeed, cooler soils from pole-facing slopes (Liu et al., 2013; Sewerniak et al., 2017) tend to have higher content of organic matter (Kutiel, 1992), moisture (Liu et al., 2013; Chu et al., 2016; Sewerniak et al., 2017), organic carbon (Liu et al., 2013; Sewerniak et al., 2017), cation exchange capacity (CEC) (Sariyildiz et al., 2005), and wider C/N ratio values (Chu et al., 2016) than equator-facing slopes. All those changes, in turn, likely impact belowground fauna and micro-organisms (Figure 1h and 1i; Mudrick et al., 1994; Begum et al., 2010; Chu et al., 2016; Gelm, 2019) as well as decomposition processes through mechanisms independent of litter species composition and soil decomposers (Figure 5.1m and 5.1n; Sariyildiz, 2008). For example, light exposure was suggested to favour decomposition by making nitrogen in plants more easily available to microbial utilisation (Foereid et al., 2010) and increasing litter colonization by basidiomycete fungi, the most active member of the soil fungal community (Newsham et al., 1999). Although litter decomposition rate has been widely investigated, much less has been done on the impact of the aspect and topography. Mudrick et al. (1994) and Sariyildiz and Küçük (2008) demonstrated that within forested watershed in North American and Turkish mountains, respectively, that decomposition was faster on north- than south-facing slopes. Mudrick et al. (1994) associated this difference to higher moisture level and micro-arthropod density on the northern aspect. They also found that litterbags containing monoculture decomposed faster than the mixed litter. Although Sariyildiz and Küçük (2008) did not consider the influence soil fauna in their experiment, they stressed the importance of microclimate and litter quality in the decomposition process within two different aspects.

The aim of this chapter is to investigate the impact of microclimate (north- and south-facing slopes), soil properties and belowground fauna on the decomposition process, and its implications for the process in a changing world. In addition to quantifying temperature, soil moisture content, and the decomposition of standard litter samples, I also considered variation in several other important soil characteristics (organic content, Nitrogen, Hydrogen and Carbon content, pH) likely to affect the decomposition process (Aerts, 1997; Walter et al., 2013; Bradford et al., 2016; Ochoa-Hueso et al., 2019). I tested the following hypotheses:

(1) Light intensity and aboveground temperature (averages and extremes) differ according to aspect; specifically higher values on south- than north-facing slopes.

(2) Soil properties vary according to aspect; specifically higher soil moisture and OM, but lower soil temperature on north-facing slopes.

(3) Litter decomposition (litter mass loss) varies with aspect and specifically, the environmental factors investigated in 1 & 2.

(4) Community structure of both soil and litter-associated fauna (i.e. species richness and relative abundance at functional and taxonomic levels) differs with aspect.

5.2. Material and methods

5.2.1. Study area

This study was carried out at four sites along highway verges of the A30 in SW England. Those sites were carefully chosen because they offered paired grassland slopes facing each other with a northern and southern aspect, with similar slope angle (about 45°)(Figure 5.3). Sites 1 near Okehampton and site 2 near Tedburn St Mary (50°44’21.1’’N, 3°54’44.7’’W and 50°43’45.5’’N, 3°41’35.9’’W, respectively) were located on the north limit of the Dartmoor National Park, while sites 3 near Bodmin Bypass and site 4 near Lanivet (50°26’27.8’’N, 4°43’04.1’’W and 50°26’23.7’’N, 4°44’42.0’’W, respectively) on the south limit of Bodmin moor (Figure 5.2). Sites were a minimum 1 km apart. Within each site, an open grassland area (1 x 4 m) was selected such that it was far enough from any trees to avoid additional shading, from where soil samples were collected, litterbags and data loggers deployed. Litterbags were placed at approximatively the same relative height (7-10 m) from the road, at all sites.

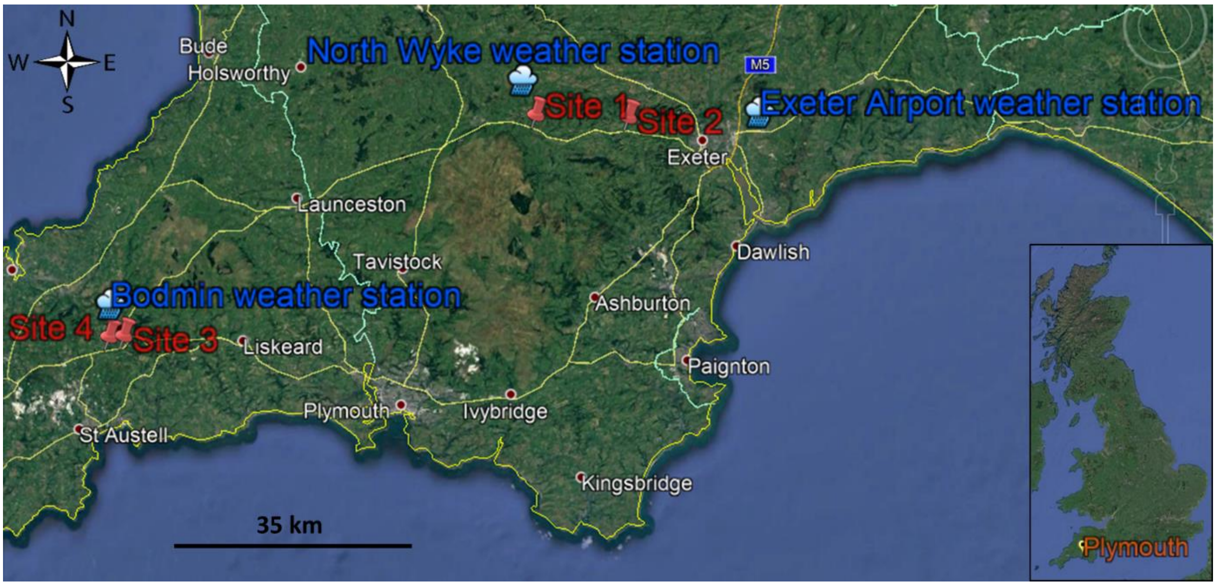


Figure 5.2: Study sites of the litterbags decomposition experiment, on north- and south-facing road verges (in red) and the local weather stations from where data was used for the whole length of experiment (in blue) in the South West of England. Sites 1 and 2 are on the verges of the highway A30 on the north of Dartmoor, and site 3 and 4 are on the verges of the same highway, but located on the south of Bodmin moor.

5.2.2. Temperature and light intensities on north- and south-facing slopes

Data loggers recording the temperature and relative humidity (iButton DS1923 Hygrochron, Maxim Integrated, San Jose, CA, USA) were deployed along road verges at the start of the experiment. Within a month, all failed due to water damage from heavy rains. Therefore, no meteorological data on the slopes’ aspect were available for the duration of the experiment.

Instead, local weather data, such as temperature and rainfall was recovered from local weather stations (shared by the Met Office).

New data loggers (HOBO UA-002-08 Pendant Temp/Light, Onset Computer Corporation, Bourne, MA, USA) were deployed on the same verges after the experiment was finished (two loggers per slope; i.e. 16 in total). Temperature and light intensity were recorded hourly for a full year (from February 2018 to January 2019 with an interruption of about 3 weeks in May) on both aspects. Each data logger was attached between 5 and 10 cm from the ground, fixed to a bamboo cane planted in the soil. This allowed capture of temperature and light intensity data near the ground without shading by surrounding vegetation. All locations were regularly visited in order to cut vegetation within a radius of about 1 meter around the bamboo cane in order to prevent additional shade.

5.2.3. Litter bag preparation, deployment and collection

Litterbags (17mm x 25mm), made of 100% nylon polyethylene with a 5 mm mesh size which allows faster decomposition than litter bags permitting interaction with microbes only (Yin et al., 2019b). In order to control litter quality, only one species - English oak (*Quercus robur*) - was used as a litter source. Since leaf chemistry (within of the same species) can vary with aspect (Sariyildiz et al., 2005), freshly fallen leaves were collected from flat ground in Central Park, Plymouth (50°22’N, 4°08’W), during the last week of October 2016. Leaves with signs of damage, decomposition, or discolouration were discarded. The remaining litter was oven-dried at 50°C for 48 hours, then once cooled, slightly crushed and broken petioles removed. Approximatively 3.5 g of foliar litter was put into each litterbag. This initial weigh was used to calculate the percentage of mass loss by the end of the experiment.

Slope position can affect both drainage (e.g., drainage deteriorates towards the bottom, leading to increasingly anaerobic soil), and soil erosion processes (e.g., finer particles moving and accumulating downhill), which then influence the abundance and diversity of soil fauna along the slope (Bardgett, 2005). Therefore, each 1 x 4 m experimental plot was positioned at the same relative height (7-10 m) from the road, at all sites. Within each plot, four 0.5 x 0.5 m sub-plots, approximately 1 m apart and arranged in a line parallel to the road, were marked and with a spade, and the turf was removed carefully . A set of four litterbags (treatment set) was placed into each sub-plot (Figure 5.3), between 10-15 cm deep, before the turf was carefully replaced on top.

Figure 5.3: Litterbag arrangement on each paired slope (north- and south-facing) of the road verges part of a decomposition experiment according to aspect. Each plot is formed by four subplots (time treatment set), containing four replicate litterbags each. The first subplot would spend only one month in the field, and would be renewed monthly, while the second subplot would spend two months, the third, three months and the last one six months.

The first set of bags was removed after a month; the second, after two months; the third, after three months; and the last one after 6 months. In addition, a new set of four litterbags (treatment set) were deployed every month; i.e. when the first set of bags was removed from the field after a month, a new set was added, and so on until the end of the experiment . The aim in so doing was to determine whether month-by-month decomposition varied and if so, for which month decomposition was faster. A total number of 288 litterbags was deployed in the field for that experiment (4 sites x 2 aspects x 4 treatment set altogether x 9 collections [1 after 2 months, 1 after 3 months, 1 after 6 months, and 1 every month of the 6-month experiment]).

5.2.4. Soil analysis

Soil properties can change with microclimate and aspect and are also known to impact litter decomposition and soil fauna (Figure 5.1). Basic soil analysis was undertaken to verify any aspect differences which could impact soil texture (e.g. soil organic matter (OM)), soil fauna and plant abundance and diversity (e.g. pH, OM, major nutrients such as carbon (C), nitrogen (N), and hydrogen (H)). Soil samples were collected from the A-horizon (circa 3 to 15 cm deep), at the beginning of the experiment (late March 2017) for chemical analysis. The soil was sieved (< 2 mm) and oven-dried at 60°C for 24 hours (or longer when moisture was still visible) and retained. Nitrogen, carbon and hydrogen were measured by coal pyrolysis analysis, which consists of an helium chromatography followed by flash combustion of the prepared samples in an oxygen rich environment using an Elemental Microanalysis EA1110 CHN Analyser (EMASyst., 1996). Soil organic matter content depends on a variety of interacting factors, such as vegetation type, climate, parent material, soil drainage, and the activity of soil biota (Bardgett, 2005), and was calculated with the dry combustion method (4 hrs at 650°C) in a muffle furnace (Goldin, 1987). Soil pH was measured on the same day of collection, on fresh sample, in deionized H_2O using a glass electrode (YSI Pro 1030) in a solution: soil paste ratio of 1:1. Moisture content was quantified monthly for each slope, by subtracting the weight of moist sieved soil (< 2 mm) by the oven-dried (until constant weight at 105°C) one. Soil temperature was recorded monthly on the same day with a field thermometer at 10 and 15 cm deep.

5.2.5. Analysis of plant material and soil-fauna

Following recovery from the field, litterbags were transported in a brown paper bag to the laboratory, where they were opened, and foliar material cleared of soil, stone, fauna, roots, etc. Micro-fauna were carefully picked from the litter before storage in 70% ethanol until identification. The litter was then oven-dried at 50°C for 48 hours before being weighed.

Earthworm's species are split into three major functional groups (Edwards and Bohlen, 1977). Epigenic earthworms, live on the soil surface or in the upper part of the mineral soil, beneath a litter layer. Anenic species create permanent or semi-permanent vertical burrows in the soil, which descend to the mineral horizon. Both epigenic and anenic earthworms feed on decomposing litter on the soil surface, but anenic species pull them into their burrows and occasionally feed directly on soil. Finally, endogenic earthworms inhabit the mineral soil horizon and consume more soil than the other groups and derive their nourishment from humified organic matter, although some species will occasionally come to the surface to feed beneath the litter layer.

In order to capture as many earthworms as possible, two combined physical and behavioural sampling methods (Cartner and Gregorich, 2008) were used. The first consist of removing a prescribed volume of soil to be hand sorted. The second, consists of pouring onto the soil surface 15 ml of hot English mustard diluted in one litre of water (Chan and Munro, 2001), known to irritate the earthworm skin and force them to leave the soil. This technique mainly targets earthworms living in deep burrows. For this study, a 25 x 25 cm quadrat was placed over the soil, and one litre of the mustard solution was poured onto it. After 15-20 min, using a spade the soil from the quadrat area was sampled to a depth of 10 cm. Two soil samples were collected for each aspect at each site. The collected soil was kept in individual plastic bags and stored in a controlled temperature room at 10-15°C (i.e. same temperature as soil in the field) until processing.

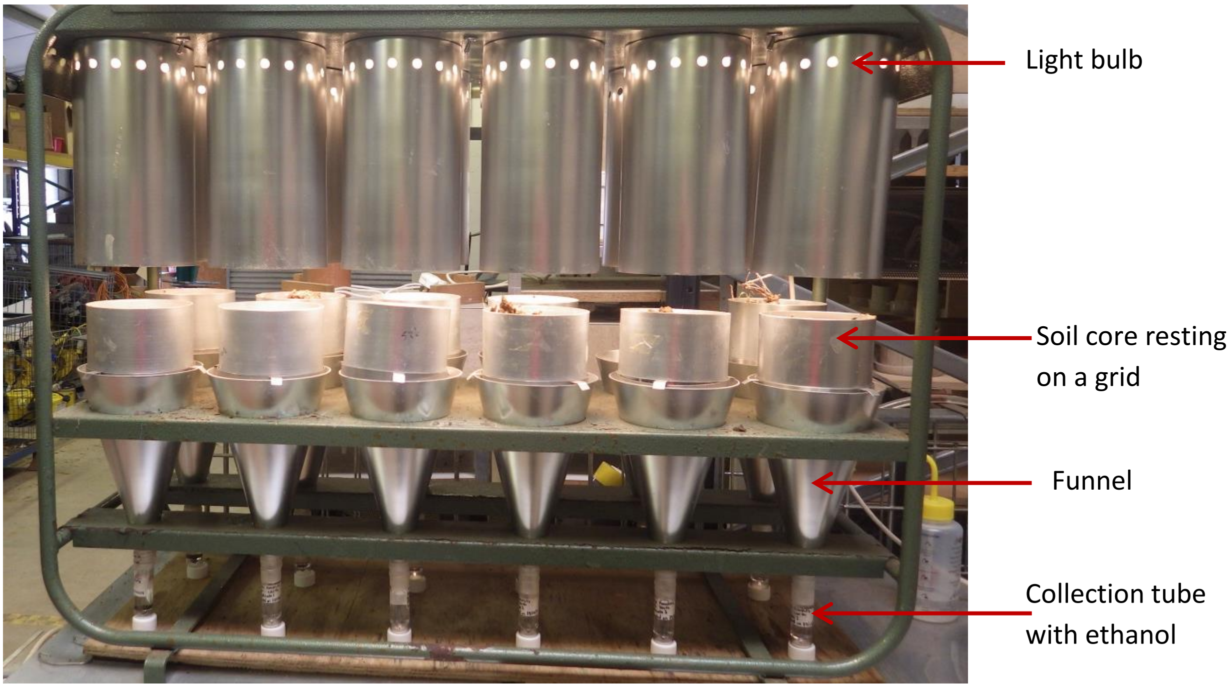


Figure 5.4: Tullgren-funnel system for micro-arthropod extraction from soil samples. The soil core, resting one a mesh, is placed on the top of a funnel. The soil is slowly warmed by a light bulb placed just above, forcing arthropods to move down the soil core to escape warmth, until they fall in the collection tube at the base of the funnel.

Mesofauna (mainly micro-arthropods) were sampled using a 30 mm deep x 50 mm wide core, and three sub-replicate cores were collected per slope. Extraction was done over 10 days using the high-gradient dynamic method (Tullgren-funnel method) (Cartner and Gregorich, 2008) (Figure 5.4). This is an active method where animals in the soil core move through it away from a repellent stimulus; i.e. a heat source using a 40W incandescent light, and toward an attractant stimulus, a tube containing the collection solution (ethanol).

5.2.6. Data analysis

5.2.6.1. Abiotic parameters analysis

Daily mean, maximum and minimum values for each aspect were calculated, and a one-way ANOVA according to aspect was performed for seasonal (winter, spring, summer and autumn) as well as annual averages. In addition, frequencies of extreme heat (i.e. above 30°C and 40°C) and cold (i.e. below 0°C and -10°C) events for each aspect were also compared. Similarly, daily means and maxima were calculated and compared according to aspect with a one-way ANOVA (Analysis of Variance) for seasonal and annual averages. The effect of aspect on soil abiotic parameters (carbon, hydrogen and nitrogen content; soil moisture; pH; OM and soil temperature) was test with a one-way ANOVA. Soil temperature, and moisture content were sampled monthly, unlike the other parameters (sampled only once). As soil temperature did not vary according to time, data temperature from all the sampled months was merged together and a mean was performed for each aspect. A two-way ANOVA was performed for the soil moisture with the factor 'Aspect' (i.e. north- and south-facing) and 'Month' (from March to September).

5.2.6.2. Soil mesofauna analysis

To examine the overall similarity of the soil measofauna communities from soil samples and litterbags, as well as the earthworm communities, a non-metric Multidimensional Scaling was undertaken using the Bray-Curtis index of similarity on 4th-root transformed abundance data of all taxa, to 'down-weight' the influence of abundant taxa and account for high numbers of zeros (Clarke et al., 2014). Differences in community structure and composition were investigated with permutational multivariate analysis of variance (PERMANOVA). Due to the well-known small-scale variation of soil mesofauna distribution, sites were used here as factor. Therefore, for the soil mesofauna the factors used in the PERMANOVA design were, ‘Aspect’ (i.e. north- and south-facing slopes), ‘Site’ (four study sites), and ‘Time’ treatment in the case of the litterbags only (i.e. one-month, two-month, three-month, and six-month treatment time). The contributions of taxa to community assemblage dissimilarities between significant factors were determined using similarity percentage analysis (SIMPER). A one-way ANOVA was then performed to examine the effect of ‘Aspect’, on earthworm species and functional groups, and other major soil mesofauna classes, in order to examine any differences not identifiable to a community level. As earthworm species can only be identified at adult stage, abundance of adults, as well as juveniles, were therefore compared with aspect.

In order to examine any relationship with (1) local weather, (2) seasonal change (over 6 months study) and (3) any change in litter mass loss, different diversity analyses were performed on the mesofauna collected from the monthly litterbags. These included : (1) Class Richness (individuals identified to class instead of species); (2) Simpson’s index of diversity ($1-\lambda$), one of the most meaningful and robust diversity measures (Magurran, 2004); and (3) total number of individuals, calculated for each individual month and aspect. Those diversity analyses were performed with the DIVERSE function in PRIMER.

5.2.6.3. Litter decomposition analysis

Decomposition was estimated by the percentage of mass loss by the litter during field deployment. For the month-by-month decomposition, a three-way ANOVA (analysis of variance) was performed with the factors ‘Aspect’ (fixed, north- and south-facing slopes), ‘Month (fixed and orthogonal, April to September) and ‘Site’ (random, four road verges). For the litterbags deployed for two, three and six months, a two-way ANOVA with the factors

'Aspect' and 'Site' was performed. The relationship between the monthly litter decomposition (percentage of mass loss) and both the monthly means of air temperature and rainfall were tested with a Pearson correlation.

All multivariate, SIMPER and diversity analyses were carried out using the PRIMER 7 (Plymouth Routines in Multivariate Ecological Research) package and the PERMANOVA add-on, and all ANOVA and correlation test were performed on the software MINITAB version17.

5.3. Results

5.3.1. Aspect and aboveground temperatures

Temperatures near the ground were consistently higher (p <0.001) on south- than on north-facing aspects (Figure 5.5 and Table 5.1), with an annual mean temperature on the south-facing road verges 1.8°C warmer (12.9 ±0.4 °C) than opposite north-facing road verges (11.1 ±0.4 °C) (Table 5.1).

Maximum temperatures were recorded during what was the warmest summer in England since the start of the Met Office in the UK in (Met Office, 2018b) and was reflected by the surprisingly high 61.7°C on the south-facing aspect of the Site 1 on the 8th of July 2018 at 14:00. By contrast, a temperature of only 33.6°C was recorded at the same time on the adjacent north-facing slope (table 5.2), a difference of over 28°C. The maximum temperature recorded on any north-facing aspect was of 46°C of the Site 2 on the 7th of July 2018 at 15:00 (Table 5.2), a difference of almost 16°C. Extremely cold temperatures were mainly reached in the short period from late February to mid-March during a severe extreme cold spell hitting Europe and the UK (Met Office, 2018a). There was no variation with aspect in the minimum temperature (-12.5°C; see Table 5.2).

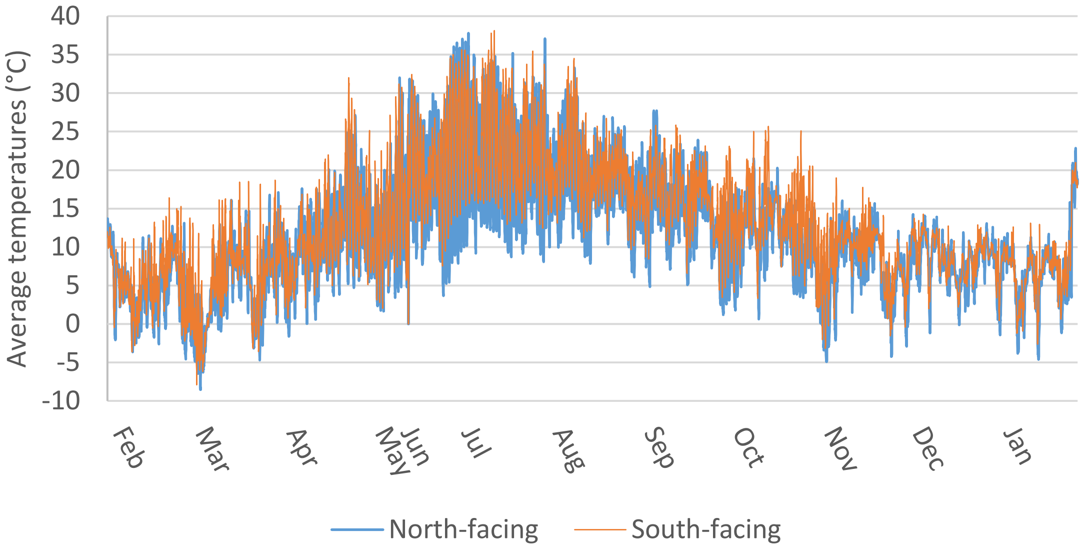


Figure 5.5: Average hourly temperature from four different locations in the SW of England, on north- (blue) and south-facing (red) slopes. Data were recorded from highway verges about 45° inclination between February 2018 and January 2019, with an interruption of 3 weeks in May.

The average daily temperature difference was highest in autumn (average 2.4 °C difference), followed by summer and spring (average difference of 2.0°C and 1.7°C, respectively). The 1°C difference recorded over the winter was not significant. Unlike minimal daily temperatures, maximum daily temperatures significantly varied with aspect consistently across all seasons (Table 5.1). The difference with aspect was highest in summer (average 10.8°C difference), followed by autumn, spring and winter (10.2°C, 7.6°C and 5.2°C difference, respectively).

There were on average significantly more extreme hot temperatures recorded on the south- than north-facing slopes, while no differences were recorded for extreme cold temperatures frequency. Although extreme high temperatures above 30°C were more frequent on southern aspect but not significantly, extreme hot events above 40°C were about 16 times more abundant on the south- than north-facing slopes. Extreme high temperatures were reached between mid- to late morning (occasionally from early morning during the middle of the summer) until mid-afternoon on the south-facing slopes, and were delayed on the north-facing slopes. Cold extreme events frequency were not significantly impacted by aspect. Extreme cold temperatures (below 0°C) tended to occur throughout the night from about 21:00-22:00 to early morning, or would start even earlier during the start of the winter, when the days are shorter. Extreme cold temperatures would tend to start slightly earlier on the south-facing slopes. Table 5.3A demonstrates important site-variations within the same region. For example, northern aspect of both sites in Cornwall (Sites 3 and 4) experienced much less hot and cold extreme temperatures than on the same aspect of both Devon sites (Site 1 and 2), and extremes such as temperatures above 40°C and below -10°C were even not reached on the northern aspect of the Cornish sites compared to the Devonian ones.

Overall, hypothesis 1 is supported; i.e. average daily mean and Max temperatures and (high >40 °C) extremes varied with aspect. These differences were apparent all year around, but there was seasonal variation and no variation in the incidence of minimum temperatures.

Table 5.1: Seasonal (winter, spring, summer and autumn) and yearly average temperature (± SE), average daily maxima (± SE), and minima (± SE) recorded on north- (blue) and south-facing (red) road verges, of four locations of the SW Peninsula of England. North- and south-facing temperatures were recorded hourly on paired slopes facing each other and were averaged daily. Significant difference in temperature ($p < 0.05$) between aspects is in bold.

	Winter		Spring		Summer		Autumn		All seasons	
	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing
Average temperatures	6.0 ±0.4	7.0 ±0.4	**8.7 ±0.5**	**10.4 ±0.6**	**19.4 ±0.3**	**21.4 ±0.4**	**10.3 ±0.5**	**12.7 ±0.4**	**11.1 ±0.4**	**12.9 ±0.4**
	$F_{1,170}$ = 2.84 , p = 0.094		**$F_{1,138}$ = 4.59 , p = 0.034**		**$F_{1,165}$ = 16.54 , p=0.000**		**$F_{1,180}$ = 13.75 , p = 0.000**		**$F_{1,658}$ = 12.12 , p = 0.001**	
Average maxima	**10.0 ±0.4**	**15.2 ±0.5**	**16.0 ±0.8**	**23.6 ±1.3**	**30.0 ±0.6**	**40.8 ±1.0**	**15.9 ±0.5**	**26.1 ±0.9**	**17.9 ±0.5**	**26.4 ±0.7**
	$F_{1,174}$ = 63.09 , p = 0.000		**$F_{1,134}$ = 23.98 , p = 0.000**		**$F_{1,166}$ = 83.42 , p = 0.000**		**$F_{1,180}$ = 93.19 , p = 0.000**		**$F_{1,660}$ = 97.94 , p = 0.000**	
Average minima	1.3 ±0.4	1.2 ±0.4	9.1 ±0.4	8.9 ±0.4	8.8 ±0.4	8.9 ±0.4	3.4 ±0.5	4.0 ±0.5	5.4 ±0.3	5.5 ±0.3
	$F_{1,174}$ = 0.00 , p = 0.946		$F_{1,134}$ = 0.09 , p = 0.771		$F_{1,166}$ = 0.04 , p = 0.839		$F_{1,178}$ = 0.75 , p = 0.387		$F_{1,658}$ = 0.12 , p = 0.733	

Table 5.2: Maximum and minimum temperatures recorded over a year period with the associated date and time, and the summer extreme from the south-facing (red) slopes paired with the temperature recorded at the same time on the north-facing (blue) road verge of the same site. All recordings were collected on highway verges at four sites in the SW of England, where the north- and south-facing verges of the same site are facing each other.

Site	Minimum temperature		Maximum temperature		Temperature on N-facing associated to S-facing max
	N-facing	S-facing	N-facing	S-facing	
Site 1	-10.8°C 28/02/18 2:45	-12.5°C 28/02/18 2:45	43.8°C 26/07/18 17:00	61.7°C 08/07/18 14:00	33.6°C
Site 2	-12.5°C 28/02/18 00:45	-10.2°C 08/02/18 1:45	46.0°C 07/07/18 15:00	56°C 08/07/18 14:00	41.3°C
Site 3	-6.4°C 28/04/18 5:45	-6.1°C 20/03/18 1:45	37.3°C 30/06/18 18:00	57.8°C 08/07/18 13:00	27°C
Site 4	-6.0°C 28/02/18 5:45	-7.7°C 27/02/18 4:45	38.0°C 29/06/18 15:00	57.6°C 22/07/18 13:00	30°C

Table 5.3: Total number and averages of extreme **A.** hot (i.e. above 30°C and 40°C) and **B.** cold (below 0°C and -10°C) events recorded over a year on north- (blue) and south-facing (red) aspects at four roadside verge sites in the SW England. Temperatures were recorded hourly.

A	Frequency of extreme hot events (>30°C)		Frequency of extreme hot events (>40°C)	
Site	North-facing	South-facing	North-facing	South-facing
Site 1	301	722	15	339
Site 2	391	646	42	220
Site 3	41	501	0	161
Site 4	65	448	0	197
Total (all sites)	798	2,317	57	917
Mean (±SE)	200 ±87	279 ±63	14 ±10	229 ±35

B	Frequency of extreme cold events (<0°C)		Frequency of extreme cold events (<-10°C)	
	North-facing	South-facing	North-facing	South-facing
Site 1	550	624	2	6
Site 2	695	520	4	1
Site 3	268	564	0	0
Site 4	298	303	0	0
Total (all sites)	1,811	2,011	6	7
Mean (±SE)	453 ±103	503 ±70	1.5 ±1	1.85 ±1.4

5.3.2. Aspect and light intensity

There was a striking significant difference in light intensity between north- and south-facing slopes ($F_{1,15664} = 667.18$, $p = 0.000$) (Figure 5.6), with the latter receiving over twice as much light than the opposite north-facing slopes (e.g., annual average of 9,015 Lux and 21,050 Lux on north- and south-facing slopes). When considering only day light data, the annual mean of light intensity was 15,208 Lux on north-facing slopes and 39,418 Lux on the opposite south-facing ones, so about 2.5 times more. The maximum light intensity was 308,624 Lux and 176,356 Lux on the south- and north-facing slopes, respectively. Therefore, maximum light intensity on south-facing slopes was 75% greater than the opposite north-facing slope. Highest light intensities were recorded in spring on south-facing slopes, and later, mainly during the summer on the north-facing ones (Table 5.5). The first and last records of light intensity during the day were roughly the same on both aspects.

On south-facing slopes, light intensity was lowest during December and January, but on north-facing slopes, this period was much longer, extending from October to beginning of March (Figure 5.6). The annual peak of light intensity appeared to be in May-June on the north-facing slopes, while maximum light intensities were evenly more spread across the year on the south-facing slopes. On the latter slopes, highest light intensities were recorded from mid-morning until mid-afternoon, while on the north-facing slopes this was spread from early morning to early evening (Table 5.5).

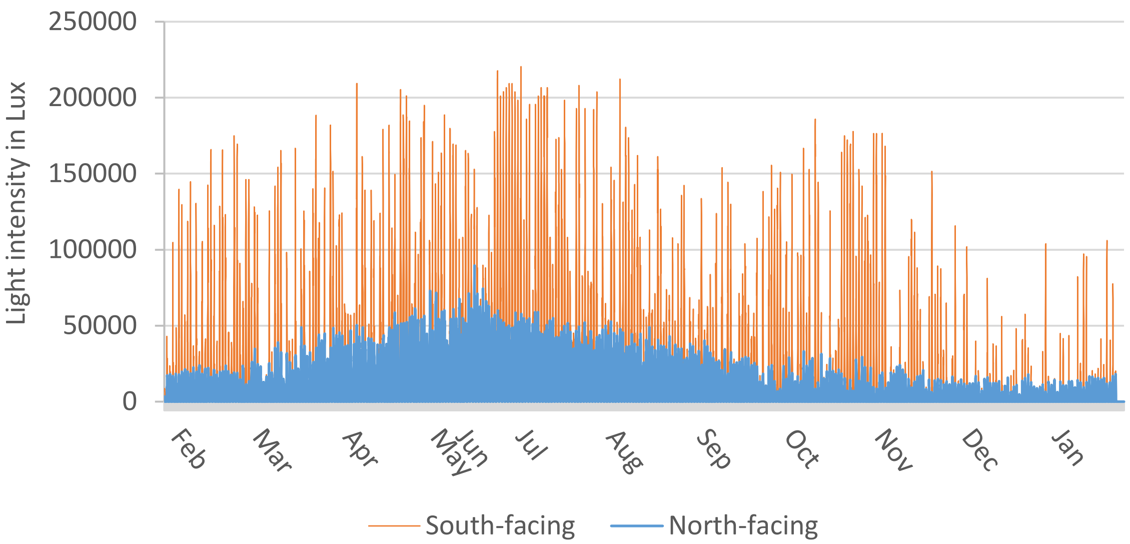


Figure 5.6: Annual light intensity (in Lux) on both north- (blue) and south-facing (red) slopes across four locations in the SW of England. The light intensity was recorded hourly, at about 5-10 cm from the ground on road verges of about 45° inclination. Start of recording was February 2018 and ended in January 2019, with an interruption of 3 weeks in May.

Table 5.4 shows that light intensity varied with aspect but differently over the different seasons. Winter was the season displaying a greater difference in light intensity according to aspect, with the south-facing slopes receiving about 4.5 more than the north-facing ones. Autumn was the second greatest with light intensity difference of 3.6 between aspect, followed by summer and then spring. Surprisingly, mean light intensity reaching the slopes was lower in the summer compared to the winter. The growing vegetation around the data loggers during the summer, which was probably not cut down frequently enough, could have contributed to this difference. The average of the daily maxima varied during all seasons (Table 5.4) with greatest maxima average in spring, followed by winter, then summer and lastly autumn. Greatest difference in maxima averages according to aspect was during the winter, where maxima light intensity were five times more intense on the south- than north-facing slopes. The second greatest difference in maxima averages with aspect was during the autumn, followed by spring and lastly summer.

Table 5.4: Seasonal (winter, spring, summer and autumn) and yearly average of light intensity in Lux (± SE), average of maxima (± SE), and minima (± SE) recorded on north- (blue) and south-facing (red) road verges, of four locations of the SW Peninsula of England. North- and south-facing light intensity were recorded hourly on paired slopes facing each other and were daily averaged. Significant difference in light intensity ($p < 0.05$) between aspects is in bold.

	Winter		Spring		Summer		Autumn		All seasons	
	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing
Average light intensity	1,964	8,852	12,284	15,744	1,572	3,052	430	1,552	3,647	9,184
	±252	±1,468	±617	±3,199	±52	±149	±22	±111	±291	±763
	$F_{1,164}$ = 21.38 , *p* = 0.000		**$F_{1,138}$ = 53.50 , *p* = 0.000**		**$F_{1,164}$ = 87.42 , *p* = 0.000**		**$F_{1,180}$ = 98.40 , *p* = 0.000**		**$F_{1,652}$ = 45.93 , *p* = 0.000**	
Average maxima	11,008	57,398	50,244	140,411	6,024	14,940	2,034	9,436	15,672	51,191
	±1,408	±8,412	±2,001	±8,836	±212	±608	±81	±566	±1,160	±3,996
	$F_{1,166}$ = 29.58 , *p* = 0.000		**$F_{1,138}$ = 99.05 , *p* = 0.000**		**$F_{1,164}$ = 191.67 , *p* = 0.000**		**$F_{1,178}$ = 167.71 , *p* = 0.000**		**$F_{1,652}$ = 72.88 , *p* = 0.000**	

Table 5.5 shows comparison between associated highest temperatures and light intensities, and *vice versa*. Without accounting for aspect, this allowed to demonstrate that light intensities and temperatures were not associated with the respective highest values. For example, the highest light intensity (308,624 Lux) was associated with only 18.2°C while the highest temperature (61.7°C) was associated with a light intensity of only 46,844 Lux, so being only 15% of the highest recorded light intensity.

Table 5.5: Maximum light intensity and its corresponding temperature, and maximum temperature with its corresponding light intensity, on both **A.** south- (red) and **B.** north-facing (blue) road verges across four Sites. The minimum light intensity is not compared, as it is zero, and is reached every day during the night-time.

A	South-facing			
	Max temp	Associated light intensity (Lux)	Max light intensity (Lux)	Associated temperature
Site 1	61.7°C 08/07/18 14:00	46,844	308,624 27/03/18 12:45	18.2°C
Site 2	56.0°C 08/07/18 14:00	37,200	264,535 28/03/18 10:45	18.0°C
Site 3	57.8°C 08/07/18 13:00	154,311	297,602 26/04/18 13:45	30.5°C
Site 4	57.6°C 22/07/18 13:00	198,400	297,602 26/04 15:45	35.0°C

B	North-facing			
	Max temp	Associated light intensity (Lux)	Max light intensity (Lux)	Associated temperature
Site 1	43.8°C 26/07/18 17:00	63,378	137,778.1 22/07/18 09:00	34.7°C
Site 2	46.0°C 07/07/18 15:00	44,089	104,712 12/06/18 15:00	22.3°C
Site 3	37.3°C 30/06/18 18:00	33,067	154,311 14/06/18 18:00	14.8°C
Site 4	38.0°C 29/06/18 15:00	16,384	176,356 14/04/18 15:00	18.2°C

5.3.3. Soil properties

Of the factors considered, only soil moisture significantly varied with aspect, averaging 31.4 ±0.8% in north-facing slopes and 26.0 ±1.2% on south-facing (Table 5.6). Carbon, hydrogen, nitrogen, and organic matter content, as well as pH, and temperature by contrast, did not differ with aspect, although a trend towards warmer soil temperature is suggested for south-facing slopes. Therefore, the second hypothesis is, in overall, refuted, as aspect does not seem to the change properties of grassland road verges soil, except for the soil moisture.

Table 5.6: Soil properties according to aspect on north- (blue) and south-facing (red) road verges in SW England. Average (± SE) soil temperatures (°C) from 10-15 cm, and soil moisture (% of dry soil weight) are average of monthly recordings (from March to September), while the other parameters are data from one sample date at the start of the experiment (March). Significant (*p* < 0.05) differences in soil properties between aspects are denoted in bold.

A	North-facing	South-facing	
C (% of dry soil weight)	7.0 ±0.7	6.6 ±0.5	$F_{1,22} = 0.24$, $p = 0.630$
H (% of dry soil weight)	2.5 ±0.2	2.3 ±0.1	$F_{1,22} = 1.20$, $p = 0.285$
N (% of dry soil weight)	0.55 ±0.03	0.54 ±0.03	$F_{1,22} = 0.08$, $p = 0.780$
pH	5.1 ±0.2	4.8 ±0.2	$F_{1,70} = 1.75$, $p = 0.190$
OM (%)	15.9 ±1.2	15.2 ±0.7	$F_{1,22} = 0.23$, $p = 0.635$
Temperature °C	11.7 ±0.6	13.0 ±0.5	$F_{1,62} = 2.76$, $p = 0.101$

B		Df	Adj MS	F-value	P-value	
Moisture (% of dry soil weight)	**Aspect**	**1**	**350.2**	**8.29**	**0.007**	N>S
	Month	**5**	**293.2**	**6.94**	**0.000**	
	Aspect x Month	5	10.6	0.25	0.937	
	Error	36	42.24			
	Total	47				

Soil moisture significantly varied month-to-month (Table 5.6), which is reflective of monthly rainfall (Figure 5.11A). Soil temperatures were recorded at 10 and 15 cm deep, however, as there was no significant difference with the factors 'Depth' (p = 0.653), and 'Aspect' (p = 0.107), nor the interaction term 'Aspect x Depth' (p = 0.963), data from both depths were merged in Table 5.6.

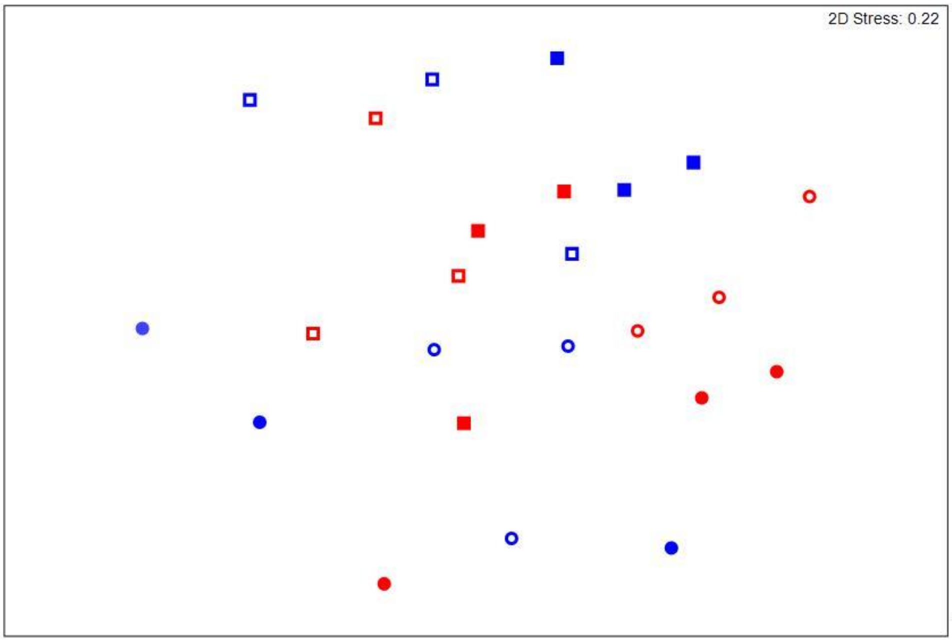
5.3.4. Soil core mesofauna and aspect

A total of 23 taxonomic groups (mainly down to order) were sampled in the soil survey, with three different types of eggs and two unknown species (Appendix 6). Aspect had no significant effect on the mesofauna community assemblage (Table 5.7, Figure 5.7) or abundance of individuals (Figure 5.8), however, trends still appeared with slightly higher abundance of the classes Nematoda, Oligochaeta (earthworms and potworms), Gastropoda (slugs and snails), Chilopoda (centripedes), Entognatha (collembola or springtails) and Arachnida (mites) on the south- than north-facing slopes (Figure 5.8). There was a site-to-site variation in the mesofauna community assemblage (Table 5.7) with similarity between sites ranging from 59 to 67%. The Acari (dominated by mites) and Collembola (Entognatha class), as well as some other classes of insects, which would vary, from a soil core or site level, mainly drove these dissimilarities. Collembola and mites were by far the most abundant soil arthropods (about 100 individuals per soil core), followed by the Oligochaeta (average 2.5 individuals per soil core) (Figure 5.8).

Table 5.7 PERMANOVA results for mesofauna community collected from soil cores on north- and south-facing slopes (factor 'Aspect') of four different paired road verges (factor 'Site'; see Figure 5.2 for locations) of the SW England. Soil cores collected late March 2017, at the beginning of the experiment.

Source	df	MS	Pseudo-F	P-values
Site	3	1196.8	2.303	**0.002**
Aspect	1	550.32	0.446	0.817
Site x Aspect	3	12332	2.373	**0.002**
Residuals	16	519.67		

Figure 5.7: Non-metric MDS ordination of Bray-Curtis resemblances between multivariate community compositions according to aspect (north/south orientation) for a total of 24 soil cores sampled from four sites of the SW England. Each symbol represents the soil mesofauna community from one core on one slope aspect at one location. Devonian sites, represented by a circle symbol, include the road Sites 1 (●) and 2 (○), while Cornish sites, represented by the square symbol, include the road Sites 3 (■) and 4 (□). The colour indicates the aspect, with blue, the north-facing and red, the south-facing substrata.



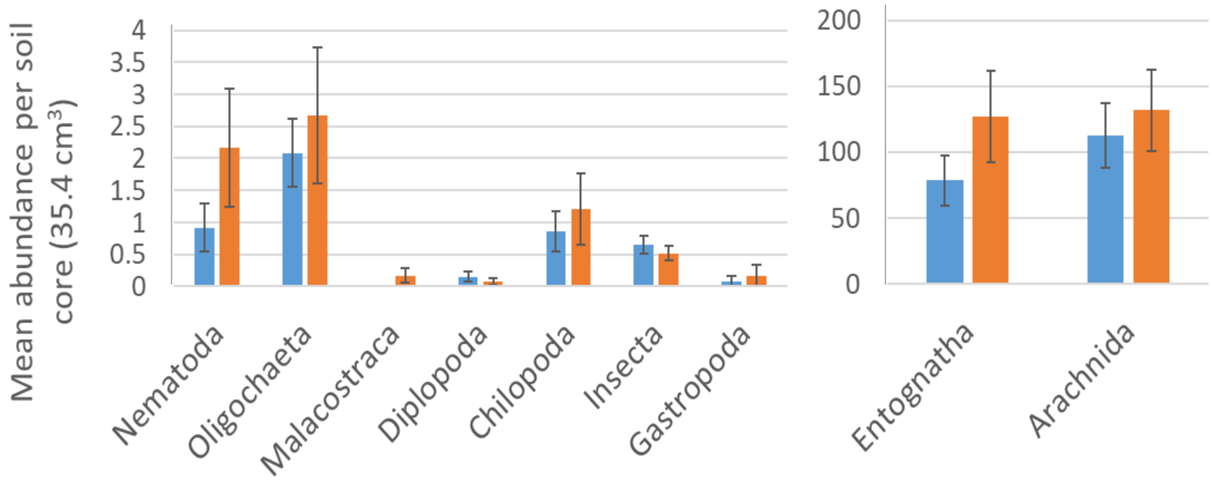


Figure 5.8: Mean abundance (± SE) of the major classes of mesofauna sampled in soil cores of 35.4 cm^3 on north- (blue) and south-facing (red) slopes from four different locations in the SW England (see Figure 5.2 for locations), collected late March 2017.

5.3.5. Earthworm survey

Overall, the whole earthworm community assemblage did not vary with 'Aspect', 'Site' or the 'Aspect x Site' interaction (Table 5.8). Overall abundance varied little with an average of 20.8 ±1.5 and 19.5 ±1.0 earthworms per soil sample (i.e. 6,250 cm^3) on the north- and south-facing slopes respectively.

Table 5.8 PERMANOVA results for all earthworm species collected late March 2017, at the beginning of the experiment, from soil samples on north- and south-facing slopes (factor 'Aspect') of four different paired road verges (factor 'Site'; see Figure 5.2 for locations) of the SW England.

Source	df	MS	Pseudo-F	P-values
Aspect	1	1307.2	0.55085	0.668
Site	3	1860.7	1.3832	0.207
Aspect x Site	3	2373	1.764	0.083
Residuals	8	1345.2		

There were on average more juveniles than adults, however, not significant (Figure 5.9A). The abundance of only one species *Apporectodea rosea*, varied according to aspect (Figure 5.9B), the species being completely absent from south-facing slopes. Other species, such as *Dendrobaena hortensis*, *Dendrobaena rubidus*, *Eisenia fetida*, *Octolasion cyaneum*, *Octolasion lacteum*, and *Satchellius mammalis* followed a similar trend with complete absence on southern aspect, but their lower abundance on north-facing slopes likely reduced statistical power. All *Lumbriscus* species, by contrast, tended to have either similar or higher abundance on south-facing slopes; *L. terrestris* being absent from the north-facing aspects. Again, low abundance and/or uneven distribution across all sites, impact statistical resolution of any

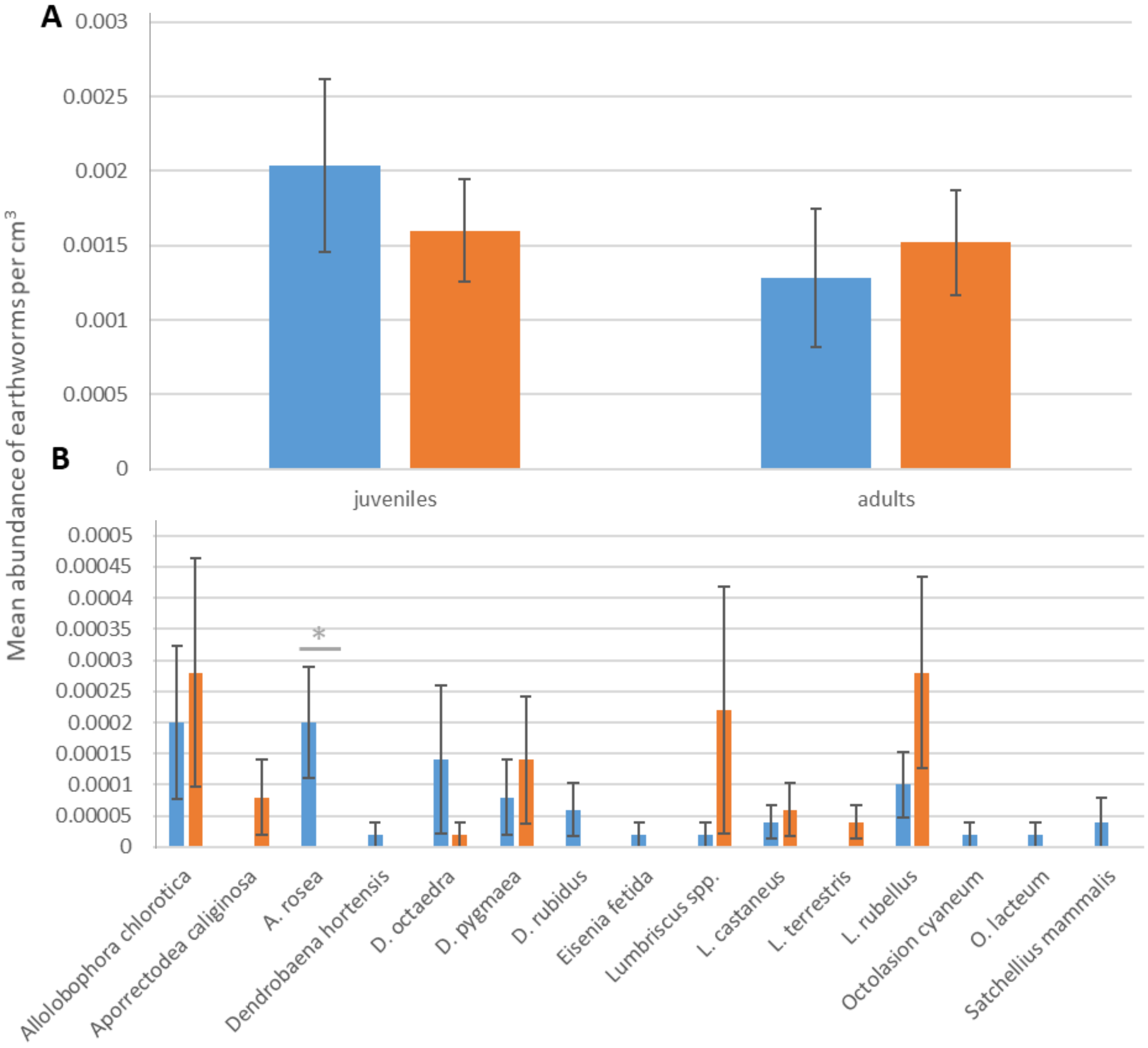


Figure 5.9: Mean abundance (± SE) of **A**. juveniles and adults earthworms, and **B**. sampled taxa, from 25x25x10 cm soil samples (volume of 6250 cm^3) on north- (blue) and south-facing (red) slopes from four different locations in the SW England (see Figure 5.2 for locations), collected late March 2017. * indicates significant difference with aspect with p <0.05.

trends. *Lumbriscus spp.* and *Allolobophora chlorotica* were the most abundant species across all sites and aspects. Both abundance and species richness of the functional groups (epigenic, anenic, and endogenic) did not vary with aspect (Figure 5.10). Epigenic earthworms tended to be more abundant and diverse on north- than south-facing slopes, while anenic ones were slightly more abundant on the other aspect, however, all none-significant. The mean abundance of each earthworm species sampled in this survey, per site and aspect, can be found in Appendix 7.

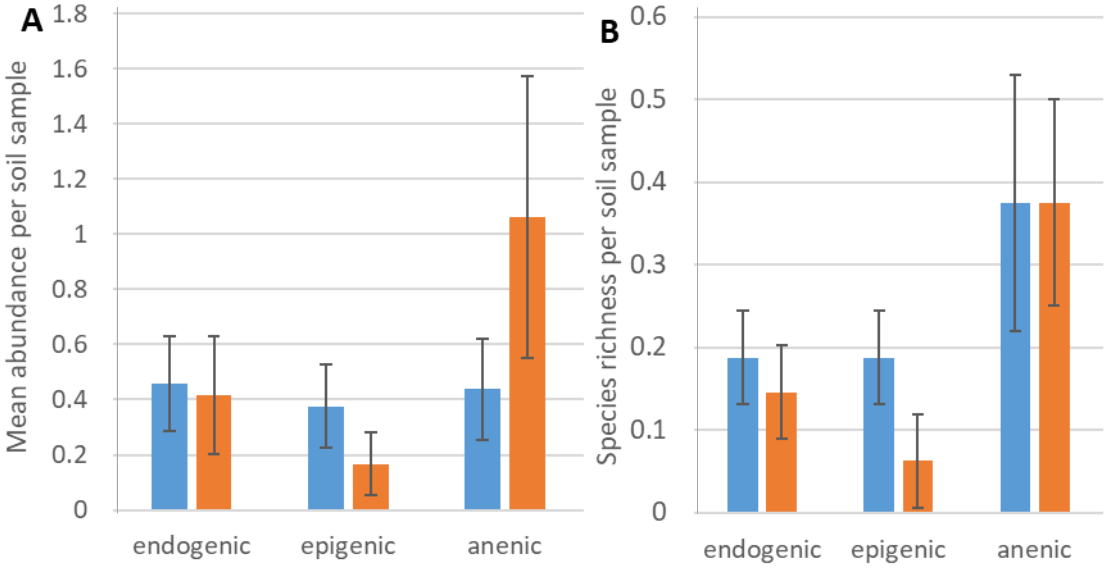


Figure 5.10: **A.** Mean abundance (± SE) and **B.** Species richness (± SE) of the earthworms functional groups (endogenic, epigenic and anenic) collected late March 2017, from 25x25x10 cm soil samples (volume of 6250 cm^3) on north- (blue) and south-facing (red) slopes from four different locations in the SW England (see Figure 5.2 for locations). No significant differences with aspect ($p > 0.05$).

5.3.6. Leaf litter decomposition, aspect and meteorological data

Decomposition (i.e. Mass loss of *Quercus robur* litter) varied according to 'Site' during all deployments (i.e. one, two, three and six months (Table 5.9)). 'Aspect' was however only significant for litterbags deployed for one and three months with greater litter mass loss on north- than south-facing slopes. All interaction terms were significant. Analysis of monthly litter mass loss revealed that decomposition was actually significantly greater on the north- than south-facing slopes in June, July and September only (Figure 5.11B), (but with no variation in April, May, and August). The effect of 'Aspect' seemed to be significant in months with warmer, greater average rainfall and soil moisture (Figure 5.11A), however, the Pearson correlation demonstrated no correlation between the litter percentage mass loss and monthly mean air temperature (*p* = 0.097), monthly mean precipitation (*p* = 0.392), nor monthly soil moisture (*p* = 0.595). Litterbags left two and six months in the field lost similar weight on both aspects, with an average of 6.7% ±0.6 and 9.3% ±0.6 grams of their initial weight, respectively.

Table 5.9: ANOVA results of the decomposition (estimated mass loss) of English oak (*Quercus robur*) litter according to 'Aspect' (north- and south-facing) and 'Site' (four road verges, see Figure 5.2) in SW England for litterbags left one month from April to September 2017 (additional factor 'Month'), two months (April to May 2017), three months (April to June), and six months (April to September 2017) in the field.

Deployment time	Source	df	MS	Pseudo-F	*p*-value
1 month	Aspect	1	35.335	12.16	**0.001**
	Site	3	32.423	11.16	**0.000**
	Month	5	67.408	23.20	**0.000**
	Aspect x Site	3	11.755	4.05	**0.008**
	Aspect x Month	5	10.597	3.65	**0.004**
	Site x Month	15	7.622	2.62	**0.002**
	Residuals	151	10.597		
2 months	Aspect	1	4.603	1.44	0.242
	Site	3	88.357	27.62	**0.000**
	Aspect x Site	3	11.611	3.63	**0.027**
	Residuals	24	3.199		
3 months	Aspect	1	20.718	13.92	**0.001**
	Site	3	109.195	73.38	**0.000**
	Aspect x Site	3	5.941	3.99	**0.019**
	Residual	24	1.488		
6 months	Aspect	1	34.16	0.40	0.535
	Site	3	301.48	3.51	**0.031**
	Residual	23	85.91		

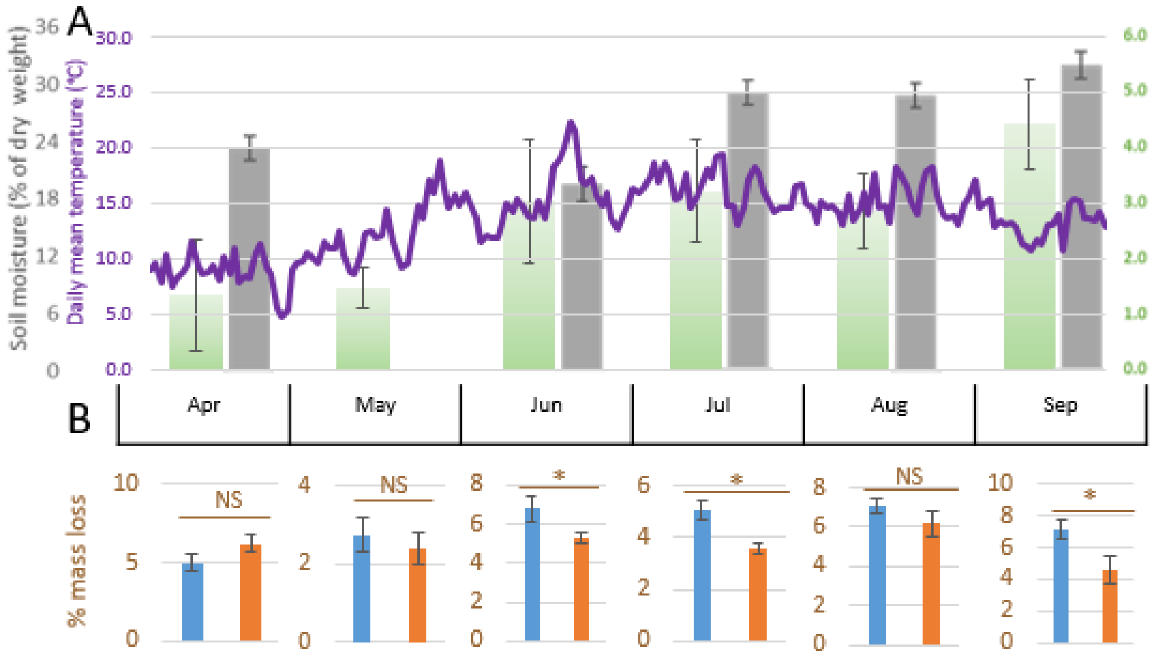


Figure 5.11: **A.** Daily mean temperature (°C) (violet) and monthly mean rainfall (mm) (green) sampled by the nearest Met Office local weather stations (see Figure 5.2), and monthly soil moisture from the A-horizon (grey), over the six month of the experiment. **B.** Monthly litter decomposition (± SE) composed of *Quercus robur* (in % of mass loss) on opposite north- (blue) and south-facing (red) slopes from four locations in the SW England (see Figure 5.2) from late March to late September 2017. NS, no significant difference; * significant with p <0.05

5.3.7. Mesofauna associated with leaf litterbags

Although 'Aspect' had no influence on the community assemblage of soil mesofauna recovered from litterbags, the factors 'Site' and 'Time treatment', as well as the interactions 'Site x Time treatment', 'Site x Aspect', and 'Time treatment x Aspect x Site', were significant (Table 5.10). Separate PERMANOVA tests performed on each monthly sampling (from April to September) revealed a significant 'Aspect' effect from the September sampling only, with on average more slugs (Gastropoda), earthworms and potworms (Oligochaeta) and Collembola (Entognatha) on the south-facing slopes. In addition, the SIMPER analysis revealed that invertebrate community assemblages varied from month-to-month, displaying a low similarity from 19% to 31%. In all monthly samples, Acari (dominated by mites), slugs, and Entognatha contributed most to sample dissimilarity. Oligochaeta (dominated by earthworms) also contributed to mesofauna community differences, but in September samples only. Some caution should be taken however, as the abundance of all species present in litterbags was extremely low (Appendix 8).

Table 5.10: PERMANOVA results for soil mesofauna community collected within oak leaf litterbags left between one and six months in the field (factor 'Time treatment'), on north- and south-facing slopes (factor 'Aspect') of four different paired road verges (factor 'Site'; see Figure 5.2 for location) of the SW England.

Source	df	MS	Pseudo-F	P-values
Site	3	28867	13.034	**0.000**
Time treatment	8	7690.8	2.037	**0.000**
Aspect	1	6559.7	0.720	0.622
Site x Time treat.	23	3795.7	1.713	**0.000**
Site x Aspect	3	9092	4.105	**0.000**
Time treat. x Aspect	8	3829.6	1.204	0.188
Time treat. x Aspect x Site	23	3191.7	1.441	**0.000**
Residuals	168			

When investigating the abundance of the most common invertebrate classes, few patterns emerged, however not significant. Both Malacostraca (i.e. Oniscidea woodlice) ($F_{1,46} = 3.12$, $p = 0.084$) and Diplopoda (millipedes *Polydesmida* spp and *Julida* spp) ($F_{1,46} = 0.08$, $p = 0.774$) were greater on north- than south-facing slopes, and Arachnida (i.e. mites) had opposite pattern ($F_{1,46} = 1.40$, $p = 0.242$) (Figure 5.12).

Other classes, most prominently the Arachnidae (spiders, pseudoscorpions, mites and harvestmen) and Insecta, tended to be more abundant on the south- than north-facing slopes, although there was considerable variation between sites. Insecta, Entognatha, Gastropoda (mainly slugs), Diplopoda, Oligochaeta had a similar abundance over the 6-month period. Chilopoda and Malacostraca had a constant abundance over time, except with a peak in July (with five times more individuals on the south- than north-facing slopes) and in June (with four time more individuals on north- than south-facing slopes) respectively. Acari (mites), by far the most abundant superclass of the Arachnida, did not vary with aspect from spring to late summer ($F_{1,46} = 1.40$, $p = 0.242$), although they tended to be more abundant on south- facing slopes in April, May and July. Peak abundance of Acari was in April and May on south-facing slopes only.

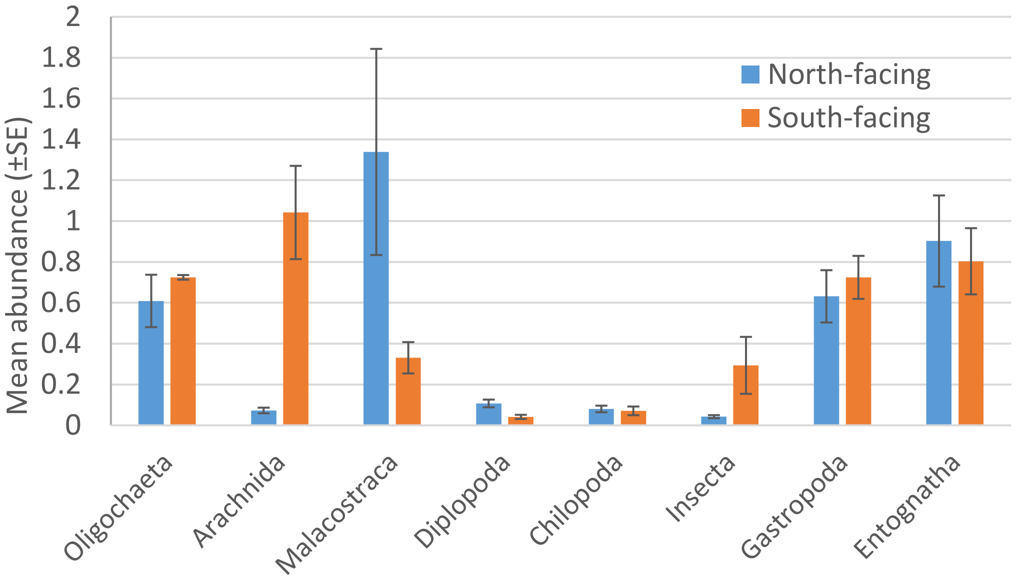


Figure 5.12: Mean abundance (± SE) of the most commonly encountered invertebrate classes collected in oak litterbags on north- (blue) and south-facing (red) slopes from four different paired road verges in the SW England, from April and September 2017 (see Figure 5.2 for locations). No significant difference was found between aspect.

Overall, there were more individuals (from all combined taxa) on the south-facing slopes in April and May, while the opposite pattern occurred in June, and no difference with aspect was found in July, August and September (Table 5.11). In April, an ant colony (Hymenoptera) settled under the grass turf replaced over the litterbags on the south-facing slope of the road verge 2. Even after excluding the number of adults' ants and pupa collected from that site, the average number of individuals sampled in April on the southern aspect was still much higher than the number collected on the opposite aspect. Overall, class richness was similar on both aspects, except in April and August where the richness was higher on the north-facing and south-facing slopes, respectively.

April samples are a good example illustrating the fact that species and taxonomic richness does not always reflect the patterns followed by the total individual numbers. Although there were more total individuals sampled on south-facing slopes, due to the ant colony in one site, there was still greater richness on the opposite north-facing slopes. This underscores the importance of using the Simpsons' index of diversity, as it accounts for evenness and dominance. However, no clear trends with aspect and seasonal changes were found. On the north-facing slopes, diversity slightly decreased (increasing index) over the 6-month experiment, with no apparent patterns on the south-facing slope. Simpsons' index of diversity was lesser on north- than south-facing slopes in April, May and July (reflecting greater diversity), while opposite pattern occurred in August and September, and no aspect-difference was found in June.

The greater mass loss of *Q. robur* litter on north- facing slopes in June, July and September (see section above), does not seem to match any concomitant changes in the litterbag mesofauna community assemblage and diversity (Table 5.11, Appendix 9).

Table 5.11: Effect of slope aspect on mesofauna communities (Total individuals (± SE), class richness (± SE) and diversity - Simpson's index of diversity (± SE)) sampled from litterbags, containing *Quercus robur* leaves, deployed monthly (April to September 2017), on north- (blue) and south-facing (red) slopes from four different paired road verges in the SW England.

	Aspect	April	May	June	July	August	September
Total Individual Number	North	5.9 ±0.9	3.4 ±0.8	16.4 ±5.3	7.6 ±2.3	8.2 ±1.3	4.4 ±0.7
	South	37.9 ±20.5	10.7 ±4.6	8.5 ±1.8	6.1 ±1.6	8.4 ±1.4	5.7 ±0.5
Classes Richness	North	12.4	12.0	15.0	13.0	16.0	17.0
	South	7.9	11.0	16	17	19	16.0
Simpson's Index	North	0.13	0.19	0.19	0.21	0.21	1.11
	South	0.28	0.34	0.19	0.24	0.16	1.04

5.4. Discussion

This study supported the first hypothesis, south-facing slopes being considerably warmer (annual difference of 1.8°C) as well as experiencing more hot extremes events, and being drier (soil 18% drier in spring and summer) than north-facing slopes, corroborating previous aspect studies (Armesto and Martínez, 1978; Bennie et al., 2008; Sidari et al., 2008). These aspect variations can likely be explained by the difference in incident solar radiation (Franzmeier et al., 1969), which was over 40% greater on south-facing slopes. The annual recording of light intensity highlighted distinct radiation peaks on north-facing slopes whereas radiation was almost uniform throughout the year with a maximum radiation spreading from spring to autumn on the opposite south-facing slopes. Franzmeier et al. (1969) found similar trends in light intensity over north- and south-facing slopes in North America. In addition to controlling above ground temperature, variation in light intensity would potentially have an important impact on photosynthesis and plant phenology, especially during key seasons of the year. For example, greater exposure to sun on equator-than polar-facing aspects has a positive impact on (1) fruit set and crop density during the growing season and especially towards the equinoxes (Khemira et al., 1993); on (2) length of flowering season, especially extending into early autumn (Cantlon, 1953), and on (3) early season dormancy breaking of buds (Cantlon, 1953). Consequently, although I found no consistent influence on litter decomposition, there may well be implications for other ecological processes. For instance, microclimate-dependant phenology (e.g., aspect) of host plant and sources of nectar would be directly linked to survival and development of pupa and adult butterflies (Weiss et al., 1988).

Overall, there was little support for hypothesis two as no abiotic soil parameters, other than moisture, varied with aspect. This would confirm that the use of road verges to examine how aspect affects aboveground processes only may be good systems assuming they also have similar slope and underlying soil materials. Results of this study would also suggest that at small scale, aspect does not alter pedoclimate, except for soil moisture, which is directly linked to aboveground climate. Soil moisture has a key importance in limiting soil temperature variation (Aschcroft and Gollan, 2013), and affecting the amount of radiation resulting in evaporation instead of temperature rise (Evans et al., 2011). It is also highly important for plants, the microbial processes and nutrient cycling (Parmesan and Hanley 2015). Drought can also potentially change soil chemistry (Hinojosa et al. 2012), and impact greatly seedling survival (Harrington, 1991). In contrast to my study, soil properties vary with slope orientation at larger scales such as mountainous systems (e.g. Mudrick et al., 1994; Yimer et al., 2006; Sidari et al., 2008; Begun et al., 2010). In those cases, it is likely impossible to distinguish the strictly aspect-dependant soil chemistry variations to the changes in vegetation and therefore litter properties, and the associated mesofauna.

Mass loss of *Quercus robur* litter was significantly influenced by aspect for litterbags deployed for one month and three months only, partially supporting hypothesis two. Higher mass loss on north-facing slopes for the wetter months of June, July and September corroborate previous studies such as Mudrick et al. (1994), Sariyildiz et al. (2005) and Seidelmann et al. (2016) who found greater decomposition rate on north-facing slopes, or in conditions with increased air temperature and soil moisture. Also this aspect-related litter mass loss was not found correlated to either rainfall, soil moisture or air temperature alone, the combination of those parameters might have driven this difference.

The combination of marked variation in temperature (averages and extremes) and the less consistent variation in litter decomposition with aspect observed here may reflect predictions in the context of global change. In a recent experimental study on the effects of ACC on litter decomposition, future climate treatments (0.55°C and 0.50°C increase of mean air and soil temperatures, respectively, combined with increase and decrease of rainfall during spring and summer respectively) decreased decomposition rate, (Yin et al., 2019a). The similar litter mass loss on both aspects, may be attributed to the similar soil temperatures and the presumably similar amount of rainfall hitting both slope aspects.

Temperature and moisture are major environmental variables affecting physical weathering (fragmentation) rates (e.g., weathering much faster in warmer climate; Bohn et al., 2001) and activity of decomposer organisms (e.g., bacteria and fungi metabolism is higher in warm, moist conditions; Edwards and Bohen, 1977; Lavelle et al., 1993). Considering that summer temperatures can exceed 60°C on a south-facing slope in the SW England, north-facing slopes would have thus been more favourable for many soil or aboveground organisms and litter decomposition in summer as moister and warm conditions (but not reaching excessively hot temperatures). Soil (and vegetation cover) is already known for its buffering property (Lu et al., 2009; Aschcroft and Gollan, 2013). The buffering process generally occurs within the few centimetres of the soil surface (Chen et al., 1999). In extreme cases of wildfire, for example, soil temperature at 2.5 cm depth was estimated at about 110°C and dropped to about 40°C at 15 cm (Beadle, 1940). Recolonisation of seeds (Beadle, 1940) and microorganisms (Bárcenas Moreno et al., 2011) successfully happened after fire, thanks to the soil-buffering effect.

Despite major differences in aboveground temperature and belowground soil moisture, there was limited variation in the soil mesofauna community between north- and south-facing slopes (i.e. little support for hypothesis three), suggesting that soil properties are likely not varying enough with aspect to influence the abundance of taxonomic and functional groups. Interestingly however, the earthworm survey did revealed that seven of 14 species were restricted to north-facing slopes only, while two (*Lumbriscus*) species were encountered on south-facing slopes only. Of these, only one, the endogeic *Aporrectodea rosea*, was consistently recovered in sufficient numbers to yield statistical evidence for greater abundance on north-facing slopes. This distribution is likely associated with its high dependency on soil moisture, also demonstrated in previous studies (Gerard, 1960; Thomson and Davies 1974; Doube and Styan, 1996). Although this species is not considered a major contributor to the litter decomposition process (e.g., its assimilation rate of the overall soil organic matter was estimated at only 0.9% by Bolton and Phillips (1976)), it has known beneficial effects on crops and pasture plants (Stephens et al., 1994a and 1994b; Doube et al., 1997; Stephen and Davoren, 1997). In addition, several earthworm species tend to be associated with each other, soil types and habitats (Edwards and Bohlen, 1977; Edwards, 2004). For example in Sweden, *A. rosea* is often associated with *Lumbriscus castaneus* and *Allolobophora chlorotica* (Nordström and Rundgren, 1973) or with *Aporrectodea* longa, *Aporrectodea caliginosa*, *A. chlorotica, Octolasion cyaneum* and *Lumbriscus spp*. in woodland mull soils (Edwards and Bohlen, 1977). Although those associations might change from one habitat and climatic region to another, out of the species listed above, only *Octolasion cyaneum* was, in my study, also restricted to the north-facing slopes. It is however difficult to identify if this prevalence to this aspect is simply relying on ecophysiological reasons, and / or being a result of a certain species association with one or more species more abundant on north-facing slopes. A month-to-month earthworm survey could eventually give better insight into potential greater variation in worms abundance and activity, as well as species that could explain observed decomposition patterns. We can expect that as ACC causes changes in environmental conditions, soil biogeochemistry and vegetation, earthworm communities will respond accordingly.

Similar to soil mesofauna, faunal community assemblages associated with litterbags did not vary with aspect. However, trends emerged, where organisms well-known for their preference in damp places, such as woodlice (Malacostraca) and millipedes (Diplopoda) (Sutton, 1972; David and Handa, 2010; Jeffery et al., 2010) were more abundant on the north- than south-facing slopes. Difference in moisture, and potentially in soil temperature during high extreme events may have a direct influence on the ecophysiology of decomposers, however, saprophagous (feeding on decaying organic litter), such as millipedes and woodlice, may preferably feed on softer and easier to chew litter on (David and Honda, 2010) located in moister soils such as on north-facing slopes, especially when leaf litter are as tough and high in lignin as *Quercus robur*.

5.5 Conclusion

This chapter has shown that north- and south-facing orientation grassland road verges offer a viable system to examine how variation in local microclimate can impact ecological process. This experiment did not however, show strong aspect-related distribution of mesofauna (in soil or litter), as expected. Although many arthropods have development behavioural and physiological mechanisms to cope with periods of dryness (David and Handa, 2010), whether such adaptations are sufficient to withstand more severe droughts due to climate change remains unclear. With global warming and the increase in both frequency and intensity of heat waves (IPCC, 2013 and 2019), the role of north-facing slopes as refuge for heat-intolerant and moist-dependant species, such as millipedes, woodlices and earthworms, might become essential.

The Chapter results also suggest that greater litter mass loss recorded on north-facing aspect over the summer is influenced principally by microclimate, with moister soil allowing (1) better microbial and soil decomposers activity and (2) litter breakdown by weathering. Although soil microbes were not investigated in this study, their response to aspect has been widely studied, mainly in mountainous systems (Kang et al., 2003; Carletti et al., 2009; Gilliam et al., 2014; Bardelli et al., 2017) where both microbial community composition and activity have shown significant differences on north- and south-facing slopes. However, investigation of aspect on soil microbes at much smaller scales are needed, especially given that geological parent material (e.g., underlaying rock and soil type) maybe the most important factor influencing soil chemistry and microbial community composition (Carletti et al., 2008). Although the soil environment in both aspects in this study was similar, it is still reasonable to assume that soil microbes could vary with aspect and have played a role in variation in litter mass loss.

Chapter 6: General discussion

Temperature is a major determinant of the physiology, fitness and distribution of organisms (Woodward 1987; Denny and Gaines, 2007; Helmuth et al., 2010b), and changing climate is therefore expected to have profound consequences on biodiversity and ecosystem functioning (Criddle et al., 2003; Lovejoy and Hannah, 2005; Lemoine and Burkepile, 2012). A better understanding of the impact of climate and changing environmental conditions on species and ecosystems has become one of the most pressing research priorities. While there is already a vast number of studies on the impact of abiotic factors on a single or few selected species, often performed through well-controlled experimental studies in laboratory conditions or in mesocosms, much more work need to be done on community structure and ecosystem processes under more realistic conditions (e.g. including species interactions and combination of factors). To fill that gap, many authors (e.g. Wernberg et al., 2012; De Frenne et al., 2013) have already stressed the need for more realistic field-based climate change experiments. In the field, responses of organisms along a thermal gradient have for example been investigated *via* latitudinal (e.g. Helmuth, et al., 2002; Wernberg et al., 2010; De Frenne et al., 2013) and altitudinal studies (e.g. Vitasse et al., 2009; Cornelius et al., 2012; Walder and Erschbamer, 2015). However, due to their large scale, they all have their limitations (e.g. local variations, different land use). Therefore, in order to minimize the limitations linked to large-scale studies, the aim of this PhD work was to study the effect of temperature variation on species and ecosystems, in the field and at a much smaller scale, using aspect (north/south facing slopes or substrata). This thesis investigated (1) abiotic variations, (2) species distribution and richness, (3) species physiology (osmotic regulation), (4) leaf-litter decomposition as a key ecological process, and (5) comparison of conspecific species with different biogeographic origins, all between north- and south-facing aspects. In addition, this work was novel as it was carried out in both terrestrial and marine (intertidal) ecosystems. In this chapter, I briefly summarize the main findings of my research in the context of these knowledge gaps.

In this thesis, I have shown that intertidal gullies and terrestrial road verges are good potential model systems to study the impact of environmental variations (especially temperature) on ecosystem patterns and process for several reasons. First, the properties of the studied substratum (e.g. intertidal rock) or medium (e.g. soil on land) varied little with aspect. On land, even though the paired north- and south-facing slopes were facing each other, and therefore not from the same hill, soil properties were the same (Table 6.1; except moisture content). Also, land use adjacent to the paired slopes was similar. In comparison, many studies investigating aspect on land have not extended the analysis of abiotic factor according to aspect further than temperature and moisture. Several studies which investigated various soil properties and found some aspect variations, also detected aboveground aspect-variations. For example, in the so-called “Evolution Canyon” mountainous microsite in Israel, well-known location to study aspect-related variations, soil properties and morphology were not completely homogenous between aspects (Nevo et al., 1998; Chikatunov et al., 1999). The authors suggested that this could be a result from the striking aboveground flora difference between aspects (steppe-like on south- *vs*. dense oak maquis forest on north-facing slope; see Nevo 1995). While no evidence was available to support this, it is reasonable to think that a completely different biota may be the result or contribute to both below- (soil) and aboveground (light intensity and temperature) variations combined.

Table 6.1: Synthesis of abiotic parameters according to aspect (north-, blue; south-facing, red) on the intertidal gullies (on four sites) and terrestrial road verges (on four sites) in the SW England. Temperature data from the intertidal was recorded from September 2016 for 12 months with a gap from February to June, which was filled the following year. Temperature and light intensity data from the land were recorded from February 2017 to January 2018. Mean soil temperatures from 10-15 cm, and soil moisture are average of monthly recordings (from March to September 2017). The other soil parameters are data from one sample date (March 2017). Significant ($p < 0.05$) differences between aspects are denoted in bold. No statistical analysis was performed on the occurrence of extreme temperatures. LW, low water (= low tide) and HW, high water (high tide), for the intertidal recordings.

			Intertidal		Terrestrial	
			North-facing	South-facing	North-facing	South-facing
TEMPERATURE (°C ±SE)	Annual average (from daily means)	LW	**11.8 ±0.1**	**13.0 ±0.1**	**11.1 ±0.4**	**12.9± 0.4**
		HW	13.2 ±0.1	13.3 ±0.1		
	Summer average		**16.9 ±0.08**	**17.8 ±0.12**	**19.4 ±0.3**	**21.4 ±0.4**
	Autumn average		**11.9 ±0.14**	**12.9 ±0.15**	**10.3 ±0.5**	**12.7 ±0.4**
	Winter average		**7.3 ±0.16**	**8.2 ±0.14**	6.0 ±0.4	7.0 ±0.4
	Spring average		**16.0 ±0.09**	**16.4 ±0.12**	**8.7 ±0.5**	**10.4 ±0.6**
	Maximum (recorded)		37.5	42.5	46.0	61.7
	Minimum (recorded)		- 3	- 3.5	- 12.5	- 12.5
	Annual maximum average		**15.8 ±0.2**	**20.0 ±0.2**	**17.9 ±0.5**	**26.4 ±0.7**
	Annual minimum average		9.3 ±0.1	9.2 ±0.1	5.4 ±0.3	5.5 ±0.3
	T > 40°C occurrence		0	1.5 ±1.5	14 ±10	229 ±35
	T > 30°C occurrence		10 ±6	63 ±20	200 ±87	279 ±63
	T < 0°C occurrence		22 ±10	23 ±7	453 ±103	503 ±70
	T < - 10°C occurrence		0	0	1.5 ±1	1.85 ±1.4
	Daily occurrence of high summer temperatures		late afternoon	late morning to mid-afternoon	mid- or late morning to late afternoon	mid- or late morning to mid-afternoon
			North-facing		South-facing	
LIGHT INTENSITY (LUX ±SE)	Annual average		**3,647 ±291**		**9,184 ±763**	
	Summer average		**1,572 ±52**		**3,052 ±149**	
	Autumn average		**430 ±22**		**1,522 ±111**	
	Winter average		**1,964 ±252**		**8,852 ±1,468**	
	Spring average		**12,284 ±617**		**15,744 ±3,199**	
	Maximum recorded		**176,356**		**308,624**	
	Annual maximum average		**15,672 ±1,160**		**51,191 ±3,996**	
	Annual period of lowest intensities		Oct to Mar		Dec to Jan	
	Annual period of highest intensities		May to Jun		evenly spread across year	
	Daily occurrence of high intensities		early morning to early evening		mid-morning to mid-afternoon	
			North-facing		South-facing	
SOIL PROPERTIES	Carbon (% of dry weight)		7.0 ±0.7		6.6 ±0.5	
	Nitrogen (% of dry weight)		0.55 ±0.03		0.54 ±0.03	
	Hydrogen (% of dry weight)		2.5 ±0.2		2.3 ±0.1	
	pH		5.1 ±0.2		4.8 ±0.2	
	Organic matter (% of dry weight)		15.9 ±1.2		15.2 ±0.7	
	Mean temperature (°C)		11.7 ±0.6		13.0 ±0.5	
	moisture (% of weight)		**31.4 ±0.8**		**26.0 ±1.2**	

Second, north- and south-facing aspects displayed both annual average temperatures and striking differences in frequency and intensity of hot extreme events (cold extremes did not vary with aspect) (Table 6.1). On land, south-facing slopes were on average 1.8°C (for both hourly recordings and daily average) warmer than the opposite north-facing ones, and on the intertidal, the temperature variation according to aspect varyied between 1.2°C (from daily means) and 1.6°C (from hourly recordings) during low tide. There was no variation during high tide (Table 6.1). This temperature variation was constant across the year on both ecosystems, except in winter on land. The maximum temperature recorded on south-facing aspect was 5°C and 15.7°C higher than on the opposite aspect on intertidal gullies and terrestrial slopes, respectively. Hot extreme events were either restricted (e.g. temperature > 40°C on the intertidal) to the south-facing slopes, or significantly more frequent (e.g., 16 times more temperatures > 40°C on land, and 6 times more temperatures > 30°C on the intertidal) on that aspect compared to the north-facing aspects (Table 6.1). No variations were found in the minimum temperature, nor the frequency and intensity of cold extreme events.

The comparison of temperature on both aspects seemed to be in line with some predictions by the IPCC (2013), such as a global increase of temperature and increase of extreme events (in intensity and frequency). Organisms living at their range boundaries are often living close to their physiological tolerance limit (Hoffman and Parsons, 1997; Williams et al., 2016), are often expected to have low genetic diversity (Eckert et al., 2008; Nadeau and Urban, 2019) and be most sensitive to environmental change (e.g. Anderson et al., 2009) compared to organisns living at the centre of the distribution. Although the fitness and potential adaptation of population at their distributional margins under climate change scenarios are poorly understood (Morta et al., 2009), extreme events, due to their large magnitude of change over short period of time are still believed to strongly affect populations, and especially at their margins (Siegle et al., 2018). Extreme events have effects on morphology, behaviour and reproduction of species, on the community dynamics and ecosystem level (Parmesan et al., 2000) as well as on the evolution of their thermal tolerance (Buckley and Huey, 2016). Evolution was suggested to even occur most likely when extreme events alter community composition (Grant et al., 2017). Although, phenological plasticity has been widely evidenced in the context of climate change, this will not always help species to adapt (Duputié et al., 2015). For example, although the boreal limpet *Patella vulgata* shifted its reproductive season withing the last few decades, likely due to the increase in sea surface temperature (SST) due to ACC, it also had an increase in reproductive failure (Moore et al., 2011). In Appendix 10, I also suggested that the extremely hot summer 2018 in the UK, which kept SST relatively high over the autumn, drove the recorded reproductive failure of this limpet species. As extreme events often involve sub-lethal thresholds (Williams et al., 2016), their more noticeable effects are in shaping species distribution. They can either lead to local contraction, extension or extinction or could allow slow recovery of species which have suffered from local extinction in the past (Wethley et al., 2011). In 2011, an unprecedented marine heat wave, on the western coast of Australia, led to an increase of SST up to 5°C for several weeks, resulted in a range contraction of about 100 km of the habitat-forming algae *Scutothalia dorycarpa* at its warm distribution limit (Smale and Wernberg, 2013). The lack of historical knowledge of most species distribution can sometimes lead, however, to misinterpretations of extreme events outcomes on species biogeography (Wethley et al., 2011b). For example, the extremely cold winter 2009-2010 allowed the boreal barnacle *Semibalanus balanoides*, which has been contracting northwards over the last century during

Table 6.2: Synthesis of results on distribution patterns according to aspect (north- (N) *vs*. south-facing (S)) in intertidal and terrestrial (above- and belowground) ecosystems in the SW England. In the intertidal, organisms were surveyed on rocky gullies in the mid-shore (on four sites) in summer and winter 2016. In the terrestrial ecosystem, plants were surveyed on hedgerow banks (on six sites) in springs 2017 and 2018, and soil invertebrates on road verges (on four sites) in spring 2018. Effect of aspect was investigated at different levels: (i) community, (ii) functional and (iii) taxonomic groups, (iv) biogeographical origin and (v) species. The different biogeographical origins are here: **U**, ubiquitous; **B**, boreal; and **L**, Lusitanian for intertidal species; **s**, distribution restricted to southern areas in Europe and absent from N Britain &/or Scandinavia; and **Sw**, distribution extending to central Europe for terrestrial plants. Species richness (SR) and abundance (in counts for most animals, and percentage covers for primary producers and few intertidal animals) were sampled and tested according to aspect. Significant ($p < 0.05$) differences between aspects (N *vs*. S) are denoted by the appropriate symbol ≠, > or <, while no significance is denoted by the symbol =.

Level of sampling	Intertidal	Terrestrial	
		aboveground (plants)	belowground (soil invertebrates)
Community composition	N ≠ S	N = S	N = S
Functional groups	SR of primary production: N > S SR of grazers: N > S SR of filter feeders N = S	SR of shrubs & herbs: N = S of ferns: S > N Abundance ferns & shrubs: S > N herbs & moss: N > S graminoids: N = S	Epigenic (earthworms) SR: N = S Anenic (earthworms) SR: N = S Endogenic (earthworms) SR: N = S
Taxonomic groups	abundance of algal groups: Chlorophyta + Rhodophyta: N > S Phaeophyta: S > N in winter only		Class richness: N = S
Biogeographical origins	SR of **B** & **L** species: N = S SR of **U** species: N > S Specific examples: *Semibalanus balanoides* (B): N = S *Chthamalus sp*. (L): S > N	SR of **s** species: S > N SR of **Sw** species: N > S Other biogeographical origins: SR: N = S	
Species	SR of all taxa: N > S (45 *vs*. 30 in summer, and 42 *vs*. 24 in winter) See chapter 2 for examples of aspect effect on species level	SR of all taxa: N = S (70 *vs*. 73) 22 species restricted to N-facing aspect 24 species restricted to S-facing aspect See Chapter 4 for further examples	*Aporrectodea rosea* abundance: N > S Earthworms: 2 restricted to S-facing, and 7 to N-facing aspect

the long term warming, to recolonize areas where it became locally extincted (Wethley et al., 2011). In addition, extreme events have also proven to limit invasive species to extend their range extension (Hilbish et al., 2010; Firth et al., 2011; Lockwood and Somero, 2011). Firth et al. (2011), for example, suggested that cold weather might have limited the invasion success of the invasive green mussel *Perna viridis* in Florida (USA).

This thesis underscored how aspect influenced species distribution at different levels (community, taxonomic group, functional group, species, and biogeographic origins; see Table 6.2), as well as variations in physiology and ecological processes. Impacts of aspect were however, more marked in the intertidal than on land. For instance, the community assemblage on the rocky intertidal significantly differed with aspect, while on land, plant community and soil invertebrates community from hedgerow banks were similar among aspects (Table 6.2). However, even on land, some species of plant (e.g., 4 species of fern, 3 of herbs, and one of shrub – consistent in at least over two sites, see Appendix 3) or soil invertebrates (e.g. 8 earthworm species, see Figure 5.9B) were restricted to one aspect.

Some similar patterns did emerge in both systems. First, species richness of terrestrial plants and intertidal organisms was consistently greater on cooler north-facing aspects. This suggests that environmental conditions, such as variation of the key parameters: temperature and moisture (on land), experienced on both aspects, may be sufficient to drive variations in species distribution in both ecosystems. Robust and probably most desiccation-resistant plants (e.g. Fucoids (Phaeophyta) on the rocky shore and ferns and shrubs in hedgerow banks) tended to be more abundant on the southern aspects. Although I did not investigate the effect of aspect on plant ecophysiology, there is, in the literature, evidence of some correlation between them. For instance, on south-facing slopes in Canada, shrubs tended to minimize drought impacts through stomatal regulation in order to limit water loss (Letts et al., 2010). In addition, *Fucus serratus*, the most common Fucoid in the intertidal survey undertaken in Chapter 2, can withstand extremely high desiccation rate (up to 90% of water loss) and perform very fast recovery (Schagerl, 2011). Aspect-induced variations in distributional patterns can, however, be dictated by other components than physiology, such as competition for space, species association (i.e., certain species tend to live together as it can be found within earthworm communities), predation or diversity of prey. For instance, higher species richness of grazers on north-facing gullies may not solely be dictated by the lesser desiccation and thermal stress on that aspect, but might also be influenced by higher diversity of food (primary production) (Table 6.2 and see Chapter 2).

Critical or lethal thermal limits, often reached during extreme events, can sometimes be used to interpret ectotherm range boundaries (Sunday et al., 2012), and congeneric species with different biogeographical origins have been demonstrated, in several cases, to have different thermal sensitivity (e.g., Jansen et al., 2007; Firth et al., 2009; Somero, 2010). Therefore, biogeographical origin of species was also a component of the intertidal and hedgerow survey according to aspect. Organisms with ubiquitous distributions were the most common on both the intertidal and hedgerow banks, however, the richness of that group only varied with aspect in the rocky shores, with prevalence to north-facing substrata (Table 6.2). Terrestrial plants with a more southwestern European distribution (absent from N Britain and Scandinavia) had greater richness on the warmer and drier south-facing slopes, while the plants with southern and more central European distribution (with a colder continental climate instead of oceanic climate on SW Europe) had greater richness on the north-facing slopes. In parallel, on the rocky shore, the Lusitanian barnacles *Chthamalus sp.* were significantly more abundant on the southern aspect. Although the abundance of several species (e.g. *Patella vulgata*, *P. depressa*, *Chthamalus sp.*) or group of species (e.g. Top shells) from the intertidal varied with aspect (Figure 2.8), some of those results were not anticipated. For instance, boreal species were not always more abundant on the north-facing aspect and *vice versa* for the Lusitanian species, as expect. Both limpets species were, for example, more abundant on the north-facing substrata, however, the Lusitanian *Patella depressa* was twice more abundant than its boreal congener *Patella vulgata* on the south-facing ones. Both species have their lethal temperature threshold slightly different from one another (lethal point 50% of 43.3°C and 42.8°C for *P. depressa* and *P. vulgata* respectively; Southward, 1958), and close to the maximum temperature recorded on the south-facing substrate (i.e. 42.5°C). In Chapter 3, I demonstrated that both species had similar osmotic regulation, suggesting that the difference in abundance of those key stone species on the southern aspect might be driven by another component of ecophysiological or behavioural thermoregulation.

Although aspect played an important part in intertidal and terrestrial plants richness and abundance, only very few aspect-related variations were found in the soil invertebrates survey. For example, only one earthworm species, *Aporrectodea rosea*, was found significantly more abundant on the north- than south-facing aspects (Table 6.2). Temperature in 10 and 15 cm deep in the soil did not vary with aspect, however, moisture did (Table 6.1). Both abiotic and biotic findings (Chapter 4, Table 6.1 and 6.2) may suggest that combined temperature and moisture content variation are required to generate consistent and significant changes in species distribution and communities' assemblage of soil invertebrates.

Litter decomposition, key ecological process involved in carbon storage, nutrient cycling and soil properties (Aerts, 1997) was investigated in grassland road verges according to aspect.

Decomposition (i.e. litter mass loss) was greater on the north- than south-facing slopes only during months that seemed to be warmer and moister. This experiment was undertaken during 6 months, which did not seem enough to capture import decomposition when using *Quercus robur* leaves, which have high concentration of lignin. A longer-term experiment (longer than 6 months) and the use of a litter species containing less lignin would have allowed greater decomposition and might have ease to detect potential greater aspect-linked variations. The absence of aspect-related change in soil mesofauna abundance seems to suggest that change of above ground temperature and moisture are the key factors driving decomposition in road verges in the SW England. Indeed, climate has long been viewed as the major factor influencing the decomposition processes at global and regional scale (Meentemeyer, 1978; Parton et al., 1988; Wall et al., 2008) with some exceptions (e.g. in Bradford et al., 2015 where plant litter traits predominated). In the context of climate change where extreme weather events such as drought and heavy rainfall will increase in frequency and intensity (IPCC, 2013; 2019), the local difference in decomposition may be more evident on slopes with different aspects.

Even when asking broadly similar questions, marine and terrestrial research projects are often conducted in isolation, by different ecologists working in different institutions, and are often published in subject-specific journals. As a result, there is often little appreciation of the large overlap in research addressing questions like thermal stresses, behavioural adaptation to environmental variations, range shifts, phenology and how anthropogenic climate change (ACC) influences ecological patterns and processes. Steele (1991) suggested that ecologists should attempt to address questions crossing the land-sea-boundary, which could lead to more general conclusions; and more recently, Webb (2012) argued that comparing both marine and terrestrial systems could be very useful at uncovering mechanisms when trying to eliminate physical differences. Similarities and variations among marine and terrestrial ecosystems have been reviewed from an ecosystem functioning and conservation (Carr et al., 2003), evolutionary (Steele et al., 2019) and climate impact (D'Alcalà, 2019) point of view, and are summarized in Table 6.3.

There is a consensus that the answer to most fundamental differences between both systems can be attributed to their contrasting physical medium, being open water in marine systems, and soil or air in terrestrial ones. The 'climate' of the ocean is unlike that of land, where in the former, short-term variations are buffered by the very large heat capacity of the ocean (Steele, 1985; D'Alcalà, 2019), and where in the later, environmental variabilities (e.g. alternation of dry and wet, or cold and warm conditions) can be large at both short- and long-term. Seawater heat capacity, being four times greater than air, would require four times more heat energy than air to change the temperature of the same amount of material (Dawson and Hamner, 2008). This principle would explain why no aspect-variation was found from data loggers (see summary of temperature recordings in Table 6.1) emerged in the sea during high tide (see Chapter 2). In addition, due to the constant movement of the seawater owing to wave actions and tidal cycles, SST would be expected to be homogenized, at least within the same bay or shoreline. Direct absorption of solar radiations during aerial exposure allowed data loggers attached to a rock surface to accumulated more or less heat, depending of the rock aspect. However, at high tide, water attenuated this absorption (Denny and Gaines, 2007), and seawater temperature would have homogenised the temperature of the rock surface on both north- and south-facing aspects. Although my study on the rocky gullies in the SW England is limited by the means that it only provides temperature differences during

Table 6.3: Key differences between marine and terrestrial ecosystems with respect to environmental, ecological and genetic features, issued from Carr et al., 2003; d'Alcalà, 2019; and Steele et al., 2019. Note that this table is not exhaustive as only the relevant features to my thesis were included here. Despite their marine origin, intertidal organisms living in the transition between terrestrial and marine ecosystems, may express or experience features in a similar way than terrestrial organisms.

Feature	Marine ecosystems	Terrestrial ecosystems
○ **Environmental**		
□ prevalence of aquatic medium	greater	less
□ "openness" of local environment (i.e. rates of import & export)	greater	less
□ climate components		
◊ temperature	organism metabolism	organism metabolism
◊ precipitation	none directly	drought / flood
◊ cloudiness	light availability	light availability
○ **Ecological**		
□ phyletic diversity	greater	less
□ life history traits:		
◊ per capita fecundity of invertebrates	higher	lower
◊ average life span	shorter	longer
□ difference in dispersal between life stages	greater	less
□ importance of pollination syndromes	minimal	greater
□rate of response to environmental variability	faster	lower
□ sensitivity to large-scale environmental variability	higher	lower
□ population structure		
◊ spatial scale of propagule transport	greater	smaller
◊ spatial structure of populations	more open	less open
◊ reliance on external sources of recruitment	higher	lower
◊ likelihood of local self-replenishment	low	high
◊ sensitivity to habitat fragmentation	less	greater
◊ sensitivity to smaller scale perturbation	less	greater
◊ temporal response to large-scale events	higher (decades)	slower (centuries)
□ trophic		
◊ turnover of primary producers	high (few perennials)	slow (many perennials)
◊ prey populations influenced by external input of predators	higher	lower
◊ reliance of carnivores on external input of prey	higher	lower
○ **Genetic**		
□ effective population size	larger	smaller
□ spatial scale of gene flow	larger	smaller
□ inter-population genetic diversity	lower	higher

low tides, intertidal organisms performance and distribution seem to be more driven by aerial conditions than marine/submerged ones (Helmuth et al., 2002; 2006; Miller et al., 2009). Therefore, the use of aspect on the rocky shore to study intertidal organisms distribution, stress, and perfance would still be valid.

There are a number of factors that vary between terrestrial and intertidal ecosystems that may contribute to observed differences in distribution patterns and ecological processes with aspect. First, soil buffers variation in temperature. Indeed, no aspect-linked temperature difference was found in the soil (Table 6.1). This effect may explain why there was little variation in belowground invertebrate communities and litter decomposition, but likely also influenced soil water availability (D'Alcalà, 2019). Second, and linked to the above, exposed bedrock in the intertidal was not only likely to be a more extreme environment than soils, but due to its heat storage properties, retain some capacity to maintain high temperatures when no longer exposed to the sun. Third, terrestrial and marine organisms have different evolutionary histories and consequently, trait variation may have played a part in differences between both systems. Terrestrial plants tend to be larger and longer-lived than plants in marine or coastal systems (Carr et al., 2003), traits that may confer tolerance of large-amplitude environmental perturbations (Steele et al., 2019). Indeed, terrestrial plants have already demonstrated delay in their response to environmental change (e.g. Lidborg, 2007; Alignier, 2018). In addition, although intertidal organisms have evolved to withstand emersion (Newell, 1976; Stillman, 2000; Denny and Gaines, 2007), and especially high shore intertidal organisms (e.g., Stillman and Somero, 1996; Sokolova and Pörtner, 2001), they are of marine origin and tend to live near their thermal and desiccation tolerance limits (Helmuth et al., 2006a, 2010; Wethey and Woodin, 2008; Hofmann and Todgham, 2010; Somero, 2010;

Chapperon et al., 2017). Therefore, intertidal organisms may respond quicker and/or be less tolerant to extreme changes in environmental conditions than terrestrial organisms. This is probably why intertidal organisms have long been considered as indicators of climate change (see Southward et al., 1995; Hawkins et al., 2009; Mieszkowska et al., 2014; for reviews).

Like every study design, investigation of aspect at small scale have drawbacks, and I will discuss two major ones. First, it is difficult to avoid confounding climate and non-climate factors. For instance, in Chapter 4, annual light intensity on south-facing slopes was almost double that the one recorded on adjacent north-facing slopes (Table 6.1). Nevo (2012) even found that in Israel, south-facing slopes had up to 800% more solar radiations than the opposite norther-facing ones. While light intensity is one of the plants' requirements (Huggett, 2004), this is often overlooked as a major factor controlling their global geographical distribution, compared to moisture and temperature (Box, 1995; Masuda, 2000; Okitsu, 2005; Sang, 2009). Light can have indirect effects on plant distribution, for example, it has been argued that slow growing alpine and arctic species are restricted to cold climate because they cannot compete for light with forest in areas of warmer climate (Dahl, 1998). In any case, it is difficult to identify if a plant is limited by climate or by competition for light as their limitation is truly multi-factorial (Dahl, 1998). Second, my study has proven that only hot extremes but not cold extremes varied with aspect at a small-scale in the SW England. Therefore, rocky intertidal gullies and terrestrial slopes can be considered as a very good tool to investigate effects of hot extremes, only, on ecosystems. As climate is changing, both hot and cold extreme events are predicted to increase in timing and intensity (IPCC, 2012; 2013). It is therefore, important to investigate effects of severe winters at species and community levels, and the use of aspect at a small-scale may not be the best field-based tool for it.

In the context of global warming, microclimate heterogeneity may have act as refugia (i.e., allowing organisms to persist in and potentially expand from under changing environmental conditions) or as stepping-stones (i.e., allowing range extension of species) (Lembrechts et al., 2006; 2018; Hannah et al., 2014; Lenoir et al., 2013; 2018). For example, canopy forest can buffer from hot temperatures (Chen et al., 1999; De Frenne et al., 2013), which have been found to hinder change of ground-layer plant communities linked to ACC (De Frenne et al., 2013), and was also associated with a reduction of non-native species invasion (e.g., in hedgerows; Wilkerson, 2014). On the other hand, warm microhabitats or complex topography may facilitates range shifts (upward and poleward) of warm-adapted species (Hannah et al., 2014; Lembrechts et al., 2018). They may allow arrival of both seasonal populations surviving beyond their margins until the next extreme temperature event (also called transient population), and populations surviving more than a year in unsuitable climatic condition until being extinct by too extreme events for repopulation or survival (also called relic population) (Helmuth et al., 2006). Thos populations would necessite acclimation and/or adaptation for full settlement (e.g. over several generation or several years). As global temperatures increase steadily and extreme events become more common (IPCC, 2013; 2019), the effect of stepping-stones and buffering will become increasingly important, especially at distributional range margins (Helmuth et al., 2006a).

This thesis has also demonstrated that north-facing of both intertidal gullies and road verge slopes buffered hot extreme temperatures (Table 6.1). Although the study sites in SW England were not situated at the range edge of any recorded species, few species still had prevalence for the cooler north-facing or warmer south-facing aspect. In addition, several species from all three surveys (intertidal, terrestrial plants and soil invertebrates) were restricted to one aspect (however, not significant for many of them due to low abundance or frequency). Micro-scale variability introduced by, for example, complex topography may serve as an ideal model to detect early signs of the impact of ACC and may inform us more specifically on which species might struggle most with ACC (Helmuth et al., 2006). This could be the case, for example, of species either restricted to north-facing aspects (or any cooler microhabitat) or with a significantly lower abundance on south-facing aspects (or any warmer microhabitat), or displaying reduced performance associated to increasing temperature and/or extreme events (e.g. reproductive failure of *Patella vulgata* see Appendix 10; and Moore et al., 2011). A good example would be the holdout population (i.e. persisting in a favourable microclimate amidst deteriorating climatic condition) of the *Zelkova abelicea* (Cretan zelkova) tree in Crete, already an endangered species, was only recorded on slopes with northerly aspect in Crete (Vogiatzakis et al., 2003). Although cooler microhabitats (e.g. pole-facing slopes) increase local climatic stability, it is difficult to say if *Z. abelicea* or any other species in a similar situation might persist or finally go locally extinct due to ACC, and if so, at which rate (which might depend on the emission of greenhouse gases that we follow).

Species distribution models (SMDs), also known as environmental niche models or ‘bioclimate’ models, represent the association of species’ distribution with climatic variables, and are widely used to make predictions and assess spatial distribution of organisms under environmental changes (Gillingham et al., 2012; Lembrechts et al., 2018b). The spatial scale at which both species distribution and climate data are collected can strongly influence the robustness of predictions (Potter et al., 2013). While macroclimatic data might be sufficient in flat terrains as well as for large mobile animals, this do not capture the apparent temperature (microclimate) experienced by each individual (especially sessile organisms) on complex topography (Potter, et al., 2013; Barton et al., 2018; Lembrechts et al., 2018b). The physiology of each organisms respond to the microclimate they live in and not large-scale climate (Hallett et al., 2004). Overlooking microrefugia (e.g. pole-facing slopes) would likely results in over-estimations of future species' range limit (Lenoir et al., 2013) and extinction rates (Willis and Bhagwat, 2009) especially at the range margins of species (Gillingham et al., 2012). Incorporating topoclimate into model would also improve their performance (e.g. Slavich et al., 2014). Assigning and appropriate spatial scale to SDMs is, therefore, particularly important across heterogeneous terrain where slope, aspect, elevation, and thus local microclimates can change dramatically over small distances (Scherrer and Körner, 2011; Suggitt et al., 2011). There is therefore a consensus among ecologists (e.g. citations above in this paragraph), of the need to downscale in order to better predict how organisms will respond to ACC. There is also an urgent need to collect more small-scale climatic data on complex topography, and incorporating mechanistic links between functional traits of organisms and their environments into SMDs (e.g., biotic interactions, behavioural thermoregulation, Kearney and Warren, 2009; Barton et al., 2019).

Even though species are adjusting their geographical distribution, phenology, and behaviour as responses to ACC; for many of them, it might not be enough to hinder the magnitude and speed of global warming and will likely decline until extinction (e.g. Sinervo et al., 2010). Extinction can be avoided if (i) populations (and not a species alone) move to favourable habitats, (ii) organisms undertake plastic changes, or (iii) population undergo evolutionary adaptation (Williams et al., 2008). Identifying evolutionary processes are needed in order to minimize biodiversity loss under rapid ACC (Hoffmann and Sgrò, 2011). As evolution is more likely to occur when extreme events alter community composition (Grant et al., 2017), thus given that intertidal community composition was, in my study, the only one being impacted by aspect-linked temperature variations, further work should be undertaken on complex topography on the rocky intertidal. Transplant experiments are useful for showing either adaptation (genetic and physiological) or phenotypic plasticity, or both (Halpin et al., 2004; Calosi et al., 2013; Gugger et al., 2015). Applying those experiments on north- and south-facing substrata on the intertidal, might allow detection of first signs of adaptation linked to (extremes) temperature variations at a very small scale. This could, therefore, help predict the prospect of the impacted species, population or community under long-term ACC.

Despite the fact that organisms might respond differently to environmental stresses depending on which life stage they are in (e.g. in limpets; Sousa et al., 2012), responses to ACC of organisms are often investigated at the adult stage, while their early life stages are rather understudied, in both seeds/seedlings (e.g. break of dormancy allowing seed to germinate) and intertidal organisms (e.g. recruitment success from newly settle juveniles or larvae on the rocky shore) (Parmesan and Hanley, 2015; Russell et al., 2012). As stressed in Chapter 1, there is a knowledge gap on the effect of aspect on intertidal species and communities, and this is even more the case regarding early-life history stages. For example, is the greater abundance of the Lusitanian barnacles *Chathamalus spp.* on the south- than north-facing substrata in the SW England (see Chapter 2), due to an initial greater settlement on this aspect? Or is this species settling evenly on both north- and south-facing substrata, and that aspect (and so thermal)-related abundance difference emerged at the recruitment stage?

As a last recommendation, in order to aim for a global understanding of the effect of microclimates such as aspect on species and ecosystems, a greatter effort should be focused on performing large scale (e.g. replications under different climates and habits across the globe) and long-term experiments or observations. As many different microclimates can be found within a much larger scale, variation from one site to another can be unavoidable. Helmuth et al. (2002) have shown a good example, where pattern of local weather, wave height, and especially tidal regime (e.g. timing of the low tide) are very different along the western coast of the USA. The authors found that body temperature of intertidal mussels in the northern part of the coast exceeded the ones from the individuals 100-1000s km farther south on the same coast.

To sum up, this thesis demonstrated that investigating aspect at small-scale, such as on road verges or intertidal gullies have proven to be potential tool to study the biotic effects of increased temperature, hot extreme events, and desiccation stress. This natural laboratory could therefore help understand what might happen to species, communities, ecological processes and ecosystem functioning under ACC. South-facing aspects are globally drier, warmer, and experience more intense and frequent hot extreme temperatures than the opposite north-facing aspects. Those abiotic fluctuations led to variations in abundance and richness of species, taxonomic, functional and biogeographic groups, as well as community composition. Patterns were clearer in the intertidal than in terrestrial ecosystem. The climatically more stable north-facing aspect, may in the future serve as refugia for cold-adapted species under ACC. Therefore, slope aspects, could grow interest in the conservation and management sector as a way to buffer locally global warming. A fuller understanding of the complexities around community-level responses to warming is still missing for successfully predict, mitigate and manage the effect of global warming. Finally, it is hoped that this work will lead to more ecological work done on parallel in marine (or intertidal) and terrestrial ecosystems.

REFERENCES

A

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*. **79**: 439-449

Aerts, R. C , and de Caluwe, H. (1999) Nitrogen deposition effects on carbon dioxide and methane emissions from temperate peatland soils. *Oikos.* **84**: 44-54

Albers, D., Migge, S., Schaefer, M., and Scheu, S. (2004) Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce. *Soil Biology and Biochemistry*. **36**: 155-164

Albon, S., and Langvatn, R. D. (1992) Plant phenology and the benefits of migration in a temperature ungulate. *Oikos*. **65**: 502-513

Alignier, A. (2018) Two decades of change in a field margin vegetation metacommunity as a result of field margin structure and management practice changes. *Agriculture, Ecosystems and Environment*. **251**: 1-10

Alistair, H. (1995) Body-size variation exhibited by an intertidal limpet: influence of wave exposure, tidal height and migratory behavior. *Journal of Experimental Marine Biology and Ecology.* **189**: 29-45

Ameztegui, A., Coll, L., Benavides, R., Valladares, F., and Paquette, A. (2012) Understory light predictions in mixed conifer mountain forests: Role of aspect-induced variation in crown geometry and openness. *Forestry Ecology and Management*. **276**: 52-61

Andrés, P., Zapater, V., and Pamplona, M. (1996) Stabilization of motorway slopes with herbaceous cover, Catalonia, Spain. *Restoration Ecology*. **4**: 51-60

Andrés, P., and Jorba, M. (2000) Mitigation strategies in some motorway embankments (Catalonia, Spain). *Restoration Ecology*. **8**: 268-275

Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., and Brook, B. W. (2009) Dynamics of range margins for metapopulation under climate change. *Proceedings of the Royal Society B: Biological Sciences*. **276**: 1415-1420

Anderson, J. T., Panetta, A. M., and Mitchell-Olds, T. (2012) Evolutionary and ecological responses to anthropogenic climate change. *Plant Physiology*. **160**: 1728-1740

Andreetta, A., Ciampalini, R., Meretti, P., Vingiani, S., Poggio, G., Matteucci, G., Tescari, F., and Carnicelli, S. (2011) Forest humus forms as potential indicators of soil carbon storage in Mediterranean environments. *Biology and Fertility of Soils*. **47**: 31-40

Angilletta Jr, M. J., Niewiarowski, P. H., and Navas, C. A. (2002) The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*. **27**: 249-268

Angilletta Jr, M. J. (2009) '*Thermal Adaptation – A theoretical and empirical synthesis'*. Oxford University Press Inc., New York.

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jonsdottir, I. S., Laine, K., Levesque, E., Marion, G. M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C. HH., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wookey, P. A. (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*. **69**: 491-511

Armesto, J. J., and Martínez, J. A. (1978) Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. *Journal of Ecology*. **66**: 881-889

Armstrong, R. A., and Smith, S. N. (1993) Radial growth and carbohydrate levels in the lichen *Parmelia conspersa* on north and south facing rock surfaces. *Symbiosis*. **15**: 27-49

Aronson, E. L., and McNulty, S. G. (2009) Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*. **149**: 1791-1799

Asch, R. G. (2014) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America.* **112**: 4065–4074

Ashcroft, M. B., and Gollan, J. R. (2013) Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: Understanding factors that promote microrefugia. *Agricultural and Forest Meteorology*. **176**: 77-89

Åström, M., Dynesius, M., Hylanders, K., and Nilson, C. (2007) Slope aspect modifies community responses to clear-cutting in boreal forest. *Ecology*. **88**: 749-758

Aude, E., Tybirk, K., and Bruus Pedersen, M. (2003) Vegetation diversity of conventional and organic hedgerows in Denmark. *Agriculture, Ecosystems and Environment*. **99**: 135-147

Ayyad, M. A., G., and Dix, R. L. (1964) An analysis of a vegetation – microenvironmental complex on Prairies slopes in Saskatchewan. *Ecological Monographs*. **34**: 421-442

B

Badano, E. I., Cavieres, L. A., Molina-Montenegro, M. A., and Quiroz, C. L. (2005) Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile. *Journal of Arid Environment*. **62**: 93-108

Baisez, A., Bach, J.-M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M., and Laffaille, P. (2011) Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research*. **15**: 265:270

Ballantine, W. J. (1961) Population dynamics of *Patella vulgata* and other limpets. PhD thesis. University of London, UK.

Ballaré, C. L., Caldwell, M. M., Flint, S. D., Robinson, S. A., and Bornman, J. F. (2011) Effects of solar ultraviolet radiation on terrestrial ecosystems. Patterns, mechanisms, and interactions with climate change. *Photochemical and Photobiological Sciences*. **10**: 226-241

Barbraud C. and Weimerskirch H. (2006) Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the United States of America.* **103**: 6248-6251

Bárcenas-Moreno, G., García-Orenes, F.,Mataix-Solera, J., Mataix-Beneyto, J., and Bååth, E. (2011) Soil microbial recolonization after a fire in a Mediterranean forest. *Biology and Fertility of Soils*. **47**: 261-272

Bardelli, T., Gómez-Branódon, M., Ascher-Jenull, J., Fornasier, F., Arfaioli, P., Francioli, D., Egli, M., Sartori, G., Insam, H., and Pietramellara, G. (2017) Effect of slope exposure on soil physico-chemical and microbiological properties along an altitudinal climosequence in the Italian Alps. *Science of the Total Environment.* **575**: 1041-1055

Bardgett, R. D. (2005) '*The biology of soil – A community and ecosystem approach'*. Oxford University Press, New York, USA

Barton, M. G., Clusella-Trullas, S., and Terblanche, J. S. (2019) Spatial scale, topography and thermoregulatory behaviour interact when modelling species' thermal niches. *Ecography*. **42**: 376-389

Bay, R. A., Harrigan, R. J., Underwood, V. L., Gibbs, H. L., Smith, T. B., and Ruegg, K. (2018) Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*. **359**: 83-86

Barton, M. G., Clusella-Trullas, S., and Terblanche, J. S.(2018) Spatial scale, topography and thermoregulatory behaviour interact when modelling species' thermal niches. *Ecography*. **42**: 376-387.

Beadle, N. C. W. (1940) Soil temperatures during forest fires and their effect on the survival of vegetation. *Journal of Ecology*. **28**: 180-192

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature*. **426**: 661-664

Begun, F., Bajracharya, R. M., Sharma, S., and Sitaula, B. K. (2010) Influence of slope aspect on soil physio-chemical and biological properties in the mid hills of central Nepal. *International Journal of Sustainable Development & World Ecology*. **15**: 438-443

Bellot, J. Maestre, F. T., and Hernández, N. (2003) Spatio-temporal dynamics of chlorophyll fluorescence in a semi-arid Mediterranean shrubland. *Journal of Arid Environments*. **58**: 295-308

Benedetti-Cecchi, L., Bulleri, F., and Cinelli, F. (2000) The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. *Oecologia*. **123**: 406-417

Bennie, J., Hill, M. O., Baxter, R., and Huntley, B. (2006) Influence of slope and aspect on long-term vegetation change in British chalk grassland. *Journal of Ecology*. **94**: 355-368

Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., and Baxter, R. (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling.* **216**: 47-59

Berg, B., McClaugherty, C. (2014) Plant Litter: decomposition, humus, formation, carbon sequestration. 3rd Edition. Springer-Verlag, Berlin, Germany

Bernal, M., Verdaguer, D., Badosa, J., Abadía, A., Llusià, J., Peñuelas, J., Núñez-Olivera, E., and Llorens, L. (2015) Effects of enhanced UV radiation and water availability on performance, biomass production and photoprotective mechanisms of *Laurus nobilis* seedlings. *Environmental and Experimental Botany*. **109**: 264-275

Beukema, J. J., Dekker, R., and Jansen, J. M. (2009) Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Marine Ecology Progress Series*. **384**: 135-145

Bickmore, C. J. (2002) *Hedgerow survey handbook: a standard procedure for local surveys in the UK*. London, DEFRA.

Biever, J. J., and Gardner, G. (2016) The relationship between multiple UV-B perception mechanisms and DNA repair pathways in plants. *Environmental and Experimental Botany*. **124**: 89-99

Biological Record Centre (2008) *Dryopteris filix-mas* - Online Atlas of the British and Irish flora. Accessed on the 30th of November 2019 [https://www.brc.ac.uk/plantatlas/plant/dryopteris-filix-mas]

Biological Record Centre (2008) *Phyllitis scolopendrium* - Online Atlas of the British and Irish flora. Accessed on the 30th of November 2019 [https://www.brc.ac.uk/plantatlas/plant/Phyllitis-scolopendrium]

Blockey, D. J., and Chapman, M. G. (2006) Recruitment determines differences between assemblages on shaded or unshaded seawalls. *Marine Ecology Process Series*. **327**: 27-36

Blower, J. G. (1995) Synopses of the British Fauna (New Series) No. 35. Millipedes. Eds. Kermack, D. M., and Barnes R. S. K. E. Brill, E. J./Dr. Backhuys, W, London, Leiden, Köln, and København

Boaden, P. J. S., and Seed, R. (1985) An introduction to coastal ecology. Blackie & Son Limited, Glasgow, UK, and New York, USA

Bohn, H. L., McNeal, B. L., and O'Connor, G. A. (2001) *Soil Chemistry*. 3rd Edition. John Wiley & Sons, Inc. New York, NY, USA

Bokhorst, S., Bjerke, J. W., Bowles, F. W., Melillo, J., Callaghan, T. V., and Phoenix, G. K. (2008) Impact of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology*. **14**: 2603-2612

Bokhorst, S., Huises, A., Convey, P., Sinclair, B. J., Lebouvier, M., Van de Vijver, B., and Wall, D. H. (2011) Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. *Polar Biology*. **34**: 1421-1435

Bolton P. J., and Phillipson J. (1976) Burrowing, feeding, egestion and energy budgets of *A. rosea* (Savigny) (Lumbricidae). *Oecologia*. **23**: 225-245

Bonebrake, T. C., and Mastrandrea, M. D. (2010) Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences of the United States of America*. **107**: 12581-12586

Bornman, J. F., and Teramura, A. H. (1993) '*Effects of Ultraviolet-B Radiation on Terrestrial Plants*', *in* Young, A. R., Björn, L. O., Moan, J., and Nultsch, W. (eds), Environmental UV Photobiology. Springer Science + Business Media, New York, USA pp 427-471

Bowman, R. S. (1981) The morphology of *Patella spp*. juveniles in Britain, and some phylogenetic inferences. *Journal of the Marine Biological Association of the United Kingdom*. **61**: 647-666

Bowman, R. S. (1985) The biology of the limpet *Patella vulgata* L. in the British Isles: Spawning time as a factor determining recruitment success. In P. G. Moore & R. Seed (eds), The Ecology of Rocky Coasts. Hodder and Stoughton, Sevenoaks (Kent): 178-193

Bowman, R. S., and Lewis, J. R. (1986) Geographical variation in the breeding cycles and recruitment of *Patella spp*. *Hydrobiologia*. **142**: 41-56

Box, E. O. (1995) Factors determining distributions of tree species and plant functional types. *Vegetatio*. **121**: 101-116

Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J.-P., Havenhand, J., Hutchins, D. A., Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., Ciotti, A., Gao, K., Gehlen, M., Hurd, C. L., Kurihara, H., McGraw, C. M., Navarro, J. M., Nilsson, G. E., Passow, U., and Pörtner, H.-O. (2018) Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—A review. *Global Change Biology*. **24**: 2239-2261

Bracewell, S. A., Spencer, M., Marrs, R. H., Iles, M., and Robinson, L. A. (2012) Cleft, crevice, or the inner thigh: 'Another place' for the establishment of the invasive barnacle *Austrominius modestus* (Darwin, 1854). *PLoS ONE*. **7**: e48863

Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H., and Newington, F. E. (2002) Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos*. **99**: 317-323

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., and Wood, S. A. (2015) Understanding the dominant controls on litter decomposition. *Journal of Ecology*. **104**: 229-238

Bradley, N. L., Leopold, A. C., Ross, J. and Huffaker, W. (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*. **96**: 9701-9704

Braun-Blanquet, J. (1932) *Plant Sociology. The Study of Plant Communities*. Authorized English translation of 'Pflanzensoziologie' by G.D. Fuller & H.S. Conard. McGraw-Hill Book Company, New York.

Branch, G. M. (1974) The ecology of Patella Linnaeus from the Cape Peninsula, South Africa. 2. Reproductive cysles. *Transactions of the Royal Society of South Africa*. **41**: 111-160

Branch, G. M. (1979) Respiratory adaptations in the limpet *Patella granatina*: A comparison with other limpets. *Comparative Biochemistry and Physiology. Part A: Physiology*. **62**: 641-647

Branch, G. M. (1981) The biology of limpets, physical factors, energy flow and ecological interactions. *Oceanography and Marine Biology: An Annual Review*. **19**: 235–379

Branch, G. M. (1985) Limpets: Evolution and Adaptation. In *The Mollusca*. Volume 10: Evolution. Ed. Trueman, E. R., and Clarke, M. R. Academic Press, Inc. London, UK

Bridge, P., Spooner, B. (2001) Soil fungi: diversity and detection. *Plant Soil.* **232**: 147-154

British Geological Survey (2017) Geology of Britain viewer. [online] Available at: http://mapapps.bgs.ac.uk/geologyofbritain/home.html URL [Accessed the 09/12/17]

Bochet, E. and García-Fayos, P. (2004) Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology*. **12:** 166-174

Brown, C. J., O'Connor, M. I., Poloczanska, E. S., Schoeman, D. S., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Pandolfi, J. M., Parmesan, C., and Richardson, A. J. (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Global Change Biology*. **22:** 1548-1560

Brown, V. K., and Gange, A. C. (1989) Herbivory by soil-dwelling insects depresses plant species richness. *Functional Ecology*. **3**: 667-671

Buckley, L. B., and Huey, R. B. (2016) How extreme temperature impact organisms and evolution of their thermal tolerance. *Integrative and Comparative Biology*. **56**: 98-109

Budd, G.C. 2007. *Cladophora rupestris* A green seaweed. In Tyler-Walters H. and Hiscock K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [Accessed on the 12th of July 2019. [https://www.marlin.ac.uk/species/detail/1471]

Buffoni Hall, R. S., Bornman, J. F., Björn, L. O. (2002) UV-induced changes in pigment content and light penetration in the fruticose lichen *Cladonia arbuscula* ssp. *mitis*. *Journal of Photochemistry and Photobiology B: Biology*. **66**: 13-20

Burggren, W. (2018) Developmental phenotypic plasticity helps bridge stochastic weather events associated with climate change. *Journal of Experimental Biology*. **221**: jeb161984

Burrows, M. T., Hawkins, S. J., and Southward, A. J. (1992) A comparison of reproduction in co-occurring chthamalid barnacles, *Chhamalus stellatus* (Poli) and *Chthamalus montagui* Southward. *Journal of Experimental Marine biology and Ecology*. **160**: 229-249

Burton, R.F. (1983) 'Ionic regulation and water balance'. In: Saleuddin, A.S.M. and Wilbur, K. M. (eds.) *The Mollusca*. Academic Press: New York ; London, pages 291-352

C

Cadenas, F. M., Rais, O., Jouda, F., Douet, V., Humair, P-F., Moret, and J. Gem, L. (2007) Phenology of *Ixodes ricinus* and infection with *Borrelia burgdorferi* sensu lato along a north- and south-facing altitudinal gradient on Chaumont Mountain, Switzerland. *Journal of Medical Entomoly*. **44:** 683-693

Caldwell, M. M., Björn, L. O., Bornman, J. F., Flint, S. D., Kualandaivelu, G., Teramura, A. H., and Tevini, M. (1998) Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology B: Biology*. **46**: 40-52

Calosi, P., Rastrick, S. P., Lombardi, C., de Guzman, H. J., Davidson, L., Jahnke, M., Giangrande, A., Hardege, J. D., Schulze, A., Spicer, J. I., and Gambi M. C. (2013) Adaptation and acclimatization to ocean acidification in marine ectotherms: an in situ transplant experiment with polychaetes at a shallow CO_2 vent system. *Philosophical Transactions of the Royal Society B*. **368**: 20120444

Camararo, J. J., Gazol, A., Sangüesa-Barreda, Gabriel, Oliva,J., and Vicente-Serrano, S. (2014) To die or not to die: early warnings of tree dieback in response to a severe drought. *Journal of Ecology*. **103:** 44-57

Campagne, P., Roche, P., and Tatoni, T. (2006) Factor explaining shrub species distribution in hedgerows of a mountain landscape. *Agriculture, Ecosystems and Environment*. **116**: 244-250

Cantlon, J. E. (1953) Vegetation and microclimate on north and south slopes of Cushetunk Mountain, New Jersey. *Ecological Monographs*. **23**: 241-270

Carey P. D., Wallis S., Chamberlain P. M., Cooper A., Emmett B.A., Maskell L.C., McCann T., Murphy J., Norton L.R., Reynolds B., Scott W.A., Simpson I.C., Smart S.M., and Ullyett J.M. (2008) *Countryside Survey: UK Results* Report *from 2007*. NERC/Centre for Ecology & Hydrology, 105pp.

Carletti, P., Vendramin, E., Pizzeghello, D., Concheri, G., Zanella, A., Nardi, S., and Squartini, A., (2008) Soil humic compounds and microbial communities in six spruce forests as function of parent material, slope aspect and stand age. *Plant and Soil*. **315**: 47-65

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., and Largier, J. L. (2003) Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. *Ecological Applications*. **13**: 90-107

Carter, B. J., and Ciolkosz, E. (1991) Slope gradient and aspect effects on soil development from sandstone in Pennsylvania. *Geoderma*. **49**: 199-213

Carter, M. R., and Gregorich, E. G. (2008) '*Soil sampling and methods of analysis'* (2nd Edition). CRC Press, Boca Raton, Florida, USA

Cattano, C., Claudet, J., Domenici, P., and Milazzo, M. (2018) Living in a high CO_2 world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecological* Monographs. **88**: 320-335

Chai, Y., Jiang, S., Guo, W., Qin, M., Pan, J., Bahadur, A., Shi, G., Luo, J., Jin, Z., Liu, Y., Zhang, Q., An, L., and Feng, H. (2018) The effect of slope aspect on the phylogenetic structure of arbuscular mycorrhizal fungal communities in an alpine ecosystem. *Soil Biology and Biochemistry*. **126**: 103-113

Chan, K.-Y., and Munro, K. (2001) Evaluating mustard extracts for earthworm sampling. *Pedobiologia*. **45**: 272-278

Channel Coastal Observatory (2019) 2018 yearly meteorological data of Looe Bay (South Devon) [http://www.channelcoast.org/data_management/real_time_data/charts/?chart=98&tab=qc&disp_option]

Chapin, F. S., Matson, P. A., and Mooney, H. A. (2002) Principles of Terrestrial Ecosystem Ecology. Springer, NY.

Chapman, L. (1994) The living history of hedgerows. A guide to date hedgerows. Orchard Publication, Newton Abbot, UK

Chapman, M. G., and Blockley, D. J. (2009) Engineering novel habitat on urban infrastructure to increase intertidal biodiversity. *Oecologia*. **161**: 625-635

Chapperon, C., Seuront, L. (2011) Behavioural thermoregulation in a tropical gastropod: links to climate change scenarios. *Global Change Biology*. **17**: 1740-1747

Chapperon, C., Le Bris, C., and Seuront, L. (2013) Thermally mediated body temperature, water content and aggregation behaviour in the intertidal gastropod *Nerita atramentosa*. *Ecological Research*. **28**: 407-416

Chapperon, C., Studerus, K., and Clavier, J. (2017) Mitigating thermal effect of behaviour and microhabitat on the intertidal snail *Littorina saxalitis* (Olivi) over summer. *Journal of Thermal Biology*. **67**: 40-48

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., and Thomas, C. D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science.* **333**: 1024-1026

Chen, J., Franklin, J. F., and Spies, T. A. (1993) Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*. **63**: 219-237

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Brookshire, B. L., and Franklin, J. F. (1999) Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*. **49**: 288-297

Chew S. F., Ho, S. Y., and Ip, Y.K . (1999) Free amino acids and osmoregulation in the intertidal Pulmonate *Onchidium tumidium*. Marine Biology, 134: 735-741

Chikatunov, V., Pavlíček, T., and Nevo, E. (1999) Coleoptera of “Evolution Canyon” lower Nahal Oren, Mount Carmel, Israel. PENSOFT Publishers, Bulgaria

Chown, S. L., Hoffmann, A. A., Kristensen, T. N., Angilletta Jr., M. J., Stenseth, N. C., and Pertoldi, C. (2010) Adapting to climate change: a perspective from evolutionary physiology. *Climate Research*. **43**: 3-15

Chu, F. J., Seaward, M. R. D., and Hodgkiss, I. J. (2000) Effects of wave exposure and aspect on Hong Kong supralittoral lichens. *Lichenologist*. **32**: 155-170

Chu, H., Xiang, X., Yang, J., Adams, J. M., Zhang, K., Li, Y., and Shi, Y. (2016) Effects of slope aspects on soil bacterial and arbuscular Fungal communities in a Boreal forest in China. *Pedosphere*. **26**: 226-234

Chuanyan, Z., Zhongren, N., and Guodong, C. (2005) Methods for modelling of temporal and spatial distribution of air temperature at landscape scale in the southern Qilian Mountains, China. *Ecological Modelling*. **189**: 209-220

Clarke, A. (2003) Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution*. **18**: 573-581

Clarke, K. R., Gorley, R. N., Somerfield, P. J., and Warwick, R. M. (2014) Change in marine communities: An approach to statistical analysis and interpretation, 3rd edition. PRIMER-E: Plymouth

Classen, A. T., Hart, S. C., Whitman, T. G., Cobb, N. S., and Koch, G. W. (2005). Insect infestations linked to shifts in microclimate: important climate change implications. *Soil Science Society of America Journal*. **69**: 2049-2057

Climate-data.org. Accessed on the 8th of November 2019 [https://en.climate-data.org]

Coleman, D. C., Crossley Jr., D. A., and Hendrix, H. F. (2004) *Fundamentals of soil ecology*. 2nd Edition. Elsevier Academic Press, Burlington, MA, USA, and San Diego, CA, USA, and London, UK. 386pp

Cornelissen J. H. C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*. **84**: 573-582

Cornelius, C., Estrella, N., Franz, H., and Menzel, A. (2012) Linking altitudinal gradients and temperature responses of plants phenology in the Bavarian Alps. *Plant Biology.* **15**: 57-69

Connell, J. H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*. **42**: 710-723

Connor, D. W., Allen, J. H., Golding, N., Lieberknecht, L. M., Northen, K. O., and Reker, J. B. (2003) The National Marine Habitat Classification for Britain and Ireland Version 03.02 JNCC, Peterborough, UK

Cook, B. J., Wolkovich, E. M., and Parmesan, C. (2012) Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*. **109**: 9000-9005

Courtney, W.A. M. (1972) The effect of wind on shore gastropods. *Journal of Zoology*. **166**: 133-139

Cox, C. L., Logan, M. L., Bryan, O., Kaur, D., Leung, E., McCormack, J., McGinn, J., Miller, L., Robinson, C., Salem, J., Scheid, J., Warzinski, T., and Chung, A. K. (2018) Do ring-necked snakes choose retreat sites based upon thermal preferences? *Journal of Thermal Biology*. **71**: 232-236

Criddle, R. S., Church, J. N., Smith, B. N., and Hansen, L. D. (2003) Fundamental causes of the global patterns of species range and richness1. *Russian Journal of Plant Physiology*. **50**: 192-199

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., and Mynsberge A. R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*. **331**: 324-327

Crisp, D. J. (1964a) The effect of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*. **33**: 165-210

Crisp, D. J. (1964b) The effect of the winter of 1962/63 on the British marine fauna. *Helgoländer wissenschaftliche Meeresuntersuchungen.* **10**:BF01626116

D

Dahl, E. (1998) The Phytogeography on Northern Europe (British Isles, Fennoscandia and adjacent areas). Cambridge University Press, UK

D'Alcalà, M. R. (2019) Similarities, differences and mechanisms of climate impact on terrestrial vs. marine ecosystems. *Nature Conservation*. **34**: 505-523

Danby, R. K., and Hik, D. S. (2007) Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology*. **13**: 437-451.

Davies, P. S. (1969) Physiological ecology of *Patella*. III. Desiccation effects. *Journal of the Marine Biological Association of the UK*. **49**: 291–304

Davie, P. S. (1970) Physiological ecology of *Patella*. IV. Environmental and limpet body temperature. *Journal of the Marine Biological Association of the United Kingdom*. **50**: 1069-1077

Davies, Z. G., Wilson, R. J., Coles, S., and Thomas, C. D. (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*. **75**: 247-256

Davis, A. J. R., and Fleur, H. J. (1903) L.M.B.C Memoirs on typical British marine plants & animals. X. *Patella* (the common limpet). Eds Herdman, W. A. Williams & Norgate, London, UK

Dawson, M. N., and Hammer, W. M. (2008) A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *Journal of the Royal Society Interface*. **5**: 135-150

De Boeck, H. J., Bloor, J. M. G., Aerts, R., Bahn, M., Beir, Cl., Emmett, B. A., Estiarte, M., Grünzweig, J. M., Halbritter, A. H., Holub, P., Jentsch, A., Klem, K., Kreyling, J., Kröel-Dulay, G., Steenberg Larsen, K., Milcu, A., Roy, J., Sigurdsson, B. D., Smith, M. D., Sternberg, M., Vandvik, V., Wohlgemuth, T., Nijis, I., and Knapp, A. K. (2019) Understanding ecosystems of the future will require more than realistic climate change experiments – A response to Korell et al. *Global Change Biology*. 26: e6-e7

Deckers, B., Verheyen, K., Hermy, M., and Muys, B. (2004) Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology*. **5**: 551-566

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Giliam, F. S., Hédl, R., Heiken, T., Hermy, M., Hommel, P., Jenkins, M. A., Kelly, D. L., Kirby, K. J., Mitchell, F. J. G., Naaf, T., Newman, M., Peterken, G., Petřik, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D. M., Walther, G.-R., White, P. S., Woods, K. D., Wulf, M., Graae, B. J., and Verheyen, K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*. **110**: 18561-18565

De Frenne, P., Graae, B. J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D. A., and Verheyen, K. (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*. **101**: 784-795

Dejonghe, W., Boon, N., Seghers, D., Top, E. M, and Verstraete , W. (2001) Bioaugmentation of soils by increasing microbial richness: missing links. *Environmental Microbiology*. **3**:649-657

Denny, M. W. and Blanchette, C. A. (2000) Hydrodynamics, shell shape, behaviour and survivorship in the owl limpet *Lottia gigantean*. *The Journal of Experimental Biology*. **203**: 2623-2639

Denny, M. W., and Gaines, S. D. (2007). Encyclopedia of Tidepools and Rocky Shores. University of California Press: Berkeley, CA.

Denny, M. W., Dowd, W. W., Bilir, L., and Mach, K. J. (2011) Spreading the risk: Small-scale body temperature variation among intertidal organisms and its implications for species persistence. *Journal of Experimental Marine Biology and Ecology*. **400**: 175-190

Department for Environment Food and Rural Affairs (DEFRA) (2007) Conserving biodiversity in a changing climate: guidance on building capacity to adapt Report

Department for Environment Food and Rural Affairs (DEFRA) (2009) Adaptation to climate change – UK Climate projections Report

Desroy, N., Dubois, S. F, Fournier, J., Ricquiers, L., Le Mao, P., Guerin, L., Gerla, D., Rougerie, M., and Legendre, A. (2011) The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellariidae) reefs in the Bay of Mont-Saint-Michel. *Aquatic conservation: Marine and Freshwater Ecosystems* **21**: 462-471

Devon City Council & Devon hedge group (1997) Devon's hedges. Conservation and management. Devon books, Tiverton, UK

DeWitt, T. J., and Scheiner, S. M. (2004) Phenotypic Plasticity: Functional and Conceptual Approaches. Oxford University Press. Oxford, UK

Dillon, M. E., Wang, G., and Huey, R. B. (2010) Global metabolic impacts of recent climate warming. *Nature*. **467**: 704-707

Dowdeswell, W. H. (1987) Hedgerows and verges. Allen & Unwin (Publishers) Ltd., London, UK

Dong, Y., Dong, S., and Ji, T. (2008) Effect of different thermal regimes on growth and physiological performance of the sea cucumber *Apostichopus japonicas* Selenka. *Aquaculture*. **275**: 329-334

Dong, Y., and William, G. A. (2011) Variations in cardiac performance and heat shock protein expression to thermal stress in two differently zoned limpets on a tropical rocky shore. *Marine Biology*. **158**: 1223-1231

Doube, B. M., and Styan, C. (1996) The response of *Aporrectodea rosea* and *Aporrectodea trapezoides* to moisture gradients in three soil types in the laboratory. *Biology and Fertility of soils*. **23**: 166-172

Doube, B. M., Williams, P. M. L., and Willmott, P. J. (1997) The influence of two species of earthworm (*Aporrectodea trapezoides* and *Aporrectoedea rosea*) on the growth of wheat, barley and faba beans in three soil types in the greenhouse. *Soil Biology and Biochemistry*. **29**: 503-509

Dover, J. W. (2019) The ecology of hedgerow and field margins. Routledge, Oxon, UK; and New York, NY, USA

Dowd, W. W., King, F. A., and Denny, M. W. (2015) Thermal variation, thermal extremes and the physiological performance of individuals. *The Company of Biologists*. **218**: 1956-1967

Dowdeswell, W. H. (1987) Hedgerows and verges. Allen & Unwin (Publishers), London, UK

Dubois, S. F., Commito, J. A., Olivier, F., and Retière, C. (2006) Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. *Estuarine, Coastal and Shelf Science* **68**: 635-646

Duputié, A., Rutschmann, A., Ronce, O., and Chuine, I. (2015) Phenological plasticity will not help all species adat to climate change. *Global Change Biology*. **21**: 3062-3073

Durant, J. M., Hjermann, D. Ø., Ottersen, G., and Stenseth, N. C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*. **33**: 271-283

E

Eckert, C. G., Samis, K. E., and Lougheed, S. C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Molecular Ecology*. **17**: 1170-1188

Edwards, C. A. (2004) Earthworms Ecology - 2nd Edition. CRC Press LLC, Boca Raton, F

Edwards, C. A., and Bohlen, P. J. (1977) Biology and ecology of earthworms – 2nd Edition. Chapman & Hall, London, Uk. pp 426

Edward, M., and Richardson, A. J., (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*. **430**: 881-884

Ehlers A., Worm B., Reusch T. B. H. (2008) Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine and Ecology Progress Series*. **355**: 1-7

Ellenberg, H. (1979) Zeigerwerte von Gefässpflanzen Mitteleuropas. *Scripta Geobotanica.* **9**, 1122

Elith, J., and Leathwick, J. R. (2009) Species Distribution Models: Prediction across space and time. *Annual Review of Ecology, Evolution and Systematics.* **40**: 677-697

EMASyst. (1996) Elemental Analyser Data System, Operation and Installation Manual (Version 4.5.01)

Enderlein, P., Wahl, M. (2004) Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. *Journal of Sea Research*. **51**: 145-155

Endresz, G., Zald-Balogh, A., and Kalapos, T. (2005) Local distribution pattern of *Brachypodium pinnatum* (*Poaceae*) – Field experiments in Xeric Loess Grassland in N.Hungary. *Phyton*. **45**: 249-265

Espinosa, F., and Guerra-García, J. M. (2005) Algae, macrofaunal assemblages and temperature: a quantitative approach to intertidal ecosystems of Iceland. *Helgoland Marine Research*. **59**: 273-285

Evans, J .P., Pitman, A. J., and Cruz, F. T. (2011) Coupled atmospheric and land surface dynamics over southeast Australia: a review, analysis and identification of future research priorities. *International Journal of Climatology*. **31**: 1758–1772

Evans, R. G. (1948) The lethal temperature of some common British littoral molluscs. *Journal of Animal Ecology*. **17**: 165-173

F

Falkenberg, L. J., Russell, B. D., and Connell, S. D. (2016) Design and performance evaluation of a mesocosm facilities and techniques to simulate ocean acidification and warming. *Limnology and Oceanography: Methods*. **14**: 278-291

Fathi, A., and Tari, D. B. (2016) Effect of drought stress and its mechanism in plants. *Journal of Life Sciences*. **10**: 1-6

Feng, H., An, L., Tan, L., Hou, Z., and Wang, X. (2000) Effect of enhanced ultraviolet-B radiation on pollen germination and tube growth of 19 taxa in vitro. *Environmental and Experimental Botany*. **43**: 45-53

Feng, H., An, L., Chen, T., Qiang, W., Xu, S., Zhang, M., Wang, X., and Cheng, G. (2003) The effect of enhanced ultraviolet-B radiation on growth, photosynthesis and stable carbon isotope composition ($\delta^{13}C$) of two soybean cultivars (*Glycine max*) under field conditions. *Environmental and Experimental Botany*. **49**: 1-8

Fernández, C. (2016) Current status and mutidecadal biogeographical changes in rocky intertidal algal assemblages: The northern Spanish coast. *Estuarine, Coastal and Shelf Science*. **171**: 35-40

Fernández, N., Alborés, I., and Aceña-Matarranz, S. (2015) Characterization of the reproductive cycle and physiological condition of *Patella vulgata* in the NW of the Iberian Peninsula: Relevant information for a sustainable exploitation. *Fisheries Research*. **164**: 293-301

Firth, L. B., and Williams, G. A. (2009) The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong. *Journal of Environmental Marine Biology and Ecology*. **275**: 70-75

Firth, L. B., and Crowe, T. P. (2010) Competition and habitat suitability: small-scale segregation underpins large-scale coexistence of key species on temperate rocky shores. *Oecologia.* **162**: 163-174

Firth, L. B., Knights, A. M., and Bell, S. S. (2011) Air temperature and winter mortality: Implications for the persistence of the invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States. *Journal of Experimental Marine Biology and Ecology*. **400**: 250-256

Firth, L. B., Mieszkowska, N., Thompson, R. C., and Hawkins, S. J. (2013) Climate change and adaptation impacts in coastal systems: the case of sea defences. *Environmental Science: Processes & Impact*. **15**: 1665-1670

Firth, L. B., Mieszkowska, N., Grant, L. M., Bush, L. E., Davies, A. J., Frost, M. T., Moschella, P. S., Burrows, M. T., Cunningham, P. N., Dye, S. R., and Hawkins, S. J. (2015) Historical comparison reveal multiple drivers of decadal change of an ecosystem engineer at the range edge. *Ecology and Evolution*. **5**: 3210-3222

Firth, L. B., White, F. J., Schofield, M., Hanley, M. E., Burrows, M. T., Thompson, R. C., Skov, M. W., Evans, A. J., Moore, P. J., and Hawkins, S. J. (2016) Facing the future: the importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. *Marine and Freshwater Research*. **67**: 131-143

Fly, E. K., and Hilbish, T. J. (2012) Physiological energetics and biogeographic range limits of three congeneric mussel species. *Oecologia*. **172**: 35-46

Foereid, N., Bellarby, J., Meier-Augenstein, W., and Kemp, H. (2010) Does light exposure make plant litter more degradable? *Plant Soil*. **333**: 275-285

Forbes, E. (1858) The distribution of marine life, illustrated chiefly by fishes and molluscs and radiata. In *The physical atlas of natural phenomena* by A. K. Johnston. William Blackwood and Sons, Edinburgh and London: 99-101 William Blackwood and Son William Blackwood and Sons, s, https://www.davidrumsey.com/luna/servlet/detail/RUMSEY~8~1~24718~940057:Map-of-the-distribution-of-marine-l

Forman, R. T. T., and Baudry, J. (1984) Hedgerows and Hedgerow networks in landscape ecology. *Environmental Management*. **8**: 495-510

Forrest, J. K. R. (2016) Complexe responses of insect phenology to climate change. *Current Opinion on Insect Science*. **17**: 49-64

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*. **5**:673–677

Franzmeier, D. P., Pedersen, E. J., Longwell, T. J., Byrne, J. G., and Losche, C. K. (1969) Properties of some soils in the Cumberland Plateau as related to slope aspect and position. Soil Science Society of America. 33: 755-761

French, D. D., and Cummins, R. P. (2001) Classification, composition, richness and diversity of British hedgerows. *Applied Vegetation Science*. **4**: 213-228

G

Galewsku, J. (2009) Rain shadow development during the growth of mountain ranges: An atmospheric dynamics perspective. *Journal of Geophysical research: Earth Surface*. **114**: F01018

Gallien, W. M. (1985) The effects of aggregations on water loss in *Collisella digitalis*. *The Veliger*. **28**: 14-17

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M. Diaz, D., Harmelin, J. G., Gambi, M., C., Kersting, D. K., Ledoux, J. B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J. C., Serrano, E., Teixido, N., Torrents, O., Zabala, M., Zuberer, F., and Cerrano, C. (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change biology*. **15**: 1090-1103

Gartner T. B., and Cardon Z. G. (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos*. **104**: 230-246

de Gasper, A. L., Eisenlohr, P. V., and Salino, A. (2015) Climate-related variables and geographic distance affect ferns species composition across a vegetation gradient in a shrinking hotspot. *Plant Ecology and diversity*. **8**: 25-35

Ge, Q. A., Wang, H., Rutishauser, T., and Dai, J. (2015) Phenological response to climate change in China: a meta-analysis. *Global Change Biology*. **21**: 265-274

Geiger, R., Aron, R. H., and Todhunter, P. (1995) The climate near the ground –Fifth Edition. Harvard University Press: Cambridge, Mass., USA

Gelm, J. (2019) Soil fungal communities reflect aspect-driven environmental structuring and vegetation types in a Pannonian forest landscape. *Fungal Ecology*. **39**: 63-79

Gerard, B. M. (1960) The biology of certain British earthworms in relation to environmental conditions. PhD thesis, London, UK

Gestoso, I., Arenas, F., and Olabarria, C. (2015) Feeding behaviour of an intertidal snail: Does past environmental stress affect predator choices and prey vulnerability? *Journal of Sea Research*. **97**: 66-74

Gibbs, P. E., Green, J. C., and Pascoe, P. L. (1999) A massive summer-kill of the dog-whelk, *Nucella lapillus*, on the north Cornwall coast in 1995: freak or forerunner*? Journal of the Marine Biological Association of the United Kingdom.* **79**: 103-109

Gilliam, F. S., Hédl, R., Chudomelová, M., McCulley, R. L., and Nelson, J. A. (2014) Variation in vegetation and microbial linkages with slope aspect in a montane temperate hardwood forest. *Ecosphere*. **5**: 1-17

Gillingham, P. K., Huntley, B., Kunin, W. E., and Thomas C. D. (2012) the effect of spatial resolution on projected responses to climate warming. *Diversity and Distribution*. **18**: 1-11

Gilman, S. E., (2006) The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment and temperature. *Ecography*. **29**: 709-720

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., and Holt, R. D. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*. **25**: 325-331

Gobat, J.-M., Aragno, M., and Matthey, W. (2004) The living soil. Fundamentals of soil science and soil biology. Science Publishers, Inc., Enfield, NH, USA. pp 603

Goldin, A. (1987) Reassessing the use of loss on ignition for estimating organic matter content in non-calcareous soils. *Communications in Soil Science and Plant Analysis*. **18**: 1111-1116

Gonçalves, M. S. (2018) Cultivation of *Osmundea pinnatifida* and *Codium tomentosum*, native seaweed species with commercial potential. Master thesis. University of Porto, Portugal

Grant, P. R., Grant, B. R., Huey, R. B., Johnson, M. T. J., Knoll, A. H., and Schmitt, J. (2017) Evolution caused by extreme events. *Philosophical Transactions of the Royal Society B*. **372**: 20160146

Gray, D. R., and Hodgson, A. N. (2003) The importance of a crevice environment to the limpets *Helcion pectunculus* (Patellidae). *Journal of Molluscan Studies*. **70**: 67-72

Griffiths, R. P., Madritch, M. D., and Swanson, A. K. (2009) The effects of topography on soil forest characteristics in the Oregon Cascade Mountains (USA): Implications for the effects of climate change on soil properties. *Forest Ecology and Management*. **257**: 1-7

Grime, J. P., Hodgson, J. G., and Hunt, R. (1988) Comparative Plant Ecology – A functional approach to common British species. Unwin Hyman Ltd., London, UK

Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., and Bennett, C. R. (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*. **105**: 10028-10032

Grove, B., Power, S. A., Buckley, G. P., and Ghazoul, J. (2007) Effects of herbicide spray drift and fertilizer overspread on selected species of woodland ground flora: comparison between short-term and long-term impact assessments and field surveys. *Journal of Applied Ecology*. **44**: 374-384

Guan, H., Zhang, x., Makhnin, O., and Sun, Z. (2013) Mapping mean monthly temperatures over a coastal hilly area incorporating terrain aspect effect. *American Meteorological Society*. **14**: 233-250

Gugger, S., Kesselring, H., Stöcklin, J., Hamann, E. (2015) Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. *Annals of Botany.* **116**: 953-962

Guiry, M. D., and Guiry, G. M. (2019) *Hildenbrandia rubra* (Sommerfelt) Meneghini. In AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Accessed on the 9th November 2019 [https://www.algaebase.org/search/species/detail/?species_id=26]

Guo, Q., Taper, M., Schoenberger, M., and Brandle, J. (2005) Spatial-temporal population dynmics across species ranges: from centre to margin. *Oikos*. **180**:47-57

Guo, Z., Li, X., He, Z., Yang, Y., Wang, W., Zhong, C., Greenberg, A. J., Wu, C.-I., Dule, N. C., and Shi, S. (2018) Extremely low genetic diversity across mangrove taxa reflects past sea level changes and hints at poor future responses. *Global change Biology*. **24**:1741-1748

Guy-Haim, T., Alexander, H., Bell, T. W., Bier, R. L., Bortolotti, L. E., Briseño-Avena, C., Dong, X., Flanagan, A. M., Grosse, J., Grossmann, L., Hasnain, S., Hovel, R., Johnston, C. A., Miller, D. R., Mucarella, M., Noto, A. E., Reisinger, A. J., Smith, H. J. and Stamieszkin, K. (2017) What are the type, direction, and strength of species, community, and ecosystem responses to warming in aquatic mesocosm studies and their dependency on experimental characteristics? A systematic review protocol. *Environmental Evidence*. **6**: 6

H

Hacker, S. D., Mange, B. A., Nielsen, K. J., Chan, F., and Gouhier, T. C. (2019) Regional processes are stonger determinants of rocky intertidal community dynamics than local biotic interactions. *Ecology*. **1000**: e02763

Häder, D-P., Lebert, M., and Helbing, E. W. (2001) Effects of solar radiation on the Patagonian macroalga *Enteromorpha linza* (L.) J. Agardh – Chlorophyceae. *Journal of Photochemistry and Photobiology B: Biology*. **62**: 43-54

Häder, D-P., Kumer, H. D., Smith, R. C., and Worrest, R.C. (2003) Aquatic ecosystems: effects of solar ultraviolet radiation and interactions with other climatic change factors. *Photochemical and Photobiological Sciences*. **2**: 39-50

Hall-Spencer, J. A., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., Rowley, S. J., Tedesco, D., and Buia, M-C. (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*. **454**: 96-99

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T.H., Pemberton, J.M., and Grenfell, B. T. (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature.* **430**: 71-75

Halpin, P. M., Menge, B. A., and Hoffmann, G. E. (2004) Experimental demonstration of plasticity in the heat shock response of the intertidal mussel *Mytilus californianus*. *Marine Ecology process series*. **276**: 137-145

Hamilton, H. J. (2017) The role of intertidal height, microhabitat use and motility on the ontogeny of stress tolerance to air temperature and desiccation in six intertidal invertebrate species. Master thesis. Thompson River University,

Hampe, A. and Petit, R. J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters.* **8**: 461-467

Hanley, M. E., Fenner, M., and Edwards, P. J. (1995) An experimental field study of the effects pf mollusc grazing on seedling recruitment and survival in grassland. *The Journal of Ecology*. **83**: 621-627

Hanley, M. E., Fenner, M., and Edward, P. J. (1996) The effect of mollusc grazing on seedling recruitment in artificially created grassland gaps. *Oecologia*. **106**: 240-246

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., and McCullough, I. M. (2014) Fine-grain modelling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Evolution & Evolution*. **29**: 390-397

Hanley, M. E., and Wilkins, J. P. (2015) On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. *Journal of Insect Conservation.* **19**: 67-74

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodroguiz, L. F., Tomanek, L., and Williams, S. L. (2006) The impact of climate change in costal marine systems. *Ecology Letters*. **9**: 228-241

Harley, C. D. G, Denny, M. W., Mach, K. J., and Miller, L. P. (2009) Thermal stress and morphological adaptations in limpets. *Functional Ecology*. **23**: 292-301

Harley, C. D. G. (2011) Climate change, keystone predation and biodiversity loss. *Science*. **334**: 1124-1126

Hartnoll, R., and Wright, J. (1977) Foraging movements and homing in the limpet *Patella vulgata* L. *Animal Behaviour.* **25**: 806-810

Harvey, B. P., Al-Janabi, B., Broszeit, S., Cioffi, R., Kumar, A., Aranguren-Gassis, M., Bailey, A., Green, L., Gsottbauer, C. M., Hall, E. F., Lechler, M., Mancuso, F. P., Pereira, C. O., Ricevuto, E., Schram, J. B., Stapp, L. S., Stenberg, S., and Santa Rosa L. T. (2014) Evolution of marine organisms under climate change at different levels of biological organisation. *Water*. **6**: 3545-3574

Harrington, G. H. (1991) Effects of soil moisture on shrub seedling survival in semi-arid grassland. *Ecology*. **72**: 1138-1149

Hättenschwiler, S., Tiunov, A. V., and Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems *Review of Ecology, Evolution, and Systematics*. **36**: 191-218

Hauck, M., Dulamsuren, C., and Mühlenberg, M. (2007) Lichen diversity on steppe slopes in the northern Mongolian mountain taiga and its dependence on microclimate. *Flora*. **202**: 530-546

Hawes, T. C., Worland, M. R., and Bale, J. S. (2010) Freezing in the Antarctic limpet, *Nacella concinna. Cryobiology*. **61**: 128-132

Hawkins S. J., and Hartnoll R. G. (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology, an Annual Review*. **21**:195-282

Hawkins S. J., Hartnoll R. G., Kain J. M., and Norton T. A. (1992) Plant animal interactions on hard substrata in the north-east Atlantic. In: John D. M., Hawkins S. J., Price J. H. (Eds) *Plant animal interactions in the marine benthos*. Systematics Association Special Vol 46. Clarendon Press, Oxford

Hawkins, S .J., Moore, P. J., Burrows, M. T., Poloczanska, E., Mieszkowska, N., Herbert, R. J. H., Jenkins, S. R., Thompson, R. C., Genner, M. J., and Southward, A. J. (2008) Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Research*. **37**: 123-133

Hawkins, S. J., Sugden, H. E., Mieszkowska, N., Moore, P. J., Poloczanska, E., Leaper, R., Herbert, R. J. H., Genner, M. J., Moschella, P. S., Thompson, R. C., Jenkins, S. R., Southward, A. J., and Burrows, M. T. (2009) Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Process Series*. **396**: 245-259

Hawkins, S. J. (2012). Marine conservation in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems.* **22**: 281-287

Hawkins, S. J., Evans, A. J., Firth, L. B., Genner, M. J., Herbert, R. J. H., Adams, L. C., Moore, P. J., Mieszkowska, N., Thompson, R. C., and Fenberg, P. B. (2016). 'Impacts and effects of ocean warming on intertidal rocky habitats'. In D. Laffoley, & J. M. Baxter (Eds.), *Explaining ocean warming: Causes, scale, effects and consequences*. Full report (pp. 147-176). Gland, CH: IUCN.

Hawkins, S. J., Mieszkowska, N., Firth, L. B., Bohn, K., Burrows, M. T., MacLean, M. A, Thompson, R. C., Chan, B. K. K., Little, C., and Williams, G. A. (2016b) Looking backwards to look forwards: the role of natural history in temperate reef ecology. *Marine and Freshwater Research*. **67**: 1-13

Healey, I. N. (1967) An Ecological Study of Temperatures in a Welsh Moorland Soil, 1962-63. *Journal of animal Ecology*. **36**: 425-434

Hector, A., Beale, A. J., Minns, A., Otway, S. J. and Lawton, J. H. (2000) Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* **90**: 357-371

Helmuth, B. S. T., and Hofmann, G. E. (2001) Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biological Bulletin*. **201**: 374-384

Helmuth, B. S. T., Harley, C. D. G., Halpin, P. M., O'Donnell, M., Hofmann, G. E., and Blanchette, C. A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science*. **298**: 1015-1017

Helmuth, B. S. T., Mieszkowska, N., Moore, P., and Hawkins, S. (2006a) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annual Review of Ecology, Evolution, and Systematics*. **37**: 373-404

Helmuth, B. S.T., Broitman, B. R., Blanchette, C. A., Gilman, S., Halpin, P., Harley, C. D. G., O'Donnell, M. J., Hofmann, G. E., Menge, B., and Strickland, D. (2006b) Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecological Monographs*. **76**: 461-479

Helmuth, B. S. T. (2009) From cells to coastlines: how can we use physiology to forecast the impact of climate change. *The Journal of Experimental Biology*. **212**: 753-760

Helmuth, B. S. T., Yamane, L., Mach, K. J., Chhotray, S., Levin, P., and Woodin, S. (2010a) All climate change is local: Understanding and predicting the effects of climate change from organism's point of view. *Stanford Journal of Law, Science & Policy.* **2**: 18-35

Helmuth, B. S. T., Broitman, B. R., Yamane, L., Gilman, S. E., Mach, K., Mislan, K. A. S., and Denny, M. W. (2010b) Organismal climatology: analysing environmental variability at scales relevant to physiological stress. *Journal of Experimental Biology*. **213**: 995-1003

Hill, M. O., Mountford, J. O., Roy, D. B., and Bunce, R. G. H. (1999) ECOFACT Research Report Series. Volume 2. Ellenberg's indicator values for British Plants. Centre for Ecology & Hydrology.

Hilbish, T. J., Brannock, P. M., Jones, K. R., Weaver, L. A., and Gilg, M R. (2002) Distribution of *Mytilus edulis*, *M. galloprovincialis*, and their hybrids in open-coast populations of mussels in southwestern England. *Marine Biology*. **140**: 137-142

Hinojosa, M. B., Parra A., Ramírez, D. A., Carreira, J. A., García-Riuz, R., and Moreno, J. M. (2012) Effect of drought on soil phosphorus availability and fluxes in a burned Mediterranean shrubland. *Geoderma*. **191**: 62-69

Hipfner, J. M. (2008) Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series*. **368**: 295-304

Hiscock, K. (2003) *Lithophyllum incrustans* An encrusting coralline alga. In Tyler-Walters H. and Hiscock K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. Accessed on the 12th of July 2019.[https://www.marlin.ac.uk/species/detail/1395]

Hiscock, K., Southward, A., Tittley, I., and Hawkins, S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic conservation: Marine and Freshwater ecosystems*. **14**: 333-362

Hodgson, C (2010) Devon Hedgerow Surveys. Farming and Wildlife Advisory Group Report.

Hoffmann, A. A, and Blows, M. W. (1994) Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution*. **9**:223–227

Hoffman, A. A., and Parsons, P. A. (1997) Extreme Environmental Change and Evolution. Cambridge University Press, UK

Hoffmann, A. A., and Sgrò, C. M. (2011) Climate change and evolutionary adaptation. *Nature*. **470**: 479-485

Hofmann, G. E. and Todgham, A. E. (2010) Living in the Now: Physiological mechanisms to tolerate a rapidly changing environment. *The Annual Review of Physiology*. **72**: 127-145

Hooper, M. D., Hoskins, W. G., Bradshaw, A. D., and Allen, D. E. (1976) Hedges and local history. Published by National Conference for Local History/The National Council of Social Service (NCSS), London, UK

Huggett, R. J. (2003) Geoecology: An evolutionary approach. Second Edition. Routledge (Taylor & Francis Group), New York, USA and London, UK

Huggett, R. J. (2004) Fundamentals of Biogeography, Second Edition. Routledge (Taylor & Francis Group), New York, USA and London, UK

Hughes, R. N., and Dunkin, S. de B. (1984) Behavioural components of prey selection by Dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus Edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology*. **77**: 45-68

Hughes, R. N., and Burrows, M. T. (1991) Diet selection by dogwhelks in the field: an example of constrained optimization. *Animal behaviour*. **42**:47-55

Hui, T. Y., Landry Yuan, F., Bonebrake, T. C., and Williams, G. A. (2018) Multifunctional behaviour in a sandy shore crab enhances performance in extreme intertidal environments. *Oecologia*. 189: 79-89

Hunt, L. J. H., and Denny, M. W. (2008) Desiccation protection and disruption: a trade-off for an intertidal marine algal. *Journal of Phycology*. **44**: 1164-1170

Hutchins, L. W. (1947) The bases for temperature zonation in geographical distribution. *Ecological Monographs*. **17**: 325-335

I

Iacarella, J. C., and Helmuth, B. (2012) Body temperature and desiccation constrain the activity of *Littoraria irrorata* within the *Spartina alterniflora* canopy. Journal of Thermal Biology. 37: 15-22

Ingólfsson, A. (1996) The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. *Sarsia*, **8**: 29-44

Inkiläinen E. N. M., McHale M. R., Blank G. B., James A. L., and Nikinmaa E. (2013) The role of the residential urban forest in regulating throughfall: A case study in Raleigh, North Carolina, USA. *Landscape Urban Planning*. **119**: 91-103

IPCC (2012) Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on

Climate Change [Field, C.B., V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M. Tignor, and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK, and New York, NY, USA,

IPCC (2013) Climate change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M. M. B., Allen, S.K., et al. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

IPCC (2014) Climate change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C. B., Barros, V. R., Dokken, D. J., Mach, K. J., Mastrandrea, et al. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

IPCC (2018) Global Warming of 1.5°C. Summary for Policymakers. Special report of the Intergovernmental Panel on Climate Change [Masson-Delotte, V., Zhai, P., Pörtner, H., Roberts, D., Skea, J., Shula, P. R. et al. (eds.)] IPCC, Switzerland,

IPCC (2019) Climate Change and Land. Summary for Policymakers. (*Approved draft*).

Ishii R., and Higashi, M. (1997) Tree coexistence on a slope: an adaptive significance of trunk inclination. *Proceedings of the Royal Society B: Biological Sciences*. **264**: 133–139

Iwasaki, K. (1995) Comparison of mussel bed community between two intertidal *mytilids Septifier virgatus* and *Hormomya mutabilis*. *Marine Biology*. **123**: 109-119

J

Jansen, J. M., Bonga, S. W., and Hummel, H. (2007) Differential cold-shock resistance among acclimated European mussel populations. *Marine Freshwater Behaviour and Physiology*. **40**:233–245

Jeffery, S., Gardi, C., Jones, A., Montanarella, L., Marmo, L.,Miko, L., Ritz, K., Peres, G., Römbke, J. and van der Putten, W. H. (eds.) (2010) European Atlas of Soil Biodiversity. European Commission, Publications Office of the European Union, Luxembourg.

Jenkins, S. R., Åberg, P., Cervin, G., Coleman, R. A., Delany, J., Della Santina, P., Hawkins S. J., LaCroix, E., Myers, A. A., Lindegarth, M., Power, A-M., Roberts, M. F., and Hartnoll, R. G. (2000) Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*. **243**: 209-225

Jennings, T., (1978) The world of a hedge. Faber and Faber Ltd, London, UK

Johnson II, S.E. (1975) 'Microclimate and energy flow in the marine rocky intertidal'. In Gates, D. M. and Schmerl, R. B. (eds.) *Perspectives of Biophysical Ecology*, pp. 559–587. Springer-Verlag, New York.

Jones, A. G., Bussell, J., Winters, A., Scullion, J., and Gwynn-Jones, D. (2016) The functional quality of decomposing litter outputs from an Arctic plant community is affected by long-term exposure to enhanced UV-B. *Ecological Indicators*. **60**: 8-17

Jones, S. J., Mieszkowska, N., and Wethey, D. S. (2009a) Linking thermal tolerance and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biological Bulletin*. **217**: 73-85

Jones, S. J., Lima, F. P., and Wethey, D. S. (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography*. **37**: 2243-2259

Jones M. M , Szyska B., Kessler M. (2011) Microhabitat partitioning promotes plant diversity in a tropical montane forest. *Global Ecology and Biogeography*. **20**:558-569

Jonsson, B., Jonsson, N. (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*. **75**: 2381-2447

Judge, R., Choi, F., and Helmuth, B. (2018) Recent Advances in data logging for intertidal ecology. *Frontiers in Ecology and Evolution*. **6**: 1-18

Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J. A., Olsen, Jeanine, L., and Hoarau, G. (2013) Climate change impacts on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and Evolution*. **3**: 1356-1373

K

Kakani, V. G., Reddy, K. R., Zhao, D., and Sailaja, K. (2003) Field crop responses to ultraviolet-B radiation: a review. *Agricultural and Forest Meteorology*. **120**: 191-218

Kampichler, C., and Bruckner, A. (2009) The role of micro-arthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews*. **84**: 375-389

Kang, S., Doh, S., Lee, D., Lee, D., Jin, V. L., and Kimball, J. S. (2003) Topographic and climatic controls on soil respiration in six temperate mixed-hardwood forest slopes, Korea. *Global Change Biology*. **9**: 1427-1437

Kaniewska, P., Campbell, P. R., Kline, D. I., Rodriguez-Lanetty, M., Miller, D. J., Dove, S., and Hoegh-Guldberg, O. (2012) Major cellular and physiological impacts of ocean acidification on reef building coral. *PLoS ONE*. **74**: e34659

Kearney, M., and Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' range. *Ecology Letters*. **12**: 334-350

Kennedy, A. D. (1995) Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology*. **1**: 29-42

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., and Franklin, S. E. (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*. **21**: 393-404

Khemira, H., Lombard, P. B., Sugar, D., and Azarenko, A. N. (1993) Hedgerow orientation affects canopy exposure, flowering, and fruiting of ‘Anjou’ pear trees. *Horticultural Science*. **28**: 984-987

Kim H-S., Palmroth S., Thérézien M., Stenberg P., and Oren R. (2011) Analysis of the sensitivity of absorbed light and incident light profile to various canopy architecture and stand conditions. *Tree Physiology*. **31**: 30-47

Kolar, C. S., and Lodge, D. M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolutio*n, **16**: 199–204

Koti, S., Reddy, K. R., Reddy, V. R., Kakani, V. G., and Zhao, D. (2004) Interactive effects of carbon dioxide, temperature, and ultraviolet-B radiation on soybean (*Glycine max* L.) flower and pollen morphology, pollen production, germination, and tube lengths. *Journal of Experimental Botany*. **56**: 725-736

Kordas, R. L., Harley, C. D. G., and O’Connor, M. I. (2011) Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *Journal of Experimental Marine Biology and Ecology*. **400**: 218-226

Kordas, R. L., Dudgeon, S., Storey, S., Harley, C. D. G. (2015) Intertidal community responses to field-based experimental warming. *Oikos*. **124**: 88-898

Korell, L., Auge, H., Chase, J. M., Harpole, S., and Knight, T. M. (2019) We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology*, 1-3

Kronberg, I. (1988) Structure and adaptation of the fauna in the black zone (littoral fringe) along rocky shores in northern Europe. *Marine Ecology Process Series*. **49**: 95-106

Kutiel, P. (1992) Slope aspect effect on soil and vegetation in Mediterranean ecosystem. *Israel Journal of Botany*. **41**: 243-250

Kuperman, R. G. (1996) Relationships between soil properties and community structure of soil macroinvertebrates in oak-hickory forests along an acidic deposition gradient. *Applied Soil Ecology*. **4**: 125-137

L

Lafon, C. W., Hanson, A. H. and Dwight, R. A. (2019) Geographic variations in fine-scale vegetation patterns: aspect preferences of montane pine stands over Southern Appalachian landscapes. *Physical Geography*. 40: 433-460

Landsberg, H. (1947) Physical climatology. School of Mineral Industries. Pennsylvania State University, 283 pp

Lane J. E., Kruuk L. E. B., Charmantier A., Murie J. O., and Dobson F. S. (2012) Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature.* **489**: 554-557

Lathlean, J. A., Ayre, D. J., Coleman, R. A., and Minchinton, T. E. (2015) Using biomimetric loggers to measure interspecific and microhabitat variation in body temperatures of rocky intertidal invertebrates. *Marine and Freshwater Research*. **66**: 86-94

Lathlean, J. A., McWilliam, R. A., Pankhurst, J., and Minchinton, T. E (2017) Altering species interactions outweighs the effects of experimental warming in structuring a rocky shore community. *Journal of Experimental Marine Biology and Ecology*. **496**: 22-28

Lavelle, P., Blanchart, E., Martin, A., Spain, A., Toutain, F., Barois, I. and Schaefer, R. (1993) A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. - *Biotropica* **25**: 130-150

Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. (2010) Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual review of Ecology, Evolution and Systematics.* **41**: 321-350

Le Coeur, D., Baudry, Jacques, and Burel, F. (1999) Field margins plant assemblages: variation partitioning between local and landscape factors. *Landscape and Urban Planning*. **37**: 57-71

Lee, J. H., and Boulding E. G. (2010) Latitudinal clines in body size, but not thermal tolerance or heat-shock cognate 70 (*HSC70*), in the highly-dispersing intertidal gastropod *Littorina keenae* (Gastropoda: Littorininae). *Biological Journal of the Linnean Society*. **100**: 494-505

Lembrechts, J. J., Lenoir, J., Nuñez, M. A., Pauchard, A., Geron, C., Bussé, G., Milbau, A., and Nijs, I. (2018a) Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. *Ecography*. **41**: 900-909

Lembrechts, J. J., Nijs, I., and Lenoir, J. (2018b) Incorporating microclimate into species distribution models. *Ecography*. **42**: 1267-1279

Lemoine, N. P., and Burkepile, D. E. (2012) Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology*. **93**: 2483-2489

Lenoir, J. Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bergendorff, C., Birks, H. J. B., Bråthen, K. A., Brunet, J., Bruun, H. H., Dahlberg, C. J., Decocq, G., Diekmann, M., Dynesius, M., Ejnæs, R., Grytnes, J.-A., Hylander, K., Klanderud, K., Luoto, M., Milbau, A., Moora, M., Nygaard, B., Odland, A., Ravolainen, V. T., Reinhardt, S., Sandvik, S. M., Schei, F. H., Speed, J. D. M., Tvraabak, L. Un., Velle, L. G., Virtanen, R., Zobel, M., and Svenning, J.-C. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology.* **19**: 1470-1481

Letcher, T. M. (2016) Climate change. Observed impacts on planet Earth – Second Edition. Elsevier

Letts, M. G., Johnson, D. R. E., and Coburn, C. A. (2010) Drought stress ecophysiology of shrubs and grass functional groups on opposing slope aspects of a temperate grassland valley. *Botany*. **88**: 850-866

Lewis J. R. (1964) The ecology of rocky shores. English University Press, London, UK

Lima, F. P., Gomes, F., Seabra, R., Wethey, D. S., Seabra, M. I., Cruz, T., and Hilbish, T. J. (2016) Loss of thermal refugia near equatorial range limits. *Global Change Biology*. **22**: 254-263

Lindborg, R., (2007) Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology*. **95**: 555–564

Liu, M., Li, W., and Wang, G. (2013) The effects of slope aspect on plant and soil properties in sub-alpine meadow of China. *Journal of Food, Agriculture and Environment*. **11**: 2639–2643

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. and Ackerly, D. D. (2009) *Nature*. **462**: 1052-1055

Lockwood, B. L., and Somero, G. N. (2011) Invasive and native blue mussels (genus *Mytilus*) on the California coast: the role of physiology in a biological invasion. *Journal of Experimental Marine Biology and Ecology*. **400**: 167-174

Lorenzen, S. (2007) The limpet *Patella vulgata* L. at night in air: effective feeding on *Ascophyllum nodosu*m monocultures and stranded seaweeds. *Journal of Molluscan Studies*: **73**: 267-274

Lovejoy, T. E., and Hannah, L. (2005) Climate Change and Biodiversity. Yale University Press, London, UK

Lowell, R. B. (1984) Desiccation of intertidal limpets: effects of shell size fit to substratum, and shape. *Journal of Experimental Marine Biology and Ecology*. **77**: 197-207

Lu, S., Ju, Z., Ren, T., and Horton, R. (2009) A general approach to estimate soil water content from thermal inertia. *Agricultural and Forest Meteorology*. **149**: 1693–1698

M

Magurran, A. E. (2004) Measuring Biological Diversity. Backwell Publishing company, Malden, MA, USA; and Oxford, UK; and Victoria, Australia.

Måren, I. E., Karki, S., Prajapati, C., and Yadav, R. K. (2015) Facing north or south: Does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan. *Journal of Arid Environments.* **121**: 112-123

Mark, A. F., Dickinson, K. J. M., Allen, J., Smith, R., and West, C. J. (2001) Vegetation patterns, plant distribution and life forms across the alpine zone in southern Tierra del Fuego, Argentina. *Austral Ecology*. **26**.: 423-440

Marshall, D. J., and McQuaid, C. D. (1992) Comparative aerial metabolism and water relations of the intertidal limpets *Patella granularis L.* (Mollusca: Prosobranchia) and *Siphonaria oculus Kr*. (Mollusca: Pulmonata). *Physiological Zoology*. **65**: 1040-1056

Marshall, D. J., McQuaid, C. D., and Williams, G. A. (2010) Non-climatic thermal adaptation: implications for species’ responses to climate warming. *Biology Letters*. **6**: 669-673

Marshall, D. J., Baharuddin, N., McQuaid, C. D. (2013) Behaviour moderates climate warming vulnerability in high-rocky-shore snails: interactions of habitat use, energy consumption and environmental temperature. *Marine Biology*. **160**: 2525-2530

Marshall, E. J. P., and Moonen, A. C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment*. **89**: 5-21

Masuda, K. (2000) A note on the climatic factors controlling the global distribution of vegetation. *Geographical Reports of Tokyo Metropolitan University*. **35**: 21-30

McCollin, D., Jackson, J. I., Bunce, R. G. H., Barr, C. J., and Stuart, R. (2000) Hedgerows as habitat for woodland plants. *Journal of Environmental Management*. **60**: 77-90

McCutchan, M. H., and Fox, G. F. (1996) Effect of elevation and aspect on wind, temperature and humidity. *Journal of Climate and Applied Meteorology*. 25: 1996-2013

McCloud, E. S., and Berenbaum, M. (1999) Effects of enhanced UB-B radiation on a weedy forb (*Plantago lanceolate*) and its interactions with a generalist and specialist herbivore. *Entomologia Experimentalis et Applicata.* **93**: 233-247.

McLaughlin B. C., and Zavaleta, E. S. (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Global Change Biology*. **18**: 2301-2312

McMahon, R. F. (1990) Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia*. **193**: 241-260

Meentemeyer, V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*. **59**: 465-472

Menneer, R. (1994) Wildlife revival in Cornish hedges. History, traditions and practical guidance. 1st Edition. Truran Publications, Redruth, UK

Mercer, C., Cherrill, A., Tudor, G., and Andrews, M. (1999) Hedgerow plant communities: relationships with adjacent land use and aspect. *Aspects of Applied Biology.* **54**: 345-352

Merckx, T., and Berwaerts, K. (2010) What type of hedgerows do Brown hairstreak (*Thecla betulae* L.) butterflies prefer? Implications for European agricultural landscape conservation. *Insect Conservation and Diversity*. **3**: 194-204

Merilä, J., and Hendry, A. P. (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications.* **7**: 1-14

Merilä, J., and Hendry, A. P. (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications*. **7**: 1-14

Met Office, Harley Centre (2019a) UK Climate Projections: Deadline Findings. Version 2.

Met Office, Harley Centre (2019b) UKCP18 Science Overview Executive Summary Report from January 2019.

Met Office (2016) South west England climate [https://www.metoffice.gov.uk/climate/uk/regional-climates/sw] Accessed 23rd of March 2019

Met Office (2018a) Snow and low temperatures February to March 2018 [https://www.metoffice.gov.uk/climate/uk/interesting/february2018-snow] Accessed 09th of June 2019

Met Office (2018b) Was summer 2018 the hottest on record? [https://www.metoffice.gov.uk/about-us/press-office/news/weather-and-climate/2018/end-of-summer-stats] Accessed 15th June 2019

Met Office (2018c) Chance of summer heatwaves now thirty times more likely [https://www.metoffice.gov.uk/about-us/press-office/news/weather-and-climate/2018/2018-uk-summer-heatwave] Accessed 15th June 2019

Meyer, J., and Riebesell, U. (2015) Reviews and Syntheses: Responses of coccolithophores to ocean acidification: meta-analysis. *Biogeosciences*. **12**: 1671-1682

Mieszkowska, N., Leaper, R., Moore, P., Kendall, M. A., Burrows, M. T., Lear, D., Poloczanska, E., Hiscock, K., Moschella, P. S., Thompson, R. C., Herbert, R. J., Laffoley, D., Baxter, J., Southward, A. J., and Hawkins, S. J. (2005) Assessing and predicting the influence of climatic change using intertidal rocky shore biota. Occasional publication No 20. Marine Biological Association of the UK.

Mieszkowska, N., Kendall, M A., Hawkins, S. J., Leaper, R., Williamson, P.,Hardman-Mountford, N. J., and Southward, A. J. (2006) Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia*. **555**: 241-251

Mieszkowska, N., Sugden, H., Firth, L. B., and Hawkins, S. J. (2014) The role of sustained observations in tracking impacts of environmental change on marine biodiversity and ecosystems. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Science*. **372**: 20130339

Midgley, G. F., Hannah, L., Millar, D., Rutherford, M. C., and Powrie, L. W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in biodiversity hotspot. *Global Ecology and Biogeography*. **11**: 445-451

Mill, P. J., and Grahame, J. (1990) Distribution of the species of rough periwinkle (*Littorina*) in Great Britain. *Hydrobiologia*. **1**: 21-27

Miller, A., Schimel, J.P., Meixner, T., Sickman, J.O., and Melack, J.M. (2005) Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology and Biochemistry*. **37**: 2195-2204

Miller, L. P., Harley, C. D. G., and Denny, M. W. (2009) The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantean*. *Functional Ecology*. **23**: 756–767

Miller, L. P., and Denny, M. W. (2011) Importance of behavioural and morphological traits for controlling body temperature in littorinids snails. *The Biological Bulletin*. **220**: 209-223

Miller, L. P., Allen, B. J., King, F. A., Chilin, D. R., Reynoso, V. M., and Denny, M. K. (2015) Warm microhabitats drive both increased respiration and growth rates of intertidal consumers. Marine *Ecology Progress Series.* **522**: 127-143.

Mislan, K. A. S., and Wethey, D. S. (2015) A biophysical basis for patchy mortality during heat waves. *Ecology*. **90**: 902-907

Monaco, C. J., Wethey, D. S., and Helmuth, B. (2016) Thermal sensitivity and the role of behaviour in driving intertidal predator-prey interaction. *Ecological Monograph*. **86**:429-447

Moosen, A. C., and Marshall, E. J. P. (2001) The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. *Agriculture, Ecosystems and Environments*. **86**: 197-202

Moore, H. B., (1936) The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *Journal of the Marine Biological Association of the United* Kingdom. **21**: 61-69

Moore, P. J., Thompson, R. C., and Hawkins, S. J. (2011) Phenological changes in intertidal conspecific gastropods in response to climate warming. *Global Change Biology*. **17**: 709-719

Morais, S. Boaventura, D., Narciso, L., Ré, P., and Hawkins, S. J. (2003) Gonad development and fatty acid composition of *Patella depressa* Pennant (Gastropoda: Prosobranchia) populations with different patterns of spatial distribution, in exposed and sheltered sites. *Journal of Experimental Marine Biology and Ecology*. **294**: 61-80

Morelli, T., Daly,C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., and Beissinger, S. R. (2016) Managing climate change refugia for climate adaptation. *PLoS ONE*. **11**: e0159909

Morignat, E., Perrin, J-B., Gay, E., Vinard, J-L., Calavas, D., and Hénaux, V. (2014) Assessment of the Impact of the 2003 and 2006 Heat waves on cattle mortality in France. *PLoS ONE*. **9**: e93176

Morritt, D., Leung, K. M. Y., De Pirro, M., Yau, C., Wai, T-C., and Williams, G. A. (2007) Responses of the limpet, *Cellana grata* (Gould 1859), to hypo-osmotic stress during simulated tropical, monsoon rains. *Journal of Experimental Marine Biology and Ecology*. **352**: 78-88

Mota, C. F., Engelen, A. H., Serrao, E. A., Coelho, M. A. G., Marbà, Krause-Jensen, D., and Pearson, G. A. (2018) Differentiation in fitness-related traits in response to elevated temperatures between leading and trailing edge populations of marine macrophytes. *PLoS ONE*. **13**: e0203666

Mudrick, D. A., Hoosein, M., Hicks Jr., R. R., and Townsend, E. C. (1994) Decomosition of leaf litter I an Appalachian forest: effects of leaf species, aspect, slope position and time. *Forest Ecology and Management*. 68: 231-250

Muñoz, N. J., Farrell, A. P., Heath, J. W., and Neff, B. D. (2015) Adaptive potential of a Pacific salmon challenged by climate change. *Nature Climate Change*. **5**: 163-166

Murphy, J. M., Sexton, D. M. H., Jenkins, G. J., Booth, B. B. B., Brown, C. C., Clark, R. T., Collins, M., Harris, G. R., Kendon, E. J., Betts, R. A., Brown, S. J., Humphrey, K. A., McCarthy, M. P., McDonald, R. E., Stephens, A., Wallace, C., Warren, R., Wilby, R., Wood, R. A. (2009) UK Climate Projections Science Report: climate change projections. Met Office Hadley Centre, Exeter.

Musil, C.F., Van Heerde, P. D. R., Cilliers, C. D., and Schmiedel, U. (2009) Mild experimental climate warming induces metabolic impairment and massive mortalities in southern African quartz field succulents. *Environmental and Experimental Botany*. **66**: 79-87

Mysterud, A., Langvatn, R., Yoccoz, N. G., and Stenseth, N. C. (2001) Plant phenology, migration, and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology*. **6**: 915-923

N

Nadeau, C. P., and Urban, M. C. (2019) Eco-evolution on the edge during climate change. *Ecography*. **42**: 1280-1297

Nakamura R. (1976) Temperature and the vertical distribution of two tidepool fishes (*Oligocottus maculosus*, *O. snyderi*). *Copeia.* **1**:143–152

Natural England and RSPB (2014) Climate Change Adaptation Manual. Report

Nevo, E. (1995) Asian, African and European biota at ‘Evolution Canyon’ Israel: local tests of global biodiversity and genetic diversity patterns. *Proceedings of the Royal Society of Biological Sciences*. **262**: 149-155

Nevo, E., Travleev, A. P., Belova, N. A., Tsatskin, A., Pavlíček, T., Kulik, A. F., Tsevetkova, N. N., and Yemshanov, D. C. (1998). Edaphic interslope and valley bottom differences at “Evolution Canyon”, Lower Nahal Oren, Mount Carmel, Israel. *CATENA*, **33:** 241–254

Nevo, E. (2012) ‘Evolution Canyon,’ a potential microscale monitor of global warming across life. *Proceedings of the National Academy of Sciences.* **109**: 2960-2965

Newell, R. C. (1976) Adaptation to environment: essays on the physiology of marine animals. Butterworth & Co (Publishers) Ltd. London, UK; Wellington, NZ; Sydney, Australia; Toronto, Canada; Durban, South Africa; and Boston, USA.

Newsham, K. K., Greenslade, P. D., Kennedy, V. H., and McLeod, A. R. (1999) Elevated UV-B radiation incidents on *Quercus robur* leaf canopies enhance decomposition of resulting leaf litter in soil. *Global Change Biology*. **5**: 403-409

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan,E. J., Mathesius, U., Poct, P., Purugganan, M. D., Richards, C. L., Valladares, F., and van Kleunen, M. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*. **15**: 684-692

Ng, T. P. T., Lau, S. L. Y., Seuront, L., Davies, M. S., Stafford, R., Marshall, D. J., and Williams, G. A. (2017) Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails. *Journal of Experimental Marine Biology and Ecology*. **492**: 121-131

Nordström, S., and Rundgren, S. (1973) Associations of lumbricids in southern Sweden. *Pedobiologia.* **13**: 301-326

Nuñez, J. D., Iriarte, P. F., Ocampo, E. H., Madrid, E., and Cledón, M. (2018) Genetic and morpho-physiological differentiation in a limpet population across an intertidal gradient. *Helgoland Marine Research*. **72**: 16

O

Ochoa-Huesco, R., Delgado-Baquerizo, M., Tuan An King, P., Benham, M., Arca, V., and Power, S. A. (2019) Ecosystem type and resource quality are more important than global change drivers in regulating early stages of litter decomposition. *Soil biology and Biochemistry*. **129**: 144-152

O'Gower, A. K., and Meyer, G. R. (1965) The ecology of six species of littoral gastropod molluscs. II. Seasonal variations in the six populations. *Marine and Freshwater Research*. **16**: 205-218

Okitsu, S. (2005) Factors controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs*. **30**: 135-151

Oksala, N. K. J., Ekmekçi, F. G., Özsoy, E., Kirankaya, Ş., Kokkola, T., Emecen, G., Lappalainen, J., Kaarniranta, K., and Atalay, M. (2014) Natural thermal adaptation increases heat shock protein levels and decreases oxidative stress. *Redox Biology*. **5**: 25-28

Oliver, P. G., and Meechan, C. J. (1993) *Synopses of the British Fauna. No 49 – Woodlice*. Field Studies Council, Shrewsbury, UK.

Oróstica Vega, M. H. (2018) Living at the edge: Ecology of *Patella* species in Britain. PhD thesis, Bangor University, Bangor, UK.

Oosenbrug, S. M., and Theberge, J. B. (1980) Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane Ranges, Yukon Territory. *Arctic*. **33**: 59-72

Orton, J. H., and Southward, A. J. (1961) Studies on the biology of limpets. IV. The breeding *of Patella depressa* Pennant on the north Cornish coast. *Journal of the Marine Biological Association of the United Kingdom.* **41**:653-662

Orton, J. H., Southward, A. J., and Dodd, J. M. (1956) Studies on the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *Journal of the Marine Biological Association of the United Kingdom.* ***35**: 149-176*

P

Parmesan, C. (1996) Climate and species' range. *Nature*. **382**: 765-766

Parmesan, C., and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. **421**: 37-42

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. **37**: 637-669

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global change Biology*. **13**: 1860–1872

Parmesan, C., Root, T. L., and Willig, M. R. (2000) Impacts of extrem weather and climate on terrestrial biota. *Bulletin of the American Meteorological* Society. **81**: 443-449

Parmesan, C., and Hanley, M. E. (2015) Plants and climate change: complexities and surprises. *Annals of Botany*. **116**: 849-864

Parton, W. J., Stewart, J. W. B., and Cole, C. V. (1988) Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry*. **5**: 109-131

Pavia, H., Cervin, G., Lindgren, A., and Åberg, P. (1997) Effects of U-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophyllum nodosum*. *Marine Ecological Progress Series*. **157**: 139-146.

Pessarrodona, A., Foggo, A., and Smale, D. A. (2018) Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. *Journal of Ecology*. **107**: 91-104

Phillips, C. L., and Nickerson, N. (2015) 'Soil Respiration'. In *Reference Module in Earth Systems and Environmental Sciences*

Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadee, G. C., and Dekker, R. (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography.* **48**:2171–2185

Picken, G. B. (1980) The distribution, growth and reproduction of the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *Journal of Experimental Marine Biology and Ecology*. **42**: 71-85

Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Johns Hopkins University Press. Baltimore, MD, USA

Plymouth Coastal Observatory (2019a). Annual Met Report 2018 – Perranporth

Plymouth Coastal Observatory (2019b). Annual Met Report 2018 – Looe

Pollard, E., Hooper, M. D., and Moore, N. W. (1974) *Hedges*, W. Collins and Sons, London, UK

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., and Richardson, A. J. (2013) Global imprint of climate change on marine life. *Nature Climate Change*. **3**: 212-225

Poloczanska, E. S, Burrows, M. T., Brown, C. J., Molinos, J G., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman, D. S., and Sydeman, W. J. (2016) Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*. **3**:62

Potter, K., A., Woods, H. A., and Pincebourde, S. (2013) Microclimatic challenges in global change biology. *Global Change Biology*. **19**: 2932-2939

Pörtner, H. O. (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A*. **132**: 739-761

Pörtner, H. O., and Farrell, A. P. (2008) Physiology and climate change. *Science.* **322**: 690– 692

Pörtner, H. O., and Peck, M. A. (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*. **77**: 1745-1779

Proesmans, W., Bonte, D. Smagghe, G., Meeus, I., and Verheyen, K. (2018) Importance of forest fragments as pollinator habitat varies with season and guild. *Basic and Applied Ecology*. **34**: 95-107

Prusina, I., Sarà, G., De Pirro, R., Dong, Y-W., Han, G-D., Glamuzina, B., and Williams G. A. (2014) Variations in physiological responses to thermal stress in congeneric limpets in the Mediterranean Sea. *Journal of Experimental Marine Biology and Ecology*. **456**: 34-40

Przeslawski, R., Davis, A. R., and Benkendorff, K. (2004) Effect of ultraviolet Radiation and visible light on the development of encapsulated molluscan embryos. *Marine Ecology Progress Series*. **268**: 151-160

Pulgar, J., Waldisperg, M., Galbán-Malagón, C., Maturana, D., Pulgar, V. M., and Aldana, M. (2017) UV radiation impacts body weight, oxygen consumption,and shelter selection in the intertidal vertebrate *Girella laevifrons*. *Science of Total Environment*. **578**: 317-322

Purvis, A., Gittleman, J. L., Cowlishaw, G. and Mace, G. M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*. **267**: 1947-1952

R

Rech, J. A., Reeves, R. W., and Hendricks, D. M. (2001) The influence of slope aspect on soil weathering processes in the Springville volcanic field, Arizona. *Catena*. **43**: 49-62

Reusch, T. B. H., Ehlers, A., Hammerli, A., and Worm, B. (2005*).* Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences.* **102**: 2826-2831

Ribeiro, P. M. A. (2008) Dispersal and connectivity of Northeastern Atlantic Patellid limpets: A multidisciplinary approach. PhD Thesis. University of Southampton, UK

Ribeiro, P. M. A., Xavier, R., Santos, A. M., and Hawkins, S. J. (2009) Reproductive cycles of four species of Patella (Mollusca: Gastropoda) on the northern and central Portuguese coast. *Journal of the Marine Biological Association of the United Kingdom.* **89**:1215-1221

Ridgwell, A., and Valdes, P. J. (2009) Climate and climate change. *Current Biology*. **19**: R563

Robinet, C., and Roques, A. (2010) Direct impacts of recent climate warming on insect populations. *Integrative Zoology*. **5**: 132-142

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*. **421**: 57-60

Rorison, I. H., Sutton, F., and Hunt, R. (1986) Local climate, topography, and plant growth in Lathkill Dale NNR. I. A twelve-year summary of solar radiation and temperature. *Plant, Cell and Environment*. **9**: 49-56

Roznik, E., and Afford, R. (2012) Does waterproofing Thermochron iButton data loggers influence temperature readings? *Journal of Thermal Biology* **37**: 260-264

Russell, B. D., Harley, C. D. G., Wernberg, T., Mieszkowska, N., Widdicombe, S., Hall-Spencer, J. N., and Connell, S. D. (2012) Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biology Letters*. **8**: 164-166

S

Sala, O. E., Chapin, F. S. III, Armesto, J. J., Berlow, E. Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000) Global biodiversity scenarios for the year 2100. *Science*. **287**: 1770-1774

Sanders, B. M., Hope, C., Pascoe, V. M., and Martin, L. S. (1991) Characterization of the stress protein response in two species of *Collisella* limpets with different temperature tolerances. *Physiological Zoology*. **64**: 1471-1489

Sang, W. (2009) Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research*. **24**: 303-314

Santini, G., Williamns, G. A., and Chelazzi, G. (2000) Assessment of factors affecting heart rate of the limpet Patella vulgata on the natural shore. *Marine Biology*. **137**: 291-296

Santini, G., Bruschini, C., Pazzagli, L., Pieraccini, G., Moneti, G., and Chelazzi, G. (2001) Metabolic response of limpet *Patella caerulea* (L.) to anoxia and dehydration. *Comparative Biochemistry and Physiology. Part A: Physiology*. **130**: 1-8

Sariyildiz, T. Anderson, J. M., Kucuk, M. (2005) Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biology & Biochemistry*. **37**: 1695-1706

Sariyildiz, T. (2008) Effects of tree canopy on litter decomposition rates of *Abies nordmanniana*, *Picea orientalis* and *Pinus sylvestris*. *Scandinavian Journal of Forest Research*. **23**: 330-338

Sariyildiz, T., and Küçük, M. (2008) Litter mass loss rates in deciduous and coniferous trees in Artvin, northeast Turkey: Relationships with litter Quality, microclimate, and soil characteristics. *Turkish Journal of Agriculture and Forestry*. **32**: 547-559

Sarlöv Herlin, I. and Fry, G. L. A. (2000) Dispersal of woody plants in forest edges and hedgerows in a southern Swedish agricultural area: the role of site and landscape structure. *Landscape Ecology*. **15**: 229-242

Schagerl, M. (2011) Drought stress, rain and recovery of the intertidal seaweed *Fucus spiralis*. *Marine Biology*. **158**: 2471-2479

Scheffers, N. R.. De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Richard, T. C., Butchart, H. M., Pearce-Kelly, P., Kovac, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., and Watson, J. E. M. (2016) The broad footprint of climate change from genes to biomes to people. *Science*. **354**: aaf7671

Scherer-Lorenzen, M., Luis Bonilla, J., and Potvin, C. (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos*. **116**: 2108-2124

Scherer-Lorenzen, M. (2008) Functional diversity affects decomposition processes in experimental grasslands. Functional Ecology. **22**: 547-555

Scherrer, D. and Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*. **38**: 406-416

Schiel, D. R., Steinbeck, J. R., and Foster, M. S. (2004) Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*. **85**: 1833-1839

Schindlbacher, A., Rodler, A., Kuffner, M., Kitsler, B., Sessitsch, A., and Zechmeister-Boltenstern, S. (2011) Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biology and Biochemistry.* **43**: 1417-1425

Shlesinger, T., and Loya, Y. (2019) Breakdown in spawning synchrony: A silent threat to coral persistence. *Science*. **365**: 1002-1007

Schoener, T. W. (1974) Resource partitioning in ecological communities. *Science.* **185**:27–39

Schroder, G. D., and Rosenzweig, M. L. (1975) Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia*. **19**: 9-28

Schwenk, K., Padrilla, D. K., Bakken, G. S., and Full, R. J. (2009) Grand challenges in organismal biology. *Integrative and Comparative Biology*. **49**: 7-14

Seabra, R., Wethey, D. S., Santos, A. M., and Lima, F. P. (2011) Side matters: microhabitat influence on intertidal heat stress over a large geographical scale. *Journal of Experimental Marine Biology and Ecology*. **400**: 200-208

Seabra, R., Wethey, D. S., Santos, A. M., and Lima, F. P. (2015) Understanding complex biogeographic responses to climate change. *Nature*. **5**: 12930

Seidelmann, K. N., Scherer-Lorenzen, M., and Niklaus, P. A. (2016) Direct vs. microclimate-driven effects of tree species diversity on litter decomposition in young subtropical forest stands. *PLoS ONE*. **11**: e0160569

Sévellec, F., and Drijhout, S. S. (2018) A novel probabilistic forecast system predicting anomalously warm 2018-2022 reinforcing the long-term global warming trend. *Nature Communication*. **9**: 3024

Sewerniak, P., and Jankowski, M. (2017) Topographically-controlled site conditions drive vegetation pattern on inland dunes in Poland. *Acta Oecologica*. **82**: 52–60.

Sidari, M., Ronzello, G., Vecchio, G., and Muscolo, A. (2008) Influence of slope asects on soil chemical and biochemical properties in a *Pinus laricio* forest ecosystem of Aspromonte (Southern Italy). *European Journal of Soil Biology*. **44**: 364-372

Siegle, M. R., Taylor, E. B., and O'Connor, M. I. (2018) Prior heat accumulation reduces survival during subsequent experimental heat waves. *Journal of Experimental Biology and Ecology.* **501**: 109-117

Sinclair, E. L. E., Thompson, M. B., and Seebacher, F. (2006) Phenotypic flexibility in the metabolism response of the limpet *Cellana tramoserica* to thermally different microhabitat. *Journal of Experimental Marine Biology and* Ecology. **335**: 131-141

Singaravelan, N., PavlÍček, T., Beharav, A., Wakamatsu, K., Ito, S., and Nevo, E. (2010) Spiny mice modulate Eumelanin to Pheomelanin ratio to achieve cryptic coloration in 'Evolution Canyon', Israel. *PLoS ONE*. **5**: e8708

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Duarte Rocha, C. F., Ibargüengoytía, N., Puntriano, C. A., Massot, M., Lepetz, V., Oksanen, T. A., Chapple, D. G., Bauer, A. M., Branch, W. R., Clobert, J., and Site Jr., J. W. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science.* **328**: 894-899

Sklenář, P. and Lægaard, S. (2018) Rain-shadow in the high Andes of Ecuador evidenced by páramo vegetation. *Arctic, Antarctic, and Alpine Research*. **35**: 8-17

Slavich, E., Warton, D. I., Ashcroft, M. B., Gollan, J. R., and Ramp, D. (2014) Topoclimate versus macroclimate: how does climate mapping methodology affect species distribution models and climate change projections? *Diversity and Distribution*s. **20**: 952-963

Smale, D. A., and Wernberg, T. (2013) Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B: Biological Sciences*. **280**: 20122829

Sokolova, I. M., and Pörtner, H. O. (2001) Physiological adaptations to high intertidal life involve improved water conservation abilities and metabolic rate depression in *Littorina saxalitis*. *Marine Ecology Progress* Series. **224**: 171-186

Somero, G. N. (2005) Linking biogeography to physiology: Evolutionary and acclimatory adjustments of thermal limits. *Frontiers in Zoology*. **2**: 1-9

Somero, G. N. (2010) The physiology of climate change: how potential for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*. **213**: 912-920

Sorte, C. J. S., and Hofmann, G. E. (2004) Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca: Gastropoda) is more stresses at its range edge. *Marine Ecology Progress Series*. **274**: 263-268

Sorte, C. J. B., and Hofmann G. E. (2005) Thermotolerance and heat-shock protein expression in Northeastern Pacific *Nucella* species with different biogeographical ranges. *Marine Biology*. **146**: 985-993

Sorte, C. J. B., Williams, S. L., and Carlton, J. T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*. **19**: 303-316

Sourour, A., Afef, O., Mounir, R., and Mongi, B. Y. (2017) A review: Morphological, physiological, biochemical, and molecular plant responses to water deficit stress. *The International Journal of Engineering and Science*. **6**: 1-4

Sousa, L. L., Seabra, R., Wethey, D. S., Xavier, R., Queiroz, N., Zenboudji, S., and Lima, F. P. (2012) Fate of a climate-driven colonisation: Demography of newly established populations of the limpets *Patella rustica* Linnaeus, 1758, in northern Portugal. *Journal of Experimental Marine Biology and Ecology*. **438**: 68-75

Southward, A. J., and Crisp, D. J. (1954). Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* (Poli) and *Balanus balanoides* L. in the British Isles. *Journal of Animal Ecology*. **23**: 163-77

Southward, A. J., and Orton, J. H. (1954) The effects of wave-action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. *Journal of Marine Biological Association of the United Kingdom*. **33**: 1-19

Southward, A. J. (1958) Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. *Journal of the Marine Biological Association of the United Kingdom*. **37**: 49-66

Southward, A. J. (1967) Recent changes in abundance of intertidal barnacles in south-west England: a possible effect of climatic deterioration*. Journal of the Marine Biological Association of the United Kingdom*. **47**: 1-29

Southward, A. J., Hawkins, S. J., Burrows, M. T. (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*. **20**: 127-155

Spehn, E. M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Dannell, K., Jumpponen, A., Koricheva, J., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Palmborg, C., Periera, J. S., Pfisterer, A. B., Prinz, A., Read, D. J., Schulze, E.-D., Siamantziouras, A.-S. D., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (2005) Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monograph*. **75**: 37-63

Staley, J. T., Bullock, J M., Baldock, K. C. R., redhead, J. W., Hooftman, D. A. P., Button, N., and Pywell, R. F. (2013) Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management. *Biological Conservation*. **167**: 97-105

Steele, J. H. (1985) A comparison of terrestrial and marine systems. *Nature*. **313:** 355-358

Steele, J. H. (1991) Can ecological theory cross the land-sea boundary. *Journal of Theoretical Biology*. **153**: 425-436

Steele, J. H., Brink, K. H., and Scott, B. (2019) Comparison of marine and terrestrial ecosystems: suggestions of an evolutionary perspective influenced by environmental variation. *ICES Journal of Marine Sciences*. **76**: 50-59

Steiner, S. C. C., Macfarlane, K. J., Price, L. M., and Willette, D. A. (2010) the distribution of seagrasses in Dominica, Lesser Antilles. *Revista de Biologica Tropical*. **58**: 89-98

Stephens, P. M., Davoren, C. W., Doube, B. M., and Ryder, M. H. (1994a) Ability of the lumbricid earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* to reduce the severity of take-all under greenhouse and field conditions. *Soil Biology and Biochemistry*. **26**: 1291-1297

Stephens, P. M., Davoren, C. W., Doube, B. M., and Ryder, M. H. (1994b) Ability of the earthworms *Aporrectodea rosea* and *Aporrectodea trapezoides* to increase plant growth and foliar concentration of elements in wheat (*Triticum aestivum* cv. Spear) in a sandy loam soil. *Biology and Fertility of Soils.* **18**: 150-154

Stephens, P. M., and Davoren, C. W. (1997) Influence of the earthworms *Aporrectodea trapezoides* and *A. rosea* on the disease severity of *Rhizoctonia solani* on subterranean clover and ryegrass. *Soil Biology and Biochemistry*. **29**: 511-516

Stewart, J. R., Lister, A. M., Barnes, I., and Dalén, L. (2010) Refugia revisited: individualistic responses of species in space andtime.*Proceedings of the Royal Society B: Biological Sciences*.**277**: 661–671

Stewart, R. I. A., Dossena, M., Bohan, D. A., Jeppesen, E., Kordas, R. L., Ledger, M. E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J. B., Suttle, B., Thompson, R., Trimmer, M., and Woodward, G. (2013) Mesocosm experiments as a tool for ecological climate-change research. *Advances in Ecological Research*. **48**: 71-181

Stillman, J. H., and Somero, G. N. (1996) Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): correlation of physiology, biochemistry and morphology with vertical distribution. *Journal of Experimental Biology*. **199**: 1845-1855

Stillman, J. H. (2000) Evolutionary history and adaptive significance of respiratory structures on the legs of intertidal Porcelain Crabs, genus *Petrolisthes*. *Physiological and Biochemical Zoology.* **73**: 86-96

Stillman,J. H., and Somero, G. N. (2000) A comparative analysis of the upper thermal tolerance limits of Eastern Pacific porcelain crabs, genus Petrolisthes: Influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiological and Biochemical Zoology*. **73**: 200-208

Storlie, C., Merino-Viteri, A., Phillips, B., VanDerWal, J., Welbergen, J., and Williams, S. (2014) Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biology Letters*. **10**: 20140576

Stoutjesdijk, P. and Barkman, J. J. (2014) 'Microclimate, vegetation & fauna' (KNNV Publishing, Netherlands)

Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B., and Thomas, C. D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos.* **120**: 1–8

Suggitt, A. J., Hodgson, J., Maclean, I., Macgregor, N., Bennie, J., and Hopkins, J. (2014) Microclimate, climate change and wildlife conservation. *British Wildlife*. **25**:162:168

Sunday, J. M, Bates, A. E., and Dulvy, N. K. (2012) Thermal tolerance and global redistribution of animals. *Nature Climate Change*. **2**:686-690

Sutton, S. L. (1972) *Woodlice*. Ginn & Company Limited, London, UK.

Suykerbuyk, W., Govers, L. L., van Oven, W. G., Giesen, K., Giesen, W. B. J. T., de Jong, D. K., Bouma, T. J., and van Katwijk, M. M. (2018) Living in the intertidal: desiccation and shading reduce seagrass growth, but high salinity or population of origin have no additional effect. *PeerJ*. **6**: e5234

Swift, M. J, Heal, 0. W., and Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley, CA, USA

T

Tagliarolo, M., Grall, J., Chavaud, L., and Clavier, J. (2013) Aerial and underwater metabolism of *Patella vulgata* L.: comparison of three intertidal levels. *Hydrobiologia*. **702**: 241-253

Tagliarolo, M., and McQuaid, C. D. (2016) Field measurements indicate unexpected, serious underestimation of mussel heart rates and thermal tolerance by laboratory studies. *PLoS ONE*. **11**: e0146341

Tillin, H.M. 2016. [*Osmundea pinnatifida*] on moderately exposed mid eulittoral rock. In Tyler-Walters H. and Hiscock K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. Accessed on the 12th of July 2019. [https://www.marlin.ac.uk/habitats/detail/84/osmundea_pinnatifida_on_moderately_exposed_mid_eulittoral_rock]

Thakur, M. P., Reich, P. B., Hobbie, S. E., Stefanski, A., Rich, R., Rice, K. E., Eddy, W. C., and Eisenhauer, N. (2018) Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change*. **8**: 75–78

Thomson, A. J., and Davies, D. M. (1974) Mapping methods for studying soil factors and earthworm distribution. *Oikos*. **25**: 199-203.

Thomas, C. D., Bodsworth, E. J.,Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M., and Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*. **411**: 577-581

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaument, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., and Williams, S. E. (2004) Extinction risk from climate change. *Nature*. **6970**: 145-148

Thomas, C. D. (2010) Climate, climate change and range boundaries. *Diversity and Distribution*. **16**: 488-495

Thompson, R. C., Roberts, M. F., Norton, T. A., and Hawkins, S. J. (2000) Feast or famine for intertidal grazing molluscs: a mis-match between seasonal variations in grazing intensity and the abundance of microbial resources. *Hydrobiologia*. **440**: 357-367.

Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G. F., Paterson, J., Schurr, F. M., Sykes, M. T., and Zimmermann, N. E. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*. **9**:137-152

Tomaneck, L., and Helmuth, B. (2002) Physiological ecology of rocky intertidal organisms: a synergy of concept. *Integrated and Comparative Biology*. **42**: 771-775

Tsuchiya, M. (1983) Mass mortality in a population of the mussel *Mytilus edulis* L. Caused by high temperature on rocky shores. *Journal of Experimental Marine Biology and Ecology*. **66**: 101-111

Tuomisto H., and Poulsen A. D. (1996). Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. *Journal of Biogeography* **23**:283–293

U

Underwood, A. J., and Jernako, V. P. (1981) Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia.* **48**:221–233

Underwood, A. J., and Jernakoff, P. (1984) The effect of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology*. **75**: 71-96

Runion, G. B., Curl, E. A., Rogers, H. H., Backman, P. A., Rodríguez-Kábana, R., and Helms, B. E. (1994) Effects of free-air CO_2 enrichment on microbial populations in the rhizosphere and phyllosphere of cotton. *Agricultural and Forest Meteorology*.**70**: 117-130

Urban, M. C. (2015) Accelerating extinction risk from climate change. *Science*. **348**: 6234

V

Valiñas, M., Helbling, E. W. (2016) Metabolic and behavioural responses of the reef fish *Patagonotothen cornucola* to ultraviolet radiation: Influence of the diet. *Journal of Experimental Marine Biology and Ecology*. **474**: 180-184

van Asch, M., Salis, L., Holleman, L. J. M., van Lith, B., and Visser, M. E. (2012) Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change*. **3**: 244-248

van der Maarel, E. (2005) *Vegetation Ecology*. Blackwell Publishing Company. Malden, MA, USA; Oxford, UK; and Victoria, Australia

Vermeij, G. J. (1971) Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology*. **10**: 308-314

Vermeij, G. J. (1973) Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology*. **20**: 319–346

Vitasse, Y., Delzon, S., Dufrêne, E., Pontailler, J.-Y., Louvet, J.-M., Kremer, A., and Michalet, R. (2009) Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology*. **149**: 737-744

Vogiatzakis, I. N., Griffiths, G. H., and Mannion, A. M. (2003) Environmental factors and vegetation composition, Lefka Ori massif, Crete, S. Aegean. *Global Ecology & Biogeography.* **12**. 121–46.

W

Walder, T., and Erschbamer, B. (2015) Temperature and drought drive differences in germination responses between congeneric species along altitudinal gradients. *Plant Ecology*. **216**: 1297-1309

Wall, D. H., Bradford, M.A, John, M. G. S., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J., Voigt, W., Wolters, V., Gardel, H. Z., Ayuke, F. O., Baskford, R., Beljakova, O. I., Bohlen, P. J., Brauman, A., Flemming, S., Henschel, J. R., Johnson, D. L., Jones, T. H., Kovarova, M., Kranabetter, J. M., Kutny, L., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabará, M. G., Salamon, J.-A., swift, M. J., Varela, A., Vasconcelos, H. L., White, D., and Zou, X. (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology.* **14**: 2661–2677.

Walter, J., Hein, R., Beierkuhnlein, C., Hammerl, V., Jentsch, A., Schädler, M., Schuerings, J., and Kreyling. J (2013) Combined effects of multifactor climate change and land-use on decomposition in temperate grassland. *Soil Biology and Biochemistry*. **60**: 10-18

Walther, G. R., Roques, A., Hulmes, P. E., Sykes, M. T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B.,Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V. E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, Vilà, M., Vohland, K., and Settele, J. (2009) Alien species in a warmer word: risks and opportunities. Trends in Ecology and Evolution. 24: 686-694

Wahindin, S., Idris, A., and Shaleh, S. R. M. (2013) The influence of light intensity and photoperiod on the growth and lipid content of microalgae *Nannochloropis sp*. *Bioresource Technology*. **129**:7-11

Wardle, D. A. and Van der Putten, W. H. (2002) Biodiversity and Ecosystem Functining (eds. M. Loreaui, S. Naeem, and P. Inchausti), Oxford University Press, Oxford

Watson, E. V. (1960) A quantitative study of the bryophytes of chalks grassland. *Journal of Ecology.* **48**: 397-414

Whalter, G-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., and Zobel, M. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*. **24**: 686-693

Webb, T. J. (2012) Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology and Evolution*. **27**: 535-541

Weiss, S. B., Murphy, D. D., and White, R. R. (1988) Slope, and butterflies: topographic determinants of habitat quality for *Euphydryas Editha*. *Ecology*. **69**: 1486-1496

Wernberg, T., and Connell, S. D. (2008) Physical disturbance and subtidal habitat structure on open rocky coasts: Effect of wave exposure, extent and intensity. *Journal of Sea Search*. **59**: 237-248

Wernberg, T., Thomsen, M. S., Tuya, F., Kendrick, G. A., Staehr, P. A., Toohey, B. D. (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implication for a warmer future. *Ecology Letters*. **13**: 685-694

Wernberg, T., Smale, D. A., and Thomsen, M. S. (2012) A decade of climate change experiments on marine organisms: procedures, patterns and problems. *Global Change Biology*. **18:** 1491-1498

Wethey, D. S. (1983) Geographic limits and local zonation: the barnacles *Semibalanus* (*balanus*) and *Chthamalus* in New England. *Biological Bulletin*.**165**: 330-341

Wethey, D. S. (2002) Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integrated and Comparative Biology*. **42**: 872-880

Wethey, D. S., and Woodin, S. A. (2008) Ecological hindcasting of biogeographic responses to climate change in intertidal zone. *Hydrobiologia*. **606**: 139-151

Wethey, D. S., Woodin, S. A., hilbish, T., J., Jones, S. J., Lima, F., P., and Brannock, P. M. (2011) Response of intertidal populations to climate: Effects of extreme events versus long-term change. *Journal of Experimental Marine Biology and Ecology*. **400**: 132-144

Williams, C. M., Buckley, L. B., Sheldon, K., S., Vickers, M., Pörtner, H.-O., Dowd, W. W., Gunderson, A. R., Marshall, K. E., and Stillman, J. H. (2016) Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. *Integrative and Comparative Biology*. **56**: 73-84

Williams, G. A., and Morritt, D. (1995) Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. Marine Ecology Process Series. 124: 89-103

Williams G. A., and McMahon B.R. (1998) *Haemolymph pH and oxygen levels in a naturally stressed tropical limpet,* Cellana grata. In: Morton BS (ed) The third international conference on the marine biology of the South China Sea, Hong Kong. Hong Kong University Press, Hong Kong, pp. 239–245

Williams, G. A., De Pirro, M., Leung, K. M. Y., and Morritt, D. (2005) Physiological responses to heat stress on a tropical shore: the benefits of mushrooming behaviour in the limpet *Cellana grata*. *Marine Ecology Progress Series*. **292**: 213-224

Williams, G. A., De Pirro, M., Cartwright, S., Khangura, K., Ng, W-C., Leung, P. T. Y., and Morritt, D. (2010) Come rain or shine: the combined effects of physical stresses on physiological and protein-level responses of an intertidal limpet in the monsoonal tropics. *Functional Ecology*. **25**: 101-110

Willians, G. A., De Pirro, M., Cartwright, S., Khangura, K., Ng, W.-C., Leung, P. T. Y., and Morritt, D (2011) Come rain or shine: the combined effects of physical stresses on physiological and protein-level responses of an intertidal limpets in the monsoonal tropics. *Functional Ecology*. 25: 101-110

Williams, G. A., Helmuth, B., Russel, B. D., Dong, Y.-W., Thiyagarajan, V., and Seuront, L. (2016) Meeting the climate change challenge: Pressing issues in southern China and SE Asian coastal ecosystems. *Regional Studies in Marine Sciences*. **8**: 373-381

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. and Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*. **6**: 2621-2626

Willis, K. J., and Bhagwat, S. A. (2009) Biodiversity and climate change. *Science*. **326**: 806-807

Wilson, R. J., Thomas, C. D., Fox, R. J., Roy, D. B. and Kunin, W. E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*. **432**: 393–396

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Monserrat, V. (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*. **13**: 1873-1887

Wilson, R. (1979) *The hedgerow book*. David & Charles (Publishers) Limited, Newton Abbot, UK

Woodward, F. I. (1987) Climate and Plant Distribution. Cambridge University Press, Cambridge

Y

Yamano, H., Sugihara, K., and Nomura, K. (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters*. **38**, L04601

Yang, X., and Chen, J. (2009) Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. *Soil biology and Biochemistry*. **5**: 910-918

Yimer, F., Ledin, S., and Abdelkadir, A. (2006) Soil organic carbon and total nitrogen stocks as affected by topographic aspect and vegetation in the Bale Mountains, Ethiopia. *Geoderma*. **135**: 335-344

Yin, R., Eisenhauer, N., Auge, H., Purahong, W., Schmidt, A., and Schädler, M. (2019a) Additive effects of experimental climate change and land use on faunal contribution to litter decomposition. *Soil Biology and Biochemistry*. **131**: 141-148

Yin, R., Eisenhauer, N., Schmidt, A., Gruss, I., Purahong, W., Siebert, J., and Schädler, M. (2019b) Climate change does not alter land-use effect on soil fauna communities. *Applied Soil Ecology*. **140**: 1-10

Yom-Tom, Y. (1972) Field experiments on the effects of population density and slope direction on the reproduction of the desert snail *Trochoidea (Xerocrassa) seetzeni*. *Journal of Animal Ecology*. **41**: 17-22

APPENDICES

Appendix 1

Summary data from the spring-summer intertidal species distribution survey (except for the different barnacles species which come from the winter survey), among four sites (Bude, Bantham, Croyde, and South Milton Sands (SMS)) according to the aspect of the gullies (north- and south-facing). The data is in percentage cover for the lichens, algae, the sponge, the worm *Sabellaria alveolata*, the barnacles, and the mussel *Mytilus edulis*. All the other organisms are represented in density per square meter. Any zero followed by (*) denote rounding where values fall below 0.1. The geographic origin (Geo origin) of the species is categorized by S (for southern species), N (for northern species), U (for ubiquitous species), and N/A (for the non-identified species, or group of organisms which could have different geograhic origins, such as the barnacles). The geographic data of the intertidal organisms comes from Firth et al, 2016; Marlin.ac.uk; Mieszkowska et al., 2005.

	Geo	Bantham		Bude		Croyde		South Milton Sands		**Total**	
Species	origin	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Lichen											
Lichina pygmaea	S	0.1 ±0.1	8.2 ±2	0	0* ±0*	0.6 ±0.5	0.9 ±0.4	0* ±0*	9.9 ±3.9	**0.2 ±0.2**	**4.7 ±1.6**
Orange-greenish lichen	N/A	0.3 ±0.1	0	0	0	0	0	0	0	**0* ±0***	**0**
Orange-yellowish lichen	N/A	0* ±0*	0	0	0	0	0	0	0	**0* ±0***	**0**
Verrucaria maura	U	0	0	0	0	0.5 ±0.5	0.8 ±0.5	0	0	**0.1 ±0.1**	**0.2 ±0.1**
Verrucaria mucosa	U	2.5 ±0.7	0.3 ±0.2	0.2 ±0.1	0.1 ±0.1	9.9 ± 2	7.1 ±1.3	4.2 ±1.1	0.2 ±0.1	**4.2 ±1**	**1.9 ±0.4**
Algae											
Blidingia minima	U	0	0* ±0*	0	0	0	0	0	0	**0**	**0* ±0***
Brown flat alveaolate-like	N/A	0.3 ±0.3	0	0	0	0	0	0.1±0.1	0	**0.1 ±0***	**0**
Brown/greenish tiny alveolate-like	N/A	0.5 ±0.4	0	0	0	0	0	0	0	**0.1 ±0***	**0**
Cladophora sp.	U	1.3 ±0.6	0.3 ±0.3	3.1 ±2.2	0	0.1 ±0*	0	0.1 ±0*	0	**1.1 ±0.7**	**0.1 ±0***

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Corallina sp.	U	0	0	0	0	0* ±0*	0* ±0*	0* ±0*	0	**0* ±0***	**0* ±0***
Fucus sp.	N	0.4 ±0.2	0.9 ±0.2	0.9 ±0.2	4.8 ±1	0.6 ±0.1	0.5 ±0.1	0.2 ±0.1	0.4 ±0.1	**0.5 ±0.4**	**1.6 ±1**
Green tiny mossy	N/A	0* ±0*	0	0	0	0	0	0.4 ±0.4	0	**0.1 ±0.1**	**0**
Green tuffed	N/A	0	0	0	0	0	0	0* ±0*	0	**0* ±0***	**0**
Leathesia difformis	U	0	0	0	0	0	0	0* ±0*	0	**0* ±0***	**0**
Lithopyllum incrustans	U	7 ± 1.7	1.3 ±0.7	2.5 ±1.5	0.5 ±0.2	1.1 ±0.4	0.2 ±0.1	2.4 ±0.9	0.1 ±0.1	**3.2 ±1.1**	**0.5 ±0.3**
Lomentaria articulata	U	0.5 ±0.3	0* ±0*	0	0	0* ±0*	0	0	0	**0.1 ±0***	**0* ±0***
Mastocarpus stellatus	N	0.2 ±0.2	0* ±0*	0.2 ±0.1	0* ±0*	0* ±0*	0	0* ±0*	0* ±0*	**0.1 ±0***	**0* ±0***
Membranoptera alata	U	0* ±0*	0	0	0	0	0	0	0	**0* ±0***	**0**
Osmundea hybrida?	U	0	0	0	0	0* ±0*	0	0* ±0*	0	**0* ±0***	**0**
Osmundea pinnatifida	U	3.3 ±0.7	0.5 ±0.4	1.6 ±0.7	0* ±0*	0.7 ±0.3	0	0.6 ±0.3	0* ±0*	**1.6 ±0.5**	**0.2 ±0.1**
Plumaria plumose	U	0.3 ±0.2	0	0.2 ±0.2	0	0* ±0*	0	0	0	**0.1 ±0.1**	**0**
Polysiphonia Atlantica	U	0.2 ±0.1	0* ±0*	0	0	0.1 ±0*	0	0	0	**0.1 ±0***	**0* ± 0***
Porphyra sp.	U	0* ±0*	0	0.1 ±0*	0	0	0	0	0	**0* ±0***	**0**
Porphyra umbilicalis	U	0* ±0*	0	0.2 ±0.1	0	0	0	0	0	**0* ±0***	**0**
Ralfsia verrucosa	U	0.1 ±0*	0	0	0	0	0	0* ±0*	0	**0* ±0***	**0**
Red tiny mossy	N/A	0	0	0	0	0	0	0.1 ±0*	0	**0* ±0***	**0**
Rhodothamniella floridula	U	0.4 ±0.2	0.6 ±0.6	0* ±0*	0	0.2 ±0.1	0	0	0	**0.2 ±0.1**	**0.2 ±0.1**
Ulva sp.	U	0.2 ±0.1	0.1 ±0*	1.9 ±0.6	0	0.1 ±0*	0.1 ±0.1	0	0	**0.6 ±0.5**	**0* ±0***

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Sponges											
Halichondria panacea	U	0*	0* ±0*	0* ±0*	0.1 ±0.1	0.1 ±0.1	0* ±0*	0	0	**0* ±0***	**0* ±0***
Worms											
Eulalia viridis	U	0	0	0.7 ±0.5	0	0	0	0	0	**0.2 ±0.1**	**0**
Lineus ruber	U	0	0	1.2 ±0.8	0	0	0	0	0	**0.3 ±0.2**	**0**
Sabellaria alveolata	S	0	0	23.8 ±7.8	0.2 ±0.1	0.2 ±0.1	0* ±0*	0	0	**6 ±2**	**0* ±0***
Anemone											
Actinia equina	U	0.2 ±0.2	0	6.4 ±2.3	9 ±2.2	1.9 ±0.7	2.2 ±1.2	0.2 ±1.2	0	**2.2 ±1.5**	**2.8 ±0.7**
Molluscs											
Acanthochitona fascicularis	U	0	0	0.3 ±0.2	0	0	0	0	0	**0* ±0***	**0**
Littorina littorea	N	0.3 ±0.3	0.2 ±0.2	0.5 ±0.2	0	0.3 ±0.3	0	0	0	**0.3 ±0.3**	**0* ±0***
Littorina saxatilis	N	5.7 ±2.8	4.3 ±2.5	0	0.2 ±0.2	2.8 ±1.7	6.2 ±2.4	18 ±1.3	0	**2.9 ±1.7**	**2.7 ±1.6**
Melarhaphe neritoides	S	0	0.9 ±0.7	0	0	0	0	0	0	**0**	**0.2 ±0.2**
Mytilus edulis	U	0	0	7.1 ±4.1	1 ±0.3	0.2 ±0*	1.6 ±0.6	0.2 ±0.2	0	**1.9 ±1.2**	**0.7 ±0.2**
Nucella lapillus	U	2.5 ±1.3	0.5 ±0.4	7.3 ±2.7	6.2 ±4	2.9 ±1.2	0.7 ±0.5	0.5 ±0.3	0	**3.1 ±1.4**	**1.8 ±1.2**
Nucella lapillus eggs	N/A	0	0	38.7 ±17	2.7 ±2.7	0	0	0	0	**9.7 ±4.2**	**0.7 ±0.6**
Onchidella celtica	S	0	0	67.5 ±24	0.8 ±0.8	0.7 ±0.7	0	0	0	**17 ±6.2**	**0.2 ±0.2**
Patella depressa	S	88.7 ±16	81.5 ±9.7	117 ±12.3	59.3 ±10.6	79 ±6.5	45.9 ±5.2	166.7 ±20.5	139 ±36.7	**112.8 ±13.8**	**81.4 ±15.5**
Patella vulgata	N	114.7 ±14.5	49.2 ±6.3	129.2 ±8.7	40.8 ±1.3	91 ±6.4	28.5 ±1	196.8 ±22.5	75.5 ±13.5	**132.9 ±13**	**48.5 ±5.6**

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Patella sp.	N/A	10.5 ±4.5	5.2 ±3.7	33.7 ±6	26.5 ±2.8	17.3 ±4	9.7 ±2.1	25.1 ±8.1	14.5 ±4.1	**21.7 ±5.7**	**14 ±3.2**
Phorcus lineatus	S	2.3 ±1	1.7 ±1	0.2 ±0.2	0	1.7 ±0.9	1.1 ±0.7	1.2 ±1.4	2.7 ±0.8	**1.3 ±0.7**	**1.4 ±0.6**
Steromphala umbilicalis	S	13.5±2.2	0.3 ±0.3	0	0.2 ±0.2	3 ±1.6	1.7 ±1.0	9 ±0.7	0.3 ±0.4	**4.5 ±1.1**	**0.6 ±0.5**
Crustaceans											
juvenile crab	U	0	0	0.2 ±0.2	0	0	0	0	0	**0* ±0***	**0**
All barnacles	N/A	15.6 ±3.8	24.4 ±4.4	35.2 ±6.8	78.8 ±7.4	71.3 ±4.4	66.9 ±4.9	17.5 ±4.9	32.2 ±6.8	**34.9 ±5**	**50.5 ±5.9**

Appendix 2

Summary data of the autumn-winter intertidal species distribution survey, among four sites (Bude, Bantham, Croyde, and South Milton Sands (SMS)) according to the aspect of the gullies (north- and south-facing). The data is in percentage cover per square meter for the lichens, algae, the sponge, the worm *Sabellaria alveolata*, 'all barnacles', and the mussel *Mytilus edulis*. The detailed barnacle species (†) are counts per 9 cm^2 using 3x3 cm quadrat as explained in the Methodology section. All the other organisms are represented in density per square meter. Any zero followed by (*) denote rounding where values fall below 0.1.. The geographic origin (Geo origin) of the species is categorized by S (for southern species), N (for northern species), U (for ubiquitous species), and N/A (for the non-identified species, or group of organisms which could have different geograhic origins, such as the barnacles). The geographic data of the intertidal organisms comes from Firth et al, 2016; Marlin.ac.uk; Mieszkowska et al., 2005.

Species	Geo ori-gin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Lichen											
Lichina pygmaea	S	0.5 ± 0*	7.3 ± 1.5	0	0* ± 0*	1.0 ± 0.9	1.7 ± 1.2	0	14.6 ± 4.6	**0.3 ±0.3**	**5.9 ±1.5**
Orange-greenish lichen	N/A	0	0	0	0	0	0	0	0	**0**	**0**
Orange-yellowish lichen	N/A	0	0	0	0	0	0	0	0.1 ±0.1	**0**	**0.1 ±0.1**
Verrucaria maura	U	0	0	0	0	0	0	0	0	**0**	**0**
Verrucaria mucosa	U	1.0 ±0.3	0.2 ±0*	0* ±0*	0* ±0*	3.0 ± 1.4	0* ±0*	3.2 ± 0.7	0.5 ± 0.1	**1.8 ±0.4**	**0.2 ±0***
Algae											
Blidingia minima	U	0	0	0	0	0	0	0	0	**0**	**0**
Brown flat alveaolate-like	N/A	0.	0	0	0	0	0	0	0	**0**	**0**
Brown flat alveaolate-like	N/A	0.	0	0	0	0	0	0	0	**0**	**0**
Brown/greenish tiny alveolate-like	N/A	0	0	0	0	0	0	0	0	**0**	**0**
Cladophora sp.	U	0	0.	1.6 ±1.5	0	0	0	0	0	**0.4 ±0.3**	**0**

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Corallina sp.	U	0	0	0	0	0* ±0*	0	0	0	**0* ±0***	**0**
Fucus sp.	N	0.6 ±0.2	1.0 ±0.4	1.3 ±0.3	5.0 ±1.3	1.0 ±0.4	0.1 ±0.1	0* ±0*	0.7 ±0.2	**0.8 ±0.2**	**1.7 ±0.3**
Green tiny mossy	N/A	0	0	0	0	0	0	0	0	**0**	**0**
Green tuffed	N/A	0	0	0	0	0	0	0	0	**0**	**0**
Leathesia difformis	U	0	0	0	0	0	0	0* ±0*	0	**0* ±0***	**0**
Lithopyllum incrustans	U	11.3 ±4.0	2.3 ±1.4	3.4 ±1.5	0.4 ±2.3	2.8 ±0.8	0.4 ±0.3	2.9 ±1.2	0.3 ±0.2	**5.1 ±1.2**	**0.8 ±0.4**
Lomentaria articulate	U	0.6 ±0.6	0	0* ±0*	0	0	0	0	0	**0.1 ±0***	**0**
Mastocarpus stellatus	N	0	0	0* ±0*	0	0* ±0*	0	0* ±0*	0	**0.1 ±0***	**0* ±0***
Membranoptera alata	U	0* ±0*	0	0* ±0*	0	0* ±0*	0	0	0	**0* ±0***	**0**
Osmundea hybrida?	U	0	0	0	0	0* ±0*	0	0* ±0*	0	**0* ±0***	**0**
Osmundea pinnatifida	U	4.6 ±1.9	0.8 ±0.5	2.9 ±0.6	0* ±0*	2.8 ±0.8	0* ±0*	0.7 ±0.3	0* ±0*	**2.6 ±0.6**	**0.2 ±0.1**
Plumaria plumose	U	0.9 ±0.9	0	0.6 ±0.6	0	0* ±0*	0	0	0	**0.4 ±0.3**	**0**
Polysiphonia atlantica	U	0.8 ±0.5	0.6 ±0.5	2.2±0.9	0	0.1 ±0*	0	0	0	**0.7 ±0.2**	**0.1 ± 0.1**
Porphyra sp.	U	0	0	0	0	0	0	0	0	**0**	**0**
Porphyra umbilicalis	U	0	0	0	0	0	0	0	0	**0**	**0**
Ralfsia verrucosa	U	0.2 ±0.1	0.3 ±0.1	0*±0*	0	0	0	0	0	**0* ±0***	**0* ± 0***
Red tiny mossy	N/A	2.1 ±0.7	0*±0*	0*±0*	0	1.0 ±0.9	0*±0*	2.1±0.8	0*±0*	**1.3 ±0.3**	**0*±0***
Rhodothamniella floridula	U	0	0	0	0	0	0	0	0	**0**	**0**
Ulva sp.	U	0* ±0*	0* ±0*	1.8 ±	0	0.1 ±0*	0* ±0*	0	0	**0.4 ±0.1**	**0* ±0***
Sponges											
Halichondria panacea	U	0* ±0*	0	0* ±0*	0	0.3 ±0.1	0	0	0	**0* ±0***	**0**

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Worms											
Eulalia viridis	U	0	0	0	0	0	0	0	0	**0**	**0**
Lineus ruber	U	0	0	0	0	0	0	0	0	**0**	**0**
Sabellaria alveolata	S	0	0	36.1 ±7.0	0.3 ±0.2	0.2 ±0.2	0	0	0	**6 ±2**	**0* ±0***
Spirobranchus lamarcki	U	0	0	0* ±0*	0	0	0	0	0	**0* ±0***	**0**
Anemone											
Actinia equina	U	0.2 ±0.2	0	6.4 ±2.3	9 ±2.2	1.9 ±0.7	2.2 ±1.2	0.2±0.2	0	**2.17 ±0.6**	**2.8 ±0.7**
Molluscs											
Acanthochitona fascicularis	U	0	0	0.2 ±0.2	0	0	0	0	0	**0* ±0***	**0**
Littorina littorea	N	0	0	0	0	0	0.1 ±0.1	0	0	**0**	**0* ±0***
Littorina saxatilis	N	10.3 ±4.3	11.5 ±3.7	0	0.2 ±0.2	2.5 ±1.9	1.4 ±1.0	4.2 ±1.8	0.5 ±0.4	**4.2 ±1.4**	**3.4 ±1.1**
Mytilus edulis	U	0*±0*	0	13.0 ±4.5	2.3 ±0.5	0* ±0*	0.7 ±0.3	0* ±0*	0*±0*	**3.2 ±1.1**	**0.7 ±0.1**
Nucella lapillus	U	1.3 ±0.5	0	4.6 ±1.6	1.8 ±1.0	1.2 ±0.7	1.1 ±0.2	0.7 ±0.5	0	**1.9 ±0.5**	**0.5 ±0.2**
Patella depressa	S	92.5 ±9.6	61 ±6.1	44.6 ±6.1	37.4 ±4.6	95 ±7.2	31.8 ±4.9	168.6 ±13.3	99.5 ±11.8	**100.1 ±6.50**	**57.4 ±4.8**
Patella vulgata	N	44.8 ±14.5	24.6 ±8.7	19.8 ±6.4	100.9 ±22.5	47.55 ±4.6	32.6 ±6.3	31.7 ±1.3	13.3 ±1	**54.3 ±13.5**	**33.0 ±2.8**
Patella sp.	N/A	32.1 ±14.5	30 ±8.7	33.8 ±6.4	40.9 ±22.5	34.2 ±2.2	20.6 ±6.3	49.6 ±1.3	14.9 ±1	**23.6 ±13.5**	**27.2 ±2.2**
Phorcus lineatus	S	2.1 ±1.0	4 ±1.3	0.2 ±0.2	0	1.5 ±0.7	2.0 ±1.1	1.5 ±1.0	2.0 ±1.0	**1.3 ±0.7**	**1.4 ±0.6**
Steromphala umbilicalis	S	24 ±5.7	6.3 ±2.5	0	0.2 ±0.2	4.5 ±1.4	1.7 ±0.9	0.7 ±0.4	0.1 ±0.1	**7.3 ±1.9**	**0.6 ±0.5**

Species	Geo origin	Bantham		Bude		Croyde		South Milton Sands		**Total**	
		North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Crustaceans											
All barnacles	N/A	18.2 ±2.9	41.5 ±5.3	76.0 ±2.4	25.1 ±4.9	40.2 ±3.1	29.0 ±5.0	89.9 ±1.7	66.9 ±8.3	**34.6 ±4.0**	**53.0 ±3.7**
† *Chthamalus montagui*	S	17.2 ±1.8	22.8 ±1.5	19.2 ±1.6	17.1 ±1.2	12 ±0.5	20.7 ±1	18.6 ±1.2	24 ±0.9	**16.8 ±0.4**	**21.2 ±0.4**
† *Chthamalus stellatus*	S	18.4 ±1.7	26 ±1.5	23.6 ±1.6	19.3 ±1.2	14.4 ±0.6	17.9 ±1	17.4 ±1.2	21.7 ±0.9	**18.4 ±0.4**	**21.2 ±0.4**
† *Semibalanus balanoides*	N	9.5 ±1.5	8 ±0.5	31.6 ±2.4	28.2 ±1.3	24.5 ±0.7	20.1 ±1.1	7.5 ±0.7	11.8 ±0.6	**18.3 ±1.3**	**17 ±1**
† Unknown adults	N/A	1.9 ±0.5	0.3 ±0.1	5.6 ±0.6	7.9 ±0.5	3.1 ±0.3	2.1 ±0.3	2.0 ±0.3	3.1 ±0.3	**3.2 ±0.2**	**3.3 ±0.4**
† Juveniles *Chthamalus*	S	11.8 ±1.3	10 ±0.6	22.7 ±1.1	17.8 ±1.2	14 ±0.6	13.5 ±0.9	10.8 ±1	12.3 ±1	**14.8 ±0.6**	**13.4 ±0.4**
† Juveniles *Semibalanus*	N	9.8 ±1	8.6 ±0.6	24.4 ±1.2	21.2 ±1.2	18.3 ±0.7	17.2 ±1.1	12.4 ±1.2	16.0 ±1.2	**16.2 ±0.7**	**15.8 ±0.6**
† Unknown juveniles	N/A	1.5 ±0.6	0.1 ±0.1	0.5 ±0.2	3.2 ±0.7	3.6 ±0.8	1.3 ±0.5	0* ±0*	0.7 ±0.2	**1.4 ±0.2**	**1.3 ±0.1**
† Total juveniles	N/A	23 ±2.4	18.7 ±1.1	47.7 ±2.3	42.2 ±2.8	35.9 ±1.3	31.9 ±2.1	23.2 ±2.2	29 ±2.2	**32.5 ±1.3**	**30.5 ±1**
† Dead barnacles	N/A	3.4 ± 0.5	3.8 ±0.4	19.7 ±2.5	22.4 ±1.8	13.11 ±1.3	10.7 ±1.2	2.6 ±0.4	3.3 ±0.4	**9.7 ±0.9**	**10.1 ±1**
Juvenile crab	U	0	0.2 ±0.2	0	0	0* ±0*	0	0	0	**0* ±0***	**0* ±0***
Idotea granulosa	N	0.1 ±0.1	0	0	0	0* ±0*	0	0.2 ±0.2	0	**0* ±0***	**0**

Appendix 3

Summary data of the plant species distribution survey on hedgerows banks, according to the aspect (north- and south-facing hedgerows), among six sites in the surroundings of Plymouth, SW England, UK. The data is in average percentage cover per quadrat (0.5 x 0.5 m) for the vegetation, and in average count for invertebrate herbivorous. The zero followed by (*) are not real zero, the data has become zero after changing the number of decimals. It is therefore possible to differenciate real absence of a specie to a real low abundance represented by 0*. The biogeographic origin (Bio-geo origin) of the plants species is categorized by **U**, ubiquitous species without well-marked gepgraphical restriction in N Europe, **S**, southern distribution with absence in northern Britain and Scandinavia; **s**, southern distribution with appearance in northern Britain or Scandinavia; **W**, largely restricted to NW Europe with distribution centred on the Atlantic seaboard; **w**, similar as W but extending to a considerable extent into central regions; and associated combined groups such as **sw**, **Sw**, **sW**; **N/A** (for the non-identified species, or groups of organisms which could have different geograhic origins, such as the graminoids and mosses). This biogeographic classification of plants in Northern Europe is issued from the book *Comparative Plant Ecology – A functional approach to common British species,* from Grime et al. (1988). Note that no plants from this survey had a northern distribution according to this classification. Species in bold, in the table, are the ones considered to be common, i.e. present in at least three sites out of six sampled during this study.

		Tinnel		**Smeaton**		**Rosedale**		**Haye**		**Lutton**		**Creacombe**		**Mean all sites**	
Species	Bio-geo origin	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**
Mushroom	N/A	0.3 ± 0.3	0	0	0	0	0	0	0	0	0	0	0	0* ± 0*	0
Ferns															
Aspleniaceae (Spleenwort family)															
Asplenium (Phyllitis) scolopendrium	SW	**3.5 ± 2.2**	**1 ± 0.7**	**0**	**0**	**0**	**8.2 ± 2.6**	**0**	**0**	**1.7 ± 1.7**	**6.4 ± 3.7**	**7 ± 4.5**	**5.4 ± 2.8**	**2 ± 0.9**	**3.5 ± 1**
Asplenium adiantum nigrum	sw	**0**	**0.8 ± 0.8**	**0**	**2.7 ± 2.1**	**0**	**1 ± 1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.7 ± 0.4**
Asplenium trichomanes	U	0	0.3 ± 0.3	0	1.6 ± 1.2	0	0	0	0	0	0	0	0	**0**	**0.3 ± 0.2**
Athyriaceae (Lady fern family)															
Athyrium filix-femina	U	0	0	0	0	0	0	0	0	4 ± 3.5	4.6 ± 4.6	0	0	0.7 ± 0.6	0.8 ± 0.8
Dryopteridaceae (Buckler fern family)															
Dryopteris affinis	sw	**0**	**1.3 ± 1.3**	**0**	**0**	**0**	**1 ± 1**	**0**	**0**	**0.3 ± 0.3**	**0**	**15.2 ± 9.8**	**0**	**2.6 ± 1.9**	**0.4 ± 0.2**

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	South	North	South	North	South	North	South	North	South	North	South	North	South
Dryopteris filix-mas	**U**	**1.8 ± 1.8**	**0**	**0**	**0**	**0.8 ± 0.8**	**6.8 ± 4.1**	**0**	**3.2 ± 3.2**	**0**	**0**	**4 ± 4**	**7.4 ± 7.4**	**1 ± 0.7**	**2.9 ± 1**
Hypolepidacea (Bracken family															
Pteridium aquilinum	**U**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.8 ± 0.8**	**0**	**5.3 ± 4.9**	**0**	**5 ± 5**	**0**	**1.9 ± 1.2**
Polypodiaceae (Polypody family)															
Polypodium vulgare	**U**	**0.3 ± 0.3**	**0.3 ± 0.3**	**8.7 ± 6.1**	**10.5 ± 3.9**	**0**	**0**	**0**	**1.2 ± 1.2**	**5.4 ± 5.4**	**0**	**0**	**0**	**2.4 ± 1.4**	**2 ± 1**
Unknown ferns															
Unknown fern 1	N/A	0	0.8 ± 0.8	0	0	0	0	0	0	0	0	0	0	0	0.1 ± 0.1
Unknown fern 2	N/A	0	0	0	0	0	0	0	0	0	0	0	0.2 ± 0.2	0	0* ± 0*
Herbs															
Apiaceae (Carrot family)															
Angelica sylvestris	U	0	0	0	0	0	0	0	0	0	0	0.7 ± 0.7	1.4 ± 1.4	0.1 ± 0.1	0.2 ± 0.2
Anthriscus sylvestris	**U**	**2 ± 2**	**0.5 ± 0.5**	**5.4 ± 3.9**	**0.2 ± 0.2**	**0**	**0**	**0**	**0**	**6 ± 4.9**	**0**	**0**	**0.4 ± 0.4**	**2.2 ± 1.1**	**0.2 ± 0.1**
Apium nodiflorum	SW	0	0	0	0	0	0	0	0	0	0	7 ± 7	0.2 ± 0.2	1.2 ± 1.2	0* ± 0*
Chaerophyllum temulum	S	0	0	0	0	0	0	0	0	2.7 ± 1.9	0	0	0	0.5 ± 0.4	0
Heracleum sphondylium	U	0	0	0	0	0	0	0	0	8.4 ± 8.4	0.7 ± 0.4	0	4 ± 4	1.4 ± 1.4	0.8 ± 0.7
Conium maculatum	S	0	0	0	0	0	0	0	0	0	0	0	1.2 ± 1.2	0	0.2 ± 0.2
Pastinaca sativa	U	0	0	0	0	0	0	0	0	4.4 ± 4.4	0	0	0	0.7 ± 0.7	0
Sison amomum	S	0	0	0	0	0	0	0	0	0	0	0	0.4 ± 0.4	0	0* ± 0*
Araceae (Arum family)															
Arum maculatum	Sw	0	0.4 ± 0.4	0	0	0	0	0	0	0	0	3 ± 1.9	0	0.5 ± 0.4	0* ± 0*
Araliaceae (Ivy family)															
Hedera helix spp helix	**U**	**22.3 ± 14.8**	**21.1 ± 9.6**	**22.5 ± 10.9**	**38.6 ± 10.2**	**20.3 13.3**	**18 ± 7.4**	**5 ± 3**	**11.5 ± 9.7**	**6.1 ± 2.7**	**25 ± 8.8**	**6.4 ± 1.6**	**5.1 ± 2.4**	**13.8 ± 3.6**	**19.9 ± 3.7**
		Tinnel		**Smeaton**		**Rosedale**		**Haye**		**Lutton**		**Creacombe**		**Mean all sites**	

Species	Bio-geo origin	North	South	North	South	North	South	North	South	North	South	North	South	North	South
Asteraceae (Daisy family)															
Achillea millefolium	U	0	0	0	0	0	0	0.5 ± 0.5	1.5 ± 1.5	0	0	0	0	0* ± 0*	0.3 ± 0.3
Arctium minus	S	0	0	0	0	3 ± 3	0	0	0	0	0	0	0	0.5 ± 0.5	0
Lapsana communis	s	0	0	0	0	0	0	0	0	3 ± 1.5	0	0	0	0.5 ± 0.3	0
Sonchus oleraceus	s	1.5 ± 1.5	0	0	0	0	0	0	0	0	0	0	0	0.3 ± 0.2	0
Taraxacum officinale	U	0	0	0	0	0	0	0.2 ± 0.2	0.8 ± 0.8	0.3 ± 0.3	0	0	0	0* ± 0*	0.1 ± 0.1
Brassicaceae (Cabbage / Crucifer family)															
Cardamine amara	S	0	0	0	0	0	0	0	0	0	0	1 ± 1	0.2 ± 0.2	0.2 ± 0.2	0* ± 0*
Cardamine pratense	U	0	0.3 ± 0.3	0	0	0.9 ± 0.6	0	0	0	0	0	0	0	0.2 ± 0.1	0* ± 0*
Rorippa nasturtium-aquaticum	s	0	0	0	0	0	0	0	0	0	0	6 ± 6	3.6 ± 3.6	1 ± 1	0.6 ± 0.6
Caprifoliaceae (Honeysuckle family)															
Lonicera periclymenum	**ws**	**0**	**0.4 ± 0.4**	**0**	**0**	**0.4 ± 0.4**	**1.4 ± 1.4**	**0**	**2 ± 2**	**1.6 ± 1.6**	**0.4 ± 0.4**	**0**	**0.3 ± 0.3**	**0.3 ± 0.3**	**0.7 ± 0.4**
Caryophyllaceae (Campion family)															
Silene dioica	**U**	**5.6 ± 5.6**	**4.8 4.8**	**0**	**0**	**0**	**5.9 ± 3.3**	**0**	**6.8 ± 3.2**	**19.4 ± 5**	**0.8 ± 0.8**	**0.2 ± 0.2**	**0**	**4.2 ± 1.7**	**3 ± 1**
Stellaria graminea	**U**	**0**	**0**	**0**	**1.4 ± 0.7**	**0**	**0**	**0**	**0**	**0**	**0.8 ± 0.8**	**0.3 ± 0.3**	**0**	**0* ± 0***	**0.4 ± 0.2**
Stellaria holostea	**s**	**2.3 ± 1.6**	**2.4 ± 1.6**	**1 ± 0.5**	**2.2 ± 0.8**	**4 ± 1.8**	**5.5 ± 3.7**	**2.9 ± 2.5**	**7.1 ± 3.5**	**7.5 ± 2.2**	**5.4 ± 3.9**	**1.4 ± 0.9**	**2.2 ± 0.8**	**3.2 ± 0.8**	**4.1 ± 1.1**
Celastraceae (Spindle family)															
Euonymus europaeus	S	0	0	0	0	0	0.3 ± 0.3	0	9	0	0	0	0	0	1.6 ± 1.6
Crassulaceae (Stonecrop family)															
Umbilicus rupestris	**SW**	**6.3 ± 6.3**	**0.4 ± 0.4**	**4.6 ± 4.6**	**11.3 ± 5**	**6.6 ± 4.8**	**0**	**0**	**0**	**6 ± 6**	**0**	**4 ± 4**	**0**	**4.6 ± 1.8**	**1.9 ± 1.1**

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	South	North	South	North	South	North	South	North	South	North	South	North	South
Convolvulaceae (Bindweed family)															
Calystegia sepium	S	0	0	0	0	1.6 ± 1.6	6.8 ± 4.6	0.8 ± 0.8	0	0	0	0	0	0.4 ± 0.3	1.1 ± 0.9
Curcubitaceae (Gourd family)															
Bryonia dioica	s	0	0	0	0	0	0	0	0	0	0.4 ± 0.4	0	9.8 ± 8.8	0	1.7 ± 1.6
Euphorbiaceae (Spurge family)															
Mercurialis perennis	s	0	0.5 ± 0.5	0	0	0	0	19 ± 8.7	21.4 ±7.3	0	0	0	0	3.2 ± 1.9	3.7 ± 1.9
Fabaceae (Pea family)															
Vicia sp.	N/A	0	0	0	0	0	0	0	0.8 ± 0.8	0	0	0	0	0	0.1 ± 0.1
Vicia cracca	U	0	0	0	0	0	0	1.2 ± 1.2	0	0	0	0	0	0.2 ± 0.2	0
Vicia sativa	**U**	**0**	**0**	**0**	**0.2 ± 0.2**	**0**	**0**	**0.6 ± 0.6**	**0**	**0.6 ± 0.6**	**0**	**0**	**0**	**0.2 ± 0.1**	**0* ± 0***
Vicia sepium	U	0	0	0	0	0	0	0	0	2 ± 2	0	0	0	0.3 ± 0.3	0
Lathyrus pratensis	**U**	**0**	**0**	**0**	**0**	**0**	**0**	**0.4 ± 0.4**	**0**	**0**	**0.6 ± 0.6**	**0**	**1.5 ± 1.2**	**0* ± 0***	**0.4 ± 0.2**
Fumariaceae (Fumitory family)															
Fumaria capreolata	s	0	0	0	0.2 ± 0.2	0	0	0	0	0	0	0	0	0	0* ± 0*
Geraniaceae (Geranium family)															
Geranium dissectum	S	0	0	0	5 ± 5	0	0	0	0	0	0	0	0	0	0.8 ± 0.8
Geranium lucidum	**Sw**	**7.1 ± 5.1**	**2 ± 1**	**12.4 ± 8.8**	**2 ± 1.5**	**5.4 ± 4.2**	**0.3 ± 0.3**	**22 ± 6.7**	**0**	**5.4 ± 4.9**	**2.8 ± 2.8**	**0**	**0**	**8.7 ± 2.5**	**1.2 ± 0.6**
Geranium pyrenaicum	S	0	0	0	0	0	0	0	0.8 ± 0.8	0	0	0	0	0	0.1 ± 0.1
Geranium robertianum	**s**	**2.8 ± 1.1**	**1.6 ± 0.8**	**2.6 ± 1.2**	**3 ± 1.1**	**1.2 ± 0.4**	**3.1 ± 1.3**	**5.1 ± 1.8**	**0.5 ± 0.3**	**14.1 ± 4**	**1.3 ± 1.3**	**2.6 ± 1.4**	**1.4 ± 0.6**	**4.8 ± 1.1**	**1.8 ± 0.4**

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	South	North	South	North	South	North	South	North	South	North	South	North	South
Lamiaceae (Dead-Nettle family)															
Ballota nigra	s	0	0	0	0	0	0	1.2 ± 1.2	2.2 ± 1.3	0	0	0	0	0.2 ± 0.2	0.4 ± 0.2
Betonica/Stachys officinalis	S	0	0	0	0	0	2.2 ± 2.2	0	0	0	0	0	0	0	0.4 ± 0.4
Glechoma hederacea	S	0	0	0	0	0	0	0	0.4 ± 0.4	0	0	1.6 ± 1.6	0.6 ± 0.6	0.3 ± 0.3	0.1 ± 0.1
Stachys sylvatica	s	0	0	0	4.4 ± 4	0	0	0	0	0	0	0	0	0	0.7± 0.7
Unknown Dead-Nettle	N/A	0	0	0	0	0	0.3 ± 0.3	0	0	0	0	0	0	0	0* ± 0*
Teucrium scorodonia	sw	0	0	0	0	0	0.7 ± 0.5	0	0	0	0	0	0	0	0.1 ± 0.1
Liliaceae (Lily family)															
Hyacinthoides non-scripta	**sW**	**0.5 ± 0.3**	**0.4 ± 0.4**	**0.9 ± 0.9**	**0**	**1.5 ± 0.7**	**7.1 ± 5.4**	**0.6 ± 0.6**	**9.1 ± 6.4**	**0**	**1 ± 0.6**	**2.2 ± 1**	**5.1 ± 1.4**	**1 ± 0.3**	**3.8 ± 1.5**
Onograceae (Willowherb family)															
Epilobium sp	N/A	0	0	0	0	0	0	0	0	1.4 ± 1	0	0	0	0.2 ± 0.2	0
Polygonaceae (Dock family)															
Polygonum convolvulus	U	0	0	0	0	0	0	0	0	2.6 ±1.3	18.6 ± 7.2	0.8 ± 0.5	1 ± 1	**0.6 ± 0.3**	**3.2 ± 1.7**
Rumex acetosa	**U**	**0**	**0**	**8.1 ± 5.4**	**0**	**1.6 ± 1.1**	**0**	**4.9 ± 3.2**	**0.4 ± 0.4**	**3**	**0**	**0**	**0**	**2.9 ± 1.2**	**0* ± 0***
Rumex obtusifolius	s	3 ±3	0	0	0	0	0	0	0	0	0	0	0	0.5 ± 0.4	0
Rumex sanguineus	S	0	0.8 ± 0.8	0	0	0	0	0	0	0.6 ± 0.6	0	0	0	0.1 ± 0.1	0.1 ± 0.1
Primulaceae (Primrose family)															
Primula vulgaris	Sw	0	0	0	0	18.8 ± 14	0	0	0	0	0	8 ± 6.8	4.2 ± 1.8	**4.5 ± 2.8**	**0.7 ± 0.4**
Ranunculaceae (Buttercup family)															
Ranunculus ficaria	s	0	0	0	0	0	0	0.5 ± 0.3	0	0	0	0	0	0* ± 0*	0

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	South	North	South	North	South	North	South	North	South	North	South	North	South
Ranunculus repens	**U**	**0**	**0**	**0**	**0**	**0**	**0.2 ± 0.2**	**7.6 ± 6.6**	**0**	**0**	**1.5 ± 1.5**	**0**	**0**	**1.2 ± 1.2**	**0.3 ± 0.3**
Ranunculus sceleratus	S	0	0.3 ± 0.3	0	0	0	0	0	0	0	0	0	0	0	0* ± 0*
Rosa (Rose family)															
Agrimonia eupatoria	S	0	0	0	0	0	0	0	0	0	0	0	1.4 ± 1.4	0	0.2 ± 0.2
Filipendula ulmaria	U	0	0	0	0	0	0	0	0	1.4 ± 1.4	0	0	0	0.2 ± 0.2	0
Fragaria vesca	U	0	0	0	0	0.6 ± 0.6	0	0	0	1 ± 0.7	0	0	0	0.3 ± 0.2	0
Geum urbanum	s	0	0	0	0	0	0	0	0	1.8 ± 1.8	0	0	0.9 ± 0.5	0.3 ± 0.3	0.2 ± 0.1
Rubiaceae (Bedstraw family)															
Galium aparine	**s**	**14 ± 7.2**	**4.6 ± 2.1**	**33.2 ± 13.5**	**7.3 ± 5.2**	**2.5 ± 1.1**	**1.3 ± 0.3**	**4.6 ± 1.8**	**3.6 ± 1.6**	**1.9 ± 0.9**	**6.2 ± 1.2**	**4.7 ± 1.1**	**9.7 ± 5.2**	**10.1 ± 3.1**	**5.5 ± 1.3**
Galium mollugo	**s**	**6.5 ± 44.3**	**12 ± 7.8**	**28 ± 8.7**	**11.7 ± 5.9**	**0.9 ± 0.7**	**7.8 ± 6.8**	**3.1 ± 1.4**	**18.1 ± 7.2**	**0.5 ± 0.5**	**3.5 ± 1.6**	**0.8 ± 0.3**	**17.1 ± 7.6**	**6.6 ± 2.4**	**11.7 ± 2.6**
Scrophulariaceae (Figwort family)															
Veronica chamaedrys	U	0	0	0.6 ± 0.6	0	0	0	0	2.4 ± 1.7	0	0	0	0	0.1 ± 0.1	0.4 ± 0.3
Veronica hederifolia	S	0	0	0	0	0	0	0	0	0	0	0.2 ± 0.2	0	0* ± 0*	0
Urticaceae (Nettle family)															
Urtica dioica	**U**	**15.8 ± 10**	**9 ± 7**	**8 ± 4.9**	**3.5 ± 2.4**	**1.4 ± 1.4**	**5.9 ± 3.7**	**0.4 ± 0.4**	**9.4 ± 3.5**	**1 ± 1**	**1.8 ± 0.9**	**8.6 ± 4.5**	**11 ± 5.9**	**5.9 ± 1.9**	**6.8 ± 1.7**
Violaceae (Violet family)															
Viola odorata	S	0	0	0	0	5.6 ± 5.6	0	0	0	0	0	0	0	1 ± 1	0
Unknown herbs															
Wild flower 1	N/A	0	0	0	0	0	0	0	0	0	0	0	0.2 ± 0.2	0	0* ± 0*

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	South	North	South	North	South	North	South	North	South	North	South	North	South
Wild flower 2	N/A	0	0	0	0	0	0	0	0	1 ± 1	0	0	0	0.2 ± 0.2	0
Wild flower 3	N/A	0	0	0	0	0	0	4 ± 4	0	0	0	0	0	0.7 ± 0.7	0
All graminoids	**N/A**	**26.1 ± 10.7**	**4.8 ± 1.6**	**7.7 ± 5.5**	**20 ± 9.8**	**7.2 ± 3.9**	**5 ± 3.6**	**55.7 ± 13.5**	**36.5 ± 8.8**	**36.4 ± 5.4**	**21.9 ± 12.5**	**29.2 ± 7.9**	**51.9 ± 10.2**	**27 ± 4.5**	**23.3 ± 4.6**
All mosses	**N/A**	**33.3 ± 15.6**	**11 ± 4.74**	**38.8 ± 11.8**	**7.2 ± 3.3**	**35.6 ± 9.3**	**6.1 ± 1.5**	**14.8 ± 6**	**2.1 ± 2.1**	**1.2 ± 1**	**0**	**0.6 ± 0.6**	**0.7 ± 0.7**	**20.7 ± 4.4**	**4.5 ± 1.1**
Shrubs															
Cornaceae (Dogwood family)															
Cornus sanuguinea	s	0	0	0	0	0	0	0	0	0	5 ± 5	0	0	0	0.9 ± 0.9
Rosa (Rose family)															
Crataegus monogyna	s	0	0	1.6 ± 1.6	0	0.6 ± 0.6	4.4 ± 4.4	0	0	0	0	0	0	0.4 ± 0.3	0.7 ± 0.7
Prunus spinosa	**s**	**0**	**10 ± 10**	**5 ± 4.2**	**2 ± 1.2**	**3.6 ± 1.7**	**6 ± 3.7**	**0**	**2.4 ± 2.4**	**0**	**0**	**0**	**0**	**1.4 ± 0.8**	**3.4 ± 1.6**
Rosa sp.	**S**	**0**	**0**	**0**	**0.4 ± 0.4**	**0.2 ± 0.2**	**6.7 ± 2.3**	**0.9 ± 0.9**	**0.7 ± 0.7**	**0**	**0**	**0.2 ± 0.2**	**1 ± 1**	**0.2 ± 0.2**	**1.5 ± 0.6**
Rubus fruticosus	**s**	**5.1 ± 4.1**	**4.3 ± 2.5**	**3.9 ± 2.4**	**1.3 ± 1.3**	**4.9 ± 1.7**	**0.3 ± 0.3**	**0.6 ± 0.4**	**4 ± 2.2**	**8.8 ± 6.2**	**6.5 ± 3.5**	**0**	**4.8 ± 2.4**	**3.9 ± 1.3**	**3.6 ± 0.9**
Betulaceae (Birch family)															
Betula pendula	U	0.3 ± 0.3	0	0	0	0	0	0	0	0	0	0	0	0* ± 0*	0
Betula pubescens	U	0.8 ± 0.8	0	0	0	0	0	0	0	0	0	0	0	0.1 ± 0.1	0
Corylus avellana	**S**	**0**	**3.8 ± 3.8**	**0**	**0**	**5.2 ± 3.2**	**25.8 ± 9.2**	**0**	**0**	**0**	**21.2 ± 5.6**	**0**	**0**	**0.9 ± 0.6**	**8.5 ± 2.7**
Ulmaceae (Elm family)															
Ulmus procera	SW	0	5 ± 5	0	0	0	0	0	0	0	0	0	0	0	0.8 ± 0.7
Olaceae (Olive family)															
Fraxinus excelsior	S	0	0	0	0.7 ± 0.7	0	0	0	0	0	0	0	0.9 ± 0.9	**0**	**0.3 ± 0.2**
Ligustrum vulgare	SW	0	0	0	0	0	0	0	0	0	10.4 ± 6.5	0	0	0	1.7 ± 1.2
Quercus robur	**S**	**0**	**0**	**2.5 ± 1**	**7.8 ± 6.8**	**0**	**0.9 ± 0.6**	**0**	**1.3 ± 1.3**	**0**	**0.2 ± 0.2**	**0**	**0**	**0.4 ± 0.2**	**1.7 ± 1.2**
Aceraceae (Maple family)															
Acer campestre	S	0	0	2.8 ± 2.8	0	0	0	0	0	0	0	0	0	0.5 ± 0.5	0

Species	Bio-geo origin	Tinnel		Smeaton		Rosedale		Haye		Lutton		Creacombe		Mean all sites	
		North	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**	**North**	**South**
Unknown shrubs															
Unknown woody plant 1	N/A	0	0	0	0	0	0	0.8 ± 0.8	0	0	0	0	0	0.1 ± 0.1	0
Unknown woody plant 2	N/A	0	0	0	0	0	0	0.7 ± 0.7	0	0	0	0	0	0.1 ± 0.1	0

Appendix 4

Ellenberg's indicators, firstly defined by the German botanist Heinz Ellenberg for European vascular plants, are based on the realised ecological niche, and the plants' tolerance to those indicators. Hill et al. (1999) intended to give the Ellenberg values in their report for the Britain and Irish native vascular plants, as typical values for GB. The considered indicators by those authors and used in this survey are the following, and fully decribed in Hill et al. (1999). Note that the original indicators T (temperature) and K (continentality) developed by Ellenberg were not used by Hill et al. (1999) due to their rather irrelevance in the oceanic climate as found in Britain. Moreover, the indicator (S) for sanity tolerance were discarded from this thesis as none of the sampled sites were coastal nor near salt-mashes. The Ellenberg's indicators used in the survey of Chapter 4 are tolerance to light (**L**), moisture (**F**), soil pH (**R** for reaction), and soil nitrogen content (**N**), and their range of values are summarize below.

Ellenberg indicator	Value	Explanation
L – Light	1	Plant in deep shade
	2	Between 1 and 3
	3	Shade plant, mostly less than 5% relative illumination, seldom more than 30% illumination when trees are in full leaf
	4	Between 3 and 5
	5	Semi-shade plant, rarely in full light, but generally with more than 10% relative illumination when trees are in leaf
	6	Between 5 and 7
	7	Plant generally in well-lit places, but also occurring in partial shade
	8	Light-loving plant rarely found where relative illumination in summer is less than 40%
	9	Plant in full light, found mostly in full sun
F – Moisture	1	Indicator of extreme dryness, restricted to soils that often dry out for some time
	2	Between 1 and 3
	3	Dry-site indicator, more often found on dry ground than in moist places
	4	Between 3 and 5
	5	Moist-site indicator, mainly on fresh soils of average dampness
	6	Between 5 and 7
	7	Dampness indicator, mainly on constantly moist or damp, but not on wet soils
	8	Between 7 and 9
	9	Wet-site indicator, often on water-saturated, badly aerated soils
	10	Indicator of shallow-water sites that may lack standing water for extensive periods

Ellenberg indicator	Value	Explanation
	11	Plant rooting under water, but at least for a time exposed above, or plant floating on the surface
	12	Submerged plant, permanently or almost constantly under water
R – Reaction	1	Indicator of extreme acidity, never found on weakly acid or basic soils
	2	Between 1 and 3
	3	Acidity indicator, mainly on acid soils, but exceptionally also on nearly neutral ones
	4	Between 3 and 5
	5	Indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soils
	6	Between 5 and 7
	7	Indicator of weakly acid to weakly basic conditions; never found on very acid soils
	8	Between 7 and 9
	9	Indicator of basic reaction, always found on calcareous or other high-pH soils
N – Nitrogen	1	Indicator of extremely infertile sites
	2	Between 1 and 3
	3	Indicator of more or less infertile sites
	4	Between 3 and 5
	5	Indicator of sites of intermediate fertility
	6	Between 5 and 7
	7	Plant often found in richly fertile places
	8	Between 7 and 9
	9	Indicator of extremely rich situations, such as cattle resting places or near polluted rivers

Appendix 5

Ellenberg's indicators values for each vascular species sampled in the survey from Chapter 4. Explanation of each values can be found in Appendix 5. The Ellenberg's indicators are the following:

- **Light** (**L**): indicates the shade or sun tolerance of a plant Scale from 1 (plant restricted to deep shade) to 9 (plant demands full sun).
- **Moisture** (**F**): indicates moisture or drought tolerance. Scale from 1 (extreme dryness, restricted to soils that often dry out for some time) to 12 (submerged plant, permanently or almost constantly under water)
- **Reaction** (**R**): indicates soil or water pH level. Scale from 1 (extreme acidity, never found on weakly acid or basic soil) to 9 (basic reaction, always found on calcareous or other higher pH soils.
- **Nitrogen** (**N**): indicates soil fertility level. Scale from 1 (extremely infertile sites) to 9 (extremely rich situations, such as cattle resting places or near polluted rivers)

Species considered to be common in the survey, i.e. present in at least three sites out of six sampled during this study, are indicated in bold.

	L	F	R	N
Ferns				
Asplenium adiantum nigrum	***6***	***4***	***5***	***5***
Asplenium trichomanes	*5*	*3*	*8*	*2*
Athyrium filix-femina	*5*	*7*	*5*	*6*
Dryopteris affinis	***5***	***6***	***5***	***5***
Dryopteris filix-mas	***5***	***6***	***5***	***5***
Phyllitis scolopendrium	***4***	***5***	***7***	***5***
Polypodium vulgare	***5***	***5***	***4***	***3***
Pteridium aquilinum	***6***	***5***	***3***	***3***
Herbs				
Achillea millefolium	*7*	*5*	*6*	*4*
Agrimonia eupatoria	*7*	*4*	*7*	*4*
Angelica sylvestris	*7*	*8*	*6*	*5*
Anthriscus sylvestris	***6***	***5***	***7***	***7***
Apium nodiflorum	*7*	*10*	*7*	*7*
Arctium minus	*6*	*4*	*7*	*5*
Arum maculatum	*4*	*5*	*7*	*7*
Ballota nigra	*7*	*4*	*8*	*6*
Bryonia dioica	*7*	*5*	*7*	*7*
Calystegia sepium	*7*	*8*	*7*	*7*
Cardamine amara	*6*	*9*	*7*	*6*

	L	F	R	N
Cardamine pratense	*7*	*8*	*5*	*4*
Chaerophyllum temulum	*6*	*5*	*7*	*7*
Conium maculatum	*8*	*5*	*7*	*5*
Euonymus europaeus	5	5	8	5
Filipendula ulmaria	*7*	*8*	*6*	*5*
Fragaria vesca	*6*	*5*	*6*	*4*
Fumaria capreolata	*7*	*4*	*6*	*7*
Galium aparine	***6***	***6***	***7***	***8***
Galium mollugo	***7***	***4***	***7***	***4***
Geranium dissectum	*7*	*5*	*7*	*6*
Geranium lucidum	***6***	***4***	***7***	***6***
Geranium pyrenaicum	*8*	*4*	*7*	*6*
Geranium robertianum	***5***	***6***	***6***	***6***
Geum urbanum	*4*	*6*	*7*	*7*
Glechoma hederacea	*6*	*6*	*7*	*7*
Hedera helix spp helix	***4***	***5***	***7***	***6***
Heracleum sphondylium	*7*	*5*	*7*	*7*
Hyacinthoides non-scripta	***5***	***5***	***5***	***6***
Lapsana communis	*6*	*4*	*7*	*7*
Lathyrus pratensis	***7***	***6***	***7***	***6***
Lathyrus pratensis	***7***	***6***	***7***	***6***
Lonicera periclymenum	***5***	***6***	***5***	***5***
Mercurialis perennis	*3*	*6*	*7*	*7*
Pastinaca sativa	*7*	*4*	*7*	*5*
Polygonum convolvulus	*7*	*4*	*7*	*5*
Primula vulgaris	*5*	*5*	*6*	*4*
Ranunculus ficaria	*6*	*6*	*6*	*6*
Ranunculus repens	***6***	***7***	***6***	***7***
Ranunculus sceleratus	*8*	*8*	*8*	*8*
Rorippa nasturtium-aquaticum	*7*	*10*	*7*	*7*
Rumex acetosa	***7***	***5***	***5***	***4***
Rumex obtusifolius	*7*	*5*	*7*	*9*
Rumex sanguineus	*5*	*7*	*7*	*7*
Silene dioica	***5***	***6***	***6***	***7***
Sison amomum	*7*	*4*	*7*	*5*
Sonchus oleraceus	*7*	*5*	*7*	*7*
Stachys officinalis	*7*	*5*	*5*	*3*
Stachys sylvatica	*6*	*6*	*7*	*8*
Stellaria graminea	***7***	***6***	***5***	***4***
Taraxacum officinale	*7*	*5*	*7*	*6*
Teucrium scorodonia	*6*	*4*	*4*	*3*
Umbilicus rupestris	***6***	***4***	***5***	***4***
Urtica dioica	***6***	***6***	***7***	***8***
Veronica chamaedrys	*6*	*5*	*6*	*5*
Veronica hederifolia	*6*	*5*	*7*	*6*
Vicia cracca	*7*	*6*	*7*	*5*

	L	F	R	N
Vicia sativa	***7***	***4***	***7***	***4***
Vicia sepium	*6*	*5*	*6*	*6*
Viola odorata	*5*	*5*	*7*	*7*
Shrubs				
Acer campestre	*5*	*5*	*7*	*6*
Betula pendula	*7*	*5*	*4*	*4*
Betula pubescens	*7*	*7*	*4*	*4*
Cornus sanuguinea	*7*	*5*	*7*	*6*
Corylus avellana	***4***	***5***	***6***	***6***
Crataegus monogyna	*6*	*5*	*7*	*6*
Fraxinus excelsior	*5*	*6*	*7*	*6*
Ligustrum vulgare	*6*	*5*	*7*	*5*
Prunus spinosa	***6***	***5***	***7***	***6***
Quercus robur	***7***	***5***	***5***	***4***
Rubus fruticosus	***6***	***6***	***6***	***6***
Ulmus procera	*5*	*5*	*8*	*6*

Appendix 6

Mean abundance of the mesofauna collected from soil cores and extracted via the Tullgren-funnel method (Figure 5.4), according to aspect (north- and south-facing slopes), and on four different locations in the SW of England (Figure 5.2). Soil cores were sampled on paired north- and south-facing road verges with about 45° slope angle, along the A30. Organisms were identified to the 'Order' level when possible and in some cases 'adults' and 'larvae' were kept separated due to their different ecology, feeding behaviour, and therefore implication in the decomposition processes. Their feeding behaviour are indicated as following: B, Blood-sucking; C, Carnivorous; D, Detritivores; H, Herbivores; N, nectar of honeydew; P, Predators, S; Scavenging (plants, animals, fungi, bacteria); N/A, not applicable, for example Ephemeroptera, only live two to 3 days and most might not feed during their adult life. Occasional feeding behaviour are in brackets. The zero followed by (*) are not real zero, the data has become zero after changing the number of decimals. It is therefore possible to differenciate real absence of a specie to a real low abundance represented by 0*.

				Site 1		Site 2		Site 3		Site 4		**All sites**	
Phylum	Class	Order		north-facing	south-facing	north-facing	south-facing	north-facing	south-facing	north-facing	south-facing	**north-facing**	**south-facing**
Nematoda			C, H	0.3 ±0.2	2.3 ±1.3	2.3 ±1.3	5.7 ±3.3	0.7 ±0.4	0.7 ±0.4	0.3 ±0.2	0	**0.9 ±0.4**	**2.2 ±0.9**
Annelida	Oligochaeta	Haplotaxida	D	2.0 ±1.2	6.3 ±3.7	2.0 ±1.2	0.7 ±0.4	2.3 ±1.3	2.3 ±1.3	2.0 ±1.2	1.3 ±0.8	**2.1 ±0.5**	**2.7 ±1.1**
Arthropoda	Arachnida	Pseudoscorpiones	p	0	0	0.3 ±0.2	1.0 ±0.6	0.7 ±0.4	0.3 ±0.2	1.7 ±1.0	0.3 ±0.2	**0.7 ±0.3**	**0.4 ±0.2**
		Araneae	P	0	0.7 ±0.4	0	0	0	0.3 ±0.2	0	0	**0**	**0.3 ±0.1**
		Acari	P,D, B (S)	332.3 ±191.9	424.7 ±245.2	170.0 ±98.1	609.7 ±352.0	532.0 ±307.2	348.3 ±201.1	313.3 ±180.9	196.3 ±113.4	**336.9 ±72.9**	**394.8 ±89.6**
	Malacostraca	Isopoda	S (H)	0	0	0	0.7 ±0.4	0	0	0	0	**0**	**0.2 ±0.1**
	Diplopoda	Glomerida	D (H)	0	0.3 ±0.2	0	0	0	0	0	0	**0**	**0.1 ±0.1**
		Julida	D (H)	0.3 ±0.2	0	0	0	0.7 ±0.4	0.3 ±0.2	0.7 ±0.4	0.3 ±0.2	**0.4 ±0.1**	**0.2 ±0.1**
		Polydesmida	D (H)	0	0	0	0	0.3 ±0.2	0	0	0	**0.1 ±0.1**	**0**
	Chilopoda	Lithobiomorpha	p	0	5.7 ±3.3	2.0 ±1.2	0	0.3 ±0.2	0	0	0	**0.6 ±0.3**	**1.4 ±0.8**
		Scolopendromorpha	P	0	0	1.0 ±0.6	0	2.3 ±1.3	2.0 ±1.2	0.7 ±0.4	2.0 ±1.2	**1.0 ±0.4**	**1.0 ±0.5**
	Entognatha	Collembola	S	46.0 ±26.6	151.7 ±87.6	50.3 ±29.1	260.7 ±150.5	153.3 ±88.5	54.3 ±31.4	64.7 ±37.3	41.7 ±24.1	**78.6 ±19.1**	**127.1 ±34.4**

Phylum	Class	Order		Site 1		Site 2		Site 3		Site 4		**All sites**	
				north-facing	south-facing	north-facing	south-facing	north-facing	south-facing	north-facing	south-facing	**north-facing**	**south-facing**
Arthropoda	Insecta	Coleoptera (larvae)	P, H, S	1.0 ±0.6	2.0 ±1.2	1.3 ±0.8	0.7 ±0.4	4.0 ±2.3	3.3 ±1.9	2.0 ±1.2	0.3 ±0.2	**2.1 ±0.7**	**1.6 ±0.4**
		Coleoptera (adult beetle)	P, H, S	0	0.3 ±0.2	0	0	0.3 ±0.2	0	0	0	**0.1 ±0.1**	**0.1 ±0.1**
		Diptera (larvae)	S	1.7 ±1.0	0.3 ±0.2	0.7 ±0.4	0	0	0.3 ±0.2	0.3 ±0.2	0.7 ±0.4	**0.7 ±0.2**	**0.3 ±0.2**
		Diptera (adult)	P, H, S	0	0	2.3 ±1.3	0	0.7 ±0.4	0	0.7 ±0.4	0	**0.9 ±0.6**	**0**
		Hemiptera (bug)	H (P)	0.3 ±0.2	1.7 ±1.0	0.3 ±0.2	1.3 ±0.8	1.0 ±0.6	0	0.3 ±0.2	0.3 ±0.2	**0.5 ±0.2**	**0.8 ±0.4**
		Hemiptera (male scale insect)	H	1.0 ±0.6	0.7 ±0.4	1.3 ±0.8	1.3 ±0.8	2.0 ±1.2	3.3 ±1.9	3.3 ±1.9	1.0 ±0.6	**1.9 ±0.5**	**1.6 ±0.5**
		Hymenoptera (Apocrita larvae)	N	0	3.0 ±1.7	0.7 ±0.4	0	0.3 ±0.2	0	0	0	**0.3 ±0.2**	**0.8 ±0.4**
		Hymenoptera (ants adults)	P (N)	0	0.3 ±0.2	0	0.3 ±0.2	0	0	0	0	**0**	**0.2 ±0.1**
		Hymenoptera (ants pupa)		1.3 ±0.8	0	0	0	0	0	0	0	**0.3 ±0.3**	**0**
		Psocoptera	H, S	0	0.3 ±0.2	0	0	0	0	0	0	**0**	**0.1 ±0.1**
		Thysanoptera	H (P)	0	0	0	0	1.0 ±0.6	1.0 ±0.6	0.7 ±0.4	0	**0.4 ±0.2**	**0.3 ±0.3**
Mollusca	Gastropoda		H	0	0	0	0.7 ±0.4	0.3 ±0.2	0	0	0	**0.1 ±0.1**	**0.2 ±0.2**
		egg 2	N/A	0	0	0	0	0.3 ±0.2	0.3 ±0.2	2.0 ±1.2	0	**0.6 ±0.5**	**0.1 ±0.1**
		egg 5	N/A	0	0	0	0	0.7 ±0.4	0	0	0	**0.2 ±0.2**	**0**
		egg 6	N/A	0	0	0	0	0	0	1.3 ±0.8	0	**0.3 ±0.3**	**0**
		unknown 1	N/A	1.3 ±0.8	0	0	0	0	0	0	0	**0.3 ±0.3**	**0**
		unknown 2	N/A	1.0 ±0.6	0	0	0	0	0	0	0	**0.3 ±0.3**	**0**

Appendix 7

Mean abundance of the earthworm species according to aspect, sampled in 25x25x10 cm soil cores in four different paired north- and south-facing road verges (with 45° slope angle) in the SW England. Sampling was undertaken using two combined methods: behavioural (use of hot mustard diluted in water, in order to capture individuals in deep burrows) and physical (hand sorted within a known volume of soil) in order to collect a variety of earthworms with different ecology. The three main ecological groups are the following: Epi, Epigenic (living on soil surface or beneath the litter layer, and feeding mainly on decomposing litter); Ane, Anecic (living in burrows down the mineral horizon, and feeding mainly on decomposing litter); Engo, endogenic (living in mineral soil horizon, and feeding mainly on soil and humified organic matter, only little role in decomposition). The zero followed by (*) are not real zero, the data has become zero after changing the number of decimals. It is therefore possible to differenciate real absence of a specie to a real low abundance represented by 0*.

				Site 1		Site 2		Site 3		Site 4		**All sites**	
Family	Genus	Species	Ecology	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Lumbricidae	*Allolobophora*	*chlorotica*	Endo	0.5 ±0.5	0	4.5 ±1.5	6.5 ±2.5	0	0.5 ±0.5	0	0	**1.3 ±0.8**	**1.8 ±0.6**
	Aporrectodea	*caliginosa*	Endo	0	0.5 ±0.5	0	1.5 ±1.5	0	0	0	0	**0**	**0.5 ±0.2**
		rosea	**Endo**	**0.5 ±0.5**	**0**	**3 ±1**	**0**	**0**	**0**	**1.5 ±1.5**	**0**	**1.3 ±0.6**	**0**
	Dendrobaena	*hortensis*	Epi	0	0	0.5 ±0.5	0	0	0	0	0	**0.1 ±0.1**	**0**
		octaedra	Epi	0	0	0	0	0	0.5 ±0.5	3.5 ±2.5	0	**0.9 ±0.7**	**0.1 ±0.05**
		pygmaea	Epi	0	1 ±1	0	0	0.5 ±0.5	2.5 ±2.5	1.5 ±1.5	0	**0.5 ±0.4**	**0.9 ±.3**
		rubidus	Epi	0	0	0	0	0.5 ±0.5	0	1 ±1	0	**0.4 ±0.3**	**0**
	Eisnia	*fetida*	Epi	0	0	0	0	0.5 ±0.5	0	0	0	**0.1 ±0.1**	**0**
	Lumbricus	*spp.*		0	5 ±5	0	0	0	0.5 ±0.5	0.5 ±0.5	0	**0.1 ±0.1**	**1.4 ±0.5**
		castaneus	Ane	0	1 ±1	0.5 ±0.5	0.5 ±0.5	0.5 ±0.5	0	0	0	**0.3 ±0.2**	**0.4 ±0.1**
		rubellus	Endo	0	1 ±0	1 ±	6 ±1	0	0	1.5 ±0.5	0	**0.6 ±0.4**	**1.8 ±0.6**
		terrestris	Ane	0	0	0	0.5 ±0.5	0	0.5 ±0.5	0	0	**0**	**0.3 ±0.09**
	Octolasion	*cyaneum*	Endo	0	0	0.5 ±0.5	0	0	0	0	0	**0.1 ±0.1**	**0**
		lacteum	Endo	0	0	0.5 ±0.5	0	0	0	0	0	**0.1 ±0.1**	**0**
	Satchellius	*mammalis*	Epi	0	0	1 ±1	0	0	0	0	0	**0.3 ±0.3**	**0**

Family	Genus	Species	Ecology	Site 1		Site 2		Site 3		Site 4		**All sites**	
				North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Unknown adults				0.5 ±0.5	1 ±1	4.5 ±3.5	0	1 ±0	8 ±8	2 ±2	1 ±1	**2 ±1**	**2.5 ±0.9**
All adults				1.5 ±0.5	9.5 ±2.5	16 ±0	15 ±2	3 ±1	12.5 ±3.5	11.5 ±9.5	1 ±1	**8 ±2.9**	**9.5 ±3.4**
All juveniles				5 ±4	14.5 ±2.5	13 ±2	14.5 ±3.5	8 ±4	7.5 ±4.5	25 ±10	3.5 ±1.5	**12.8 ±3.6**	**10 ±3.2**

Appendix 8

Mean abundance of the mesofauna found in oak leaves litterbags according to aspect (north- and south-facing slopes), from four different paired north- and south-facing road verges in the SW England (See Figure 5.2 for location) with about 45° slope angle. Abundance is the mean of organisms' count from litterbags left one, two, three and six months in the field, from April to September 2017. Organisms were identified to the 'order' level when possible and in some cases 'adults' and 'larvae' were kept separated due to their different ecology, feeding behaviour, and therefore implication in the decomposition processes. Their feeding behaviour are indicated as following: B, Blood-sucking; C, Carnivorous; D, Detritivores; H, Herbivores; N, nectar of honeydew; P, Predators, S; Scavenging (plants, animals, fungi, bacteria); N/A, not applicable, for example Ephemeroptera, only live two to 3 days and most might not feed during their adult life. Occasional feeding behaviour are in brackets. The zero followed by (*) are not real zero, the data has become zero after changing the number of decimals. It is therefore possible to differenciate real absence of a specie to a real low abundance represented by 0*.

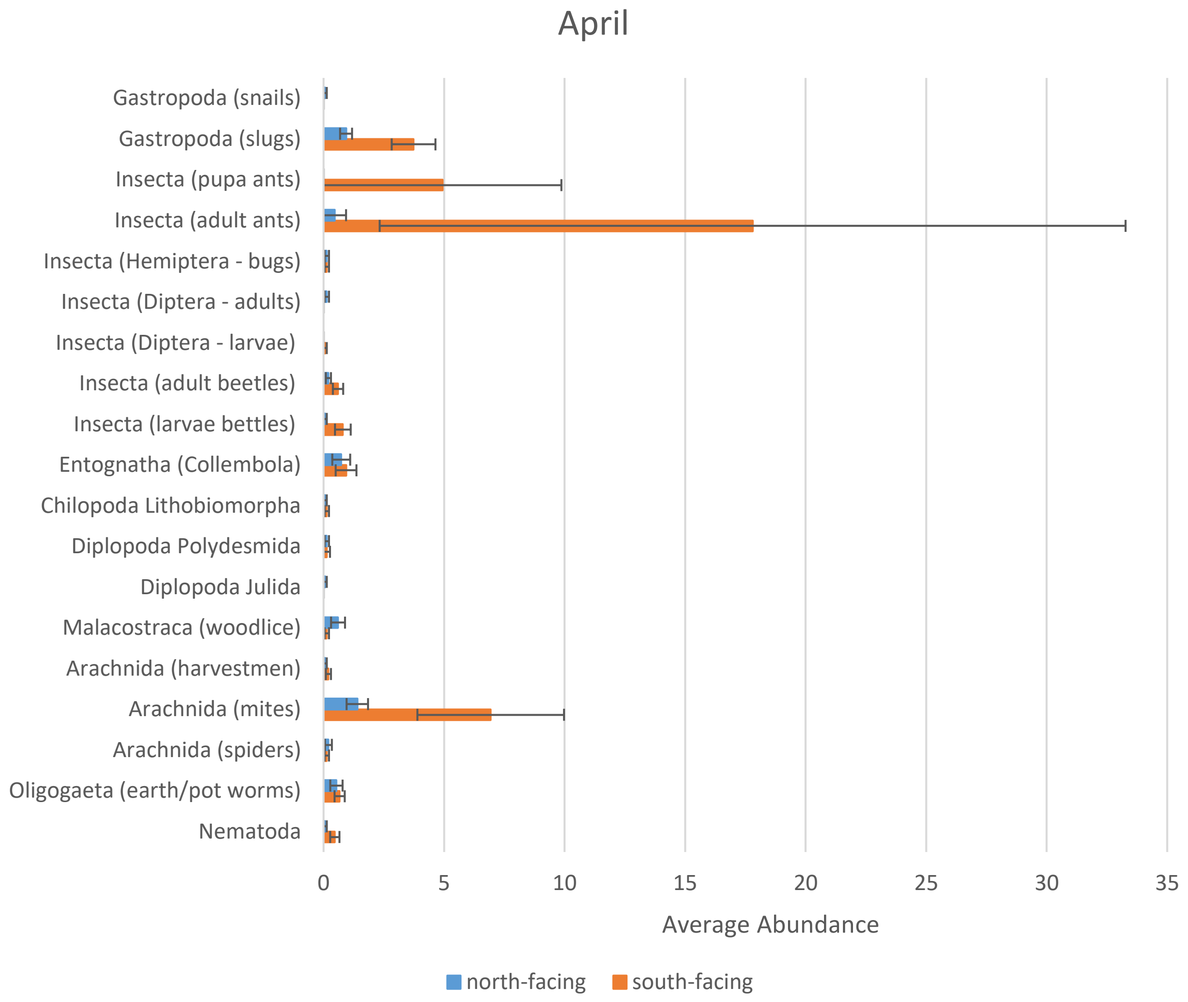
Phylum	Class	Order	Feed-ing behav	site 1		site 2		site 3		site 4		**All sites**	
				North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Nematoda			C, H	0	0.2 ±0.1	0.2 ±0.1	0* ±0*	0.3 ±0.1	0.2 ±0.1	0.2 ±0.1	0.1 ±0.1	**0.2 ±0***	**0.1 ±0***
Annelida	Oligo-chaeta	Haplotaxida	D	0.1 ±0.1	0.9 ±0.3	0.2 ±0.1	0.1 ±0.1	0.5 ±0.2	1.0 ±0.3	1.5 ±0.4	0.8 ±0.3	**0.6 ±0.1**	**0.7 ±0.1**
Arthro-poda	Arach-nida	Pseudoscorpiones	P	0	0.1 ±0.1	0.1 ±0*	0.3 ±0.1	0	0	0.1 ±0*	0* ±0*	**0*0***	**0.1 ±0***
		Araneae	P	0.1 ±0*	0.2 ±0.1	0.3 ±0.1	0.4 ±0.1	0* ±0*	0	0.1 ±0.1	0.1 ±0*	**0.1 ±0***	**0.2 ±0***
		Opiliones	P (S)	0* ±0*	0.1 ±0.1	0.1 ±0.1	0* ±0*	0.1 ±0*	0	0.1 ±0.1	0.0 ±0*	**0.1 ±0***	**0.1 ±0***
		(Acari)	P,D, B (S)	0.2 ±0.1	5.2 ±2.5	1.5 ±0.8	1.2 ±0.4	2.5 ±0.4	1.9 ±0.5	2.0 ±0.4	2.8 ±0.6	**1.6 ±0.2**	**2.9 ±0.7**
	Malacos traca	Isopoda	D, S (H)	0.1 ±0.1	0.6 ±0.3	5.1 ±2.0	0.6 ±0.1	0* ±0*	0.2 ±0.1	0.3 ±0.2	0	**1.3 ±0.5**	**0.3 ±0.1**
		Isopoda (moulting)	N/A	0	0* ±0*	0	0.1 ±0.1	0* ±0*	0	0	0	**0* ±0***	**0.0 ±0***
	Diplo-poda	Chordeumatida	D (H)	0	0* ±0*	0	0	0* ±0*	0	0	0	**0* ±0***	**0.0 ±0***
		Glomerida	D (H)	0	0.1 ±0*	0	0	0* ±0*	0	0	0	**0* ±0***	**0.0 ±0***
		Julida	D (H)	0.1 ±0.1	0.2 ±0.1	0.1 ±0*	0* ±0*	0.1 ±0.1	0* ±0*	0.4 ±0.1	0* ±0*	**0.2 ±0***	**0.1 ±0***
		Polydesmida	D (H)	0.2 ±0.1	0.1 ±0.1	0.3 ±0.2	0	0.2 ±0.1	0.1 ±0.1	0.3 ±0.1	0* ±0*	**0.2 ±0.1**	**0.1 ±0***

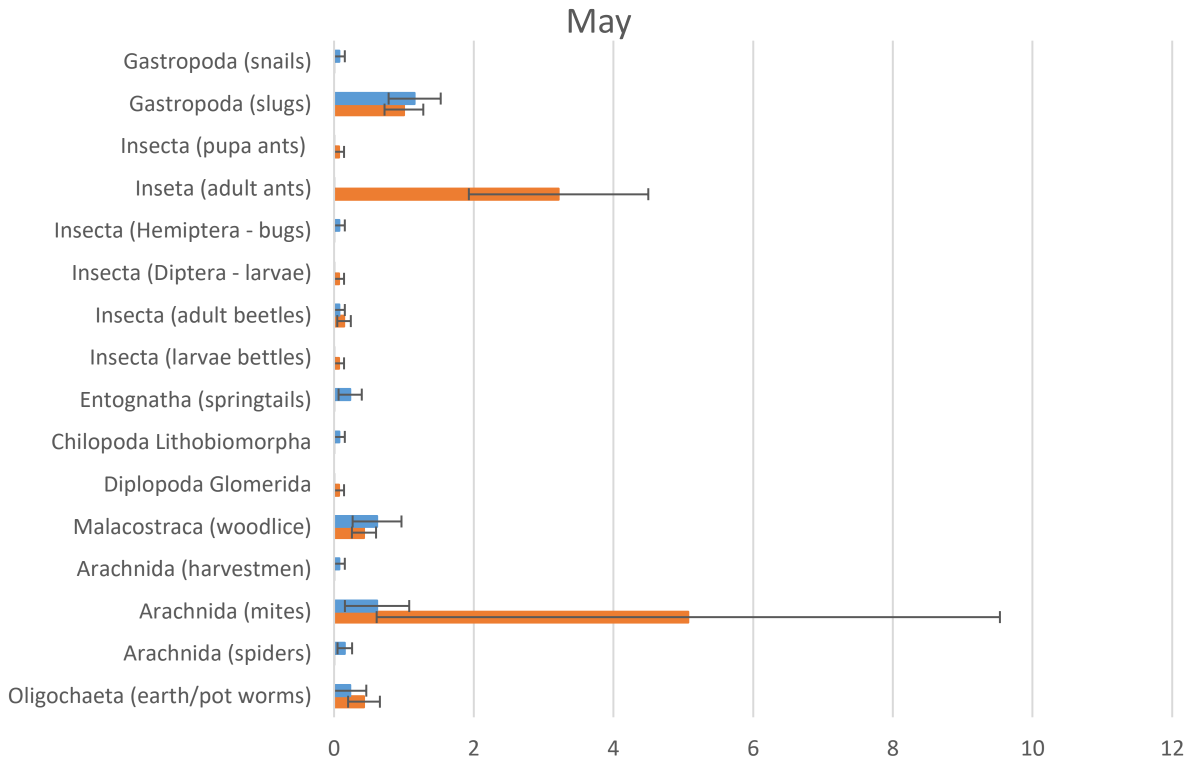
Phylum	Class	Order	Feeding behav	site 1		site 2		site 3		site 4		**All sites**	
				North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Arthropoda	Chilopoda	Geophilomorpha	P	0	0	0.1 ±0*	0	0* ±0*	0* ±0*	0* ±0*	0* ±0*	**0* ±0***	**0.0 ±0***
		Lithobiomorpha	P	0.1 ±0.1	0.6 ±0.2	0.4 ±0.1	0* ±0*	0* ±0*	0* ±0*	0.1 ±0.1	0.1 ±0.1	**0.2 ±0***	**0.2 ±0.1**
		Scolopendromorpha	P	0* ±0*	0	0.1 ±0.1	0	0.1 ±0*	0	0.1 ±0.1	0	**0.1 ±0***	**0**
	Entognatha	Collembola	S	0.2 ±0.1	0.7 ±0.2	1.2 ±0.3	1.0 ±0.3	0.2 ±0.1	0.1 ±0.1	2.1 ±0.8	1.3 ±0.5	**0.9 ±0.2**	**0.8 ±0.2**
	Insecta	Coleoptera (larvae bettle)	P, H, S	0.1 ±0.1	0.4 ±0.2	0	0	0.4 ±0.1	0.1 ±0*	0.2 ±0.1	0.3 ±0.1	**0.2 ±0***	**0.2 ±0.1**
		Coleptera (adult bettle)	P, H, S	0* ±0*	0.2 ±0.1	0.2 ±0.1	0.2 ±0.1	0* ±0*	0.2 ±0.1	0.1 ±0.1	0.1 ±0.1	**0.1 ±0***	**0.1 ±0***
		Coleoptera (Weevil beetle larvae)	P, H, S	0	0	0	0	0	0* ±0*	0	0	**0**	**0* ±0***
		Diptera (larvae)	S	0	0* ±0*	0	0	0* ±0*	0.1 ±0*	0* ±0*	0	**0* ±0***	**0* ±0***
		Diptera (adult)	P, H, S	0	0* ±0*	0* ±0*	0	0* ±0*	0	0* ±0*	0* ±0*	**0* ±0***	**0* ±0***
		Ephemeroptera	N/A	0* ±0*	0	0	0	0	0	0	0	**0* ±0***	**0**
		Hemiptera (bug)	H (P)	0.1 ±0*	0* ±0*	0.1 ±0.1	0*±0*	0* ±0*	0* +0*	0.1 ±0*	0.1 ±0.1	**0.1 ±0***	**0.1 ±0***
		Hemiptera (male scale)	H	0	0.1 ±0.1	0	0	0	0	0* ±0*	0	**0* ±0***	**0* ±0***
		Hymenoptera (Apocrita)	N	0	0	0	0	0	0	0.1 ±0.1	0	**0* ±0***	**0**
		Hymenoptera (ants adult)	P (N)	0.5 ±0.3	0.8 ±0.4	0.2 ±0.2	9.8 ±8.8	0.1 ±0.1	0.8 ±0.4	.0* ±0*	0.9 ±0.5	**0.2 ±0.1**	**2.9 ±1.9**
		Hymenoptera (pupa)		0	0	0	2.6 ±2.6	0	0	0	0	**0**	**0.6 ±0.6**
		Siphonaptera	B	0	0	0	0	0	0	0	0.1 ±0.1	**0**	**0* ±0***
		Thysanoptera (adult)	H (P)	0	0	0	0	0* ±0*	0.1 ±0.1	0* ±0*	0.1 ±0*	**0* ±0***	**0* ±0***
		Thysanoptera (larvae)	H (P)	0	0	0	0* ±0*	0	0	0	0* ±0*	**0**	**0* ±0***
Mollusca	Gastropoda	(slugs)	H	2.4 ±0.9	1.8 ±0.5	0.1 ±0*	0.2 ±0.1	0.7 ±0.1	0.8 ±0.2	1.6 ±0.3	2.3 ±0.5	**1.2 ±0.2**	**1.3 ±0.2**

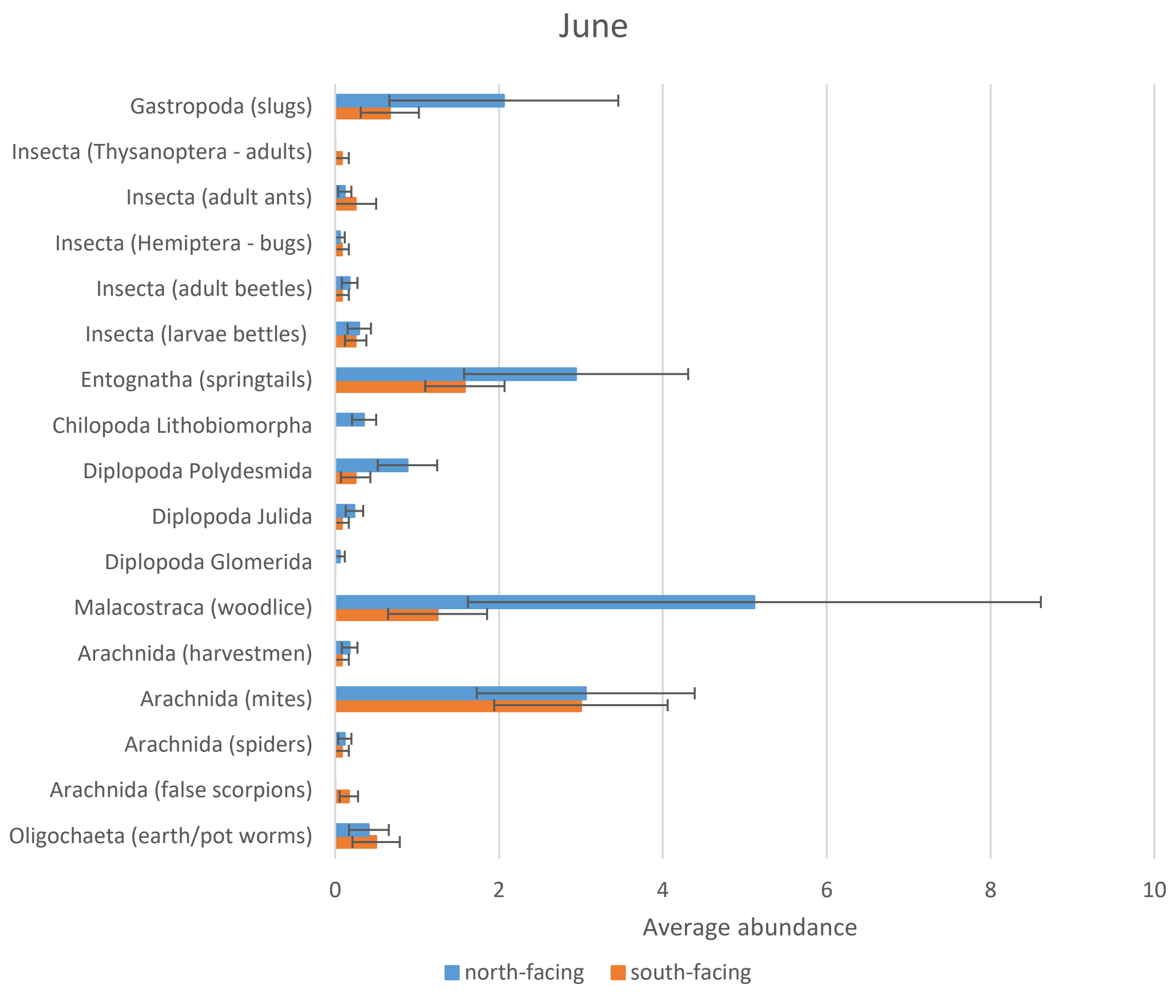
Phylum	Class	Order	Feeding behav	site 1		site 2		site 3		site 4		**All sites**	
				North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	North-facing	South-facing	**North-facing**	**South-facing**
Mollusca	Gastropoda	(snails)	H	0.1 ±0.1	0.3 ±0.1	0.1 ±0.1	0	0.1 ±0*	0	0	0.2 ±0.1	**0.1 ±0***	**0.1 ±0***
		(empty shells)	N/A	0	0* ±0*	0.1 ±0*	0	0	0	0	0.1 ±0*	**0* ±0***	**0* ±0***
		Unknown egg 1	N/A	0	0* ±0*	0	0	0.1 ±0.1	0	0	0.1 ±0.1	**0* ±0***	**0* ±0***
		Unknown egg 2	N/A	0	0	0.1 ±0.1	0	0	0	0	0	**0* ±0***	**0**
		Unknown egg 3	N/A	0	0	0	0	0.1 ±0.1	0	0	0	**0* ±0***	**0**
		Unknown egg 4	N/A	0	0	0	0	0* ±0*	0	0	0	**0* ±0***	**0**
		Unknown 1	N/A	0* ±0*	0.1 ±0.1	0	0	0	0	0* ±0*	0.1 ±0.1	**0* ±0***	**0* ±0***
		Unknown 2	N/A	0	0* ±0*	0	0	0	0	0	0	**0**	**0* ±0***
		Unknown 3	N/A	0	0	0	0	0* ±0*	0	0	0	**0* ±0***	**0**
		Unknown 4	N/A	0	0	0	0	0*±0*	0	0	0	**0* ±0***	**0**
		Unknown 5	N/A	0* ±0*	0	0	0	0	0	0	0	**0*±0***	**0**

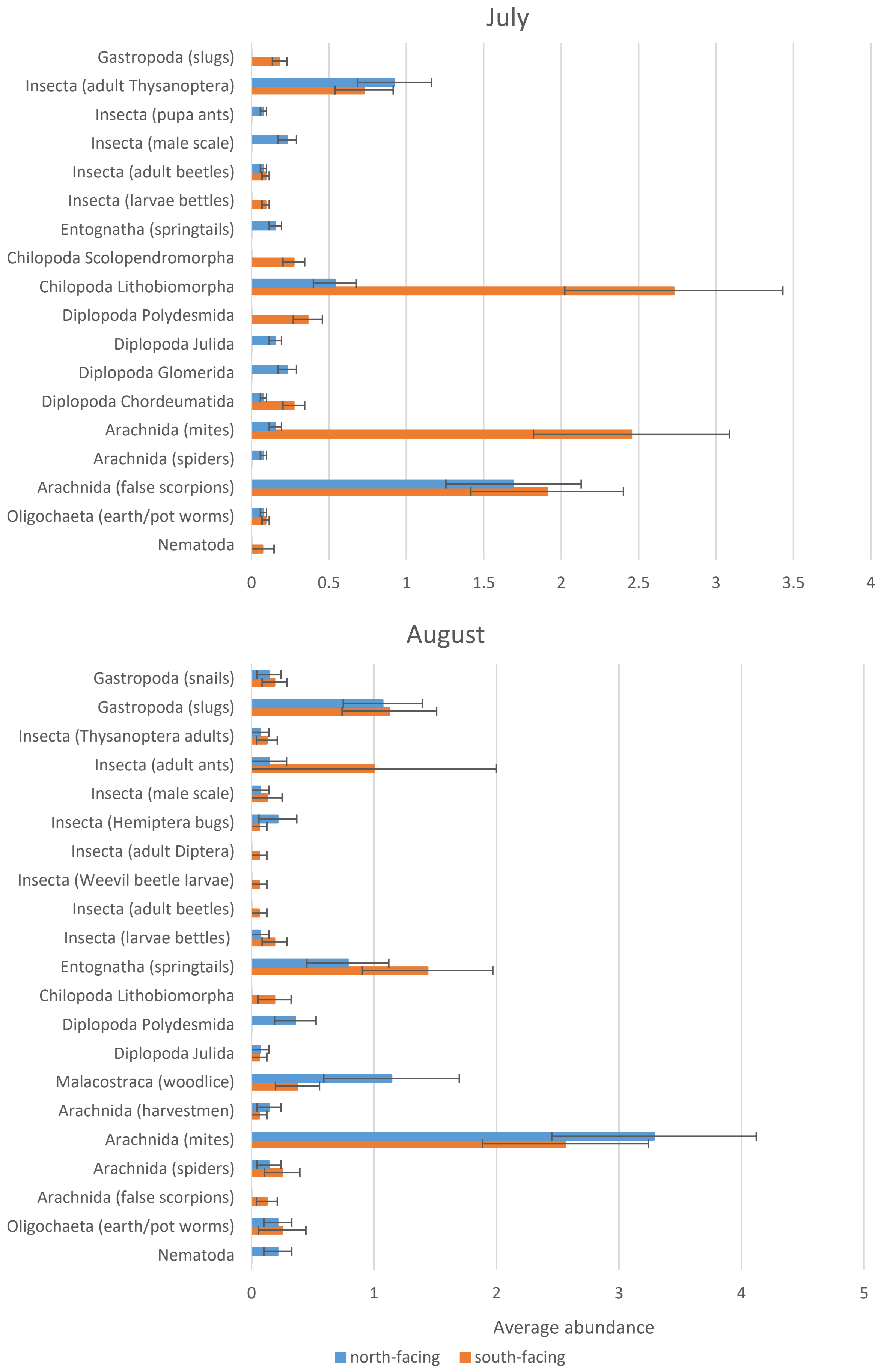
Appendix 9

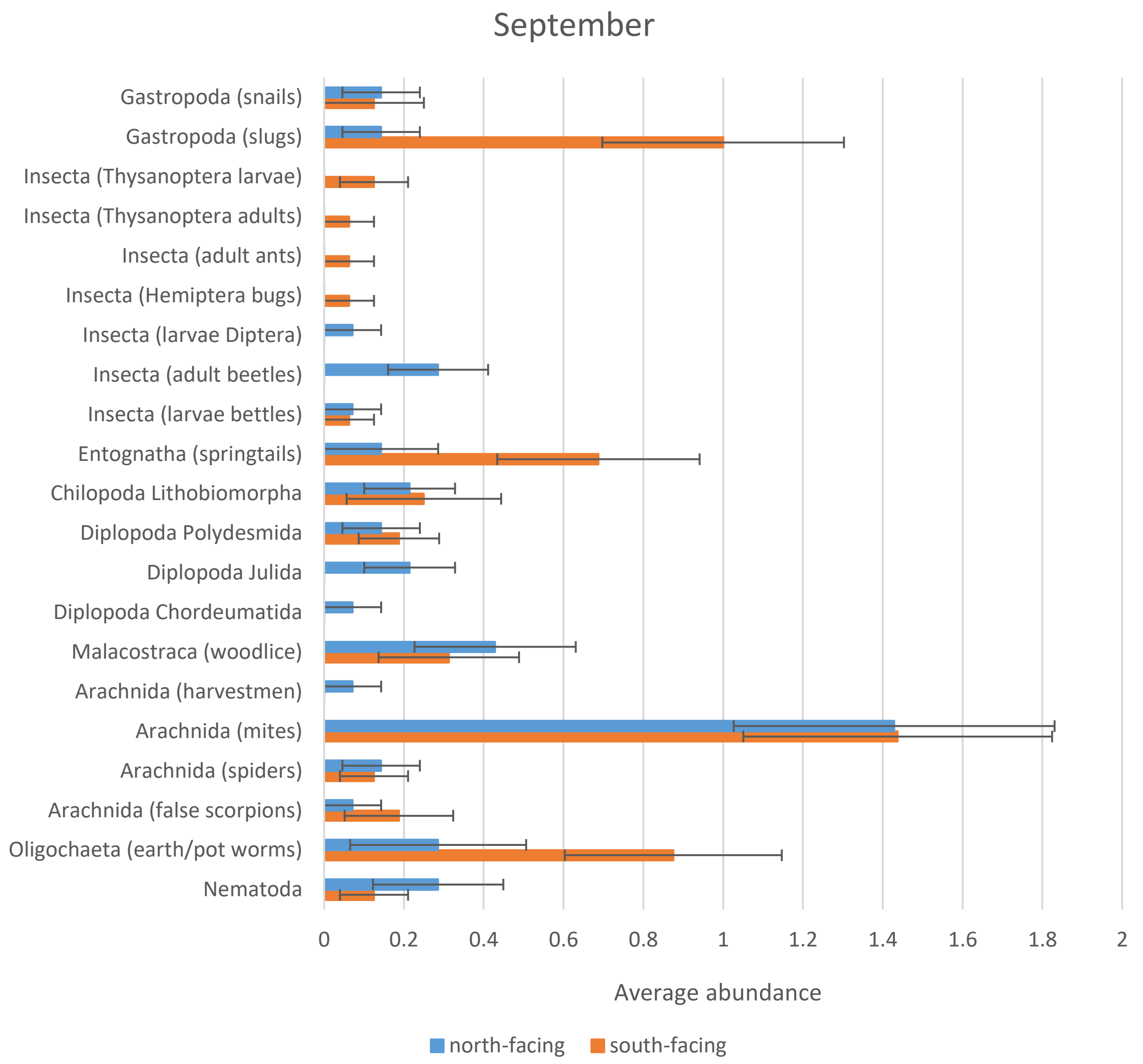
Diagrams of average abundance of the mesofauna sampled from oak leaves litterbags according to aspect, from four different paired north- (blue) and south-facing (red) road verges in the SW England (See Figure 5.2 for location) with about 45° slope angle, collected monthly from April to September 2017. Organisms were identified to the 'order' level when possible and in some cases 'adults' and 'larvae' were kept separated due to their different ecology, feeding behaviour, and therefore implication in the decomposition processes. Their feeding behaviour can be found in Appendix 5.1.




May
Gastropoda (snails)
Gastropoda (slugs)
Insecta (pupa ants)
Inseta (adult ants)
Insecta (Hemiptera - bugs)
Insecta (Diptera - larvae)
Insecta (adult beetles)
Insecta (larvae bettles)
Entognatha (springtails)
Chilopoda Lithobiomorpha
Diplopoda Glomerida
Malacostraca (woodlice)
Arachnida (harvestmen)
Arachnida (mites)
Arachnida (spiders)
Oligochaeta (earth/pot worms)
0
2
4
6
8
10
12


June
Gastropoda (slugs)
Insecta (Thysanoptera - adults)
Insecta (adult ants)
Insecta (Hemiptera - bugs)
Insecta (adult beetles)
Insecta (larvae bettles)
Entognatha (springtails)
Chilopoda Lithobiomorpha
Diplopoda Polydesmida
Diplopoda Julida
Diplopoda Glomerida
Malacostraca (woodlice)
Arachnida (harvestmen)
Arachnida (mites)
Arachnida (spiders)
Arachnida (false scorpions)
Oligochaeta (earth/pot worms)
0
2
4
6
8
10
Average abundance
north-facing
south-facing


July
Gastropoda (slugs)
Insecta (adult Thysanoptera)
Insecta (pupa ants)
Insecta (male scale)
Insecta (adult beetles)
Insecta (larvae bettles)
Entognatha (springtails)
Chilopoda Scolopendromorpha
Chilopoda Lithobiomorpha
Diplopoda Polydesmida
Diplopoda Julida
Diplopoda Glomerida
Diplopoda Chordeumatida
Arachnida (mites)
Arachnida (spiders)
Arachnida (false scorpions)
Oligochaeta (earth/pot worms)
Nematoda
0
0.5
1
1.5
2
2.5
3
3.5
4
August
Gastropoda (snails)
Gastropoda (slugs)
Insecta (Thysanoptera adults)
Insecta (adult ants)
Insecta (male scale)
Insecta (Hemiptera bugs)
Insecta (adult Diptera)
Insecta (Weevil beetle larvae)
Insecta (adult beetles)
Insecta (larvae bettles)
Entognatha (springtails)
Chilopoda Lithobiomorpha
Diplopoda Polydesmida
Diplopoda Julida
Malacostraca (woodlice)
Arachnida (harvestmen)
Arachnida (mites)
Arachnida (spiders)
Arachnida (false scorpions)
Oligochaeta (earth/pot worms)
Nematoda
0
1
2
3
4
5
Average abundance
north-facing
south-facing


September
Gastropoda (snails)
Gastropoda (slugs)
Insecta (Thysanoptera larvae)
Insecta (Thysanoptera adults)
Insecta (adult ants)
Insecta (Hemiptera bugs)
Insecta (larvae Diptera)
Insecta (adult beetles)
Insecta (larvae bettles)
Entognatha (springtails)
Chilopoda Lithobiomorpha
Diplopoda Polydesmida
Diplopoda Julida
Diplopoda Chordeumatida
Malacostraca (woodlice)
Arachnida (harvestmen)
Arachnida (mites)
Arachnida (spiders)
Arachnida (false scorpions)
Oligochaeta (earth/pot worms)
Nematoda
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Average abundance
north-facing
south-facing

Appendix 10

Additional study on the effect of aspects and a hot extreme event on the phenology of limpets

1. Introduction

Patella vulgata and *Patella depressa* are very common intertidal limpet species in SW England. They occupy similar niches (Hawkins et al., 2009) and exploit similar food resources (Thompson et al., 2000). The first part of this chapter suggested that they also have similar osmotic response to desiccation and dilution stress. However, body temperature affects almost every facet of organismal physiology (Denny and Gaines, 2007), and thus, has the potential to affect processes such as survival, growth and reproduction. In addition to their distributional range, *P. vulgata* and *P. depressa* also differ in their period of spawning. Comparing historical data collected in the 1940s (1946-1949) and recent data from the 2000s (2003-2007), Moore et al. (2011) were able to investigate the effect of global warming on the phenology of *P. depressa* and *P. vulgata*. Gonad development in *P. depressa* advanced by ~10.2 days per decade, had a longer reproductive season, and higher proportion of the population were reproductively active. This advance in peak reproduction was positively correlated with sea surface temperature (SST) in late spring/early summer, which increased between 1940s and 2000s. In contrast, gonad development in *P. vulgata* was delayed by ~3.3 days per decade, increased the reproductive failure years, and had a reduction in the proportion of the reproductively active population.

The distribution of Patella *vulgata* extends from the North of Norway to the Mediterranean, and is known as a winter breeder, although in southern locations reproduction happens earlier (Bowman, 1981; Fernández et al., 2015). A clear latitudinal gradient was therefore found in its main spawning season across its distributional range (Bowman and Lewis, 1986). Near the northern range margin, spawning started in the summer (i.e. July/August in Tromsø, Norway), shifted to September/October in NE England and Scotland, and December/January in North Portugal (Bowman and Lewis, 1986). A latitudinal gradient was also apparent for spawning season length. Very rare ripe gonads were found unspawned mid-December in the north of the UK, while major spawning could expend as late as January in the south, and into March in Portugal (Bowman and Lewis, 1986). Yet, in some years, spawning season might start earlier than usual and extend for a much longer period (e.g. years 1977-78 in Scotland and NE England; Bowman and Lewis, 1986), or might start relatively late with little or no redevelopment of gonads (e.g. years 1973-74 in Scotland; Bowman, 1985 cited in Bowman and Lewis 1986). This yearly variation already triggered that climatic factors might be involved in limpet reproduction. Bowman (1981) and Bowman and Lewis (1986) found that the main spawning time for each region occurred during the period when mean sea temperature dropped below 12°C. In addition, populations located in sheltered sites matured earlier than the exposed ones, and spread over a longer period (Fernández et al., 2015). Similarly, storms and heavy swells favour gamete release (Bowman and Lewis, 1986).

Patella depressa, is found on the Atlantic coast from South Portugal to North Wales. In the UK, it is a summer-breeding species but with similar yearly variation to *P. vulgata*. For example, *P. depressa* spawns from April/May until June/July (Orton and Southward, 1961), or from May/June until October/November (Bowman and Lewis, 1986) in SW England. Some years, this species will have multiple spawning events and redevelopment similar to *P. vulgata,* but sometimes so extensive that they resemble separate breeding seasons (e.g. in 1978, spawning in June/July followed by later spawning in October/November in SW England;

Bowman and Lewis, 1986). Moore et al. (2011) even found an increase in the number of peaks per reproductive season, associated with climate change, and especially increase in sea surface temperature (SST) over time. As for *P. vulgata*, exposure of the shore was shown to influence maturity of *P. depressa* gonads (Morais et al., 2003).

In Chapter 2, I found that *Patella depressa* had a much greater abundance than *P. vulgata* on both aspects, and that both species had a much greater abundance on the north- than south-facing substrata. The difference in the distribution of both *Patella* species according to aspect was assumed to be connected with the annual mean temperature and probably more to the difference in hot extreme events. The aim of this study was to investigate if and how small-scale temperature variations, as recorded on north/south facing gullies, reflected also variation and shift in the gonads development of both limpet species. In addition, as the annual average temperature difference between aspects (about 1°C) aligns closely with the 0.85°C global warming since the late 19th century, I predict any aspect-related variations in gonad development to follow similar patterns as variations associated with global change (findings from Moore et al., 2011). Therefore, the tested hypothesis are the following:

H1: Delayed and reduced reproduction of *Patella vulgata* on the south- compared to the north-facing substrata.

H2: Advanced, prolonged *Patella depressa* reproductive season and increased numbers of reproductively mature individuals on south-facing substrata.

2. Material and methods

2.1. Sea-surface temperature (SST)

This current study was performed after the year-long deployment of the data loggers used in Chapter 2. Therefore, SST was obtained from the Western Channel Observatory for the period mid-May to end of December 2018. Data were recorded hourly at the L4 Autonomous Buoy (0°15.0'N; 4°13.0'W), not far from Plymouth, and about 25 km from the limpet collection site. Due to annual maintenance of the buoy, no data were collected in January 2019. SST was graphed so that the suggested 12°C limit for triggering gonads development of *P. vulgata* (Bowman, 1981; Bowman and Lewis, 1986) could be inferred. No statistical analysis was performed using the SST data.

2.2. Study sites, limpet sampling and analysis

Limpets were collected from Bantham Beach on the south coast of the SW peninsula of England (see Chapter 2, Figure 2.2A). Limpets were sampled from the mid-shore level from 1-5 m high, on almost vertical gullies, offering paired north- and south-facing aspect separated by only a few meters (See Chapter 2, picture 2.2B). All selected gullies were perpendicular to the sea and parallel to each other, so that wave action was similar across aspects and gullies. Fifty limpets of each species, ranging from 25-45 mm long were collected from each aspect monthly (50 x 2 species x 2 aspects = 200 limpets), placed in a labelled bag, brought back to the laboratory and frozen (T = -18.0°C) until later dissection. This shell size range corresponds to adult size, where gonad development is detectable, and resulting in approximately similar ratio of female and male; More et al., 2011. Freezing limpets does not change the development stage of the gonads, compared to fresh samples (Moore et al., 2011). Gonad development of *P. depressa* was investigated in this experiment from May to September, and from September to February in *P. vulgata*.

Dissection of the limpet foot, to reveal their gonad, was carried out closely following the method of Orton et al. (1956). The sex of the limpet was determined by internal colour; males have pinkish white or cream gonads, while females have green or brown ones (Orton et al., 1956). Individuals with no clear gonad development but containing a discrete reddish brown kidney-shaped structure were considered ‘neuters’. When gonads were visible, they were allocated to one of the arbitrary stages described in detail by Orton et al. (1956), and listed below (See Figure A10.1for pictures):

- Neuter: Either rudimentary virgin stage or resting after discharge of gametes
- Stage 1: Beginning to develop, and sex detectable, but only slight increase in size
- Stage 2: Developing to one-third full size
- Stage 3: Between one-third and two-thirds full size
- Stage 4: Two-thirds full size
- Stage 5: Fully developed

When spawning occurs, not all eggs or sperm are shed at once and gonads gradually regress from stage 5 to neuter. Gonads undergoing progressive development (towards stage 5) or regression (from stage 5 to neuter) are difficult to distinguish, and criteria separating them are undoubtedly subjective and difficult to describe (Orton et al., 1956). In some cases, microscopic section of the gonads can help identify regression or development (Orton et al., 1956). Therefore, in the current study, no distinction was made between regressing and developing gonads following Moore et al. (2011).

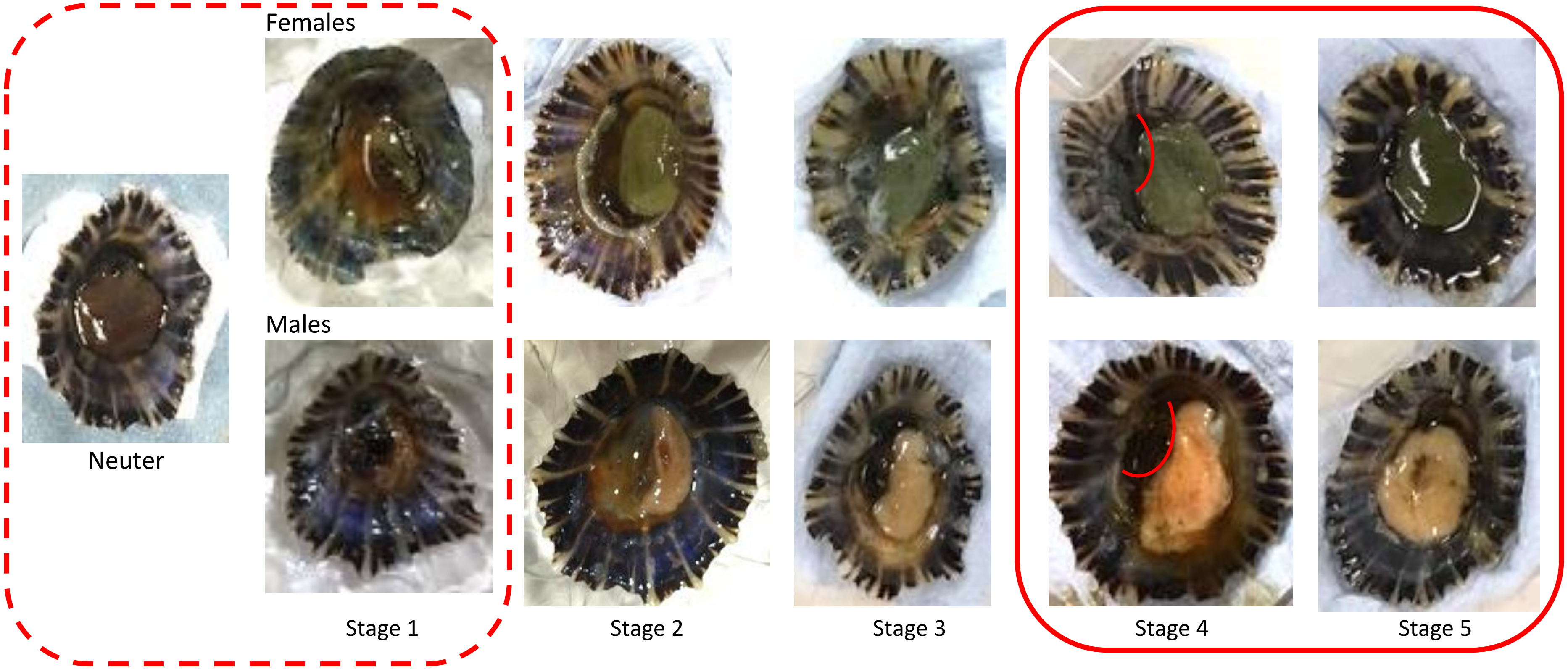


Figure A10.1: Images of the arbitrary gonads development stages of the limpet *Patella depressa*, first described by Orton et al. (1956), used in Chapter 3.3 on *Patella depressa* and *Patella vulgata*. Note that gonad development is similar in shape and colour in both species. The limpet on the left is a neuter, limpet with no developed gonads and therefore no sex yet (brown-ish colour). The top row represents stages 1 to 5 of females, identifiable with olive-green to light brown gonads colour. The bottom row represents stages 1 to 5 of male limpets, distinguishable with their orange to creamy coloured gonads. Stages 4 and 5 (in red box) are fully developed/mature stages, where limpets can release gametes. Both neuter and stage 1 were referred as the undeveloped gametes (red dashed box).

The reproductive cycle of each species was described by the monthly variation in the proportion of reproductively active limpets with gonads in advanced stages (stage 4 & 5; Moore et al., 2011) and non-reproductively active ones, with undeveloped gonads (neuters and stage 1). By doing so, spawning events can be identified by a drop in the proportion of full gonads (stage 4 & 5) and a concomitant increase in the percentage of empty gonads (neuter and stage 1) (Ribeiro et al., 2009). Stages 2 and 3 are referred to, here, as intermediate stages, but will not be plotted, nor analysed.

To test if the peak of proportion of limpets in advanced stages of gonad development had changed between north- and south-facing substrata, for both species, one-way ANOVAs were performed.

3. Results

3.1. Aspect and gonad development in *Patella depressa*

At the beginning of the study for *P. depressa*, in May, the gonad development had already started on both aspects, and there was a significantly higher proportion of advanced gonads in limpets on the south- than north-facing substrata ($F_{1,92} = 9.42$, $p = 0.03$; Figure A10.2). There was already 40 % advanced gonads in limpets on the south-facing substrata and about 10% of empty gonads. In addition, the much lower proportion of undeveloped gonads on the south- facing substrata suggested that there were more intermediate stage gonads compared to the north-facing. The peak of reproduction (65-70% of advanced gonads) was reached in July, on both aspects, and did not vary with aspect, and was immediately followed by a drop of about 45-50% of advanced gonads the following month. This peak started gradually in June on the north-facing substrata, while the peak was more sudden on the south-facing substrata.

A difference between aspects was noticeable in the regression rate of gonads (from full to empty), which can be a sign of gametes release when following an increase of advanced gonads proportion. This process seemed to have happened relatively slowly and constantly from July to September on the south-facing substrata, while it was increasing rapidly in a peak from August to September on the north-facing ones.

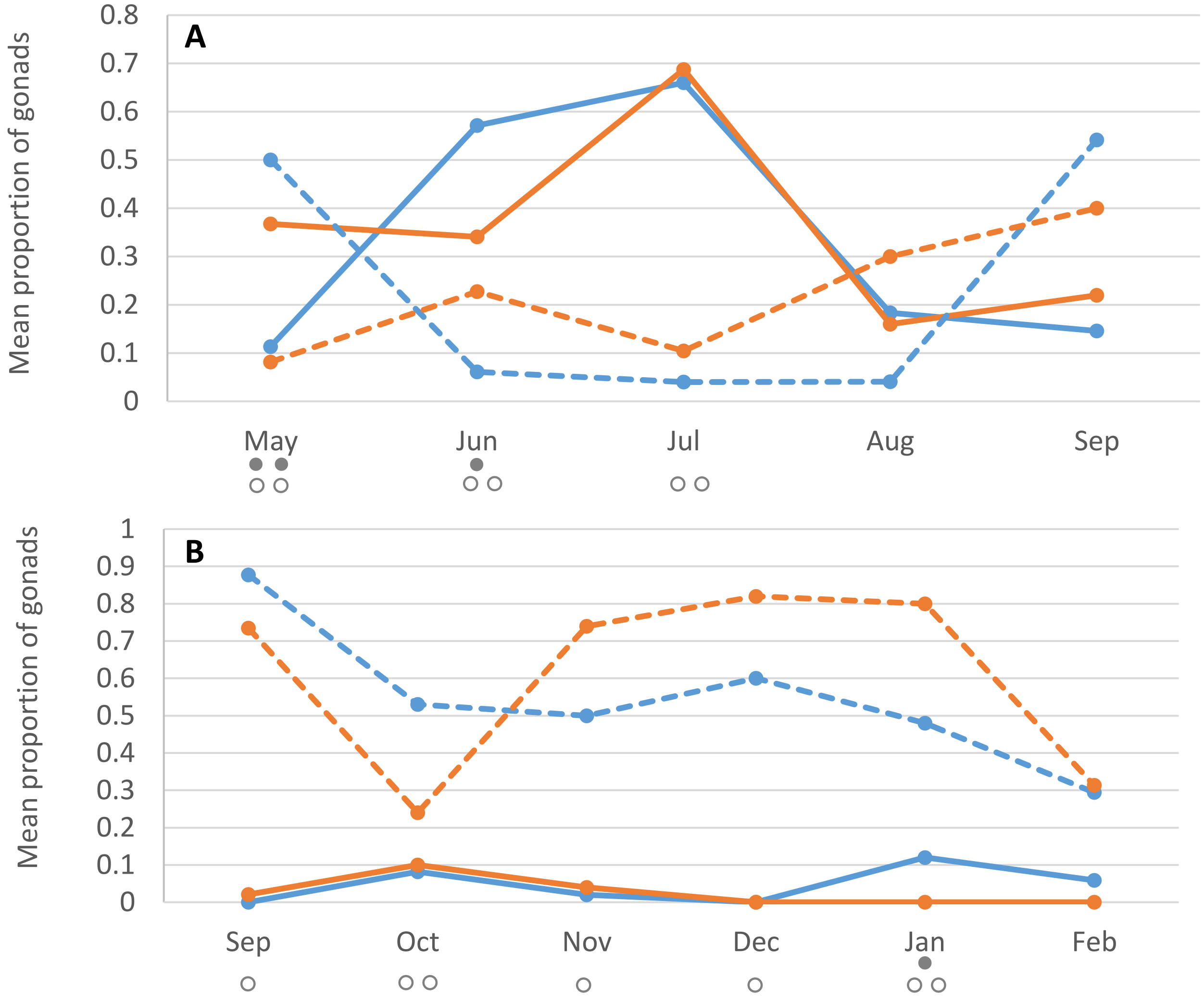


Figure A10.2: Mean proportion of gonads in advanced (stages 4 and 5; in full line) and undeveloped (neuters and stage 1; in dashed line) state, between May 2018 and February 2019, of **A.** *Patella depressa* – Lusitanian summer-breeder, and **B.** *Patella vulgata* – boreal winter-breeder, according to aspect. Limpets were collected from Bantham, SW England, on north- (blue) and south-facing (red) substrata, during their respective reproductive season. Symbols ● (advanced stages) or ○ (undeveloped stages) indicates significance within the same month with $p \leq 0.05$, and ○○ or ●● with $p \leq 0.01$.

3.2. Aspect and gonad development in *Patella vulgata*

At the start of the gonad development investigation in September, SST was almost 16°C and steadily dropped to reach temperatures of below 12°C as late as December (Figure A10.3).

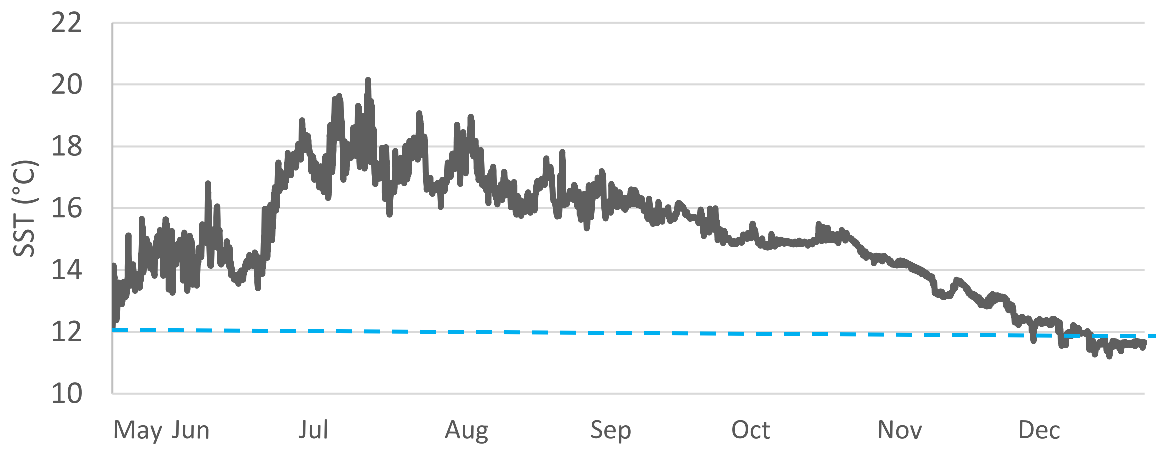


Figure A10.3: Sea Surface Temperature (SST) in °C, from the L4 Autonomous Buoy (see Western Channel Observatory) near Plymouth, SW England. SST data correspond to hourly recording from mid-May to end of December 2018. The suggested 12°C limit for triggering gonads development of *P. vulgata* (Bowman, 1981; Bowman and Lewis, 1986) is represented by the dashed blue line.

The proportion of developed stages of *P. vulgata* gonad was extremely low from September to February, suggesting that *P. vulgata* had a failure in reproductive ability during the winter 2018-19. At the start of the study (September) the most of the gonads were undeveloped in both aspects, and from September to October a drop in their proportion reflected a development of gonads principally to intermediate stages, and about 10% to mature gonads (stage 4 & 5) on both aspects. This slight increase of mature gonads did not last nor increased, and gradually decreased to zero in December, when a second slight increase in the proportion of mature gonads (up to 10%) occurred, but this time on the north-facing substrata only. Although this increase was low, it was still significantly different to the opposite south-facing aspect, for both January ($F_{1,92} = 9.42$, $p = 0.03$) and February ($F_{1,97} = 6.72$, $p = 0.011$). The decrease of undeveloped gonads happening at the same time of the increase in mature gonads suggested a release of gametes during both those small peaks in October and January. During the period from September to February, the proportion of undeveloped gonads stayed very high on both aspects, but was lower on the north- than south-facing substrata from November to February, suggesting that more gonads developed to intermediate stages.

4. Discussion

Comparison of the gonad development of *Patella depressa* and *P. vulgata* on north- and south-facing substrata suggests that aspect can impact their reproduction at a small scale. The proportion of advanced gonads in *P. vulgata* was so low that is was impossible to detect any start to the reproductive season; therefore, hypothesis 1 could not be tested. Although, despite the very low proportion of advanced gonads in *P. vulgata*, more were found on north- than south-facing substrata. Due to the limited sample period for *P. depressa*, the full reproductive season was not recorded and so I was unable to detect any advancement and lengthening of the season with respect to aspect, although it was clear that the proportion of advanced gonads in *P. depressa* on south- and north-facing substrata was similar.

Over the five months of the experiment, the proportion of advanced gonads in *P. depressa* was similar on both aspects and the peak of reproduction recorded in mid-summer happened at the same time and same amplitude on north- and south-facing substrata. From May, where the proportion of advanced gonads in *P. depressa* was rather low, to the peak in July, the progressive development of gonads appeared to be slower and constant on the warmer south-facing substrata, although rapid development (in one month) was recorded on north-facing substrata. Due to the timing of this experiment, the start of the reproductive season of *P. depressa* was not captured, not allowing me to verify whether gonad development of this species started earlier on the warmer south-facing substrata than on the cooler north-facing ones. However, the data from my experiment (May to July) suggests that gonad development in *P. depressa* might be more concentrated around the peak of reproduction on the north-facing substrata, suggesting that development of gonads might be more operative when it is warmer.

P. vulgata experienced a 'reproductive failure' year (Brown and Lewis, 1986; Moore et al., 2011). Peak of *P. vulgata* reproduction from 1973 to 1984 in SW England happened on average around November (Brown and Lewis, 1986), or more generally between October and December depending on the year (e.g., 1946-49; Orton et al., 1956). A latitudinal investigation in the UK of reproductive cycle of this limpet species along its distributional range, uncovered a link between spawning events and drop of SST below 12°C across all studied locations (Bowman and Lewis, 1986). This temperature recorded around late summer/autumn in 1980s in England, is thought to be an important cue for gonad development in *P. vulgata* (Bowman and Lewis, 1986). A relationship between the change in SST and spawning phenology has been described in other marine molluscs. For example, the Antarctic limpet *Nacella concinna* spawns about three weeks after the coastal seawater exceeds -1.4°C (Picken, 1980); or the clam *Mercenaria mercenaria,* which appeared to spawn in North Carolina (USA) when temperatures rose above 10°C (Porter, 1964). Conversely, spawning was induced by a decrease of mean seawater temperature from 30 to 25°C during the reproductive season of the scallop *Argopecten irradians* in Florida (USA) at its southern distributional limit, while the temperature threshold was lower towards the north of its distributional range (Barber and Blake, 1983).

With increasing SST *P. vulgata* seemed to have adapted to this warming by delaying its reproductive season (Moore et al., 2011). In 2018, during my experiment, a SST of 12°C was first recorded early December, which could explain why *P. vulgata* did not reproduce during what should be its ‘normal’ reproductive window in this part of Britain. This atypical delay in the decrease in SST was very likely due to the extremely hot summer experienced in Europe, (the hottest summer in the UK since the first records in 1910 (MetOffice, 2018)). A minor spawning event was detected in January and February, suggesting that reaching 12°C SST in December started the maturation process of some gonads. A longer sampling season would have allowed assessing whether or not this small detected spawning event would have increased and eventually started on the south-facing substrata.

From the 1940s to 2000s, a reduction of the proportion advanced gonads was found in *P. vulgata* during its reproductive season, and was associated to ACC and more especially with increase of SST (Moore, et al. 2011). Similarly, during the minor spawning event in January and February, no reproductively active limpets were found on warmer south-facing substrata, while the only mature limpets where recorded on the cooler north-facing slopes. Although Moore et al. (2011) demonstrated a positive correlation between SST and the proportion of reproductively active limpets, I demonstrated in Chapter 2 that during low tide, south-facing substrata were on average 1.5°C warmer than the opposite north-facing substrata, and that no difference was found during high tide. Therefore, the difference in proportion of advanced gonads in *P. vulgata* according to aspect found in my experiment, however quite low, could suggest that air temperature could also have an impact on gonad maturation for limpets.

As a result of increased SST over the decades due to ACC Moore et al. (2011) reported an increase in the frequency of *P. vulgata* failure years. In addition to an increase of SST, hot extreme events, like those in 2018, are predicted to become more frequent, intense, and longer-lasting (IPCC, 2012). Although both *P. depressa* and *P. vulgata* have about 4 months interval in their reproduction cycle, which limits hybridization (Orton and Southward, 1961), ACC-driven changes might trigger *P. vulgata* to delay even more its reproductive season and *P. depressa* to advance (as already found by Moore et al., 2011), leading to a risk of hybridization. In addition, although limpets tend to correlate their spawning with food abundance in the water column (Branch 1974, 1981) for their planktotrophic trochophore larvae (Ribeiro, delaying their spawning due to change in SST might lead to a mismatch with autumn plankton blooms on which the limpets' larvae feed on. A decline in *P. vulgata* could therefore be expected, starting by its southern range limit, and *P. depressa* is already predicted to replace this species, as a result of climate change (Hawkins et al., 2016; Letcher, 2016). On the other hand, warm-adapted species, such as *P. depressa* (Moore et al., 2011), often have extended their reproductive season. This longer reproductive season might be beneficial as it could allow to still coincide with potential delays or advancements of planktonic blooms.

Although clear aspect-related patterns did not emerge from this study, mainly due to the too short length of the experiment, and to the reproductive failure of *P. vulgata*, reproduction cycles of both *P. depressa* and *P. vulgata* are known to vary from one year to another (Orton et al., 1956; Orton and Southward, 1961; Bowman and Lewis, 1986; Ribeiro et al., 2009; Moore et al., 2011). Therefore, a longer-term study (capture full reproductive season and over several years) might illustrate clearer patterns and variations between aspects. More reproduction cycles should also be analysed following extremely hot summers and cold winters, in order to associate any differences to those events. As south-facing substrata are on average warmer and experience frequently more hot extreme temperatures during low tide, than on the north-facing substrata, cold-adapted species, such as *P. vulgata*, might have better success of reproduction on the cooler aspect. Therefore, in the context of global warming, the importance of gullies might grow, as they might offer reproductive refugia for certain species, or at least act as temperature buffer.