The relative importance of microclimate and land use to biodiversity

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Abstract

The extent of species' distributions, and their abundance within them, can be affected by many factors. At coarse resolutions and large spatial extents, climatic variables are often found to be important in determining the boundaries of species' ranges. However, several authors have postulated that variables such as land cover or species interactions are more important in determining where species will be found at finer resolutions within a landscape. Climatic variables are often not available at the fine resolutions necessary to test this hypothesis. In this study, I first show that topography is important in influencing the temperature that will be experienced at a particular location. Temperatures generally decrease with elevation (known as the lapse rate). However, extremes of temperature, such as absolute maxima and minima, can also be influenced by the angle and aspect of a slope. Whilst high resolution elevation data are occasionally included in climatic models of species' distributions, the effects of slope and aspect have so far been ignored. My second data chapter uses all three topographical variables (elevation, slope and aspect) to interpolate temperatures for three landscapes. These interpolated temperatures, along with land cover variables and an index of soil moisture, are included in exploratory analyses which suggest that microclimate is at least as important as land cover in determining spatial patterns of abundance for 20 species of ground beetle. Given this potential importance of microclimate in determining where species will be found at fine resolutions, I then show that different resolution data layers generate different predictions about the amount of a landscape that will remain suitable following climatic warming. Fine resolution layers predict a slower loss of thermally suitable habitat for a northerly-distributed species in a reserve located at its southern range margin. I therefore conclude that, in topographically diverse areas, where a wide range of temperature conditions can be encountered, climatic variables should be considered at spatial resolutions relevant to individuals of species whose distributions are modelled using the 'climate-envelope' approach rather than the coarse-resolution data that are currently used.

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Declaration

The material in this thesis is my own work, except where specific references have been given to the work of others. Where data have been obtained from external sources, this is specified in the text and in the acknowledgements.

A large part of Chapter 4 is printed in Oikos as part of a joint paper between myself, Andrew Suggitt and all of our supervisors (Suggitt *et al.* 2010). All the analyses included in Chapter 4 were undertaken by me. However, Figure 4.1 was created by Andrew Suggitt from values calculated by me. In addition, paragraphs 5 - 8 of the discussion for Chapter 4 have been modified by me from the original text of the paper. This part of the discussion was originally written mainly by Andrew Suggitt, with corrections from me and our co-authors.

1 General Background to Study

1.1 Rationale for thesis

Much of ecology is concerned with the niches of species. These can be divided into fundamental and realised niches. The fundamental niche refers to the combination of conditions that a species could, in theory, occupy. Many factors can contribute to the fundamental niche, and one of these is the temperature experienced. Other factors could include moisture availability, the presence of a suitable food source or nest site. However, in reality, most species do not occupy all of the areas that appear suitable for them. In many cases, there might be geographical boundaries preventing movement into a suitable area. Evidence for this comes from the large number of species that are considered ‘invasive’ when introduced to countries other than those they originated in. When conditions are suitable, such species can establish resident populations in the country they have been introduced to, and in some cases expand quickly both in population size and area covered. Examples of such invasive species are the cane toad in Australia (Sabath *et al.* 1981), which was introduced from central America by man, and the harlequin ladybird in Great Britain (GB, Brown *et al.* 2008). Some areas have been affected more than others by invasive species; in Hawaii many native species have gone extinct, and these extinctions have been attributed to the success of a variety of invasive species, many of which were introduced by man (Stone 1999).

The factors affecting realised niches are extremely complex, and are likely to interact with each other such that, in some areas, a particular combination of abiotic conditions result in the persistence of a species, whereas in other areas, with different host plants, predators and parasites, the same combination of abiotic factors may not be occupied by that species. However, factors contributing to the fundamental niche are a little simpler to interpret. Temperature has a direct, physiological effect on the metabolisms of organisms. Whilst individuals can tolerate a range of conditions, if the environment is too hot, the organism will desiccate (Woodman *et al.* 2007), may grow more slowly in response to reduced water availability (Jump *et al.* 2006), experience molecular damage, or even cardiac dysfunction (Somero 2010). If the environment is too cold, the organism will potentially suffer damage due to freezing (Bayram & Luff 1993) or lack of movement, possibly leading to starvation (particularly in endothermic organisms). Persistent low temperatures can also result in slower than usual development rates, with fewer individuals completing key parts of their life cycles (Leirikh *et al.* 2009). The presence of temperatures (be it minimum, maximum or some accumulation of heat or cold) outside the range encompassed by the fundamental niche of a species will therefore result in individuals of that species not surviving to reproduce and therefore occupy the area.

In some cases, the presence of extreme temperatures has led some species to evolve to tolerate these extreme conditions; the presence of antifreeze proteins (Duman *et al.* 2004) and water transporting proteins known as aquaporins, (Phillip *et al.* 2008) within cells, such that if cell do freeze they are not damaged due to the larger volume of ice than water, may allow persistence in extremely cold environments. Water conserving abilities and behavioural modifications can enable tolerance of extreme heat. However, such adaptations may put the species in question at a competitive disadvantage in more temperate climes, as they can be metabolically costly to maintain, resulting in lower fecundity or slower growth rates in the species that have evolved them (Loehle 1998). Thus, species have different temperature optima (Sayeed & Benzer 1996), and accordingly different fundamental niches.

It is well known that the global climate has already warmed, and temperatures are predicted to continue rising in the future (IPCC 2007). Because temperature is directly important to the survival of individuals (see above), there has been some concern about the effects of climatic warming on the persistence of species. Climatic warming could potentially change the ecology of many species in many ways. Species may be able to colonise areas that were previously too cool for them (Thomas *et al.* 2001; Davies *et al.* 2006), or suffer higher levels of death (Hari *et al.* 2006; Pounds *et al.* 2006) or lower levels of growth and fecundity in geographical areas that were previously considered within their thermal tolerances (Jump *et al.* 2006). Additionally, some species might be expected to evolve either to cope with the changed conditions in an area (Hoffman

2010) or to disperse more quickly and easily to newly suitable areas (Hochkirch & Damerau 2009). However, the most vulnerable species may have evolutionary constraints on their potential for local adaptation (Somero 2010), and such adaptation will only rarely result in changes to absolute tolerance limits (Berg *et al.* 2010). Yet other species might advance the phenology of events within their lives, perhaps flowering (Amano *et al.* 2010) or emerging earlier (Dell *et al.* 2005) in response to climatic warming, such that the absolute temperatures at which phenological events take place is conserved. There is the added complication that, for some plants, phenology advances may result in higher exposure to spring frosts (Bennie *et al.* 2010) and therefore increased mortality. Since species are likely to respond differentially to climatic warming, showing some or all of these expected effects, this could result in the presence of novel communities in the future (Pacala & Hurtt 1993; Walther 2010).

This thesis concentrates on the effects of temperature on species' distributions. By relating the abundances of species to the temperature conditions encountered at the locations of capture, I aim to determine what currently affects where mobile (non-sessile) species are able to survive within a geographical area. This may be the temperature encountered, or other factors such as the land use, presence of a particular vegetation type or the wetness of the substrate. This is an important first step in recognising management options to enable species to survive under future climatic warming. For example, the climate encountered by individuals (the "microclimate") could be modified by providing a higher level of canopy cover, thereby increasing shadiness, and decreasing the maximum temperatures of some areas to provide cool refugia. This action might therefore be expected to increase the likelihood of a cold-adapted species to persist in an area undergoing climatic warming.

1.2 Outline for introduction

In order to understand the relative effects of microclimate and land use on biodiversity, it is first necessary to examine what will cause differences in the microclimate experienced by an organism. In this chapter, literature is reviewed concerning the effects of topography on the temperatures experienced within a landscape. To give an idea of the effects that climatic variables can have on species' distributions, I then review studies that examine the effects of temperature and recent climatic changes on species' geographical ranges, altitudinal distributions, the slope aspects that can be colonised and abundance within an area.

1.3 The effects of topography on temperature

It is well known that temperatures decrease with increasing elevation, this decrease being known as the lapse rate. Lapse rates are generally 5.5 - 6.5 °C per 1000m (Hodkinson 2005), but maximum temperatures decrease more rapidly than means, whilst minimum temperatures decrease less rapidly with elevation (Grace & Unsworth 1988). Lapse rates can also vary seasonally. Guan *et al.* (2009) found the highest values (i.e. more rapid decreases with increasing elevation) in Taiwan in late spring and summer. They also found that the relationship between temperature and elevation was non-linear for the first three months of the year. Similarly, Rolland (2003) observed higher lapse rates in summer than in other months. Lapse rates may even vary between different mountains and overall elevation levels (Gottfried 1999). Despite these seasonal and geographical differences, because the relationship between elevation and temperature is relatively well recorded and has been for quite some time (e.g. Perring 1960; Geiger 1973), elevation (or elevational range) is often either included as a predictor in climate envelope models of species' distributions (Luoto & Heikkinen 2008; Virkkala *et al.* 2010), or used to interpolate temperature records to finer resolution (Nalder & Wein 1998).

However, several authors have found that adding other topographic variables such as slope and aspect improves the reliability of temperature interpolations between weather stations (Lookingbill & Urban 2003; Rolland 2003; Engler *et al.* 2004). This is likely to be because temperature is strongly influenced by levels of radiation, which is itself influenced by the angle of a surface in relation to incoming radiation (Oke 1992; Oliver 1992), such that in the northern hemisphere a steep north-facing slope will receive far less direct radiation than a steep south-facing slope. Such a steep, north-facing slope would therefore be expected to be much cooler than a steep south-facing slope at equivalent latitude and elevation, and indeed this has been observed in the field (Rorison *et al.* 1986; Thomas *et al.* 1999).

There can also be differences in the relative amounts of direct and indirect radiation received by a site due to cloud cover (Nunez 1980). Most topographically diverse areas, at least in the UK, are associated with high levels of cloud (Grace & Unsworth 1988), and hence increased levels of indirect radiation in relation to direct radiation. The amount of indirect radiation received by a site is not affected by the aspect of that site (Nunez 1980), so that temperatures might be more similar across a topographically diverse area on cloudy days than clear, sunny days (e.g. Davies *et al.* 2006).

One possible solution might be to include other topographical predictors such as slope and aspect both when modelling species' distributions using a climate envelope approach and when interpolating temperatures from coarse resolution records. Both slope and aspect have been found to be significant predictors of species' distributions (Lassueur *et al.* 2006). However, using indirect predictors such as topography to model species distributions means that the resulting model can only be applied to a limited geographical extent (and time span if climate is changing), since in different regions, the same topographic position will reveal a different combination of direct (i.e. temperature) and resource (i.e. soil nutrient levels, soil moisture levels) gradients (Guisan and Zimmerman 2000). Therefore, the use of a model that incorporates these factors to interpolate temperatures might be expected to be more generalisable across space and time (e.g. Wang *et al.* 2003; Bennie *et al.* 2008).

1.4 Climate change predictions

The microclimate of any site will be influenced by the prevailing macroclimatic conditions as well as its topography. It has been shown that global temperatures have increased in recent years and are likely to increase further in the near future (IPCC 2007). Responses of climate variables are not uniform in relation to CO_2 elevation, as coastal interactions make a difference to predictions (Schneider 1993). Regional scenarios have suggested 3.5 °C increases in Great Britain by 2100, and 0.47 °C of warming has already been observed between 1901 and 1995 (Conway 1998).

Several different models have been developed to predict future climate change, which give very different outcomes (IPCC 2007). However, at least some of the uncertainty in future climate projections reflects policy uncertainties since we do not yet know by how much anthropogenic emissions of greenhouse gases will be cut by future governments (Sala *et al.* 2000; http://www.metoffice.gov.uk/climatechange/science/projections/).

1.5 Effects of recent climatic change on species' distributions

Many studies have looked at the effects of recent climatic change on the distributions of species. Changes in temperature have variously been found to have an effect on the range limits of species, on the altitudinal limits where species are found, on the aspects that species can occupy and on the relative abundance of northerly and southerly distributed species at a site. These will be examined more thoroughly in this section.

1.5.1 Range shifts

At the European scale, species have been predicted to show a general shift from the south-west to the north-east in order to track suitable climate space (Harrison *et al.* 2006; Ohlemüller *et al.* 2006). Potential gains (areas previously unsuitable that will become suitable in the future) may balance losses (areas that are currently suitable but will not be in the future) for many species (Harrison *et al.* 2006). However, increases are also predicted in the area experiencing non-analogous climates; that is to say combinations of climatic variables that have not existed in the recent historical past (Ohlemüller *et al.* 2006). These patterns of change have not only been characterised in relation to recent climate change; species have also been observed to shift their distributions in response to climate change in the past (Davis & Shaw 2001; Huntley *et al.* 2004).

In addition to studies encompassing the entirety of a species' range, many authors have looked at the movement of range margins in recent years. Meta-analyses over a range of terrestrial taxa show that in general the cold margin of species' distributions has moved in the direction expected (Parmesan & Yohe 2003; Root *et al.* 2003; Hickling *et al.* 2006), i.e. northwards in the northern hemisphere and southwards in the southern hemisphere. This holds for marine copepods as well, which have shown a northwards extension of over 10° latitude in warm water species, with a corresponding decrease in cold water species (Beaugrand *et al.* 2002). Expansion at the cold range margin can sometimes result in disruption to trophic interactions, but these are not always deleterious to the species in question. Menéndez *et al.* (2008) showed that the Brown Argus butterfly, *Aricia agestis,* experienced lower levels of parasitism, resulting in lower levels of mortality, in newly colonised areas at the cold margin. However, even with climatic warming, habitat loss can outweigh any potential positive effects of climatic warming (that might allow a species to expand into a previously unoccupied area) at the cold range margin (Warren *et al*. 2001; Opdam & Wascher 2004). In addition, dispersal limitations mean that expansion at cold range margins can lag behind changes in climate (Warren *et al.* 2001; Willis *et al.* 2009).

Vegetation changes can also lag behind climate change. For example, the grass *Brachypodium pinnatum* can establish beyond its current range if transplanted, suggesting that lack of dispersal is currently preventing its northwards expansion (Buckland *et al.* 2001). This sort of response is especially likely considering the current fast rate of change in climatic variables, and novel future climates are expected to produce novel communities (Pacala & Hurtt 1993) as lags behind suitable climate will differ depending on the dispersal abilities of species. Most ectotherms have ranges that are not limited by vegetation directly, and so may expand north as rapidly as dispersal allows. This is likely to be at different rates for different species, as some species have higher powers of dispersal than others. In the cricket *Metrioptera roeselii,* dispersal into new areas is undertaken by long-winged individuals (Thomas *et al.* 2001; Hochkirch & Damerau 2009). A trade-off has been found between dispersal ability and reproductive ability in this and three other cricket species (Simmons & Thomas 2004), and long-winged morphs of a further cricket species, *Velarifictorus ornatus,* are less fecund than their short-winged counterparts (Zhao *et al.* 2010). This raises the possibility that ongoing climatic change could result in a higher proportion of long-winged individuals, with potential consequences for the persistence and evolution of the species.

Species that are limited by vegetation can only move north as quickly as the vegetation allows. Since dispersal is often slower in plants than animals, and species respond differentially to climatic change, this is expected to result in major changes to the constituents of communities (Pacala & Hurtt 1993; Root 1993). Floral community composition has already been observed to change over an altitudinal gradient in response to recent climatic warming (Le Roux & McGeoch 2008), although the full extent of potential for disruption in trophic interactions remains unclear (Walther 2010).

As well as expansion at cold range margins in response to climate warming, we might also expect to observe contractions at warm range margins as the climate becomes unsuitable. Early studies looking for contraction at warm range margins either did not observe any such declines (Thomas & Lennon 1999) or the retraction that occurred was slower than corresponding expansion at cold range margins (Parmesan 1999), leading to the hypotheses that species might be responding to slower climate related changes in vegetation, or that the warm range margins observed tend to be more mountainous and hence contain a wider range of microclimates that might allow persistence.

However, some insect species have now been observed to retract at their warm range margin (Hickling *et al.* 2005; Franco *et al.* 2006). Increases in the numbers of pathogens (Pounds *et al.* 2006) and temperature related disease (Hari *et al.* 2006) have also been shown to decrease the abundances of species at their warm margins.

Different types of species might have their warm range margins determined in different ways. For tree species, it has been postulated that the southern range margin can be determined not directly by the deleterious effect of too warm an environment but by the presence of faster growing competitors, because adaptations to cold can cause reduced growth (Loehle 1998). Similar competitive interactions have been found at low altitude boundaries of plants in Norway (Klanderud & Birks 2003). However, temperature warming has more recently been found to directly cause slower growth rates of beech trees at their southern (warm) range margins (Jump *et al.* 2006), which may eventually lead to death and therefore retreat at the southern range margin under future climatic warming. Such retreats may happen at a slower rate than the associated invasion of warm-adapted species, potentially resulting in a transient increase in species richness within some areas (Walther *et al.* 2002).

Studies using coarse resolution data may well miss changes in distributions of species at their warm margins, as all populations within a grid cell would have to go extinct before that grid cell was recorded as being empty (Thomas *et al.* 2006). Large grid cells may contain topographically diverse landscapes that provide some areas that are climatically suitable. Therefore, studies looking at altitudinal changes in distribution or changes in abundance might be better placed to elucidate changes occurring at these margins and smaller range shifts may *only* be detectable by analysing change in the mean altitude of presence records rather than the upper or lower range boundaries (Shoo *et al.* 2006).

1.5.2 Altitudinal changes

A shift in altitude of 150 m corresponds to approximately 100 km in latitude in terms of the temperature encountered (Hodkinson 2003). If species are to move to areas that are more climatically suitable in response to climatic warming, the distances that would have to be travelled are much less if tracking suitable temperatures within topographically diverse areas rather than moving latitude. Therefore, it might be expected that warm-adapted species would respond to climate warming by colonising locations at higher altitudes than previously possible. For cold-adapted species, mountain tops may provide refugia where the temperature is cool enough to allow persistence (Hodkinson 2005).

Several insect species have been shown to shift their altitudinal limits in this way. Wilson *et al.* (2005) observed that 17 of the 23 butterfly species they studied retracted an average of 212 m uphill at their warm margins, accompanying a 1.3 °C rise in temperature (which led them to expect a 225 m rise in altitude). Franco *et al.* (2006) also observed upwards retreat of a butterfly species. Still within the Lepidoptera, the Pine Processionary moth expanded 110 - 230 m uphill over around 30 years, which has been attributed to increased winter survival (Battisti *et al.* 2005). Parmesan (1996) found that extinctions of local populations of Edith's Checkerspot butterflies significantly decreased with altitude, suggesting that looking for changes in abundance at relatively fine resolutions may be necessary to elucidate patterns in species distribution at warm margins.

Movement uphill in response to climate warming has also been found in plants (Grabherr *et al.* 1994; Klanderud & Birks 2003), although not as quickly as expected, probably due to the slower dispersal in plants in relation to climate warming. In marine environments, species can shift their depth in response to climate warming (Perry *et al.* 2005; Dulvy *et al.* 2008). However, not all species necessarily move to higher altitudes in response to climate warming (Archaux 2004), perhaps changing their phenology instead.

Looking solely at elevation is a first step, but may be an overly simplistic way of describing the changes in species distributions in topographically diverse areas. I have already described how other variables such as slope and aspect can have an effect on temperatures (see above). The elevational limits of bird species have been shown to vary regionally and can be different on different sides of a particular mountain (Sekercioglu *et al.* 2008). This is as might be expected if temperature is the driving force behind distributions, since suitable temperatures will be encountered at different altitudes at different latitudes and on slopes that face in different directions. In addition, Lakhani & Davis (1982) found that aspect was an important predictor of the presence of *Helianthum chamaecistus* (*H. nummularium*) at a site in England, with an optimal aspect of between 192° and 205°, corresponding with some of the warmest areas in the landscape.

1.5.3 Changes in aspect occupied

Very few studies have considered the potential for species to colonise cooler aspects following climate warming, or that some aspects may become too warm. One example is that of *Hesperia comma*, which was found only on south facing slopes at its northern (cool) range margin in 1982. In more recent years it has colonised other aspects (Thomas *et al.* 2001; Davies *et al.* 2006). Other species have been found to occupy different aspects at their warm and cool range margins. For example, the herb *Cirsium acaulon* was limited to south-westerly (warmer) aspects at the edge of its range in northern Britain, but was able to occupy all aspects in northern France (Pigott 1968). Similar patterns have also been recorded for the butterfly *Plebeius argus*, the ant *Myrmica sabuleti*, the grasshopper *Chorthippus vagans*, and the lizard *Lacerta agilis* (Thomas *et al.* 1999). Since aspect has an effect on the temperature of a site (see above), microclimate may be important in determining where species are found within the landscapes they occupy.

1.5.4 Abundance changes

Using abundance data can potentially reveal patterns that are not picked up by presence/absence data alone. Many studies looking at the effects of temperature on the abundance of species have concentrated on marine taxa in the Northern hemisphere (Barry *et al.* 1995; Sagarin *et al.* 1999; Hughes 2000). All found that southerly-distributed species increased in numbers in relation to recent climate warming, whilst northerly-distributed species declined in abundance. Marine copepods have responded particularly sensitively to temperature changes; warm adapted species increased in abundance during warmer periods and cold adapted species increased in abundance during cooler periods. These patterns were observed seasonally as well as over longer time periods (Southward *et al.*1995). More recently, and again in the Northern hemisphere, declines have been observed in plant species at their southern range margins (Lesica &McCune 2004; Pauli *et al.* 2007) alongside increases in the cover of northerly-distributed plants (Pauli *et al.* 2007). These changes were observed over relatively short periods (13 and 10 years respectively), showing how much more powerful abundance data can be than presence/absence data.

1.6 Summary

Recent climatic change has been shown to influence the range boundaries of species' geographical distributions, the altitudes and aspects that can be colonised and the relative abundances of warm and cool adapted species at a site (see above). In addition, it is possible that some species may occupy vegetation types that produce different microclimatic conditions depending on the prevailing macroclimatic conditions (Oliver *et al.* 2009).

This leads to the suspicion that microclimatic differences can be important to the survival of individuals, and thus can influence patterns of distribution within a landscape. Indeed, McCarty (2001) claims that it is necessary to conserve microclimatic variation within a habitat type to enable populations to survive. Efforts to predict the future distributions of species using a scale-dependent hierarchical framework to integrate between continental and regional climate effects, with land cover, a dispersal model and connectivity model included, recognised the potential importance of microclimate to species, but did not include it within the framework (del Barrio *et al.* 2006).

2 Technical Introduction

In this section I present background information on the types of landscape sampled during this study, the study taxa (Carabidae) and a discussion of various invertebrate sampling techniques and their limitations both in general and with respect to carabid beetles. I also consider various statistical modelling techniques commonly used in climate-envelope approaches to model the distributions of species.

2.1 Upland moorland as a habitat

All sampling took place in the uplands of Britain. The oceanic climate of Britain is fairly unusual elsewhere in a global context; there is low seasonal variation in cloudiness, precipitation and temperature (Ratcliffe & Thompson 1988), with a comparatively low average temperature. Blanket bog requires these continuously cool and wet conditions to form over sloping terrain, hence is almost exclusively found in temperate hyperoceanic areas (Charman 2002). Britain is therefore an internationally important location for blanket bog, containing 7-13 % of the global total, although much of this is in bad condition (Ratcliffe & Thompson 1988). The British uplands have 19 constituent plant communities, of which five are virtually confined to Great Britain (GB), and six more are better represented here than anywhere else (Thompson & MacDonald 1995) and *Sphagnum*, *Eriophorum* and *Calluna* are the chief peat forming genera. Peat has a high water holding capacity; it can retain up to 500 % of its dry weight, which results in the water table being typically high, from the soil surface to 30 cm below in drier areas. Peat soils also have a low pH, with little seasonal or between site variation (Heal & Perkins 1978).

Grazing and burning, which are used to manage heather and prevent the encroachment of *Betula* scrub, account for widespread erosion of blanket bog in many areas due to the exposure and subsequent maintenance of areas of bare peat (Yeloff *et al.* 2006). In addition, atmospheric pollution can cause the loss of peat-forming sphagnum (Ratcliffe

& Thompson 1988). Historically, many upland landscapes have been drained by the addition of drainage channels (grips) that, it was hoped, would improve the land for agricultural purposes (but see Coulson *et al.* 1990). The realisation that these grips can lead to soil erosion (Newson 1980) has led to the re-blocking of these drainage channels in many places (e.g. http://www.blanketbogswales.org/) in order to improve the condition of blanket bog, raise the water table and prevent continuing soil erosion, so providing cleaner water supplies.

Most ongoing management chiefly involves the removal of some vegetation, which leads to greater fluctuations in temperature and moisture regimes in managed areas (Barclay-Estrup 1971). The patchy removal (often for grouse) typical in most upland areas results in heterogeneous microhabitat being available (Hobbs & Gimingham 1987). Temperatures of bog surfaces can therefore reach several degrees above the ambient air temperature (Heal & Perkins 1978).

This combination of conditions poses a variety of challenges to the organisms that inhabit the uplands. Limiting factors for animals include the humic acid content of soil water, large fluctuations in temperature and the low nutrient content of peat soil (Charman 2002), as well as the potential for drowning of soil-living invertebrates in waterlogged peat. Invertebrate diversity can be related to the structural diversity of the surrounding vegetation as well as that present at a trapping location (Hobbs & Gimingham 1987), as insects are mobile and may move into and out of unsuitable areas. The invertebrate fauna is dominated by the Diptera, with few pollen or nectar feeders. Homopterans are the only abundant above ground invertebrate herbivores. Due to the high levels of moisture present in the soil, there is little risk of desiccation, so aquatic invertebrates are well represented. Predators are represented by the Carabidae and Staphylinidae, with 2 - 4 carabids per m^{-2} being typical on blanket bog, corresponding to seven beetles per trap-year (Heal & Perkins 1978).

2.2 Carabid beetles as a study group

The beetles that make up the family Carabidae are mainly predatory and carrion eaters, although some species are thought to be bound to a particular vegetation type (Thiele 1977). In Europe, some species are herbivorous or mixed feeders (Lövei & Magura 2006). However, the majority are predatory or omnivorous, with only members of the Amarini having herbivorous adults in Britain, and most Harpalini being at least partly herbivorous as larvae (Luff 1998). Within the insects, herbivores and detritivores have been found to be much more specific to different upland habitat types than predators (Coulson 1988). There are 27 species within the Amara genus in GB, of an estimated 350 carabid species (Luff 2007). An unknown number of these are exclusively herbivorous. Therefore, the majority of carabid species (which are either exclusively or mainly predatory) should not be limited to certain vegetation types *per se*, although if their prey species are restricted to certain vegetation types then some restriction may occur. Carabids as a group are relatively well recorded, with published distribution atlases available (e.g. Luff 1998). 142 species of carabid (34 % of species) are considered endangered in Western Europe (Kotze *et al.* 2003), making them an important group from the point of view of conservationists. 350 species have been recorded from Britain and Ireland, with several species having biodiversity action plans in Britain, and many more appearing on Red Data Book lists (Luff 1998).

Many declining species of carabids are thought to be thermophilic, and so the loss of natural and semi-natural habitats, along with the intensification of agriculture in southern Britain, has been postulated to cause this decline, rather than climate warming (Desender *et al.* 1994). Large and medium species can move around 10m in a day, whereas the smaller species tend to disperse by flight (Rushton *et al.* 1991), so may be able to cover much larger distances in one-off dispersal events. This means that ground beetles ought to be able to respond fairly quickly to any change in conditions.

At the GB scale, carabid community composition has been shown to be related to land cover. Eyre *et al.* (2003) found nine distinctly different groups of carabids associated with different land cover types. Although most species occurred in all of the groups, their relative abundances changed, reinforcing the notion that the use of abundance data may be more powerful for detecting patterns in distribution (see introduction). Smaller scale analyses also find that carabids are affected by land cover (Gardner 1991). Particular stages of moor degradation in north-eastern Germany can be characterised by specific assemblages of carabids (Kampichler & Platen 2004), and a higher diversity of species is found on heaths surrounded by structurally diverse vegetation such as woodland (Webb *et al.* 1984). Size of habitat patches can also be important; DeVries (1994) found that species with low powers of dispersal were almost absent from small or isolated patches of heath in the Netherlands. Whilst relatively high numbers of carabids have been found on intensively managed sites in Scotland, these tended to belong to species with broad habitat requirements, short life-cycles and high reproductive capacity (Cole *et al.* 2005), and are thus of lower concern to conservationists than the fauna typical of rarer habitats like blanket bog.

Land cover is not the only factor known to affect carabid distributions. Blake *et al.* (2003) defined 15 different carabid communities (again with different proportions of many of the same species) within just 5 broad habitat categories in Scotland, and expected that ground beetles would be more likely to respond to soil factors rather than vegetation as most are predators (i.e. not restricted to certain plants, see above) with soil dwelling larvae. The species/abundance composition of plant communities is often related to soil moisture levels (Daubenmire 1968), so it is possible that the perceived responses of carabids to the vegetation are actually driven by other factors, which also affect the vegetation.

Habitat preferences can also change over geographical distance or altitude. For example, *Pterostichus madidus* is found in oak-hornbeam forest in Central Europe, open country and cultivated soil in Britain, and is intermediate between these in the Netherlands (Turin *et al.* 1991). Since the different vegetation types are likely to modify the prevailing macroclimatic conditions in different ways (Suggitt *et al.* 2010), such changes in habitat preference may be caused by a response to the microclimate rather than a preference for any one vegetation type *per se*.

Carabids have previously been shown to have preferences for particular temperatures, both at a national scale (Eyre 2006) and within regions (Martinez *et al.* 2009). Other important determinants of their distributions will vary depending on species, but may include light levels, humidity, substrate types and possibly pH and salt levels (Thiele 1977), as well as soil moisture (Holmes *et al.* 1993; Gardner *et al.* 1997; Antvogel & Bonn 2001; Eyre 2006). This latter is usually thought to be because many carabids have soil-dwelling larvae. However, soil moisture can be important even to adults; Ewers (2008) found that adult carabids can suffer mortality as a result of dry soil conditions, although this can take some time to take effect; a forest dwelling species was found to be able to survive for considerable periods in drier areas outside of moist forest habitats.

For some species, it is possible that temperature is not an important predictor of abundance. Loreau & Nolf (1994) found no effect of temperature on the total catch of the carabid *Abax ater* (which is not found in GB). However, this could have been due to the low observed differences in temperature at their study site, or because their experiment was limited to May and June, whereas temperature at different times of year could be important.

Different temperature variables have been found to affect different aspects of carabid life histories. Mean May temperature is a significant predictor of the net reproduction of *Carabus autonitens,* but ground running activity is influenced by air temperature during early night (Althoff *et al.* 1994). Depending on the phenology and physiology of the species in question, temperatures during various different months of the year could have a proportionally larger effect on reproductive success, and high maxima or prolonged periods of high temperature or low minima could affect survival through desiccation or freezing of individuals. Temperatures could also be perceived as more important to individuals depending on where in their geographical range is sampled. At their warm or cold margins, where the average background climate is unsuitable, it might be expected that the species in question is limited to a few, thermally suitable areas of the landscape, but other factors could be more important determinants of variation in density or distribution in more central parts of the geographic distribution (where the macroclimate is suitable).

The majority of Carabids are nocturnal, but a large minority are diurnal (Thiele 1977). In the UK, 60 % of species are nocturnal and 20 % diurnal, the remainder either showing no preference, having individuals that are both, or switching preferences over their life span (http://www.earthlife.net/insects/carabids.html). Even within a genus there can be both diurnal and nocturnal species. Of six *Nebria* species in the Austrian Alps (Gereben 1995), four were nocturnal and two were diurnal. The diurnal species preferred higher temperatures and survived low humidity conditions for longer than the nocturnal species. These nocturnal species were also found at higher altitudes than the diurnal ones, where temperatures will be cooler (see introduction). Genders may also have different temperature preferences. Atienza *et al.* (1996) found during field observations that females were more conservative with regards to temperature (showing less activity during the hottest parts of the day) than males of the same species, which they attributed to physiological differences inherent in the breeding period.

Carabids are well suited as indicator species of the effects of environmental change on other organisms. They are generally fairly large, and as such are relatively easy to identify, especially with the recent publication of an excellent field guide (Luff 2007). Within Great Britain, they are fairly well recorded, with national distribution maps and the underlying data being widely available (Luff 1998; http://data.nbn.org.uk/). Antvogel & Bonn (2001) found that carabids were particularly sensitive to small-scale modifications of habitats, and gave a better habitat indication than plant survey data. Additionally, the species richness of carabids can be considered as indicative of the richness of other beetles (Oliver & Beattie 1996).

2.3 Invertebrate trapping methods, with particular emphasis on pitfall trapping

2.3.1 Invertebrate sampling techniques in the uplands

Techniques used for sampling upland invertebrates include sweep netting, pitfall trapping and suction sampling. Pitfall traps have been recommended for monitoring presence and yearly fluctuations of epigeal Coleoptera and spiders, whereas a combination of sweep netting and suction sampling is better for estimating density and species richness (Standen 2000). However, this recommendation only holds for epiphytic Hemiptera and Diptera as well as herbivorous beetles and Linyphiid spiders. D-vac (a kind of suction sampler) sampling is inadequate for sampling heavy insects (Mommertz *et al.* 1996). Large species from the genus *Carabus* were caught almost exclusively in pitfall traps, and were not picked up by suction sampling in their study. Although some suction devices may be more effective than the D-vac (e.g. Wilson *et al.* 1993), results are not easily reproduced by others due to the level of equipment modification required. In addition, suction sampling devices have been found to inflate the number of species captured due to the edge effects of lateral suction (Samu *et al.* 1997), and may not be efficient in dwarf shrub vegetation, such as that encountered at our field sites, due to the structural complexity of such shrubs (Webb & Hopkins 1984).

2.3.2 Pitfall trapping for ground beetles

One major problem with pitfall traps is that catches depend on a combination of population size, locomotor activity and susceptibility to capture. Several carabid species have been found to show a positive correlation between their levels of activity and mean daily temperature (Neve 1994), thus increasing the likelihood of an individual encountering a trap. Locomotor activity also varies between species (Baars 1979), and even between different habitats (Kennedy 1994), possibly due to the different energetic requirements posed by different vegetation structures (Greenslade 1964), or the indirect effects of vegetation cover on temperature (Suggitt *et al.* 2010). Species also have different susceptibility to capture once a trap is encountered (Halsall & Wratten 1988), and may avoid capture either by avoiding traps having detected them, or recovering their balance on the lip of the trap. Therefore, the ecological characteristics of species (such as their size, speed of movement, microhabitat use and diel pattern) will all contribute to the likelihood of capturing a particular species, although vision/olfaction may be less important, since Greenslade (1964) found that baiting and/or camouflaging traps caused no variation in catches.

Despite such variation, Baars (1979) found that two species of Carabid (and indeed of six more species from data gathered by others) showed a linear relationship between the mean density of the population and the number of individuals caught in pitfall traps over a year. Pitfall catch for a whole season can be taken as a measure of relative population density for a given species in a particular habitat, thereby avoiding the problem of the possible bias introduced by the differential activity of beetles when considering isolated samples (Ribera *et al.* 2001). If resources are limited, sampling restricted to spring and summer pitfall samples can be considered to be representative of more intensive sampling (Oliver & Beattie 1996).

2.4 Modelling species' distributions

Given that many species have been shown to shift their range margins in response to climatic warming (see Introduction), it has become increasingly popular in recent years to relate the presences and absences of species to current climatic conditions, then project these models onto predicted future climate surfaces to predict where, if anywhere, will remain climatically suitable for the species following climatic warming (e.g., Huntley *et al.* 1995; Iverson & Prasad 1998; Hill *et al.* 2002; Huntley *et al.* 2007). This approach is known as "climate envelope modelling", and many different statistical modelling techniques have been developed to deal with different kinds of data (i.e. presence-only data, presence/absence data and abundance data) and applications. Here, I will discuss some problems inherent with statistical climate-envelope models, and then consider some of the various techniques available for their implementation.

One major problem with using climate envelope models is that distributions may include sources and sinks, and not all occupied habitat may be suitable (Davis *et al.* 1998). By including habitat variables, working at a relatively fine resolution and using abundance (such that less suitable areas may still be expected to contain some individuals, but fewer than the most suitable areas) rather than presence/absence data we minimise the risk of this confounding our results. Of course, this still assumes that pitfall traps sample the same species in the same way across the sampled landscapes, and so may result in the mistaken conclusion that a species is more likely to be present in a given vegetation type (for example), when in fact that vegetation type might be easier to move through, resulting in higher activity levels and therefore higher catch rates. In addition, if individuals of a species are either attracted or repelled from a location if other beetles have been caught (for example if they are attracted to decomposing material), this could also bias the results.

Climate envelope models have been criticized for being "static" representations of populations that are constantly responding to environmental flux (Zurrell *et al.* 2009), and Individual Based Models (IBMs) are likely to provide more accurate predictions of future distributions due to their mechanistic nature (e.g. Travis *et al.* 2010). However, sufficiently detailed data is just not available for the majority of species to enable the use of IBMs, and information on fine-scaled spatial distributions of species is far from complete, even for surrogate groups (Ferrier *et al.* 2002). Climate envelope models have been shown to successfully retrodict population trends (Green *et al.* 2008), and can predict the responses of far-dispersing species fairly well (Zurell *et al.* 2009) which suggests they have at least some utility for predicting future patterns of distribution, despite their many flaws. Lastly, the climate-envelope approach assumes that species are in equilibrium with their environments, and that the environmental gradient has been adequately sampled (Elith & Leathwick 2009). The extent to which species are in equilibrium with their preferred environmental conditions is often uncertain, although the recent deliberate introductions of several species (Buckland *et al.* 2001) to sites further north than previously occupied, and their subsequent survival and establishment implies the assumed equilibrium is not always achieved.

There is a large amount of debate surrounding the subject of the "best" modelling technique to use when relating climate variables to records of species' occurrence (e.g. Tsoar *et al.* 2007; Elith & Graham 2009), and the conclusion often varies depending on the desired usage of the resulting model. Many modelling techniques perform very well according to the commonly used metrics such as area under the receiver operating characteristic curve (AUC) and Kappa values, but would be less appropriate for generalisation to other areas or for prediction into the future (Randin *et al.* 2006). Some techniques are specific to certain types of data, using presence-only data (see Tsoar *et al.* 2007) whilst others require records of both presence and absence (e.g. GARP (Genetic Algorithm for Rule-set Production), Stockwell & Peters 1999), or generate "pseudoabsences" if true absence data is lacking (e.g. Phillips *et al.* 2004; Zarnetske *et al.* 2007). However, regression techniques are the only statistical methods available that allow for explicit, ecologically realistic modelling of species' responses to environmental variables (Elith & Burgman 2003). Generalised Linear Models (GLMs) are relatively well understood by the majority of ecologists, and dependent variables can include presence/absence, proportion or abundance data. Although commonly found to perform less well than other techniques when discriminating between areas of likely presence and absence of a species (i.e. low AUC scores; Randin *et al.* 2006; Heikkinen *et al.* 2007; Virkkala *et al.* 2010), GLMs are more appropriate for generalisation to other geographical areas than non-parametric techniques such as Generalised Additive Models (Randin *et al.* 2006), as they do not tend to over-fit to the sample dataset.

Physiologically based approaches such as IBMs should also provide ecologically realistic modelling, but the required data is not available for most species (especially the rarer species that tend to be of more interest to conservationists). Rushton *et al. (*1996) modelled the colonisation and spread of the carabid *Leistus rufomarginatus* in Britain. As data on growth, fecundity and survivorship were not available for this species, they used data for similar species with similar habits to parameterise the model. Their model predicted the spread to have been slower than was actually observed, which indicates that substituting unknown parameters into the model may have been inappropriate. Dynamic population models can have additional problems since different populations of the same species can respond differentially to climatic change (Schwager *et al.* 2008), or may even begin to adapt differentially to climatic warming (O'Neill *et al.* 2008).

3 Field sites and methods

3.1 Field sites

Sampling took place at three sites; Lake Vyrnwy Royal Society for the Protection of Birds (RSPB) reserve in Wales; Glen Finglas Woodland Trust reserve in Scotland; and the High Peak in the Peak District National Park in England (Figure 5.1a).

Lake Vyrnwy is situated adjacent to Snowdonia National Park (52° 47′ 09″ N, 03° 30′ 49″ W), covers *ca.* 9,700 hectares, lies between *ca.* 350 and 620 m a.s.l. and contains several different vegetation types. All sampling was undertaken in heathland dominated by *Calluna vulgaris* (heather), the commonest habitat type in the reserve (Figure 3.1). The heathland is actively managed for wildlife using a mixture of mowing, burning and grazing to maintain a mosaic of heather and graminoids over a mainly peat soil base. This site is at the southern range margin of many species with northerly distributions within Great Britain (e.g. Figure 5.2).

Figure 3.1: A catchment at the Lake Vyrnwy site

Glen Finglas is situated within the Loch Lomond and the Trossachs National Park, (56° 16′ 01″ N, 4° 23′ 20″ W). The whole site covers *ca*. 4,100 hectares and lies between *ca.* 150 and 821 m a.s.l.. It contains several different habitats, and open areas are maintained by a combination of sheep and cattle grazing. Sampling was undertaken in heathland dominated by *C. vulgaris* and upland unimproved grassland (Figure 3.2).

Figure 3.2: A catchment at the Glen Finglas site. © Mutt Lunker,

http://en.wikipedia.org/wiki/File:Glen_Finglas.JPG

The High Peak site is situated within the Peak District National Park, Derbyshire (53° 31′ 25″ N, 01° 52′ 50″ W) and lies between *ca.* 250 and 580 m a.s.l.. The site is partially grazed by sheep, and some areas are managed for grouse shooting with a burning regime to maintain a mosaic of different age classes of *C. vulgaris*. Sampling took place in dwarf-shrub heathland, upland unimproved grassland and on bare peat (Figure 3.3). Again, this site is at the southern range margin of many species that are northerly-distributed within Great Britain (e.g. Figure 5.2).

Figure 3.3: A catchment in the High Peak site

3.2 Sampling strategy

During the 2007 field season, 50 locations were selected at Lake Vyrnwy and the Peak District on the basis of a stratified random sample with proportional representation of 12 categories of combinations of slope, aspect and elevation. This ensured that a wide range of the microclimates present at the site were sampled. For the 2008 field season, the strategy was changed to include 40 sample locations at Lake Vyrnwy and the Peak District (Figure 5.1 c-d), again determined using a stratified random sample, but this time with equal representation of the 12 categories of combinations of slope, aspect and elevation with an additional four locations within the areas of lowest elevation. The change allowed better representation of the rarer topographic categories and ensured that the warmest locations within the landscape were sampled. In addition, 48 locations were sampled in Glen Finglas in the same way in 2008 (Figure 5.1b), the additional locations to allow better representation of the more topographically diverse terrain present there. Sample locations were georeferenced in the field using a handheld Global Positioning System (Garmin GPS 60), and were at least 50 m apart in order to reduce spatial autocorrelation, or in other words to ensure that the sample locations were as independent as possible (given other constraints such as time and available sampling area).

3.3 Temperature measurements

One Tinytag datalogger (Gemini, model TGP-4520) was deployed at each sampling location at the Lake Vyrnwy and High Peak sites. At Glen Finglas, the more recently available, cheaper HOBO pendant loggers (Onset, model UA-002-64K) were deployed. Each logger recorded hourly temperature, with a specified accuracy of ±0.4°C, and 0.02°C resolution (for the Tinytag loggers) or ±0.47°C and 0.1°C resolution (for the HOBO loggers). Temperature probes were placed at the soil surface as determined by dropping a 150 g weight from 1.5 m. The probes were therefore placed beneath the vegetation present at the sampling location. Vegetation shaded the loggers at all sample points and was not cut back, although the height and density of vegetation above loggers varied. Due to livestock interference, data were not available for all sample points for the study period; fewer than 15 sites in the High Peak and Lake Vyrnwy sites had records for the entire sampling period because of destruction of logger parts during some months.

3.4 Other environmental variables

Vegetation height was measured at each sampling location at each visit during the summer field season. This was by way of a drop disc (Stewart *et al.* 2001) lowered gently on to the top of the vegetation over the datalogger location, until the first piece of vegetation was encountered. In addition, a qualitative description of the vegetation present within the 5 x 5 m cell sampled was made. These qualitative descriptions were summarised into categories describing how much the vegetation branched (i.e. category 1 included grass, sedge or juncus; category 2 included some juvenile dwarf shrub; category 3 was mature dwarf shrub and category 4 was bracken). In this way I attempted to categorise a continuum from more to less branched, however, the mosaic of vegetation types tended to intermingle, such that I found it very difficult to impose this categorisation with any real certainty. Unfortunately, I did not have any better method available at the time, although instruments do exist for determining the amount of canopy gap present which would appear to be a better measure in such landscapes. Soil moisture was measured at the Lake Vyrnwy site during a single day in March 2009 using theta probes (Delta-T, model ML2x) at six points (next to the temperature probe and all five pitfalls) within each sampling location. The sampling took place on a single day to minimise the effect of rain on the data gathered. Repeat sampling had been planned for further days, but a period of heavy rain during the designated period would have rendered the data useless. The best solution would have been to gather data on soi moisture continuously over the entire trapping period, using dataloggers as for the temperature sampling. However, the equipment required for this was well out of the budget of this study, and has already been seen, would also have been vulnerable to livestock damage, such that there would be no certainty of a good dataset even with this method. The data that was gathered was extremely variable, with more variability within location than between, and a large amount of variability between the two probes used. However, the majority of locations contained at least one point that was considered to be completely saturated.

3.5 Sampling of ground beetles

Ground beetles were collected by pitfall trapping during two field seasons; from the start of May to the end of August 2007 and from the start of May to the end of August 2008. At each sample point five pitfall traps were deployed in a circle with 2 m diameter, such that all traps were located within a single 5m grid cell. Traps consisted of two standard plastic vending cups nested together and sunk into the soil so that the rim of the inner cup was flush with the soil surface. Each cup was filled to a 2.5 cm depth with ethylene glycol antifreeze. Traps were covered with a lid made up of a terracotta coloured plastic saucer suspended 11 cm above the surface with galvanised wire. This served the dual purpose of limiting liquid loss by evaporation and limiting flooding from rainfall. A surround of chicken wire (mesh diameter 20 mm) completed the lid, with the aim of excluding small mammals from the trap (Figure 3.4).

Invertebrates from all five pitfalls at each sample location were pooled then transferred to 100% ethanol for transport back to the lab. Ground beetles were sorted from other invertebrates captured and were identified to species in the laboratory following Luff (2007). The entire season's catch for each trapping location was then pooled for analysis to give a measure of the relative population density present at any one location; the pooling procedure averaged out the effects of sample error and of extreme weather events on activity of individuals during different months of trapping (Ribera *et al.* 2001), giving a more reliable estimate of population density than could be achieved from one month alone.

3.6 Other invertebrate sampling

Sweep net transects were walked in 5 x 5m squares around the pitfall traps during the 2007 sampling season. Due to the nature of the field sites, this sampling technique was found to be ineffective as it could only be employed when the vegetation was dry. Suction sampling using a Vortis$^{©}$ (Burkland Ltd, UK) was also trialled in September 2007. Again, the wetness of the sites meant that samples could not be collected from some locations with extremely saturated soils.

Figure 3.4: A pitfall trap with lid and mesh surround

3.7 Microclimate modelling

A recently published microclimatic model (Micromaker: Bennie *et al.* 2008) was used to predict the microclimate for each of the three sites[1]. Hourly radiation, wind speed and air temperature data were obtained for the meteorological stations recording radiation data that were closest to each of the three study sites (Lake Vyrnwy, 52° 45′ 25″ N, 03° 38′ 45″ W, Manchester Hulme Library, 53° 28′ 01″ N, 02° 15′ 00″ W and Strathallan Airfield, 56° 19′ 33″ N, 3° 43′ 44″ W) from the British Atmospheric Data Centre (BADC, www.badc.rl.ac.uk). Digital Elevation Models (DEMs) at 25 m^2 horizontal resolution and 1 m vertical accuracy for the three sites were obtained from the NERC

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[1] recoded from a Bash script running under the open source GIS program GRASS to a standalone C++ program by Joseph Chipperfield

Earth Observation Data Centre (NEODC, neodc.nerc.ac.uk). Slope and aspect values for each 5 x 5 m cell were calculated using the standard functions in ArcMap v 9.2 (ESRI, 2008). The microclimate model used this information to generate hourly predicted temperatures at the top of the vegetation layer at 25 m^2 resolution from the start of September 2007 until the end of August 2008.

The microclimate model adjusted the temperature values from the meteorological stations to take account of the elevation difference between the meteorological station and each 25 m^2 grid cell in the landscape, as well as differences in direct and indirect radiation associated with different slopes and aspects at different times of the day and year (including effects of hill-shading; Bennie *et al.* 2008). These hourly values were then summarised into monthly mean, maximum and minimum values, which were then further summarised to annual mean, maximum and minimum values for use as explanatory variables in species distribution modelling.

3.8 Statistical Modelling

Details of the particular statistical analyses used varied for each dataset, and so these methods are described in detail in the relevant data chapters. In the main, I used Generalised Linear Models (GLMs) for species' distribution modelling, which are useful predictive tools, compared to other methods, which are relevant for describing patterns of presence and absence across ranges (see 2.4). I also trialled the use of Generalised Additive Models (GAMs), but these always appeared to overfit the data, and subsequent exploration of the quadratic relationships suggested using GLMs always resulted in a completely non-significant model (as suggested in Guisan & Zimmerman 2000). Lastly, the presence-only method Maximum Entropy (Phillips *et al.* 2004; 2006) was trialled. However, the Area Under the Receiver Operating Characteristic Curve (AUC) scores achieved using this method led me to reject these models. The AUC statistic compares four categories when predicting species' distributions; the number of correctly predicted presences, the number of correctly predicted absences, the number of absences that were incorrectly predicted to be presences, and the number of presences that were incorrectly predicted to be absences. The low AUC scores achieved by using the MaxEnt technique on my datasets is most likely due to the fact that I have abundance data for a small number of locations, rather than presence data for a larger number of locations. By using presence-only or presence/absence modelling techniques, I would have ignored some of the information available to me, therefore reducing statistical power.

4 The effects of topography on microclimate

4.1 Abstract

Most multicellular terrestrial organisms experience climate at scales of millimetres to metres, yet most species-climate associations are analysed at resolutions of kilometres or more. Because individuals experience heterogeneous microclimates in the landscape, species sometimes survive where the average background climate appears unsuitable, and equally may be eliminated from sites within apparently suitable grid cells where microclimatic extremes are intolerable. Local topography can be important in determining fine-resolution microclimate, but most climate-envelope models either do not include topographic variables, or limit their inclusion to elevation alone. Here, I show that temperature differences associated with topographic variables (including slope and aspect) can reach 7 °C, potentially allowing the survival of species in areas where the average climate is physiologically unsuitable. I then go on to ground truth a recently published microclimate model, to prove its utility for interpolating temperatures across different landscapes. Hence, I argue that the microclimatic effects of topography must be included in studies (and that this is increasingly easier to achieve) if we are to obtain sufficiently detailed projections of the ecological impacts of climate change to develop detailed adaptation strategies for the conservation of biodiversity.

4.2 Introduction

It has long been recognised that temperature can have an effect on the distributions and abundance of species (see Introduction). So called "climate envelope" models have been used to model the current distributions of species, to quantify recent changes in distribution in relation to climatic warming (Warren *et al.* 2001) and to predict where species might be located following a certain amount of future warming (e.g., Huntley *et al.* 1995; Iverson & Prasad 1998; Hill *et al.* 2002; Huntley *et al.* 2007). These models are usually fitted using data at resolutions of 100 km² or coarser. However, coarse grid cells can cover a wide range of thermal conditions, with differences in temperature of up to 33.8 °C within one 50 x 50 km cell (Ashcroft *et al.* 2009). To account for this, several authors have included the topographical variable elevation as a predictor when modelling species' distributions (Luoto & Heikkinen 2008; Virkkala *et al.* 2010), since temperatures are known to decrease with increasing altitude (Perring 1960; Geiger 1973). However, the temperature experienced at a location may be influenced by factors other than elevation (see Introduction chapter). This means that current methods may still be underestimating the range of conditions experienced by organisms.

There is therefore a real need for fine-resolution environmental data, as species distribution models using such variables at fine resolutions perform better than those using coarser resolution data (Ferrier *et al.* 2002). However, precise, physiologically meaningful microclimate measurements can be difficult to obtain in a spatially explicit way (Engler *et al.* 2004), presumably due to the high cost both in time and money associated with locating and servicing measuring equipment across landscapes. One alternative to collecting a large amount of data in the field is to interpolate temperature from coarser-resolution weather station records. Models that interpolate temperatures often include elevational lapse rate (Nalder & Wein 1998; Price *et al.* 2000), but these suffer from the same problem as species' distribution models that include elevation as a predictor term; namely that the microclimate experienced at a particular location can be affected by variables other than elevation. More recently, attempts have been made to include a range of other topographical variables when interpolating temperatures from meteorological station records (Bennie *et al.* 2008, Ashcroft *et al.* 2008). Temperature surfaces that are interpolated based on several topographical variables can predict the distributions of species better than the inclusion of elevation as an explanatory variable alone (Ashcroft *et al.* 2008).

Problems can still occur with interpolated temperatures. There might be gaps in the data recorded due to damage, a lack of sufficient station data within an area, or stations that are present may not record the full variability in temperature that occurs (Guisan and Zimmerman 2000). This could occur if cost and ease of access to a location were the main deciding factors in the location of weather stations, leading to most stations being located at relatively low elevation sites, in areas with limited topographical diversity. Indeed, in many countries, mountainous areas have a lower density of meteorological stations than flatter areas that are closer to population centres (Guan *et al.* 2009). In addition, the urban heat island effect produced by urban areas (Oke 1982) could result in temperature interpolations that are artificially high in many areas.

In this chapter, I use temperature loggers to record temperatures at a fine spatial resolution within two landscapes. I first investigate whether the topographical variables slope and aspect add explanatory power to the prediction of temperatures at fine resolutions compared to models based solely on elevation. I then compare the predictions of my statistical models to those generated by a recently published microclimate model (Bennie *et al.* 2008), which uses the topographical variables slope, aspect and elevation in a series of equations to interpolate temperatures from meteorological station records. In this way, I can check whether the published model predicts the full range of microclimates present at a site.

4.3 Methods

4.3.1 Fieldwork

I used two sites in which the vegetation was relatively homogenous, but where there was considerable variation in topography; enabling me to examine the impact of slope, aspect and elevation on temperature without the need to consider thermal variation associated with variation in habitat type. The two sites were Lake Vyrnwy Royal Society for the Protection of Birds reserve in Wales, and the High Peak in the Peak District National Park in England.

Lake Vyrnwy is adjacent to Snowdonia National Park (52° 47' 09" N, 03° 30' 49" W) and covers around 9,700 ha. It contains several different habitat types, but all data loggers were placed in heather (Ericaceae) moorland, the commonest habitat type in the reserve. The heather moorland is actively managed for wildlife with a mixture of mowing, burning and grazing to maintain a mosaic of heather and grassland over a mainly peat soil base. The lowest areas of the reserve are around 350 m a.s.l., with the highest being around 620 m a.s.l. Thus, a range of elevations and topographical features were represented.

The second site studied is in the High Peak, Derbyshire (53° 31' 25" N, 01° 52' 50" W). The site is partially grazed by sheep, with some areas managed as grouse shooting moors with a heather burning regime to maintain a mosaic of age structures of heather. The lowest areas of this site are around 250 m a.s.l., with the highest around 580 m a.s.l. Again, this site provided elevational and topographical heterogeneity.

A total of 50 Tinytag dataloggers (Gemini, model TGP-4520) were deployed at each site throughout September 2007 and January 2008 in a stratified random design to ensure representation of the full range of slopes, aspects and elevations present. Each logger recorded hourly temperature, with a specified accuracy of ±0.4 °C, and 0.02 °C resolution. At each sample location, temperature probes were placed at the soil surface as determined by dropping a 150 g weight from 1.5 m. The probes were therefore placed beneath the vegetation present at the sampling location. Vegetation shaded the loggers at all sample points and was not cut back, although the height and density of vegetation above loggers varied. Due to livestock interference, data were not available for all sample points for the study period. In Wales, 48 loggers collected data during September 2007, and 44 in January 2008. The damage from livestock was worse in the Peak District, where only 25 loggers collected full datasets for September 2007, and 33 for January 2008.

4.3.2 Statistical analyses

Five temperature-related bioclimatic variables were derived from the temperature time series data to summarise the microclimate. These were: monthly mean temperature (T_{mean}), monthly minimum temperature (T_{min}), monthly maximum temperature (T_{max}), monthly temperature range (T_{range}) and growing degree days above 5 °C (GDD+5). These variables were taken to represent ecologically important or physiologically limiting variables commonly applied to a range of taxa in bioclimatic studies (e.g. Thuiller *et al.* 2006b; Preston *et al.* 2008; Svenning *et al.* 2008). GDD+5 was calculated by subtracting 5 °C from the hourly temperature readings, totalling these for each day (removing negative values), then dividing by 24 to obtain hourly values, before totalling for each month. In this way hourly information on the temperature regime is preserved.

The covariates in each case were elevation (metres above sea level), slope (degrees) and aspect. Aspect was transformed to degrees from 200, the aspect found to have the hottest temperatures, as described in Lakhani and Davis (1982). Finally, a slope x aspect interaction term was included. These predictor variables were computed in ArcMap v. 9.2 (ESRI, 1999-2006) from a 5 m resolution Digital Elevation Model provided by the National Environment Research Council's Earth Observation Data Centre (NEODC, neodc.nerc.ac.uk).

I first looked for correlations between the explanatory variables using both Pearson and Spearman correlation coefficients. I then used Multimodel Inference (MMI, Burnham & Anderson 2002) to choose the best supported model. All possible variable combinations were presented in a Generalised Linear Model (GLM) format with the identity link function, assuming normal error structure. Coefficients were calculated for all variables retained in the best model in each case. In addition, the explanatory variables were standardised to distributions with mean = 0 and standard deviation = 1 to help identify which explanatory variable had the greatest effect on each temperature variable. Diagnostic plots were examined and any sample site with a Cook's Distance (denoting a very large effect on the coefficient) of more than 1 was excluded from the analysis. This was a maximum of one sampling location per field site, per month sampled. Tests were carried out separately for each time period and for the two different field sites. All analyses were carried out in R version 2.8.1 (R Development Core Team 2008). The resulting models were extrapolated across the sampled landscapes in ArcMap v. 9.2 (ESRI 1999-2006).

Hourly wind speed, air temperature and global radiation were obtained from the nearest meteorological stations for each site (Manchester Hulme Library 53° 28′ 01″ N, 02° 15′ 00″ W, Lake Vyrnwy 52° 45′ 25″ N, 03° 38′ 45″ W). These were used as input variables in a recently published microclimate model ("Micromaker", Bennie *et al.* 2008) along with the elevation, slope and aspect layers generated for the landscape models. Micromaker used these topographical variables to interpolate temperature for a 5 x 5 m resolution grid across the landscape at hourly intervals (temporal resolution limited by the meteorological station records, spatial resolution limited by the DEM resolution). From these layers, the monthly mean, maximum, minimum and Gdd5 (T_{mean}, T_{max}, T_{min} and GDD) were extracted for both sites for September 2007, and for January 2008 at the Peak Site. Due to a problem with the input data, only T_{mean} could be calculated by Micromaker for the Welsh site for January 2008.

For both modelling approaches, the predicted temperature was extracted to a 100 x 100 m resolution grid (rather than 5 x 5 m resolution, as available computing power was not sufficient to deal with such a large amount of data in R). The pairs of variables (i.e. T_{max} as calculated by the statistical model and by Micromaker) were then checked to see whether their predictions were correlated using Spearman's and Pearson's correlation coefficients. Note that it is the strength of the correlation that is relevant, not its statistical significance, given the potential spatial autocorrelations in both surfaces. In addition, a generalised linear model (GLM) assuming normal error structure and identity link function was fitted to see how well Micromaker predicted the surface generated by the landscape model.

4.4 Results

4.4.1 Landscape Model

Interpretation of slope and aspect effects on recorded temperatures is complicated by slope x aspect interactions, where a steeper southerly-facing slope is generally hotter than a flat slope, yet a steeper northerly-facing slope is cooler than a flat slope (Table S1). Hence the results can best be summarised by using the GLMs produced to compare the differences in temperatures on steep (15 °) southerly hillsides (200 °, corresponding to the warmest aspect) with those on equally steep northerly hillsides (020 °).

The most interesting (in that variables other than elevation were considered important) results were for maximum and minimum temperatures. In the Peak District, T_{max} was estimated to be 6.98 °C warmer on southerly than on northerly hillsides in September (Figure 4.1), and 5.67 °C warmer on southerly than on northerly hillsides in January. The raw data show differences of over 20 °C between temperature maxima at different logger locations, so the GLM estimate seems reasonable and possibly conservative (e.g., northerly-facing WayPoint 52 experienced a T_{max} of 16.4 °C, and southerly-facing WayPoint 77 experienced a T_{max} of 37.7 °C, both in September in the Peak District). However, aspect was non-significant in Wales, suggesting that topographic effects on microclimates may be geographically variable (see below).

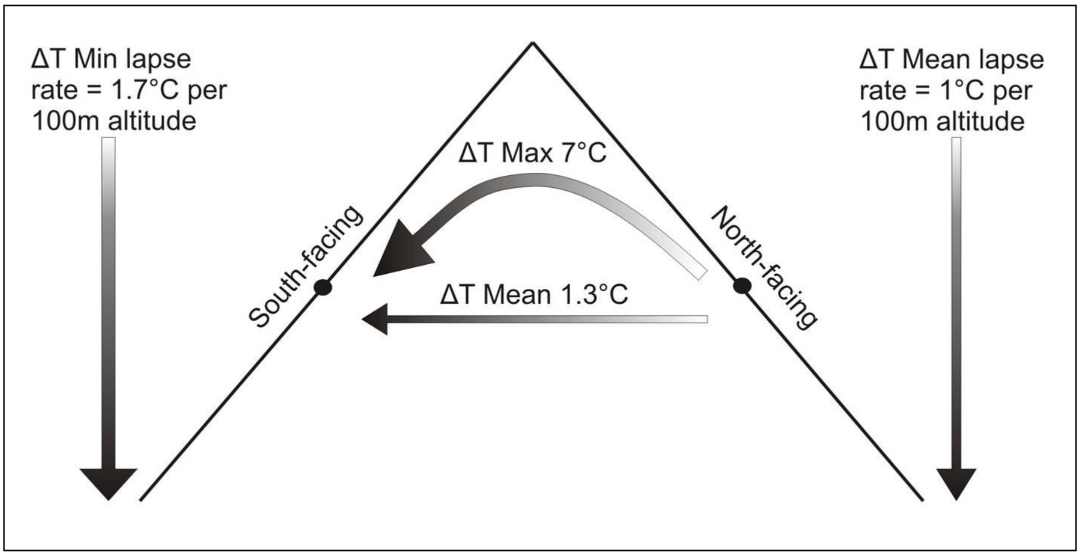

Figure 4.1: Modelled changes in bioclimatic variables experienced when switching between north (020°) and south (200°) facing aspects. Slope angle is held constant at 15°. Values are for September 2007, at the Peak District field site.

For the minimum temperatures, elevation was usually the only variable retained in the best model, with the exception of the Welsh site in January (for which the model was not significant at all). Where elevation had a significant effect on T_{mean}, lapse rates were broadly consistent with previously published rates (Table S1; September: Wales; β = -0.0108; Peak District; β = -0.0101,, January: Wales; β = -0.0043; Peak District; β = -0.0049; a β value of -0.005 is equivalent to 0.5 °C cooling for each 100m increase in elevation). The results for GDD+5 followed a similar pattern, being lower at higher elevations, significantly so for September measurements at both locations (Table S1). Elevation was rarely included in the best model for T_{max} or thermal range (Table S1), and it had little explanatory power on those occasions when it was retained, suggesting that other factors are more important for these variables over the ~ 300 m elevational ranges considered here.

The microclimate differences between the English and Welsh field sites appear to be associated with differences in their regional climates. In Wales, the principal result was that elevation affected T_{mean} and GDD+5; whereas in the Peak District, slope and aspect frequently affected the temperatures recorded. Lake Vyrnwy in Wales is in one of the cloudiest parts of England and Wales; data from the UK Met Office (UKMO 2009) indicate that it had only 20 - 30 hours of sunshine, as opposed to 40 - 50 hours in the Peak District during the measurement period of January 2008. The Peak District also received more sunshine than did Vyrnwy in September. Effects of slope and aspect on microclimate depend most strongly upon differences in direct, incident sunshine, especially for maximum temperatures, so the lack of sunshine at Vyrnwy perhaps curtailed the influence of slope and aspect during the months considered.

4.4.2 Comparison of landscape model and Micromaker output

For most variables, correlation between the landscape model predictions and Micromaker predictions was extremely high (see Table 1). In general, T_{min} predictions showed the highest correlations, whereas T_{max} predictions showed low correlations (maximum correlation coefficient was 0.39 in Wales in September). T_{mean} and GDD predictions were generally highly correlated, although correlation coefficients were lower for September in the Peak District. The September landscape models for T_{mean} and GDD in the Peak District retained slope and aspect (See Table S1 B), and the relative simplicity of the linear functions fitted appear to have produced some very high and very low predictions for certain areas of the landscape (see Figure 4.2). The more complex equations used in Micromaker predicted a much lower range of values than did the landscape models.

The GLMs relating the two sets of predictions tell a similar story, with high to very high amounts of the variability in the landscape model predictions being explained by the micromaker predictions, with the exception of T_{max}. However, the ß-coefficient relating the two sets of predictions was almost never close to 1 (which would be expected if both models predicted the same value), being as high as 2.56 for T_{min} in the Peak District in September, and as low as 0.37 for GDD in the Peak District in January (disregarding the values for T_{max}). The capacity of the Micromaker model to predict the landscape model output was generally strong (median model $R^2 = 0.82$), but this variation in the slopes indicates that it is the relative, rather than absolute, temperatures of different locations that are predicted accurately. Again, a very large proportion of the variability in T_{max} predicted by the landscape model remains unexplained by the Micromaker predictions. The highest amount of explained variability was again found for the T_{min} models, with R^2 again being generally high for T_{mean} and GDD, but lower for both in September in the Peak District.

Table 4.1 - Correlation coefficients and ß-coefficients (for GLMs) for predictions of the landscape model generated from my data and micromaker interpolations. Notionally significant coefficients are indicated by ***. The R^2 value for the GLM is also given.

Site	Date	Variable	Spearman	Pearson	GLM β	R^2
Lake Vyrnwy	09/2007	T_{mean}	0.9044***	0.9034***	1.7139***	0.8161
Lake Vyrnwy	09/2007	T_{max}	0.3614***	0.3854***	0.4152***	0.1485
Lake Vyrnwy	09/2007	T_{min}	0.9973***	0.9983***	2.0662***	0.9966
Lake Vyrnwy	09/2007	GDD+5	0.9077***	0.9071****	1.7390***	0.8227
Lake Vyrnwy	01/2008	T_{mean}	0.9641***	0.9779***	0.6470***	0.9564
High Peak	09/2007	T_{mean}	0.7448***	0.7765***	1.3340***	0.6029
High Peak	09/2007	T_{max}	0.1341***	0.1583***	0.5373***	0.0251
High Peak	09/2007	T_{min}	1.0000***	1.0000***	2.5570***	1.0000
High Peak	09/2007	GDD+5	0.7970***	0.8230***	1.8550***	0.6773
High Peak	01/2008	T_{mean}	0.9975***	0.9976***	0.7479***	0.9952
High Peak	01/2008	T_{max}	0.0586***	0.0684***	0.1018***	0.0047
High Peak	01/2008	T_{min}	1.0000***	1.0000***	0.9077***	1.0000
High Peak	01/2008	GDD+5	0.9953***	0.9909***	0.3656***	0.9820

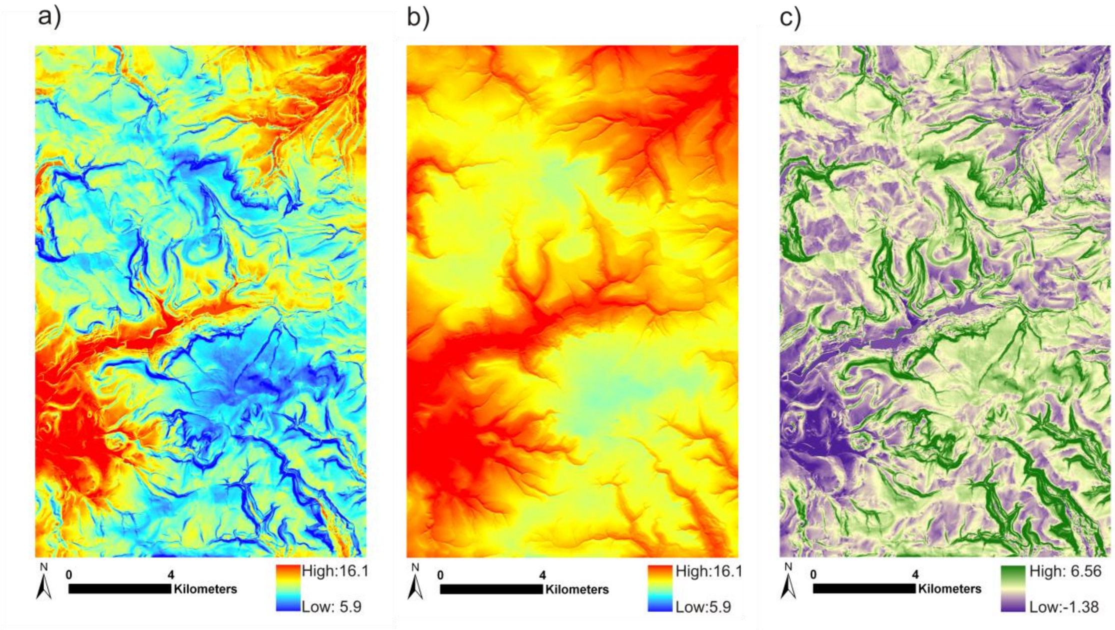

Figure 4.2: Modelled mean temperature for September 2007 at the Peak District site using two different modelling techniques; a) The statistical model based on topography (the landscape model) developed here; b) Micromaker. c) Shows the absolute difference between the two techniques. Units are in ºC

4.5 Discussion

Thermal differences between slopes and aspects (as affected by these variables and the interaction between the two) were of the same order of magnitude as projected increases in global average surface temperatures. In some cases, microclimate variation exceeded estimates of warming under any of the IPCC SRES marker emissions scenarios, which range from a 1.1 to a 6.4 °C rise in global mean temperatures (IPCC 2007). At the site in northern England, maximum temperatures were recorded as almost 7 °C hotter on south-facing than on north-facing hillsides, in September. This conclusion for topography only held for the English landscape, presumably due to flatter slope angles, more uniform vegetation, and greater cloud cover in the Welsh site. In a shorter study, Thomas *et al.* (1999) reported that daytime temperatures (near to maximum) were 4 – 5 °C warmer on a south-facing than on a corresponding north-facing hillside, in sunny March weather. These large temperature differences provide opportunities for individual organisms that are able to move short distances to escape unfavourable microclimates, and populations may shift microhabitats (slopes, aspects and vegetation density) in response to inter-annual variation in the climate.

In contrast, mean temperatures and accumulated degrees (GDD+5) varied more with elevation than with slope and aspect (see Table S1). The Welsh landscape had no significant effect of slope or aspect, which suggests that conventional modelling approaches may represent means and accumulated degrees reasonably well, at least in some landscapes, given that lapse rates are already incorporated into interpolated surfaces for temperature and that these can be deployed at high spatial resolution if required. However, for organisms that are limited by extremes of temperature or thermal range, modelling frameworks that are commonly used are unlikely to be sufficient (cf. Bennie *et al.* 2008, Kearney & Porter 2009).

I also showed that a recently published microclimate model (Bennie *et al.* 2008) produced predictions that generally showed a very high correlation with the predictions of landscape models generated from my temperature data. This raises the possibility that slope and aspect can be more easily incorporated into future climate-envelope models, especially for species that are limited by extremes of temperature or in topographically diverse landscapes. This model is based on well understood mechanisms (including lapse rate, hill-shading and radiation levels), meaning that it should be more generalisable to other areas than statistical models generated from temperature data collected within a particular site.

Using spiders as an illustrative example of the resident fauna in my study areas, it is possible to show the potential effect that fine-scale microclimates can have on real-world distributions. Taking the Peak District to illustrate the effects of slope and aspect, *Alopecosa pulverulenta*, has a mean supercooling point of -1.61 °C (Bayram & Luff 1993), meaning it is unlikely to survive below this temperature threshold. The UKMO meteorological station nearest to this site (at Emley Moor, West Yorkshire) records an absolute minimum of -7.5 °C in January 2008, suggesting that this species was unlikely to survive at the site. However, the landscape models, when projected across the Peak District site, suggest that only 18 % of the site would have had a minimum temperature below the -1.61 °C threshold, and hence the remainder could have been thermally suitable for survival in January 2008. Of course, other species will have different thresholds for survival. A species that could not survive below a threshold of 0 °C might not be expected to be able survive well according to the meteorological station temperature, and indeed, only 7 % of the landscape would be predicted to be suitable for such a species using my temperature models.

These results indicate that the incorporation of topographical information is essential for species that are at least partially limited by temperature extremes. Most species have some capacity to undertake shifts of slope and aspect to areas that are thermally more suitable for them. In this study I have concentrated on the effects of topography on the temperature encountered at a location, but still other factors could also influence microclimate. Even small differences in vegetation height can generate very large differences in ground-level temperatures (Thomas 1983; Thomas *et al.* 1999). There is already evidence that a butterfly species has shifted its host plant association in some areas due to climatic warming (Thomas *et al.* 2001) - moving into habitats that were previously considered too cool. The extent to which the global, regional and habitat distributions of species are limited by temperature extremes, rather than by averages, is uncertain. Nevertheless, many studies document strong impacts of observed or experimental thermal extremes on the performance of individuals and populations (e.g. Easterling *et al.* 2000), so the incorporation of topographical and/or vegetation data should improve the accuracy of climate-envelope models for such species.

There are also a number of studies that indicate the effect of microclimatic variation on species' distributions in practice (see Introduction). Individual insects can thermoregulate by selecting appropriate microhabitats and topographies (e.g. Ashton *et al.* 2009). They may also lay their eggs in sites with microclimates which facilitate the survival of their offspring (Weiss *et al.* 1988), choosing host plants that grow in hotter locations when conditions are relatively cool (Davies *et al.* 2006). Kindvall (1995) found that *Metrioptera bicolor* crickets performed best in short turf in cool years, but in longer grass in hot, dry years; and Thomas *et al.* (1996) found that a catastrophic frost (≈T_{min}) eliminated *Euphydryas editha* butterflies from one habitat type but not from another. Furthermore, large-scale variation in species’ habitat associations along climatic gradients implies that such effects are likely to be commonplace (Oliver *et al.* 2009). I conclude that thermal variation described here is highly relevant to a wide variety of species, and hence cannot simply be excluded from studies examining landscape-scale population biology.

These findings also have important implications for conservation efforts. Current prospective policies for preserving biodiversity under climate change include wildlife corridors (e.g. Vos *et al.* 2008), increasing connectivity (e.g. Opdam *et al.* 2006) and translocation or assisted colonisation of species (e.g. Hoegh-Guldberg *et al.* 2008; Heller & Zavaleta 2009). I suggest that maintaining a thermally diverse landscape could also prove a useful and cost-effective conservation approach, assuming species' other requirements are met by the prospective habitats. Areas with high topographic variability provide a diversity of thermal conditions that may enable populations to survive limited levels of warming (Hopkins *et al.* 2007). Microclimatic refugia with respect to suitable slopes and aspects are likely to operate in the landscape in a similar way to topographic refugia derived from the cooler temperatures available with higher elevations. Thus, it should be possible to identify existing areas that are thermally diverse. Further work on the thermal diversity of different vegetation types (Suggitt *et al.* 2010) may additionally allow the identification of management options to increase thermal diversity in some situations.

The use and application of bioclimatic modelling is growing and a number of limitations have already been recognised (Pearson & Dawson 2003). Commonly modelled and interpolated temperature surfaces are very different from those directly experienced by organisms. With the exception of some spiders, few species actually live inside standard Stevenson screens at 1.5 m above the ground (where temperatures are recorded by meteorological stations). If we are to understand the effects of climate (and climate change) on species’ populations in ways that can inform conservation, we should develop fine scale (sub 1 km resolution) temperature data for modelling studies, including fine resolution habitat data and model parameterisations that incorporate habitat-climate and topography-climate interactions. These approaches are increasingly feasible (see Bennie *et al.* 2008, Kearney & Porter 2009).

In summary, local variation in topography can generate large temperature differences. These should be quantified and included if we are to properly understand, predict and undertake adaptive management as part of conservation efforts in response to climate change.

5 The relative importance of climate and habitat in determining the distributions of species at different spatial scales

5.1 Abstract

5.1.1 Aim

To evaluate the importance of different environmental variables on carabid species distributions at different spatial scales

5.1.2 Location

Three field sites in Great Britain: Lake Vyrnwy in Wales; Glen Finglas in Scotland; and the Peak District National Park in England. Data were also used from the overall distributions of species within Great Britain.

5.1.3 Methods

The abundances of 20 beetle species of the family Carabidae were determined across the three study sites by pitfall trapping, and their distributions at the national scale were obtained from monitoring data. Statistical models were constructed to determine which of four sets of environmental variables (topographical, temperature, soil moisture or broad habitat) best accounted for the observed data at the local landscape scale, and whether climate or habitat models performed better at the national scale.

5.1.4 Results

Topographical models were the most frequently selected to best describe species' distributions at the local scale, followed by temperature models. Habitat models were occasionally selected as the best way to model species' abundances at such scales, with soil moisture never being considered the best model. Habitat models were always better than temperature models at describing coarse scale distributions within Great Britain. None of the variables was able to explain the presence or absence of ubiquitous species as well as they did those species with a northerly distribution.

5.1.5 Main conclusions

Temperature can be an important determinant of the local abundance of species within

landscapes. It is therefore important to include temperature variables in finer-scale analyses in addition to coarse-scale analyses where temperature is usually included. Consideration may need to be given to temperature variables when considering management of reserves for the conservation of selected species.

5.2 Introduction

It is widely recognised that climatic variables are important determinants of species' distributions at relatively coarse grains and over large spatial extents, but no consensus yet exists about the role of climate in determining finer-resolution distributions that approach the scales that individuals actually experience (Pearson and Dawson 2003; Harrison *et al.* 2006; Elith and Leathwick 2009). This uncertainty arises, in part, because there is a large difference between the spatial resolutions at which individuals experience the environment, and the spatial resolutions at which distributions and climate are usually represented and modelled. Most individuals of terrestrial invertebrates spend the majority of the non-dispersing phases of their lives in areas of 10^{-4} to 10^{5} m^{2}; even species which are more mobile usually experience a potentially selective series of such local environments, rather than the “average” conditions of a much larger area. In contrast, the distributions of species are typically represented at resolutions that are three to fourteen orders of magnitude coarser than this. For example, grid resolutions of 10^{8} to 10^{10} m^{2} (i.e. 10^{2} to 10^{4} km^{2}) are commonly used for the production of distribution atlases (e.g. Luff 1998; Harvey *et al.* 2002), to help quantify recent distribution changes in response to climate change (e.g., Thomas & Lennon 1999; Warren *et al.* 2001; Hickling *et al.* 2006), and for the purposes of modelling species’ distributions and projecting the responses of species to climate change (e.g., Huntley *et al.* 1995; Iverson & Prasad 1998; Hill *et al.* 2002; Thomas *et al.* 2004; Huntley *et al.* 2007; McKenney *et al.* 2007).

Given this mismatch, it is unclear whether coarse-resolution analyses are sufficient to understand current distributions, or to project future potential changes and conservation priorities. For example, different resolution bioclimatic models may give rise to quite different expectations of species' distributions and abilities to survive climatic change (e.g., Randin *et al*., 2009).

Climate may not even be the key factor determining where species are found at finer scales (Pearson and Dawson 2003). Within a particular landscape, the background climate may be similar from place to place, such that fine-resolution spatial variation in the distributions of species and in the composition of communities could be determined predominantly by non-climatic factors, such as differences in land cover and management (e.g., Butterfield and Coulson 1983; Eyre *et al.* 2003; 2005a), or by the geological substrate and soil type (e.g., Blake *et al.* 2003).

In reality, climatic and non-climatic variables are likely to combine to determine fine-resolution distributions. Littlewood *et al.* (2006) found that plant species composition was the most important variable in determining hemipteran assemblages, but that temperature was also a significant predictor. However, the relative importance of climate and land cover is difficult to deduce, partly because land cover is itself often related to climate. Some species may be restricted to favoured locations or habitats (where population growth rate is generally highest) in regions where the background climate is marginal, but occur in a wider range of habitats where the climate is more favourable (Lennon *et al*., 2002). Different topographies, shading and vegetation directly alter microclimatic conditions, such that only some combinations (e.g., sparse vegetation on south-facing slopes at northern range boundaries) provide suitable microclimates for population growth (J A Thomas *et al.* 1999; Suggitt *et al.,* 2010). Thermoregulatory behaviour that involves, for example, the selection of suitable microhabitats for basking (where available) may enable species to inhabit regions far outside the geographical limits that might otherwise be expected (Bryant *et al.* 2002). These interactions give rise to temperature-related geographic gradients of habitat associations (Stefanescu *et al.* 2004; Merrill *et al.* 2008; Oliver *et al.* 2009), and underlie shifts in the habitat affiliations of species following climatic warming (Thomas *et al.* 2001; Davies *et al.* 2006). Hence, even when non-climatic factors appear to be the most important determinants of the local distributions of species (when climate is measured at a coarse scale), it is not evident whether it is the microclimatic conditions that these locations provide that are important, or whether other non-climatic differences are more important.

Assessments of the relative importance of climatic *vs.* non-climatic factors at different spatial scales require the availability of both species' distribution and environmental data at equivalent resolutions. Point values of temperature have been used to describe species' distributions (Littlewood *et al.* 2006). Elevational lapse rates in concert with topographical variables, such as aspect, have been used to predict vegetation composition at landscape and regional scales (Gottfried 1999). Some studies, such as that of Gutiérrez Illán *et al.* (2010), have found elevation and solar insolation to be the principal factors in determining species range and abundance. However, fine-resolution temperature surfaces have yet to be combined in the same analyses as land cover or habitat variables. This may in part be due to a lack of availability of climatic data for use in landscape scale studies, but the recent publication of a fine scale microclimate model (Bennie *et al.* 2008; 2010) enables us to investigate the relative importance of climatic and habitat variables for selected species at a much finer resolution than has previously been explored. In this study, we develop this approach in relation to the distributions of a group of mainly predatory ground beetles (Carabidae) that should not be intrinsically limited to a particular type of vegetation, although habitat may be limiting in the prey it provides and the manner in which its structure modifies the climate experienced on the ground (Cernusca & Seeber 1981). Judas *et al.* (2002) found that distribution patterns of carabid beetles were not reproduced between years in relation to topography and canopy age. This is exactly as might be expected if temperature was the main factor driving the spatial distribution of this group, since the prevailing macroclimatic conditions will interact with topography and vegetation at the landscape scale to provide conditions at a location that may be suitable in some years but not in others. Here, we examine the relationship between microclimatic variation and other habitat features and the distributions of 20 carabid species at 25 m^2 spatial resolution, in three areas of the British uplands. We compare these results with deductions based on coarse-scale (100 km^2 resolution) distribution models for the same species across the whole of Great Britain.

5.3 Methods and Analysis

5.3.1 Field Sampling

Invertebrates were collected by pitfall trapping between the beginning of May and the end of August 2008. Trapping took place at three sites: Lake Vyrnwy Royal Society for the Protection of Birds (RSPB) reserve in Wales; Glen Finglas Woodland Trust reserve in Scotland; and the High Peak region in the Peak District National Park in England (Figure 5.1).

Lake Vyrnwy is situated adjacent to Snowdonia National Park (52° 47′ 09″ N, 03° 30′ 49″ W), covers *ca.* 9,700 hectares, lies between *ca.* 350 and 620 m a.s.l. and contains several different vegetation types. Trapping was undertaken in the commonest habitat type in the reserve, heathland dominated by *Calluna vulgaris* (heather) This habitat is actively managed for wildlife using a combination of mowing, burning and grazing to maintain a mosaic of heather and graminoids over a mainly peat soil base, such that a several different vegetation categories occur within the site, but the full range of vegetation encountered in GB is not present This site is at the southern range margin of many species with northerly distributions within the UK (Figure 5.2).

Glen Finglas is situated within the Loch Lomond and the Trossachs National Park, (56° 16′ 01″ N, 4° 23′ 20″ W). The whole site covers *ca.* 4,100 hectares and lies between *ca.* 150 and 821 m a.s.l.. It contains several different habitats, and open areas are maintained by a combination of sheep and cattle grazing. Trapping was undertaken in heathland dominated by *C. vulgaris* and upland unimproved grassland.

The High Peak site is situated within the Peak District National Park, Derbyshire (53° 31′ 25″ N, 01° 52′ 50″ W) and lies between *ca.* 250 and 580 m a.s.l.. The site is partially grazed by sheep, and some areas are managed for grouse shooting, with a burning regime imposed to maintain a mosaic of different age classes of *C. vulgaris*. Trapping took place in dwarf-shrub heathland, upland unimproved grassland and on bare peat.

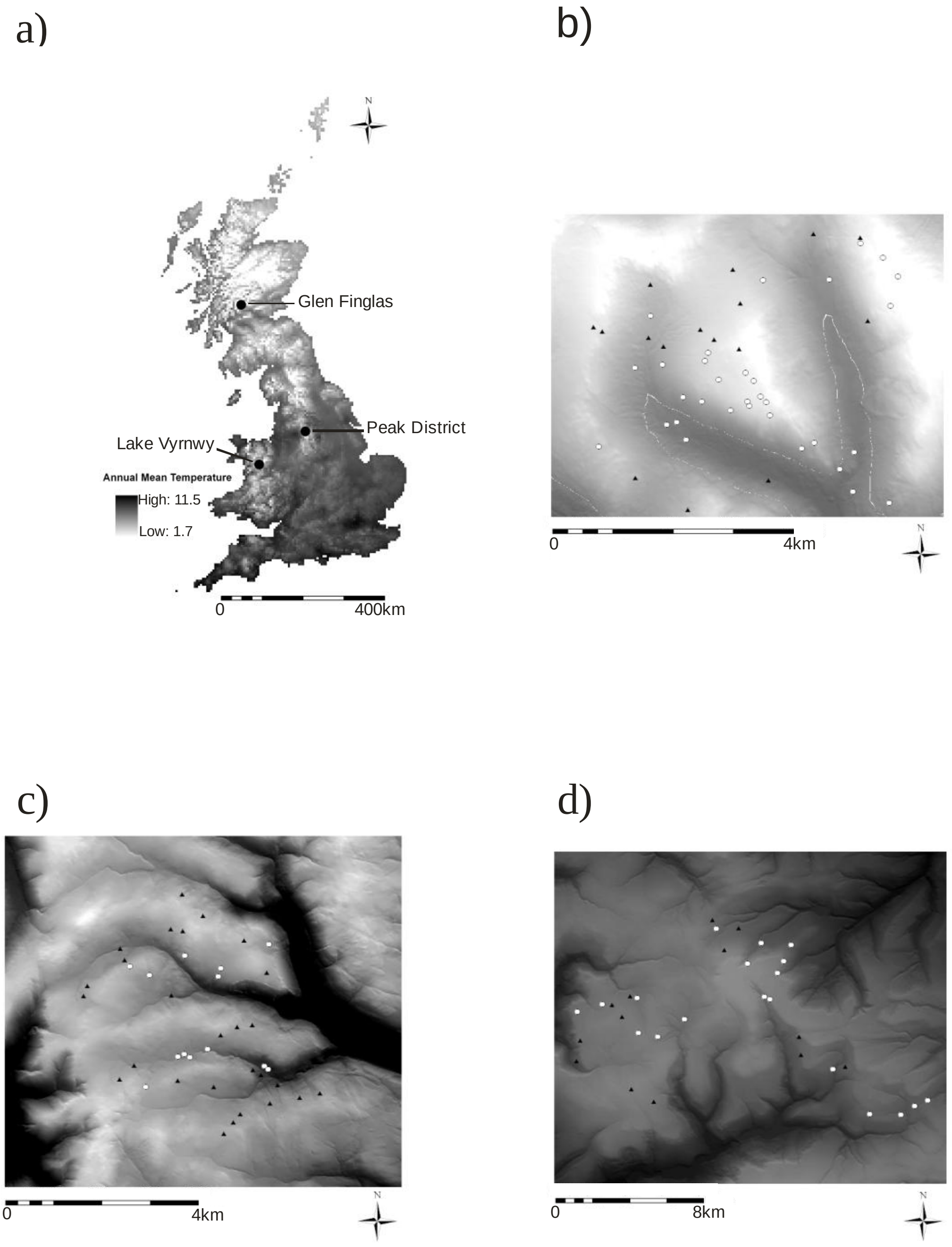

Figure 5.1 a) Location of the three field sites within Great Britain in relation to annual mean temperature (ºC) during the period 1961-90 at 5 km resolution; (b,c,d) Examples of the presence (black triangles) and absence (white circles) of individual species at the three study sites in relation to modelled annual mean temperature (ºC) at 5 m resolution: b) *Carabus glabratus* at Glen Finglas, c) *Carabus glabratus* at Lake Vyrnwy, d) *Pterostichus adstrictus* at the Peak District.

Forty locations were sampled at both Lake Vyrnwy and the Peak District, these being determined using a stratified random sampling strategy with equal representation of twelve categories determined on the basis of slope, aspect and elevation, plus a further four sites in the lowest elevation areas. This strategy was designed to give a comprehensive representation of the range of microclimates present at each site. Forty-eight locations were sampled at Glen Finglas, locations being selected in the same way, the additional locations allowing better representation of the more topographically diverse terrain present there. Sample locations were georeferenced in the field using a handheld Global Positioning System (Garmin GPS 60), and were at least 50 m apart in order to reduce spatial autocorrelation. Vegetation type was not considered when locating sample points, as this information was not available before sampling commenced, and as discussed earlier was difficult to determine accurately whilst in the field.

At each sample location, five pitfall traps were deployed in a circle of 2 m diameter. Traps consisted of two standard plastic vending cups nested together and sunk into the soil so that the rim of the inner cup was flush with the soil surface. Each trap was filled to a 2.5 cm depth with ethylene glycol antifreeze. Traps were covered with a lid made up of a terracotta coloured plastic saucer suspended 11cm above the ground and trap using galvanised wire. This served the dual purpose of limiting liquid loss by evaporation and limiting flooding from rainfall. A surround of chicken wire (mesh diameter 20 mm) completed the lid, with the aim of excluding small mammals and livestock from the trap. Traps were emptied on a monthly basis, and the antifreeze solution was replaced as necessary. Invertebrates from all five pitfalls at each sample location were pooled then transferred to 100% ethanol for transport back to the lab. Ground beetles were sorted from other invertebrates captured and were identified to species. The entire season's catch for each trapping location was then pooled for analysis to give a measure of the relative population density present at any one location; the pooling procedure averaged out the effects of sample error and of extreme weather events on activity of individuals during different months of trapping (Ribera *et al.* 2001).

Figure 5.2 – The distribution of *Carabus glabratus* within Great Britain. Black squares are where the species has been recorded as present, grey squares are where the species has not been recorded, but a record of at least one other carabid exists. White circles show the locations of the three field sites that were sampled for carabid beetles in 2008

5.3.2 Microclimatic Modelling

A recently published microclimatic model (Micromaker: Bennie *et al.* 2008) was used to predict the microclimate for each of the three sites[2]. Hourly radiation, wind speed and air temperature data were obtained for the meteorological stations recording radiation data that were closest to each of the three study sites (Lake Vyrnwy, 52° 45′ 25″ N, 03° 38′ 45″ W, Manchester Hulme Library, 53° 28′ 01″ N, 02° 15′ 00″ W and Strathallan Airfield, 56° 19′ 33″ N, 3° 43′ 44″ W) from the British Atmospheric Data Centre (BADC, www.badc.rl.ac.uk). Digital Elevation Models (DEMs) at 25 m^2 horizontal resolution and 1 m vertical accuracy for the three sites were obtained from the NERC Earth Observation Data Centre (NEODC, neodc.nerc.ac.uk). Slope and aspect values for each 5 x 5 m cell were calculated using the standard functions in ArcMap v 9.2 (ESRI, 2008). The Micromaker used this information to generate hourly predicted temperatures at the top of the vegetation layer at 25 m^2 resolution from the start of September 2007 until the end of August 2008. From these data, annual mean (ANMEAN), mean over the sampling period (May to August, MAMEAN), annual maximum (ANMAX) and annual minimum (ANMIN) temperatures were extracted for each sampling location to model the distributions of the selected species.

5.3.3 Landscape Scale Modelling

Species were selected for distributional modelling if they were present at five or more sampling locations in a site, with at least 10 individuals across the site, and were only modelled at the sites where these criteria were met. Abundance was used as the response variable in a Generalised Linear Model (GLM) with Poisson error structure and log link function. P-values were further corrected using a dispersion factor calculated by dividing the sum of the squared Pearson's residuals by the residual degrees of freedom

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[2] recoded from a Bash script running under the open source GIS program GRASS to a standalone C++ program. C++ code available on request from PKG

(see Gardner *et al.* 1995). Predictor variables available for possible inclusion were split into four sets: temperature; habitat; soil moisture; and topographic variables. The temperature set comprised ANMEAN, MAMEAN, ANMAX and ANMIN in degrees Celsius as calculated by Micromaker. There were two habitat variables (land-cover, extracted from the CEH Land Cover Map 2000 dataset): local dominant habitat (LOCH, the category recorded at the sampling point) and the number of land-cover categories present within a 100 m diameter buffer around each point (NH). There were five different land cover categories sampled at the Lake Vyrnwy site, with seven being sampled at both the High Peak site and Glen Finglas. Values of NH ranged from one to four at all sites. Only one soil moisture variable was used, a topographical index of potential soil moisture (SWI, calculated in ArcGIS following Murphy *et al.* 2009). Lastly, three topographical variables were used; elevation (E, m a. s. l.), slope (S, degrees, calculated in ArcGIS) and aspect (A, degrees, calculated in ArcGIS and expressed as the deviation from 200°, the warmest aspect, as described by Lakhani and Davis (1982)). To account for damage to traps caused by grazing livestock, a trapping effort variable was calculated and included as a log-offset in all models, corresponding to the proportion of the trapping effort that was lost to such damage at each location (e.g., loss of two of the five pitfall traps at a given location in one month). Linear and quadratic relationships were explored, and best models were built using a forwards stepwise procedure using the Akaike Information Criterion (AIC) as the basis for rejection or inclusion within each set of variables (e.g. topographical, temperature, soil moisture and broad habitat). This procedure was used in order to retain the trapping effort variable as the first term in all models, since it was a feature of the experimental design. Finally, a single best overall model for each species was developed starting with the best single variable set model and offering the other models in addition. Variables were then removed from these combined models using a backwards stepwise procedure, again using AIC as the basis for rejection. All statistical analyses were carried out in R version 2.82 (R Development Core Team 2008). Residuals from the overall best models were checked for spatial autocorrelation using Moran's I in ArcGIS.

5.3.4 ‘National’ Scale Modelling

To compare the perceived effects of different study scales, we used distribution records from the National Biodiversity Network (NBN) Gateway (http://data.nbn.org.uk), at 10 x 10 km grid resolution (i.e., 100 km^2 cells) for Great Britain. Long term average climatic variables for 1961- 90 were obtained at 25 km^2 resolution from the UK Climate Impacts Programme (UKCIP, http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/), and summary percentage cover of the broad habitat categories at 1 km^2 resolution was obtained from the CEH Land Cover Map 2000 (CEH, www.ceh.ac.uk/sections/seo/lcm2000_home.html). The resolutions were then harmonised by summarising the climatic and land cover data to 100 km^2 resolution in ArcGIS, to match the distributional data; the mean was used for the temperature variables, and the total area covered for the habitat categories. Species’ presences were taken as 100 km^2 grid cells where a given species had been recorded, using all data available from the NBN gateway. Because sampling of carabid beetles in Britain is not exhaustive, a species may be truly present in some cells where it has not been recorded. To reduce this concern, “absences” were taken to be only those 100 km^2 grid cells that were known to have been sampled for ground beetles (i.e., other carabid species had been recorded from them, Figure 5.2). For each species, a layer of presences and absences for the UK was generated. This was used as the response variable in a GLM with binomial error structure and logit link function, and was fitted to the percentage cover of each of 15 habitat categories (based on the Level one categorisation carried out by CEH), and to mean, maximum and minimum temperatures in a combined model using the BIOMOD package for R (Thuiller 2009). Area under the receiver operating characteristic curve (AUC) was calculated using a 70/30 data split.

5.4 Results

5.4.1 Landscape scale distribution modelling

35 species of Carabidae were caught at Glen Finglas, 29 at Lake Vyrnwy and 19 in the Peak District; the cumulative total across the three sites being 41 species (see table 5.1). Twenty of these species fulfilled the modelling criteria at one or more sites. The models based on the four different types of variable (see tables S1-S3, supplementary materials, appendix 2) show that there were many correlates of abundance across the landscape when modelling at 25 m^2 resolution. Summarising across sites and species, temperature variables were considered the *most important* (best model selected by AIC) for 17 out of 41 species/location combinations (Glen Finglas 9/18 species; Lake Vyrnwy 7/14; Peak District 1/9), whereas habitat class (LOCH) produced the best model in only 3 of the 41 analyses. Even with a cautious interpretation of this result, temperature may be considered to be at least as important as habitat as a predictor of the abundance of species at finer resolutions. This is reinforced by examining the variables retained in the overall best models for each species (see tables S4-S6, supplementary materials). Two temperature variables (ANMAX and MAMEAN) were retained in 16 of the 41 best models, ANMEAN was retained in 15, and ANMIN in nine. Dominant habitat type (LOCH) was retained in 17 models, with local habitat diversity (NH) explaining some variation in 11 models.

Spatial autocorrelation in the predictor variables retained in the best models accounted for any autocorrelation in the abundances of species across the landscapes, in most models. The residuals from the best models were significantly clumped in only three of the 41 analyses, and p-values for the Moran's I statistic were typically close to the threshold of 0.05. Additionally, residuals were over-dispersed in one of the 41 analyses. There is therefore only weak evidence for remaining spatial autocorrelation in the abundances of the species examined, once spatial autocorrelation in the environmental variables has been accounted for.

Table 5.1: The abundance of the twenty selected species at each field site. Species present at a site, but not fulfilling the modelling criteria, are designated by *.

Species	Peak	Lake Vyrnwy	Glen Finglas
Abax parallelepipedus	0	48	66
Agonum fuliginosum	15	89	38
Amara lunicollis	15	10	37
Carabus arvensis	0	53	191
Carabus glabratus	0	437	162
Carabus problematicus	126	19	159
Carabus violaceus	110	125	167
Cychrus caraboides	11	45	13
Loricera pilicornis	6 *	0	81
Nebria brevicollis	22	0	0
Notiophilus biguttatus	6 *	10	0
Patrobus assimilis	4 *	0	24
Poecilus versicolor	0	50	337
Pterostichus adstrictus	85	0	75
Pterostichus aethiops	0	0	12
Pterostichus diligens	139	240	43
Pterostichus madidus	2 *	123	620
Pterostichus melanarius	0	0	134
Pterostichus niger	0	76	468
Pterostichus nigrita	86	1752	623

Northerly and southerly-distributed species largely behaved in predictably different ways. The northerly species that were sampled in sufficient abundance to analyse were *Carabus glabratus*, *Patrobus assimilis* and *Pterostichus adstrictus* (Nelson 1971; Luff 1998). *C. glabratus* exhibited a positive linear correlation with elevation at Glen Finglas, being more abundant at higher (cooler) elevations; at Lake Vyrnwy this species showed a negative linear correlation with ANMAX, being more abundant in cooler areas of the site. *P. assimilis* abundance showed a negative linear relationship with MAMEAN at Glen Finglas, again being most abundant where the temperature was coolest. The abundance of the third northerly-distributed species, *P. adstrictus*, was positively correlated with elevation at Glen Finglas, again occurring in greatest abundance in locations where the temperature is coolest. In the Peak District, this species was positively correlated with elevation, but only after a strong negative association with ANMIN was taken into account. In contrast, we sampled one southerly-distributed species, *Abax parallelepipedus*, which reaches the northern margin of its global distribution in Scotland (Luff 1998). This species shows a positive linear relationship with annual maximum temperature at Glen Finglas, and a quadratic relationship with elevation in Wales such that it shows a non-linear decrease in abundance with increasing elevation; as expected it is more common in warmer areas.

Although a few species could be recognised as distinctly “northern” or “southern” in Britain, all species can be represented on a continuous “northerliness” scale by the mean of their latitudinal records in Great Britain. The slope of the regression of each species’ abundance at each site (where present) against annual mean temperature (at 25 m^2 resolution) and its northerliness index were negatively correlated (Figure 5.3; Spearman's $r = -0.4677$, $n = 20$, $p=0.0196$). This negative correlation confirms that more northerly species tend to occur at greater abundance in cool locations within landscapes (negative regression coefficients), whereas more southerly species tend to be more abundant in relatively warm places (positive regression coefficients). The three species that appear to diverge from this trend (*Loricera pilicornis, Nebria brevicollis and Agonum fuliginosum*) are all represented by at least some winged individuals, suggesting that chance occurrences of species capable of flight could create unexpected patterns in their abundance.

Another interesting result is that SWI (soil moisture) was never the variable explaining most variation, and was only occasionally (6 of the 41 analyses) retained in the best models (Tables S1-S6, supplementary materials, appendix 2).

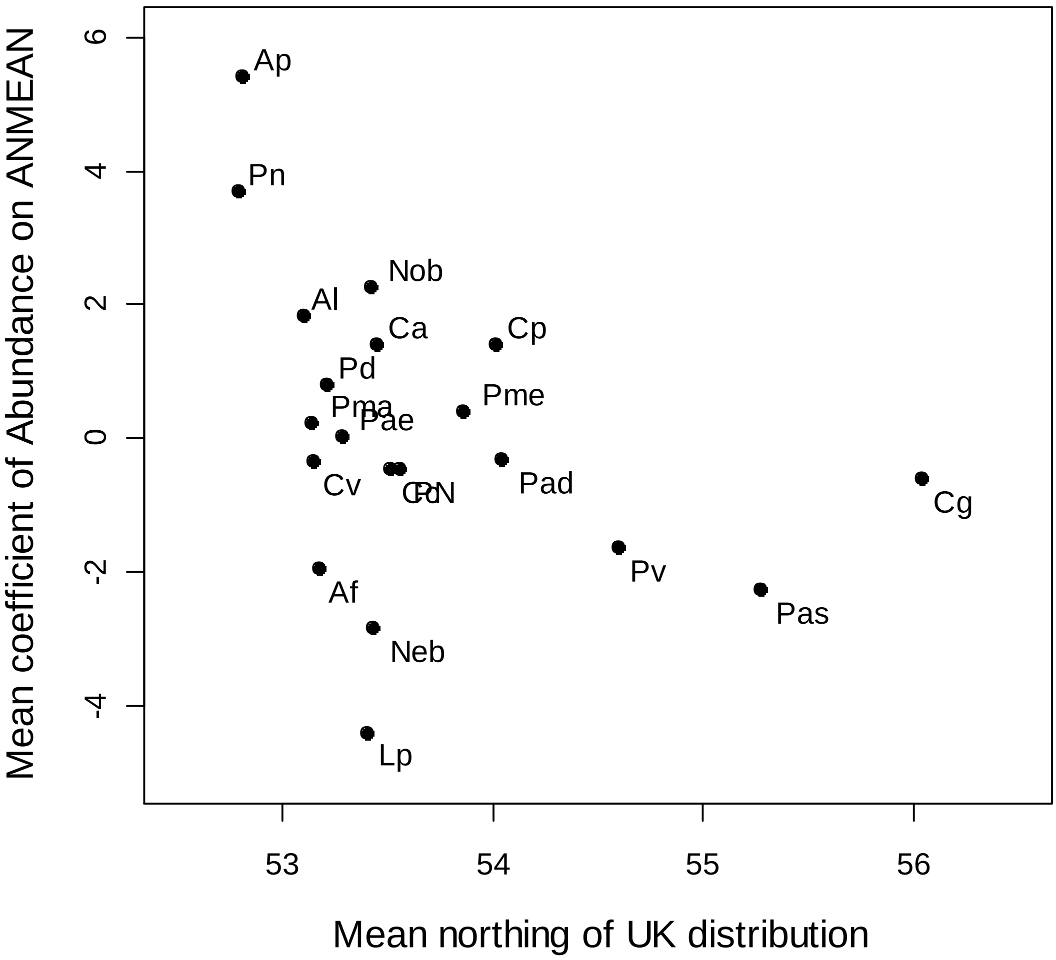

Figure 5.3 – The relationship between the mean regression coefficient of species abundance on modelled annual mean temperature (ANMEAN) and the mean latitude of the GB distribution of the 20 selected Carabid species. For the purposes of illustration, all models were constrained to use ANMEAN (the mean annual temperature in °C), despite other temperature variables often being better predictors of the abundance of species. Labels denote codes for each species; Af = *Agonum fuliginosum*, Al = *Amara lunicollis*, Ap = *Abax paralllelepipedus*, Ca = *Carabus arvensis*, Cg = *C. glabratus*, Cp = *C. problematicus*, Cv = *C. violaceus*, Cc = Cychrus *caraboides*, Lp = *Loricera pilicornis*, Neb = *Nebria brevicollis*, Nob = *Notiophilus biguttatus*, Pas = *Patrobus assimilis*, Pad = *Pterostichus adstrictus*, Pae = *P. aethiops*, Pd = *P. diligens*, Pma = *P. madidus*, Pme = *P. melanarius*, Pn = *P. nigrita*, PN = *P. niger*, Pv = *Poecilus versicolor*.

5.4.2 ‘National’ scale distribution modelling

Our analysis revealed that habitat models were better than temperature models at predicting the presence/absence of all species modelled. In general, model fit was poor (AUC scores below 0.7) However, both habitat and temperature models performed better for the more northerly-distributed species (Table 5.2). The poor fit may be additionally attributable to using habitat data for one year only (2000) and average temperature data for only 1961-90, whereas species' records have been gathered over many decades. In addition, it was not possible to include factors such as variation in recorder effort leading to an unknown numbers of false negatives being present in the NBN data.

Table 5.2 – Summary of relationships between both broad habitat models and the temperature variable considered best by AIC value and species presence/absence for the UK distributions of the 20 selected species. Values of AUC below 0.7 indicate a poor fit of the model to the observed data, which may be caused by poor prediction of presence, absence, or both.

Species	Mean Latitude	Habitat retained	AIC	AUC	Best temp model	AIC	AUC
Carabus glabratus	56.04	9	843	0.90	+ANMEAN -ANMAX -ANMIN	942	0.87
Patrobus assimilis	55.27	8	1100	0.84	-ANMEAN +ANMIN	1197	0.82
Pterostichus adstrictus	54.60	7	1045	0.81	-ANMEAN	1137	0.78
Pterostichus aethiops	54.04	5	533	0.85	-ANMAX	625	0.73
Carabus problematicus	54.01	7	2574	0.67	-ANMEAN -ANMAX	2689	0.61
Pterostichus niger	53.85	7	2932	0.60	+ANMIN	2994	0.51
Pterostichus nigrita agg.	53.55	9	2937	0.62	+ANMIN	3026	0.51
Cychrus caraboides	53.51	5	2616	0.65	+ANMAX	2730	0.54
Carabus arvensis	53.44	9	1157	0.72	-ANMAX +ANMIN	1255	0.60
Notiophilus biguttatus	53.43	7	2922	0.65	+ANMAX -ANMEAN	2991	0.61
Nebria brevicollis	53.42	7	2898	0.66	-ANMEAN +ANMAX +ANMIN	2997	0.58
Loricera pilicornis	53.40	8	2929	0.65	+ANMAX	3018	0.59
Pterostichus diligens	53.27	7	2541	0.67	+ANMAX -ANMEAN +ANMIN	2681	0.55
Pterostichus madidus	53.20	8	2783	0.70	+ANMAX	2933	0.63
Agonum fuliginosum	53.17	11	2665	0.66	+ANMAX -ANMEAN +ANMIN	2733	0.61
Carabus violaceus	53.14	9	2614	0.68	+ANMAX -ANMEAN	2766	0.59
Pterostichus melanarius	53.13	10	2741	0.67	+ANMAX	2809	0.63
Amara lunicollis	53.10	8	1843	0.67	+ANMAX	1928	0.55
Abax parallelepipedus	52.81	9	2515	0.74	+ANMAX +ANMIN -ANMEAN	2708	0.66
Poecilus versicolor	52.75	8	1740	0.66	+ANMEAN	1785	0.62

5.5 Discussion

Climatic and land-cover variables were both important determinants of the distributions of species, at both fine (25 m^2 resolution within landscapes) and coarse (100 km^2 cells across Britain) scales. Northerly species, which are more frequently reported from cool regions of Britain, were most abundant in cool micro-sites within landscapes. Southerly species showed the reverse pattern, with greatest abundance in warm environments within landscapes. However, the effects of climatic variables were not restricted to species at the thermal edges of their geographic distributions, and many “widespread” species, such as *Pterostichus madidus,* were statistically associated with particular thermal environments within landscapes. The strength and direction of the relationships between abundance and temperature variables correlated with the mean latitude that the species was found at in GB By using high resolution (25 m^2) surfaces that reflect local thermal environments, the within-landscape distributions of species could frequently be explained in terms of climatic variables. In contrast, land cover was always more important in analyses of species’ distributions at the national scale.

These results appear to run counter to the commonly-held perception that habitat and vegetation variables will be most important at a local scale, whereas climatic variables will predominate in apparent importance at more extensive scales (Pearson and Dawson 2003, Harrison *et al.* 2006, but see Tingley and Herman 2009). Our explanation for this apparent discrepancy relates to the spatial resolutions and extents of the analyses.

High resolution, within-landscape analyses of the distributions and abundances of species rarely consider the importance of microclimates on species’ local distributions, although microclimates are recognised as being important towards the edges of species’ geographic distributions (J A Thomas *et al.* 1999), and may be important in determining species' survival in the context of environmental stochasticity (Weiss *et al.* 1988; Kindvall 1995; 1996; Oliver *et al.* 2010). In the absence of high resolution microclimatic data, local distributions of species are typically explained in terms of the types of variables that are commonly available at such resolution; such as resource, habitat and vegetation variables. The distributions of these “habitat” variables may themselves be correlated with climatic variation within a landscape (different vegetation types may be associated with different slopes, aspects and local elevations), such that a statistical association between a species and a particular habitat type cannot unambiguously be ascribed to habitat or to microclimate. In our study, the number of different habitat types was limited (up to seven in Glen Finglas and the High Peak), which may have limited the variation in abundance that was explained by habitat. However, this is likely to be the case in other studies done at such scales, so the amount of variation attributable to habitat should be generalisable to other similar studies covering similar sized areas.

This is further confounded by the fact that different habitats not only *occur* predominantly in different microclimates but that they also *generate* different microclimates through variation in vegetation density and height. For example, Schneider and Eugster (2005) found that converting peat wetlands to productive agricultural land reduced the temperature range experienced by the area by 0.6 ºC. Similarly, Suggitt *et al.* (2010) found that the minimum temperature in woodlands was 4 - 6 ºC warmer than in nearby heathlands and grasslands, and Thomas (1983) reported that short-turf can generate 8 ºC higher surface temperatures than tall turf, within the same grassland. Hence, it is possible that, in the absence of appropriate high-resolution microclimatic data, much of the within-landscape variation in species' abundance and distribution is being mistakenly attributed to habitat-related factors, thereby under-estimating the role of climatic variables (and hence climatic change) in affecting species' local distributions. Because our analyses only considered microclimatic variation associated with topography, and did not consider other sources of microclimatic variation related to habitat type, we may still have underestimated the role of thermal variation in determining within-landscape distributions. The fine-scale vegetation structure data required to determine this indirect effect of land cover are not yet available for most areas, although the increasing availability and use of high resolution LiDAR data may provide a solution (Müller and Brandl 2009).

Soil moisture appeared in our study to be of less importance than other factors in determining patterns of species' abundance within a site. Previous studies (Butterfield and Coulson 1983; Gardner 1991; Eyre 1994) have found soil moisture to be very important to carabid beetles. This seems reasonable as many carabid species have soil-dwelling larvae, and larvae may drown in soils that are too wet or desiccate in those that are too dry. This disagreement may have arisen because SWI was derived from the topographical variables slope and upslope area, which were themselves derived from a DEM. This presents opportunities for error propagation, and the resultant surface may not be completely reliable. Topographically similar sites may also have differing soil structures or peat depths, and so may retain different levels of moisture. In addition, surface temperatures can affect evaporation rates (Bennie *et al.* 2008), so that more moisture may be lost to the atmosphere on warmer slopes than on cooler slopes with equivalent SWI. Simple topographic (drainage) wetness indices such as the one we used, although commonly used by hydrologists thanks to their relative ease of computation, are recognised as being less accurate than some other methods available to calculate the wetness of soils (Murphy *et al.*, 2009). Given the nature of the data currently available, we remain cautious in our interpretation of the role of soil moisture.

For the national scale analysis that was carried out for the geographic extent of Great Britain, local climatic variation associated with different topographies and vegetation types within 100 km^2 cells may be as large as, or greater than, the climatic variation between cells (e.g. we observed a range of over 6 ºC in maximum temperatures within the Peak District site in any one month). This thermal variation may partly be captured by the frequencies of different land cover types; it is possible that our British-scale analysis assigns greatest importance to land cover type simply because vegetation types provide proxies for the range of local microclimatic conditions within each 100 km^2 grid cell. Likewise, including elevational range within coarse grid cells can improve the fit of distribution models because this reflects the likelihood that suitable local climates will be found somewhere within the grid cell (Luoto & Heikkinen 2008). For widespread species, climate may contribute to variation in presence or abundance, but such variation is only weakly correlated with the smoothed 100 km^2 climatic surfaces that were available to use in the 100 km^2 resolution analysis of Britain.

For northerly distributed species that are close to their climatic margins within Britain, temperature variables were also found to be important in the 100 km^2 resolution analyses (Table 5.2). If we presume that these species are truly at their thermal margins, only the coldest 100 km^2 grid cells are expected to contain microclimatic conditions that are sufficiently cold and moist for northern species to survive and reproduce; such species are expected to be restricted to microclimates that are cooler than the average conditions of coarse grid cells, as seen in our landscape-scale analyses. Similarly, southern species are only expected to find sufficiently hot microclimates within the warmest 100 km^2 grid cells.

At yet coarser resolutions, land cover may cease to be important in analyses (Luoto *et al.* 2007) because all grid cells contain a diversity of topographies (south- and north-facing slopes) and vegetation types (which vary in shadiness, for example), providing a wide range of local climates. Such coarse-resolution grids give the impression of solid distributions of species within the core parts of their ranges, with a relatively “sharp” climatic margin, giving rise to the conclusion that climatic variables dominate distributions at very coarse resolution, particularly when analysed over much larger extents than Britain (continents).

We are left with the somewhat uncomfortable conclusion that the perceived relative importance of climatic and non-climatic determinants of species' distributions may have as much or more to do with the nature of the data available, and the resolution and extent of the analysis, as with the real separate and combined effects of climatic versus non-climatic variables.

More positively, finer-resolution microclimatic approaches, such as those adopted here, may begin to provide projections of species’ responses to climatic change at a scale that is relevant to conservation planning. Thermally-driven shifts in species’ vegetation associations (Davies *et al.* 2006) may enable us to identify ways of adapting management regimes to maintain suitable microclimates for species, and to identify heterogeneous landscapes and climatic refugia where species may be most buffered against extinction (Weiss *et al.* 1988.; Kindvall 1995; 1996; Oliver *et al.* 2010). Microclimatic modelling could also be used to improve assessments of conservation status by refining estimates of the area of land occupied by species. The conservation status of species is often determined, in part, by estimates of the extent of occurrence (from coarse resolution maps) or area of occupancy (from finer resolution maps) (IUCN 2001; 2010). The coarse-grained extent of occurrence may include large areas that are unsuitable for a species, and hence it is preferable to use area of occupancy criteria. However, this more accurate measure is unknown for 98 % of all birds (Sekercioglu *et al.* 2008), which are a relatively well studied group. Fine-resolution models incorporating microclimatic variation as well as other appropriate high-resolution data could be used to assess current status and project future trends more realistically than is possible with coarser-resolution models (Williams *et al.* 2003).

6 Reprieve for a northerner: very fine resolution models predict reduced losses of bioclimatic space at a warm range margin.

6.1 Abstract

Climate-envelope models have recently become popular for mapping potential habitat availability to species under current and future climatic conditions. However, the coarse-resolution climatic layers typically used in these studies do not represent the range of local climatic conditions present in topographically diverse grid cells. A few high-resolution analyses have considered the impacts of variation in elevation (lapse rates) on local climatic conditions, but not the effects of slope and aspect, which are equally important. We show that the distribution of a predatory beetle *within* a 10 x 10 km grid cell can be predicted from estimates of local (down to 5 x 5 m) climatic conditions (based on a microclimate model that incorporates the effects of variation in slope, aspect and elevation). The area perceived to be thermally suitable following climatic warming, and the expected abundance, is dependent on the resolution of the input data. Finer resolution data lead us to predict that more of the landscape will remain thermally suitable in the future (a 5 x 5 m resolution model predicted 31 % of the landscape would remain suitable with 2.5 °C warming compared to 2 % using a 900 x 900 m model). A comparable pattern is predicted for total abundance. In our study system, lower resolution analyses (as commonly reported in the literature) appear to underestimate the ability of populations to survive climatic warming, but further studies of different taxa, in different terrains and at different latitudes are required before more general conclusions can be drawn. Higher resolution analyses are not only likely to provide more accurate estimates of expected patterns of decline, but also to highlight potential microclimatic refugia for the conservation of species that otherwise might appear to be threatened with regional or global extinction.

6.2 Introduction

Many studies use climatic variables such as temperature to define the range of conditions that species can occupy. At large spatial extents, such climatic variables are commonly found to be associated with the presence and absence of species (Peterson 2001). Environmental “niche” or “bioclimate” models, which are based on these associations of species’ distributions with climatic variables, are often then used to predict changes in the area available to species following future climatic change (e.g. Huntley *et al.* 1995; Leathwick *et al*. 1996; Peterson *et al*. 2001; Thomas *et al.* 2004; Elith & Leathwick 2009; Kearney *et al.* 2010) and changes in species' richness within an area following climatic warming (Hannah *et al.* 2005; Menéndez *et al.* 2006; Huntley *et al.* 2007). In the past, these climate envelope studies have normally considered the associations between climate and species’ distributions at relatively coarse resolutions (usually 1 km^2 or coarser; commonly around 100 km^2 resolution in Britain, or 2500 km^2 in Europe), corresponding to the availability of species' distribution data (e.g. National Biodiversity Network, http://data.nbn.org.uk) and/or of climate surfaces, and have given the capacity to run models quickly for large geographic areas. However, some distribution records are submitted with greater spatial precision (http://data.nbn.org.uk) and climate surfaces are increasingly downscaled to finer resolutions (Guan *et al.* 2009) as computational power continues to increase. This makes the prospect of producing high-resolution bioclimatic models increasingly realistic (e.g. Montoya *et al.* 2009; Seo *et al.* 2009). Here we consider the implications of modelling distribution change at different spatial resolutions.

A number of previous studies suggest that the spatial resolution of analysis could affect estimates of species declines and extinction. Thomas and Abery (1995) found that the observed decline rates of 12 British butterfly species were 35 % higher when estimated using a 4 km^2 grid than when based on a 100 km^2 grid; and that the loss of 90 % of the local populations of *Plebejus argus* resulted in a loss of only 56 % of 4 km^2 grid squares. Similarly, Thomas *et al.* (2006) found that much higher rates of retraction at low latitude/elevation range boundaries were detected when they were measured using a 1 km^2 grid than when using a 100 km^2 grid. This may be a particular issue in mountainous regions, where coarse-resolution grid cells may contain a wide range of environments and population densities (Shoo *et al.* 2006). Within such a grid square there is likely to be a wide range of microclimatic conditions (Ashcroft *et al.* 2009) potentially resulting in the presence of locally-suitable conditions for species at their thermal margins, the existence of which might not be apparent at a coarser resolution. Many species are associated with locally suitable microclimates at their range margins, where the coarser-scale mean climate is less suitable than at the centres of their ranges (Thomas *et al.* 1999; Bryant *et al.* 2002; Lennon *et al.* 2002; Stefanescu *et al.* 2004). Thus, models that utilise fine resolution data should be more accurate than those using coarse resolution climate data (Ferrier *et al.* 2002) in areas of high relief and for predicting the likely persistence of species in small areas such as individual nature reserves.

These resolution issues mean that estimates of rates of decline under climatic change may be either too high or too low when using low resolution data and model projections. There is a possibility that low resolution models will overestimate the area available to species (Trivedi *et al.* 2008) if, for example, a species only lives in the coldest 1 % of a coarse-grained grid cell containing a heterogeneous mix of different microclimatic conditions, but statistically appears to be able to inhabit the mean temperature of the grid square. Under modest climate warming, the coldest 1 % may become unsuitable for the species, even if the average temperature of the grid square still appears to remain suitable. Under this circumstance, a low resolution model may be slow to predict the disappearance of thermal refugia, and may therefore underestimate the rate of decline. Alternatively, however, high resolution models may predict the persistence of these thermal refugia for longer into the future with climatic warming than do low resolution models (Randin *et al.* 2009). So far, there are very few studies that have attempted to discover whether over- or under-estimation of declines is likely to be projected using low resolution models. Those that have been attempted have been restricted to plants, which, being sessile, might be expected to have a different propensity to survive in spatially restricted thermal refugia than more mobile organisms.

Previous studies that explored the implications of using models at different spatial resolutions interpolated high-resolution climate surfaces using lapse rates (i.e., adjusting local temperatures to take account of the local elevation; Trivedi *et al.* 2008; Randin *et al.* 2009). However, variation in aspect and slope can have even larger effects than elevation on local temperature (Suggitt *et al*. 2010). Given this uncertainty, and contrasting conclusions in the literature, it is not clear whether high-resolution analysis is expected to predict reduced (Trivedi *et al.* 2008) or increased (Randin *et al.* 2009) persistence, compared to low-resolution analyses. Here, we present the first study to compare the effects of different resolution models where the effects of slope, aspect, hill-shading and elevation on local temperatures are all included.

In this study, we sampled the abundance of ground beetles from within a single 10 x 10 km square from an area with substantial topographic variation, which thus gives a range of predicted temperatures depending on the resolution of the data (Figure 6.1). Because our records have a spatial precision of 5 m and include abundance data rather than presence/absence data, we are able to use them to answer several questions:

1) How does the spatial resolution used when modelling alter our perceptions of the importance of climate variables in determining where a species may be found?

2) Does the projected percentage of a landscape that will remain suitable for a species following climatic change vary with the resolution of the distribution model?

3) How does spatial resolution affect our perception of the carrying capacity of a landscape?

6.3 Materials and Methods

6.3.1 Field Sampling

Ground beetles were collected by pitfall trapping from the start of May to the end of August 2008. Trapping took place on the Royal Society for the Protection of Birds (RSPB) Lake Vyrnwy reserve.

Lake Vyrnwy is situated adjacent to Snowdonia National Park in Wales (52° 47′ 09″ N, 03° 30′ 49″ W) and covers around 9,700 hectares. It contains several different vegetation types, but all trapping was undertaken in the commonest vegetation type on the reserve; heathland dominated by *Calluna vulgaris* (heather) that occurs mainly on peaty soils. The area is actively managed for wildlife with a combination of mowing, burning and grazing being employed to maintain a mosaic of heather and grassland. The lowest areas of the reserve are around 350 m a.s.l.; the highest around 620 m a.s.l. The location and elevational range of the site means it is at the southern range margin of many species with northerly distributions within the UK.

Stratified random sampling was used to select 40 locations, as described previously, see chapters 4 and 5. A 5 x 5 m grid was laid across the landscape, then grid cells were stratified into twelve categories on the basis of combinations of slope, aspect and elevation, with a thirteenth category for areas at the lowest elevations; three sampling locations were then randomly positioned within each of the first 12 strata, and four in the last. This ensured that a wide range of microclimates present at the site was sampled, whilst giving the maximum chance of capturing species with both northerly and southerly distributions within the UK. Sample points were georeferenced in the field using a handheld Global Positioning System (Garmin GPS 60). At each sample location, five pitfall traps were deployed in a circle of 2 m diameter. Traps consisted of two standard plastic vending cups of 7 cm diameter nested together and sunk into the soil so that the rim of the inner cup was flush with the soil surface. Each trap was filled to a 2.5 cm depth with ethylene glycol antifreeze. Traps were covered with a lid made up of a terracotta coloured plastic saucer suspended 11 cm above the ground and trap using galvanised wire. This served the dual purpose of limiting liquid loss by evaporation and limiting flooding from rainfall. A surround of chicken wire (mesh diameter 20 mm) completed the lid, with the aim of excluding small mammals from the trap.

Traps were emptied at monthly intervals, with the antifreeze solution being replaced when necessary. Catch was pooled for all five traps across the entire sampling season for each location. All carabid beetles were identified to species, and *Carabus glabratus*, a northerly distributed species found at approximately half of the sample locations was selected for distributional modelling. No species considered by experts to be southerly-distributed were captured during this study (Hickling pers comm.). *C. glabratus* is a large ground beetle with a northerly distribution within the UK, which we might therefore expect to be found only in the colder and/or moister areas of the site. Additionally, the relatively high frequency of capture (compared to other northerly-distributed species) was likely to result in a model with greater statistical power than would be obtained for less frequently occurring species.

6.3.2 Microclimate modelling

A recently published microclimate model (Bennie *et al.* 2008) was coded into C++ (Programme available on request from PKG). Wind speed, air temperature and radiation data was obtained for the Vyrnwy meteorological station (52º 45′ 25″ N, 03º 38′ 45″ W) from the British Atmospheric Data Centre (BADC, www.badc.rl.ac.uk). A digital elevation model (DEM) at 5 x 5 m resolution (hereafter referred to as 5 m resolution) and 1 m vertical precision for the site was obtained from the NERC Earth Observation Data Centre (NEODC, neodc.nerc.ac.uk). Slope and aspect values for each 5 m cell were calculated using standard functions in ArcMap. The microclimate model used this information to generate hourly predicted temperatures at vegetation surface height at 5 m resolution from the start of September 2007 until the end of August 2008.

The microclimate model adjusted the temperature values from the Vyrnwy meteorological station to take account of the elevation difference between the met station and each point in the landscape, as well as differences in direct and indirect radiation associated with different slopes and aspects at different times of the day and year (including effects of hill-shading, and assuming homogenous cloud cover across the entire site; Bennie *et al.* 2008). From these hourly surfaces, annual mean, maximum temperature in July (T_{max}) and minimum temperature in December (T_{min}) were extracted for use in the distribution model at 5 m resolution.

6.3.3 Statistical Modelling

Abundance of *C. glabratus* was the response variable to which predictor variables were fitted using a Generalised Linear Model (GLM) with Poisson error structure and a log link function. The annual mean (T_{mean}), July maximum (T_{max}) and December minimum (T_{min}) temperatures as calculated by the microclimate model were included as predictor variables. Habitat variables were not included as they have been previously found to be less important for this species in this site (see Appendix 2 table S2), and in any case changes in vegetation are difficult to project into the future as they depend on management by humans. Trapping effort, corresponding to the proportion of the trapping effort that was lost to damage at each location (e.g., loss of two of the five pitfall traps at a given location in one month), was included as a log-offset in all models to allow for variations in catch caused by damage to pitfall traps. In addition, the topographical variables Slope (degrees), Aspect (degrees, transformed as deviation from 200 °, the warmest aspect, following Lakhani and Davis (1982)) and Elevation (m.a.s.l.) were included as independent variables, along with a topographic soil wetness index (SWI, described in Murphy *et al.* 2009). Forwards stepwise regression using AIC was used to determine the best model. The forwards procedure was used in order to keep the log trap effort as the first term in the model, as this was an inherent part of the experimental design. In addition, p-values were modified to take account of any overdispersion of data using a dispersion factor calculated by dividing the sum of the squared Pearson's residuals by the residual degrees of freedom (see Gardner *et al.* 1995). All topographical variables were calculated in ArcMap version 9.2 (ESRI 2008). All statistical analyses were carried out in R version 2.9.0 (R Development Core Team 2008).

Coarser resolution temperature surfaces for the site were generated by blocking up the data in 100 m increments using the mean value of the enclosed 5 m cells in ArcMap, to a maximum of 1 km resolution (for examples see Figure 6.1, note that resolution refers to the length of the side of each cell, such that 100 x 100 m cells are referred to as “100 m resolution”). GLMs were refitted to these lower resolution layers as before to compare how the variation explained by a variable changes with resolution. Where more than one sampling location fell within a given coarse resolution cell, both abundance and trapping effort values were pooled to create one value per cell. R^2 for all resolutions was partitioned between T_{max} (the climate variable that was retained in the “best” model; see Results) and the trapping effort variable using the hier.part package in R version 2.9.0.

6.3.4 Future Projections

The microclimate model was used to predict hourly temperature surfaces for the site at temperature increases in half degree steps to 6 ºC, which is the central estimate of the maximum predicted by 2085 for the UK under the maximum emissions scenario (http://ukclimateprojections.defra.gov.uk). This approach was used in order to compare the effects of data resolution on future predictions and it is not within the remit of our study to comment on the likelihood of future scenarios of climatic change. The 5 m resolution layer of the climate variable that was always retained, T_{max}, was used to predict the future abundance of *C. glabratus* in traps given a maximum sampling effort of 4 months of continuous capture in five pitfall traps, which corresponds to our sampling season with no damage to traps. The 5 m resolution future temperature surfaces were again blocked to the resolutions previously used, and the respective model equations derived previously were applied to these coarser surfaces to predict the abundance of *C. glabratus* under the degrees of warming. A threshold of one or more individuals predicted to be present within a cell was used to estimate the percentage of the total landscape that is expected to be climatically suitable for the species with each 0.5 ºC temperature increase.

6.4 Results

6.4.1 Microclimate surfaces

The microclimate surfaces are illustrated using July maximum temperatures (T_{max}), the climate variable that was shown to have the strongest association with the distribution of *C. glabratus* (below; Figure 6.1). The range of T_{max} temperatures decreased greatly as one moved from a 5 m resolution analysis (11.2 ºC range; 22.4 ºC to 33.6 ºC) to 1000 m resolution (3.9 ºC range; 26.1 ºC to 30.0 ºC). This compares to the maximum temperature of 23.5 °C recorded at the Lake Vyrnwy meteorological station for July 2008. In general, as the resolution of the analysis became coarser, the range of temperatures declined, with the coolest observable locations being warmer and the highest observable temperatures being cooler (Figure 6.2a).

6.4.2 Current Distributions

T_{max} was the only variable apart from the log-offset trapping effort to be retained in the best models at 5 m resolution. It showed a strong negative effect ($\beta = -0.7355$, $n = 40$, $p = 0.0004$) on the abundance of *C. glabratus*. The maximum temperature explained 22.9 % of the total variation in abundance of this species, which accounted for almost 25 % of the variation remaining once trapping effort had been taken into account. This means that there were fewer *C. glabratus* in areas with warmer maximum temperatures, as expected for a species at the southern limit of its distribution.

Using the 100 m resolution temperature surface yielded a similar result. Maximum temperature had a strong negative effect ($\beta = -0.7564$, $n = 40$, $p = 0.0002$) on the abundance of *C. glabratus.* This model explained slightly more variation than the 5 m model, with 26.9 % attributed to T_{max} (over 29 % of the variation remaining once trapping effort had been taken into account). This result is replicated at the 200 m and 300 m resolutions, with very similar regression coefficients and R² values (Table 6.1).

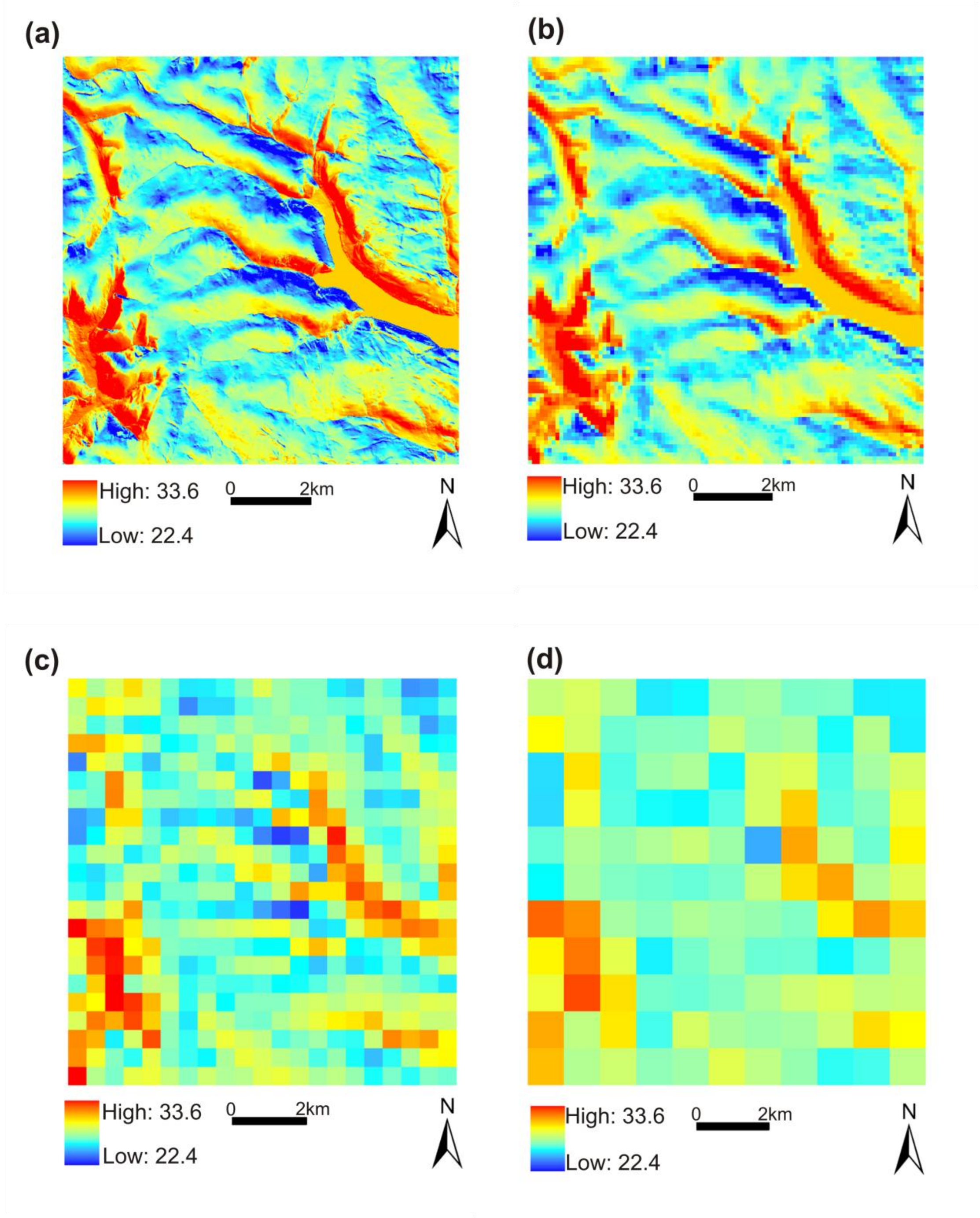

Figure 6.1: The maximum temperature in July 2008 (T_{max}) across the Lake Vyrnwy field site, shown at four different resolutions a) 5 m b) 100 m c) 500 m d) 1000 m

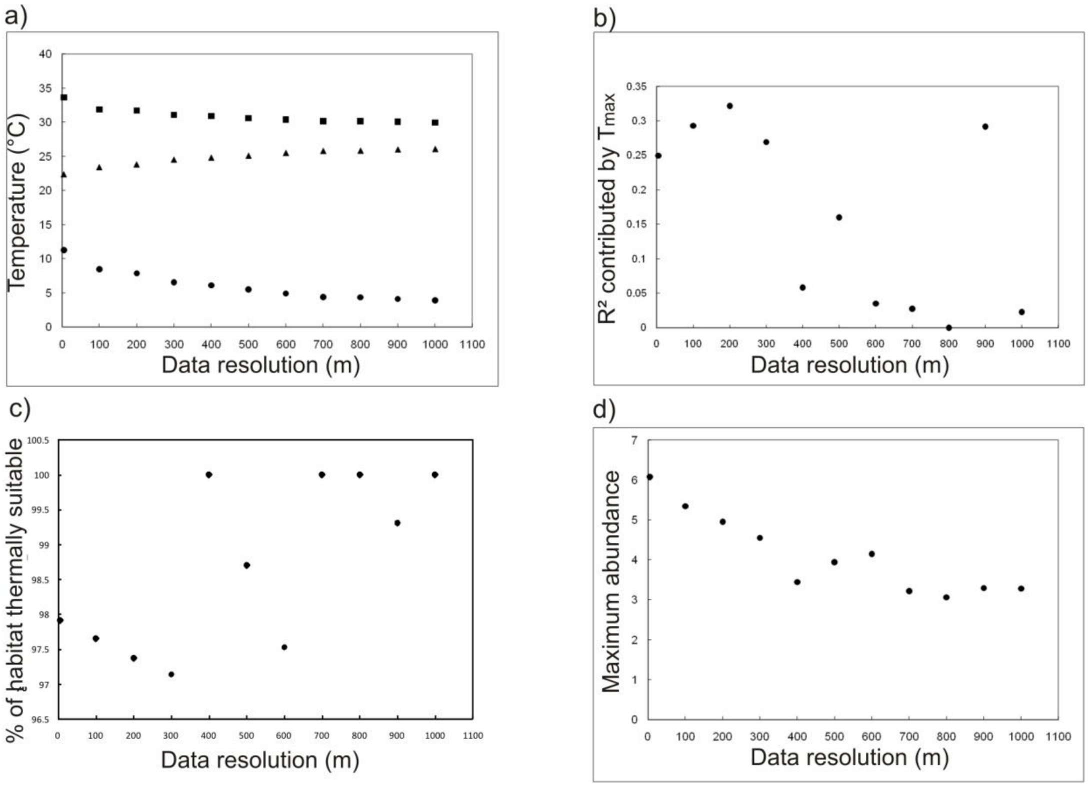

Figure 6.2: The relationship between input data resolution and perception of various parameters at 2008 conditions a) The maximum of T_{max} (squares), minimum of T_{max} (triangles) and range of T_{max} (circles) in the landscape, b) the variation in abundance of *Carabus glabratus* explained by T_{max}, c) The percentage of the landscape currently thermally suitable and d) the maximum modelled abundance for a trapping season of four months using 5 pitfall traps

The slope of the relationship between abundance and T_{max} was negative at all resolutions (i.e. increasing abundance in cooler locations), although the statistical significance varied with resolution (partly because of a reduction in sample size at coarser resolutions, see Table 6.1). However, there was a general trend towards lower explanatory power with increasing coarseness of input data (R^2 for T_{max} Table 6.1), with the relationship between maximum temperature and abundance always explaining less variation at resolutions of 400 m or coarser than in the models fitted at 300 m resolution or finer (Figure 6.2b). Although it does appear that the explanatory power of T_{max} peaks at intermediate resolutions (i.e. 32 % of remaining variation explained at 200m resolution), we would be cautious in claiming this as it is not possible to tell whether or not this is significantly more than the 25 % of remaining variation explained by the 5 m resolution model.

The apparent peak in explanatory power of the 900 m model appears to be an artefact of the pooling procedure, such that, by chance, more similar locations in terms of topography and thus predicted temperatures were pooled together. Moving the grid on both axes in 100 m chunks for both the 900 m and 1 km models resulted in a range of β co-efficients for T_{max}, with most models being non-significant (see Appendix 3 Tables S1-2). Three of the ten models run at 900 m resolution were considered significant, with estimated β-coefficients ranging from -0.81 to 0.11, whilst four of the ten models run at 1 km resolution were considered significant, with estimated β-coefficients ranging from -0.74 to 0.1. There was also a large range in the variation explained by Tmax in the models, from less than 1% to over 20% explained for the 900 m models, and less than 1% to over 25% being explained by the 1 km models.

Several other parameters were also influenced by the resolution of the explanatory variable T_{max}. Coarser resolution surfaces predicted that slightly more of the landscape was thermally suitable (more than one individual predicted to be caught using our trapping methodology) than the finer resolution analyses under current climatic conditions (Figure 6.2c), but predicted much lower maximum abundances (Figure 6.2d). Carrying out our trapping methodology in the most suitable areas of the landscape would be predicted by the 5 m resolution model to yield a maximum of six individuals in the five traps deployed at a sampling location (for full recording effort, depending on the exact location sampled), but the same methodology would only be predicted to capture a maximum of three individuals per sampling location by the 900 m resolution model. However, this effect was not observed on mean density per sampling location (Figure 6.3), suggesting that this is due to the averaging effect of coarse resolutions, such that the best cells at coarse resolutions do not appear to be as good as the best fine resolution cells in the same area, despite containing these cells.

Table 6.1: Summary of the Generalised Linear Models fitted at each resolution (Res), with number of sample locations N. Shown are the β-coefficient of the relationship between abundance of *Carabus glabratus* and maximum temperature in July (βT_{max}) with standard errors in brackets, and between abundance and trapping effort (βTrap) along with their associated p-values and the intercept of the combined model. Lastly, the variation attributed to T_{max} (R^2T_{max}), and the variation explained by T_{max} once trapping effort has been taken into account ($R^2T_{max}\%$) are shown

Res (m)	N	βT_{max}	p	βTrap	p	Intercept	R^2T_{max}	$R^2T_{max}\%$
5	40	-0.7355 (0.2081)	0.0004	1.7640	0.0455	11.3325	0.2294	0.2495
100	40	-0.7564 (0.2023)	0.0002	1.5159	0.0855	13.4209	0.2693	0.2929
200	40	-0.7720 (0.2038)	0.0002	1.1228	0.1450	16.2103	0.2959	0.3218
300	38	-0.8067 (0.2124)	0.0001	0.7899	0.1021	19.2970	0.2679	0.2693
400	34	-0.3790 (0.2331)	0.1039	0.8467	0.0582	7.4634	0.0552	0.0584
500	31	-0.7676 (0.2142)	0.0003	1.5302	0.0004	13.4668	0.1374	0.1603
600	28	-0.9457 (0.4787)	0.0482	1.2344	0.0504	20.4034	0.0338	0.0349
700	26	-0.4546 (0.3217)	0.1577	0.9653	0.0135	8.8002	0.0248	0.0277
800	22	-0.2753 (0.3883)	0.4784	0.8594	0.0424	4.7100	0.0001	0.0001
900	20	-0.8096 (0.2729)	0.0030	1.2081	0.0007	16.6539	0.2066	0.2918
1000	21	-0.7385 (0.5253)	0.1597	1.1591	0.0007	15.1597	0.0131	0.0228

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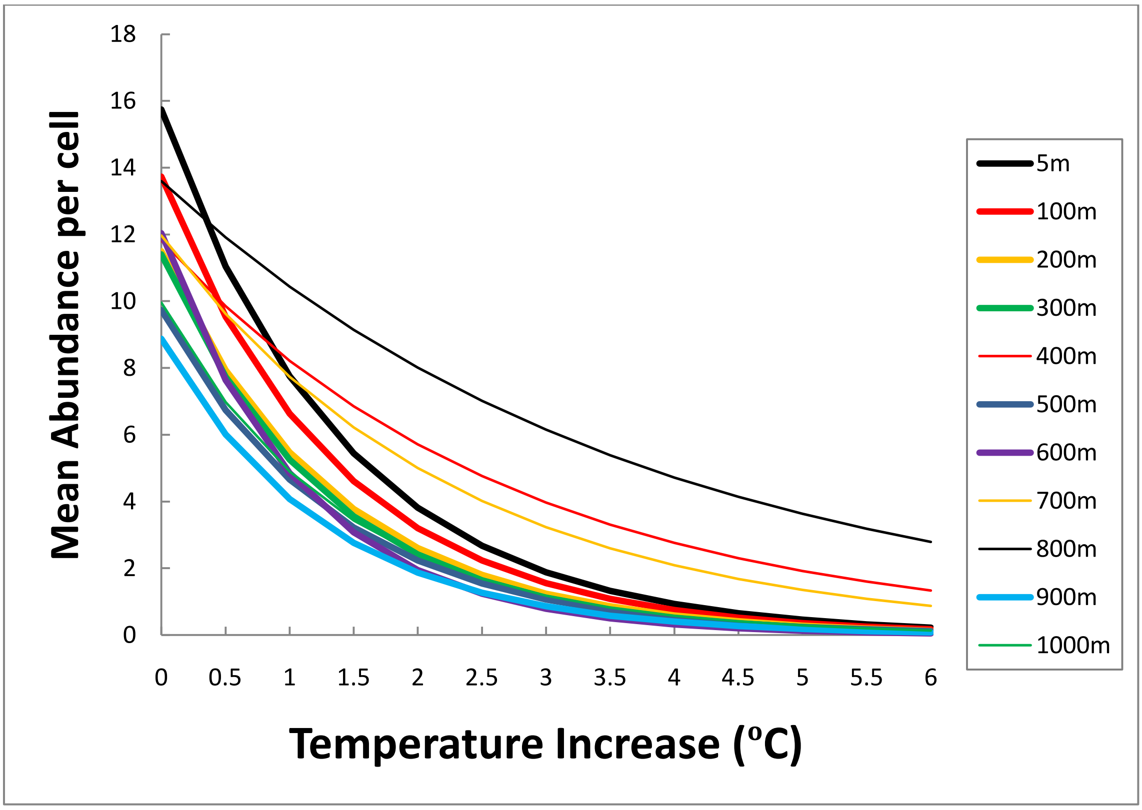

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Figure 6.3: The mean abundance of *Carabus glabratus* per grid cell modelled over the Lake Vyrnwy landscape in relation to projected temperature change and resolution of data. Significant models (P<0.05) are shown by heavy lines, non-significant ones by fine lines

4.3 Future distributions

The area projected to remain thermally suitable for *C. glabratus* within the study landscape, following climatic change, decreases in a non-linear fashion for all resolutions of analysis (see Figure 6.4). At current temperatures, the percentage of landscape perceived to be thermally suitable (i.e. we would expect to catch one individual or more in five pitfall traps over a four month period) is similar for the significant models across the resolutions examined (minimum 97 % at 300 m resolution, maximum 99 % at 900 m resolution). However, the finer resolution data/model resulted in a slower decline in the percentage of thermally suitable habitat associated with increasing temperatures (Figure 6.4). Following a 4 °C rise in temperature, the 5 m resolution model predicted that just over 28 % of the landscape could still be occupied, whilst the 900 m resolution model (the coarsest statistically significant model) predicted that just over 1 % of the landscape would be thermally suitable, and intermediate resolutions predicted intermediate percentage declines (i.e. the 100 m resolution model predicted the second slowest declines, the 200 m resolution model predicted a slightly faster decline, up to the 600 m resolution model, which predicted a decline only slightly slower than that of the 900 m resolution model). As another illustration, the amount of warming required to reduce the predicted landscape suitability to < 20 % remaining habitable was 3.5 °C for the 900 m resolution model, but 4.5 °C using the 5 m resolution model. However, the localised climatic refugia associated with fine-resolution models are only retained up to a point: almost all statistically significant models predict that the entire landscape would be thermally unsuitable following a 6 °C rise in temperature, with the exception of the 5 m, 100m and 200m resolution models in which just 2.4%, 1.1% and 0.3% respectively of the landscape was perceived as remaining suitable.

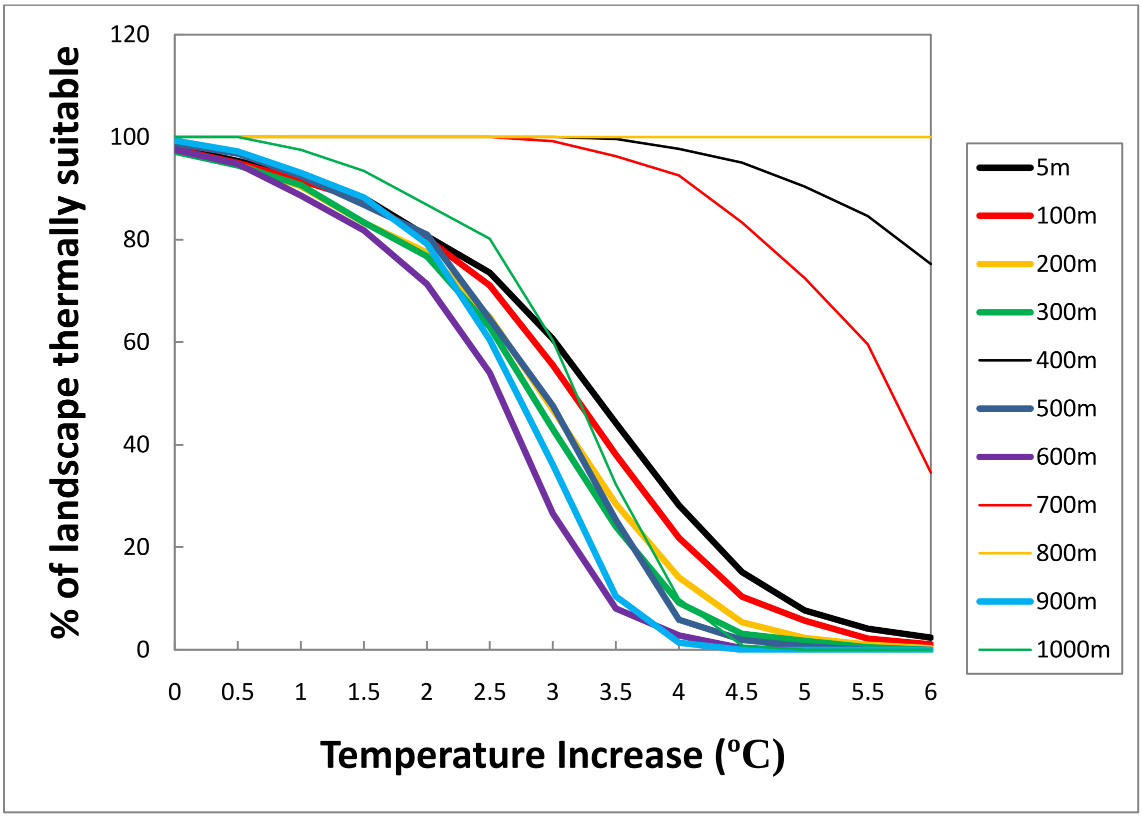

Figure 6.4: The percentage of the landscape predicted to remain thermally suitable following climate warming. Significant ($p<0.05$) models are drawn with heavy lines, non-significant models with fine lines.

As well as predicting a slower decline in the total amount of landscape remaining suitable with climatic warming, the finer resolution models consistently predicted a higher mean (Figure 6.3) and maximum (Figure 6.5) abundance within the landscape following climatic warming than did the coarser resolution models.

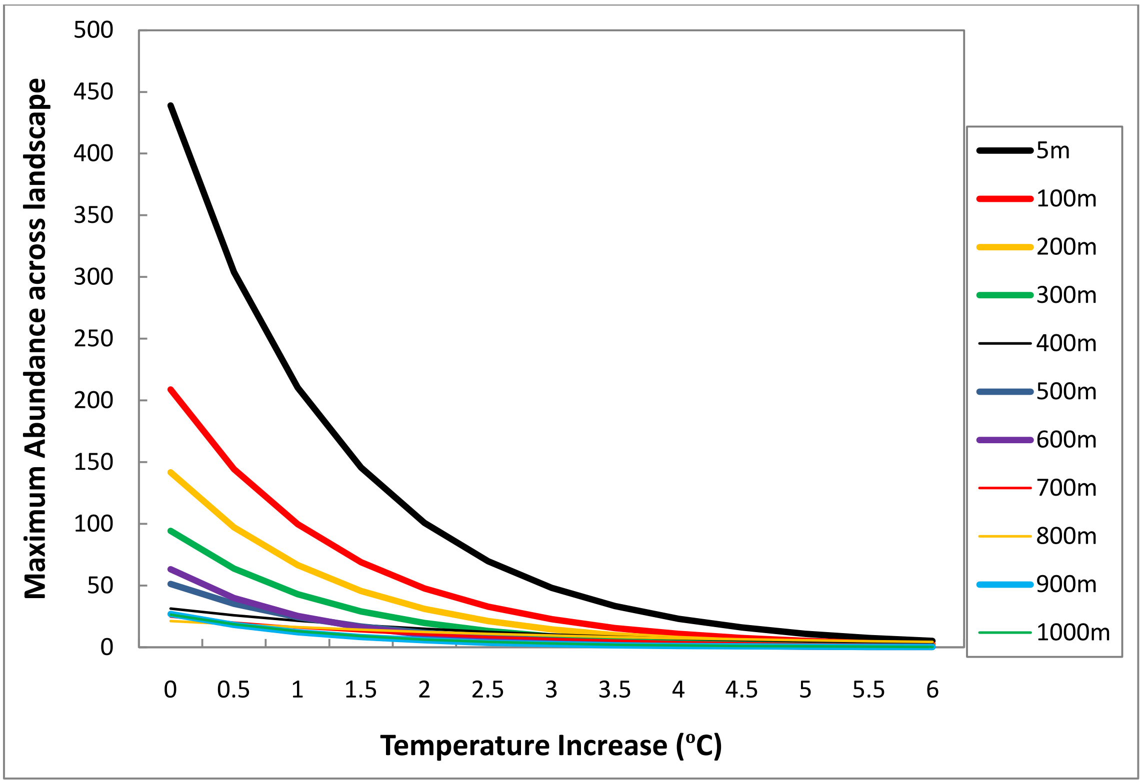

Figure 6.5: The maximum abundance at any grid cell within the Lake Vyrnwy landscape in relation to projected temperature change and resolution of data. Significant models ($P<0.05$) are shown by heavy lines, non-significant ones by fine lines

6.5 Discussion

The abundance of a northern beetle species, *C. glabratus*, was more closely associated with cold environments when analysed at fine resolutions than at coarser ones (Figure 6.2b). Fine resolution analyses ensured that the temperatures associated with sample locations were appropriate for the actual topographic conditions found at each location rather than the average of those over several hectares. At a site such as ours, topography can change markedly over a scale of tens to hundreds of metres, such that a coarser resolution cell may contain both north and south-facing slopes, as well as several hundred metres of elevational range. These differences in topography and thus temperature conditions presumably result in many coarse grid cells containing some areas that are suitable for *C. glabratus* and other areas that are not (see Figure 6.6).

Finer resolution models also predicted that, for a given amount of climatic warming, more of the landscape would remain thermally suitable for a northern species. Indeed, not only was the area remaining suitable following climatic change predicted to be greater when using fine resolution data (Figure 6.4), the most suitable areas were also predicted to support larger numbers of individuals of *C. glabratus* (Figures 6.3 and 6.5). Thus, by modelling at resolutions far coarser than the environments individuals actually experience we underestimated both the area of “suitable” conditions and the species' density where present. Small-scale refugia have also been found in other studies that have used fine-resolution models (Gottfried *et al.* 1999; Williams *et al.* 2003; Seo *et al.* 2009), although these studies did not expressly compare model resolutions.

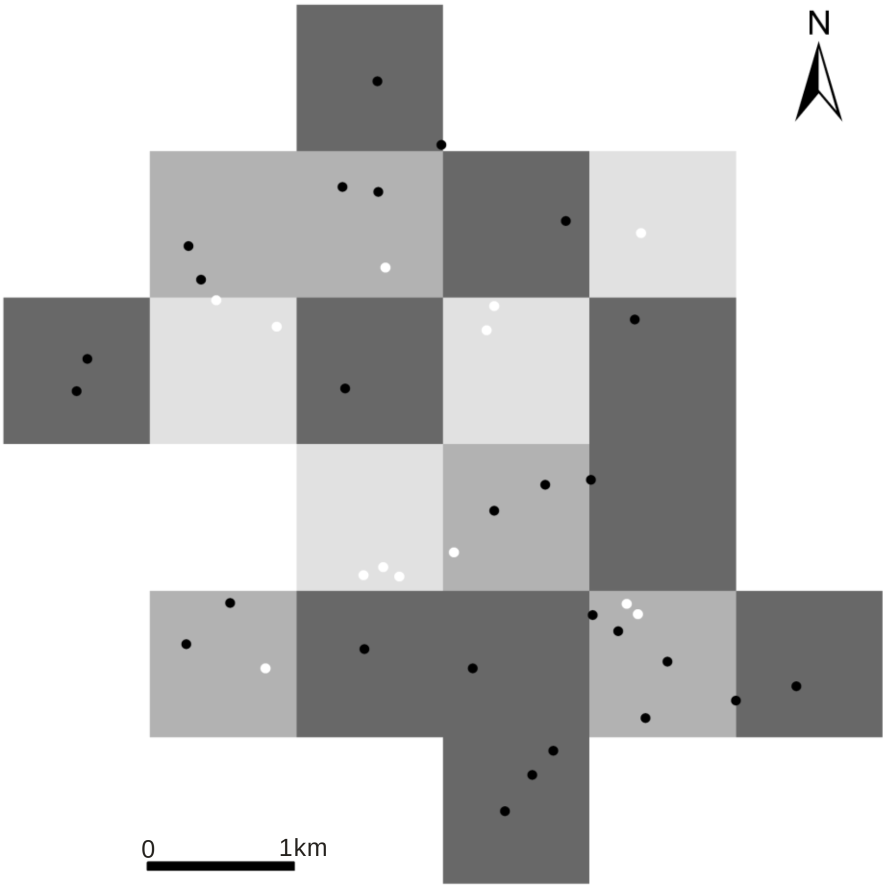

Figure 6.6: Locations within the landscape that were sampled for *Carabus glabratus.* Presences (black circles) and Absences (white circles) are shown on a 1km resolution grid of cells with presence only (dark grey), absence only (pale grey) and containing both presence and absence records (mid grey).

Of the two most comparable studies, our results are consistent with those of Randin *et al.* (2009), who projected higher levels of persistence for high-resolution models of plant distributions in the Swiss Alps; but show the opposite pattern to those of Trivedi *et al.* (2008), who found lower projected persistence in high resolution models of Scottish plants than in coarse resolution models. However, both studies used elevation as the sole means for interpolating temperature to finer resolutions (i.e. colder at higher elevations), without considering the effects of slope and aspect. North and south facing slopes can differ by as much as 7 ºC (Suggitt *et al.* 2010), so the coldest place within a landscape may not be at its highest point. However, topographic effects depend on the climatic variable considered (Suggitt *et al.* 2010). Low elevation areas may experience lower minimum temperatures than mid-elevations due to cold air pooling (Geiger 1973), and maximum temperatures are commonly found on steep south (in the northern hemisphere) facing hillsides rather than at the lowest elevations (Bennie *et al.* 2010; Suggitt *et al.* 2010), whilst the lowest maxima (i.e. areas that are suitable refugia for species preferring cooler conditions) occur at moderate rather than high elevations in some landscapes (Ashcroft *et al.* 2008), where some shelter is available from hot, dry winds. Hence we suggest that elevation-only models are insufficient for high resolution modelling of climatic effects on species' distributions. We suspect that the opposite results of Randin *et al.* (2009) and Trivedi *et al.* (2008) may arise partly because of the higher elevational, and hence temperature (based on lapse rate), range of Switzerland than Scotland.

The fact that changing the locations of the coarse grids produced a range of different models poses a whole new problem when using models at coarse resolution. Most examples of climate-envelope approaches use readily available national records, with presence or absence taken as a response to climatic variables. This presence or absence is often based on an underlying collection of records, such that some grid cells contain several records of a species, whilst others contain none or only one. It is clear therefore that pooling of a sort does occur frequently in the literature, with records pooled based on the national grid. These national grids may well group together records from more suitable locations in some areas, whilst not in others. Re-analyses of these data using a similar procedure for moving the grid axes may help to shed some light on the extent of this problem for climate-envelope models.

The observed discrepancy between the perceptions of fine and coarse scaled models, along with the fact that finer resolution models have been found to perform better than coarser ones in predicting species' distributions (Engler *et al.* 2004), leads us to conclude that more modelling should be done at a range of resolutions across different taxa and regions, at least until we understand the circumstances leading to the prediction of higher or lower estimations of extinction when fine resolution data are used. Further research on the capacities of species from different taxonomic groups to persist in local microclimates is also needed. Small areas of suitable microclimates do not necessarily imply that sufficient area will survive to ensure long-term population persistence.

One potentially positive note from this work is that the loss of species from landscapes may not occur quite so quickly as previously predicted. For example, the recently published European climatic risk atlas for butterflies (Settele *et al.* 2008) is based on a 50 km grid. Many of the 50 km grid cells in which species are predicted to go extinct could easily contain suitable microclimates than enable survival past the temperature increases predicted in the atlas. However, since this study only focuses on one species, and agrees with one out of two studies done by other groups, more work is necessary for a wide range of taxa in a range of landscapes to determine the extent to which this pattern actually occurs.

A challenge is the need for high resolution analyses over large spatial extents, and a more systematic approach to sampling would be beneficial (Eyre *et al.* 2005). To date, studies (including ours) often focus on relatively small geographical extents when modelling at a fine resolution. This is because it is impractical to collect distribution data at the fine resolution required for such studies throughout the whole of a species' range. However, the approach that we advocate may become increasingly feasible because: (a) as in this study, one only needs data from a sample of precisely georeferenced locations (it is not necessary to cover every cell); (b) 100 m resolution models yielded similar coefficient and intercept estimates to those at 5 m resolution; (c) many existing records are already at 100 m grid resolution (http://data.nbn.org.uk); and

(d) cheap GPS units mean that many records are now submitted with location data that have a precision of < 20 m. Such records could be used to model species distributions at a fine resolution across whole countries in order to make a fair comparison between coarse and fine resolution models across large geographical extents.

7 General Discussion

In this chapter, I will first discuss the results of each data chapter in turn, then consider the wider implications of the findings of this thesis for conservation efforts. Many key points have already been covered in the chapters themselves, so I will try to limit my discussion here to additional points not already mentioned.

7.1 Chapter 4 – The effects of topography on microclimate

In Chapter 4, I showed that the inclusion of the topographic variables slope and aspect produced better models for the prediction of extreme temperatures than elevation alone. I then showed that a recently published microclimate model (Bennie *et al.* 2008) could be used to interpolate temperatures across a landscape by incorporating information on slope, aspect and elevation. Here I will discuss these results with regards to other studies looking at temperature within landscapes, as well as potential future climatic warming and possible management strategies to give thermally constrained species the best possible chance of surviving in an area following climatic warming.

In my study, I found that a lower percentage of temperature variability within the landscapes was explained by the best supported model (using MMI, Burnham & Anderson 2002) for January 2008 than for September 2007. Guan *et al.* (2009) similarly found higher errors associated with their temperature models in winter than the rest of the year. Their GAMs explained a high percentage of variation (> 97 %), which is far higher than the percentages achieved by my models, although GAMs have a tendency to over-fit and so are less generalisable to other landscapes than GLMs (Randin *et al.* 2006). This suggests that factors other than those explored here are important in determining temperatures during winter months. Such factors could include frost hollow effects, where areas of low elevation such as valley bottoms collect pools of cold air, creating a temperature inversion (Geiger 1973). Far more work is necessary to fully understand all the factors that can affect the temperature of an area before models can truly represent the range of microclimates available. However, models such as Micromaker, which incorporates more information than elevation alone, are an important first step in understanding microclimatic diversity within sites.

I also found very different values for the lapse rate, across the range of temperature variables, in September 2007 and January 2008. For models that retained elevation as an explanatory variable, lapse rates were higher (i.e. temperatures decreased more rapidly with increasing elevation) for extreme rather than mean temperatures, this effect being most pronounced for maximum temperatures; and lapse rates were higher in September than in January. Gottfried *et al.* (1999) similarly found a daytime lapse rate of 1.31 °C per 100m (when temperatures are at their warmest), with a night-time lapse rate of just 0.7 °C. These differences in lapse rate across the different variables and seasons may help to explain the large variation in ß-coefficients for the GLMs relating the predictions of my landscape model (which generates a different lapse rate for each variable and for each month) to the predictions of Micromaker (which uses the same lapse rate in all calculations). Models such as Micromaker may therefore benefit from the development of a set of lapse rate values to be used under different circumstances.

The fact that slope and aspect were retained in some of the 'best' models is perhaps not surprising, since altitudinal gradients, aspect and specific landforms such as narrow gullies have all been found to play a crucial role in the persistence of plant species following climate change (Lavorel 1999), presumably because they influence temperature (and therefore desiccation) and so result in some areas remaining thermally suitable. Future climatic change could also have differential effects in topographically diverse regions. Ashcroft *et al.* (2009) found that a 1 °C rise in ambient air temperature resulted in an average rise of 0.71 °C across a topographically diverse site in Australia, with a larger rise observed on west-facing slopes than east-facing slopes, and more warming occurring further from the coast.

Models may benefit even further from the inclusion of habitat (vegetation) variables. Ashcroft (2006) found that average summer maximum temperature was not accurately predicted by elevation alone, but predictions were much better when also including percentage canopy cover and low pass filtered radiation. In upland sites such as those visited during this study, vegetation variables may need to be recorded in some detail to give a full view of the range of microclimates available within a landscape. For example, different temperature conditions are associated with different stages of the *Calluna* life cycle. The pioneer (juvenile) phase shows far more extreme temperatures than the more mature phases, with differences of up to 40 °C being recorded between maxima and minima in a single week (Barclay-Estrup 1971). Even within grassland (which is structurally simpler than heather), conditions are different within and above the vegetation layer. Wind velocity within a grass canopy has been recorded to be just 15 - 30 % of that recorded at 2 m (Cernusca & Seeber 1981). This resulted in temperature differences of up to 25 °C from those recorded within a standard Stevenson screen, with warmer maxima being recorded outside the screen. Lyons (1994) also found important differences in temperature between those recorded by meteorological stations and those experienced in insect habitats, whilst Hornbuckle & England (2005) found a vertical gradient in temperature within the canopy of a maize field that varied over the night/day cycle. Temperature interpolations based on slope, aspect and elevation are an important first step towards a more complete understanding of the conditions experienced by organisms, but, as previously discussed, further work is needed to give full consideration to the potential effects of vegetation on these conditions.

There are other considerations to be made if Micromaker is to be used to project fine-resolution temperature changes caused by changes in global climate. Conditions may change in ways not covered by the model. For example, daily minimum temperatures have increased relative to daily maxima (Easterling *et al.* 1997), possibly due to increased cloudiness, which blocks incoming solar radiation whilst reducing radiative heat losses at night (Pounds *et al.* 1999). However, in more recent years (1974-2004), maximum and minimum temperatures have increased at the same rate (Vose *et al.* 2005). The incorporation of a cloudiness index may therefore go some way to increasing the reliability of future projections, and this uncertainty should be remembered when making claims about the possible future distributions of species following climatic change. Models that do not include this disproportionate warming may be either over- or under- optimistic, depending which climatic variables have the greatest effect on the physiology and population growth of the species in question.

It is clear that large ranges in temperature can be present in landscapes with even modest topographical heterogeneity. I found expected differences in maximum temperatures of almost 7 °C between north and south facing slopes in the Peak District. Larger mountain ranges are likely to show even larger differences, due to the sharper relief found there. McCarty (2001) suggested that microclimatic variation must be conserved within habitat types to aid conservation of species during climate change, and topographic diversity has been shown to be important for the long term population persistence of some species (Weiss *et al.* 1988), probably due to the presence of a range of microclimates. The large temperature differences recorded during this study imply that creating reserves in topographically diverse areas would help to protect areas with a wide range of microclimates within a small geographical area. This tactic has only recently been recognised as being useful for conserving biodiversity in the face of climate change (Heller & Zavaleta 2009; Oliver *et al.* 2010), despite the relative ease with which species can move to an area with suitable climate within such a topographically diverse area, when compared to the distances that would otherwise have to be travelled to track suitable climate.

The possibility of management of habitat to further increase the range of microclimates should also be investigated. Previous advice for the management of heather moorland has been to leave a higher proportion of unburned heather, especially on north-facing slopes at high altitude (Thompson & MacDonald 1995), but no reasons were given for this. However, since mature heather buffers extreme temperatures (see above), this management option would presumably result in the retention of areas with particularly low maximum temperatures, possibly providing refugia for cold-adapted species under climatic warming. Maintaining a heterogeneous vegetation cover could also be important (Oliver *et al.* 2010), as temperature minima will be higher under tall (wooded) vegetation (Suggitt *et al.* 2010). Any species relying on low minimum temperatures would therefore be disadvantaged by covering an entire landscape with such vegetation.

However, such management options may be complicated for species that rely on a particular vegetation type for survival. Some species are shifting their habitat associations in response to climate warming (Davies *et al.* 2006), so traditional management may not be appropriate in the future. These shifts in habitat associations in relation to temperature have also been observed seasonally (Roy & Thomas 2003), such that species have different habitat requirements at different times of year. Any management plan should therefore balance the management of vegetation in order to provide a wide range of thermal environments with the (possibly changing) requirements of habitat specialists.

In summary, topographically diverse areas provide a unique opportunity for the conservation of microclimatic refugia that may allow the persistence of cold-adapted species in an area undergoing climatic warming. These refugia may further be enhanced for species in higher trophic levels by sympathetic management of the vegetation present, although further research will be necessary to untangle the indirect effects of vegetation on the persistence of species via modification of the temperature experienced and any direct effects the vegetation present may have, such as the provision of food and nest sites.

7.2 Chapter 5 – The relative importance of climate and habitat in determining the distributions of species at different spatial scales

In chapter 5, I showed that climatic variables can be at least as important as habitat variables in determining the distributions of carabid species at small spatial scales, depending on the landscape sampled However, habitat variables were always better predictors of the presence and absence of the same species at the GB scale. Soil moisture was almost never a predictor of the abundance of carabids at small spatial scales, despite the expectation that it should be important to carabids, which often have soil-dwelling larvae (see introduction).

One reason that soil moisture may not be important to all of the species I modelled is that some species have surface-active larvae. Of the species I modelled, *Carabus problematicus, C. violaceus, Nebria brevicollis* and *Pterostichus niger* are known to have surface active larvae, and have previously been found to have no relationship with soil moisture levels (Eyre 1994). This does not explain the lack of importance of soil moisture to all species modelled however. Other authors (Sanderson *et al.* 1995) found that vegetation cover was not a significant predictor of carabid distributions once soil conditions had been taken into account. This suggests that soil moisture could be more important to the distributions of carabids than vegetation cover, which is almost opposite to the results of my study. Of course, another possibility is that soil moisture levels and vegetation cover are correlated, such that any variation attributable to soil moisture might actually be down to the vegetation cover (or possibly even the microclimatic conditions induced by this). These effects are likely to be difficult to disentangle, and would benefit from a more experimental approach.

Many species I modelled are known to fly, including *Agonum fuliginosum, Amara lunicollis, Loricera pilicornis, Nebria brevicollis, Notiophilus biguttatus, Pterostichus diligens, P. nigrita* and *Poecilus versicolor* (van Huizen 1980). These species should therefore have relatively high powers of dispersal, and it is possible they could therefore be captured a long distance from habitats that are actually suitable for them. This would at least partly explain the high levels of variation not explained by the best models in many cases.

One unexpected feature of this study was that the best topographic model often outperformed the best model based on predictions from Micromaker, despite the fact that Micromaker uses the same topographical variables to generate its predictions. However, topography can affect other variables than temperature; for example, the partial pressure of gases decreases with altitude (Hodkinson 2005), and slope can account for gravitational processes such as snow avalanches and rockfall (Randin *et al.* 2006) and soil erosion (Duley & Hays 1932). Vegetation structure can also vary with aspect (Armesto & Martinez 1978). Topographic variables may therefore contain hidden information about factors not otherwise considered in this study, so it is perfectly possible for the best topographic model to perform better than the best temperature model under some circumstances, despite the fact that Micromaker's temperature interpolations are calculated using topographical variables.

In agreement with my study, Arundel (2005) found that plant species in the same community are limited by different climatic variables. Extremes of temperature, whether hot or cold, may cause mortality to some species (see introduction), whereas others may require a certain number of days above a certain threshold temperature (GDD) to complete development (Sharratt *et al.* 1989). The temperature variable considered most important to a species may also change throughout its life cycle. For example, Weiss *et al.* (1988) found that a butterfly species developed more quickly on warm south-facing slopes, but showed greater survival on cooler north-facing slopes where their host plants did not desiccate. Depending on the species in question, it may well be necessary to include temperature extremes in climate-envelope models in order to give a true representation of the likely consequences of climatic warming.

The results of my GB extent modelling are similar to those of Eyre *et al.* (2005), who found that climate or altitude explained over 20% of the variation in presence and absence of only 10 of 137 species modelled. The best predictions were for species considered typical of either lowland damp wetlands or upland moorland. The agreement with my results is perhaps not surprising since I used the same distributional data as these authors, but does confirm that the patterns I observed are likely to be replicated across the Carabidae in general. I also found that vegetation variables were better correlated with carabid distributions than were climatic variables, which was the opposite result to that at my sampling sites. In the context of my study, this could be because my sample locations typically contained only 3 – 8 different habitat types, whereas the GB extent modeling incorporated information on 15 different categories of vegetation cover. In addition, Stefanescu *et al.* (2004), working in Europe, found that the range limits of butterfly species were correlated with climatic variables rather than the distribution of host plants (i.e. climate is important at large extents, even more so than the specific food plants used by caterpillars, which seems to run counter to my study). Carabid beetles, for the most part, do not utilise living plants as food, raising the question of why land cover might in fact be important to them. One possibility is that, in my study, land cover type gives a better indication of the microclimates available to species than the coarse-resolution climatic variables. Again amongst butterfly species, generalists have been found to be directly influenced by climatic conditions, whilst habitat specialists may additionally be indirectly influenced via the effects of climate on vegetation (Menéndez *et al.* 2007). For other taxa, vegetation structure may also be important. Not only might there be different microclimates found under different vegetation structures, the structure itself can be important to invertebrates that live within this layer. For example, some types of spider can create webs in structurally complex vegetation, but do not inhabit grasslands (Coulson & Butterfield 1986).

In summary, I have shown that climate can influence the distributions of species when modelled at fine resolutions, and may be at least as important as vegetation cover in determining where individuals will be found within a landscape. Climate can also affect the vegetation cover found at a site, and vegetation cover can in turn modify the microclimate experienced by organisms. These effects are likely to be difficult to disentangle fully, however this study is a first step in understanding that not all previously perceived responses to vegetation cover have necessarily been due to the vegetation cover itself, but could at least in part be due to microclimatic differences.

7.3 Chapter 6 – Perceptions of possible future landscape use by a northern species

In chapter 6, I showed that the perception of the seriousness of future climatic warming to a cold-adapted species differed depending on the input resolution of data. Finer resolution data predicted longer persistence of the species than did coarse-resolution data. These results have already been discussed in relation to other studies looking at the effects of data resolution on the predictions of climate-envelope models, so this will not be covered here.

However, this study clearly supports the hypothesis that although species' distributions are related to temperature, retraction at southern range margins will be slower than expansion at northern margins in response to climatic change (see introduction). I showed that with 3 °C warming, at least some areas of a 100 km^2 grid cell at the southern range margin of *C. glabratus* would remain suitable. Therefore, in a study based on data at this resolution, retraction at the southern range margin would not be expected to occur until over 3 °C warming from the current level was achieved. Most studies relating recent climatic warming to expansions of the cold range margin have dealt with warming of around 0.55 °C, which has occurred since the 1970s (IPCC 2007) . With this amount of warming, my fine resolution models show a decrease in the area that is thermally suitable for *C. glabratus* at the warm range margin, but based on these models I would not expect retraction of the range until 3 °C above current temperatures was reached. For 10 km of expansion to be recorded at the northern range margin,all that is required is one extra record at this resolution beyond the current range boundary, such that expansion appears to be quicker than contraction, even if individuals of species find that the area suitable at their warm range margin is decreasing when considered at a finer resolution.

Other studies looking at the effects of climatic warming have similarly shown that large areas of habitat that are currently suitable will be lost to species following modest warming. In Queensland, Australia, all 65 endemic vertebrate species were predicted to lose all their core habitat at 7 °C warming, and with 3.5 °C warming 30 lost all their core habitat, the other 35 retaining less than 11.5 % of their current habitat (Williams *et al.* 2003). Similarly, Leathwick *et al.* (1996) predicted a marked forest-climate disequilibrium following 2°C warming. This compares with my results for all resolution models, which suggest that most available area is lost with 3 °C of warming. Given that models predict that temperatures will continue to increase even if emissions are stabilised at 2000 levels (Meehl *et al.* 2005), which seems extremely unlikely, this suggests that options other than simply protecting large areas may be necessary to conserve some species.

The use of abundance data collected across climatic gradients (as in this study) gives a better understanding of population size changes than presence/absence data (Shoo *et al.* 2005), and changes in population size is a key criterion in determining IUCN status (IUCN 2001). It is important to understand how using different resolution datasets affects our perception of population size changes as well as the possible percentage of a landscape that will remain suitable, so that climate-envelope and other modelling approaches may be used to inform the decision making process when determining the risk of extinction of species under climatic warming.

Of course, temperature is not the only variable that might change in future which might affect the area that will remain suitable for a species. Bird abundances have been found to vary with precipitation within a landscape (Martin 2001), so similar studies should be considered on such variables. However, confidence in future projections is higher for temperature variables than rainfall patterns (Conway 1998), and the effects of topography on temperature are far better understood than its effects on precipitation (Singh *et al.* 1995; Prudhomme & Reed 1998) and hydrology (Wilson *et al.* 2010), and soil moisture levels are further complicated by soil type and depth.

At very coarse scales, other variables may be perceived to be more important the climate experienced. For example, *Euphdryas aurinia* was perceived to survive best in core areas of its range within Great Britain, and this was replicated within occupied counties in Great Britain. However, at the European scale it appeared to survive best in countries located to the south and east, associated with geographical variation in agricultural intensification at these coarse scales (Thomas *et al.* 2008).

Habitat fragmentation and dispersal ability can also play a role in tracking climate. Poor dispersers have been predicted never to be able to track climate, but some movement is predicted to occur on correlated habitat, whilst species with high colonisation rates may track climate better in fragmented habitat (McInerny *et al.* 2007). One problem with this in the uplands is that both thermally suitable areas and suitable vegetation can be fragmented, so that any attempts to understand the potential future invasion of southerly-distributed species would need to consider the dispersal abilities of these species, and conservationists may even consider the translocation of individuals to areas of climatic suitability in order to facilitate the northwards movement of species' ranges (Heller & Zavaleta 2009).

To summarise, fine-resolution models of species' distributions following climatic warming produce different (and often more optimistic) views of the potential for survival than coarse-resolution models. Although in most cases sufficient data is not available to model across species' ranges at such fine resolutions, the further development of remote sensing techniques (e.g. Garrigues *et al.* 2006) may enable the extension of such fine-resolution analyses in future.

7.4 Wider context and conservation

It has been recognised that peat biotopes can support a wide range of species. In the Humberhead levels (lowland raised mires), both northerly- and southerly-distributed carabid species are supported (Telfer & Eversham 1996). It seems likely, in the context of my study, that this is because the low elevation mires found there contain warm enough microclimates to support species that are typically found in the south of Britain, whilst also being damp enough to support a more northerly fauna. Management of moorland by burning can result in a more diverse fauna than that found on unmanaged moors, as mature heather is favoured by characteristic upland species, whereas an open canopy allows more widespread species to invade (Gardner *et al.* 1997), presumably due to the differing microclimatic conditions offered by the different life stages of heather (see above). However, stakeholders often favour historically local species, which are likely to be replaced by more southerly and lowland species following climatic change (McCarty 2001). Conservation priorities will therefore need to be considered and perhaps updated to include a more globally coherent strategy in the face of the potential movements of species in relation to climatic change.

Conservation targets of increased sphagnum and cottongrass in peaty areas would result in too high a water table for carabids like *Bembidion humerale* (which is rare in Britain) and other dry heath fauna, but may be ideal for more stringent bog species such as *Agonum ericeti* (Telfer & Eversham 1996). Conservation management for plants on peatland biotopes is not always beneficial (and is sometimes harmful) to invertebrates (Holmes *et al.* 1993), and similarly the designation and utilisation of areas for carbon storage may not result in the most effective utilisation of resources for the protection of biodiversity (Anderson *et al.* 2009). However, management strategies can potentially benefit several taxa at once. Low intensity grazing has been recommended as the management strategy that will maximise bird diversity in the British uplands (Evans *et al.* 2006), and the same strategy is correlated with a higher diversity of moth species in the British uplands, particularly providing habitat for species that have been documented as having declined in the UK (Littlewood 2008).

In all conservation management actions, species will therefore need to be prioritised in terms of overall risk, and the potential effects of climatic change will need to be incorporated into this. My study shows that, even at smaller extents such as individual reserves, climatic variables can play an important part in determining how much of the landscape species are able to occupy, and how many individuals these occupied areas are likely to be able to support. Potential risks from climatic change can be complicated by fragmentation of habitat due to land use by humans. 30 of 35 British butterfly species failed to track recent climate change due to a lack of suitable habitat (Hill *et al*. 2002). Topographically diverse areas, such as those visited during my study, record a large temperature range within a small area. In these areas, the vegetation is fairly homogeneous, so there would be no such problems with moving between thermally suitable areas within such a landscape, up to the extent that the landscape is able to provide refugia from temperature changes. As discussed above, the creation or protection of reserves in areas of topographical diversity should therefore be considered as a strategy for managing risks to biodiversity in the face of climatic change.

Appendix 1: Supplementary Materials for Chapter 4

Included are tables of overall means for all field data and analyses. Note that values for maxima and minima (and therefore range) are means of absolute values for that month, not means of daily highs/lows.

Table S1. Values represent the slope (*β*) of the relationship between temperature and the corresponding explanatory variable in the GLM, with SE the standard error. SxTrA is the interaction term between Slope and Transformed Aspect. Underlined values indicate where the best model under multi-model inference includes non-significant terms. The word "dropped" indicates that the term was dropped from the model considered to be best when using Multi-Model Inference. Where waypoints have been removed from the dataset due to a large Cook's Distance, this is indicated.

Non-standardised models.

(A) for Wales

September 2007 – 0.01 m measurement height. N = 47 loggers (with waypoint 47 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	*β*	SE	*β*	SE	*β*	SE	
Tmean	-0.0108	0.003	0.0512	0.0299	-0.0035	0.0021	dropped		0.3089
Tmax	-0.0178	0.0163	dropped		dropped		dropped		0.0040
Tmin	-0.0136	0.0076	dropped		dropped		dropped		0.0446
Trange	-0.0042	0.0207	dropped		dropped		dropped		-0.0213
Gdd+5	-0.3213	0.0890	1.4782	0.8897	-0.1033	0.0619	dropped		0.3040

January 2007 – 0.01 m measurement height. N = 43 loggers (with waypoint 16 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	β	SE	β	SE	β	SE	
Tmean	-0.0043	0.0022	dropped		-0.0022	0.0012	dropped		0.1199
Tmax	-0.0093	0.0069	dropped		dropped		dropped		0.0217
Tmin	dropped		dropped		-0.0029	0.0052	dropped		-0.0167
Trange	dropped		0.0676	0.1075	dropped		dropped		-0.0146
Gdd+5	-0.0503	0.0301	dropped		dropped		dropped		0.0411

(B) for Peak District

September 2007 – 0.01 m measurement height. N = 24 loggers (with waypoint 77 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	β	SE	β	SE	β	SE	
Tmean	-0.0101	0.0034	-0.1064	0.0409	-0.0074	0.0025	dropped		0.4076
Tmax	dropped		-0.5489	0.2905	-0.0338	0.0189	dropped		0.1490
Tmin	-0.0166	0.0071	dropped		dropped		dropped		0.1565
Trange	dropped		-0.5275	0.3528	dropped		dropped		0.0490
Gdd+5	-0.3287	0.1025	-2.7723	1.2790	-0.1948	0.0754	dropped		0.3498

January 2007 – 0.01 m measurement height. N = 32 loggers (with waypoint 71 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	β	p	β	p	β	p	
Tmean	-0.0049	0.0015	dropped		dropped		dropped		0.2245
Tmax	dropped		0.2099	0.0785	0.0073	0.0065	-0.0021	0.0008	0.2115
Tmin	-0.0059	0.0068	dropped		dropped		dropped		-0.0079
Trange	dropped		0.5006	0.1935	0.0291	0.0160	-0.0054	0.0020	0.1359
Gdd+5	-0.0382	0.0214	dropped		dropped		dropped		0.0661

Standardised models

(A) for Wales

September 2007 – 0.01 m measurement height. N = 47 loggers (with waypoint 47 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	p	β	p	β	p	β	p	
Tmean	-0.4433	0.1223	0.2113	0.1234	-0.358	0.2131	dropped		0.3089
Tmax	-0.7262	0.6676	dropped		dropped		dropped		0.0040
Tmin	-0.5547	0.3126	dropped		dropped		dropped		0.0446
Trange	-0.1716	0.8452	dropped		dropped		dropped		-0.0213
Gdd+5	-13.132	3.639	6.1	3.672	-10.588	6.341	dropped		0.304

January 2007 – 0.01 m measurement height. N = 43 loggers (with waypoint 16 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	β	SE	β	SE	β	SE	
Tmean	-0.1349	0.0696	dropped		-0.1228	0.0696	dropped		0.1199
Tmax	-0.293	0.2107	dropped		dropped		dropped		0.0217
Tmin	dropped		dropped		-0.1657	0.2983	dropped		-0.0167
Trange	dropped		0.2739	0.4352	dropped		dropped		-0.0145
Gdd+5	-1.5863	0.9478	dropped		dropped		dropped		0.0607

(B) for Peak District

September 2007 – 0.01 m measurement height. N = 24 loggers (with waypoint 77 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	β	SE	β	SE	β	SE	
Tmean	-0.4617	0.1536	-0.5156	0.1981	-0.4275	0.1461	dropped		0.4076
Tmax	dropped		-2.660	1.408	-1.956	1.097	dropped		0.149
Tmin	-0.7593	0.3251	dropped		dropped		dropped		0.1565
Trange	dropped		-2.557	1.71	dropped		dropped		0.0490
Gdd+5	-15.016	4.680	-13.436	6.198	-11.276	4.367	dropped	ns	0.3498

January 2007 – 0.01 m measurement height. N = 32 loggers (with waypoint 71 removed).

Variable	Elevation		Slope		Transformed Aspect		SxTrA		$R^2_{adjusted}$
	β	SE	*β*	SE	*β*	SE	*β*	SE	
Tmean	-0.2515	0.0796	dropped		dropped		dropped		0.2245
Tmax	dropped		-0.1173 †	0.2261 †	-0.37	0.1907	-0.6096	0.2447	0.2115
Tmin	-0.3053	0.3510	dropped		dropped		dropped		-0.0079
Trange	dropped		-0.5640 †	0.5570 †	-0.4256 †	0.4698 †	-1.5885	0.6028	0.1359
Gdd+5	-2.218	1.067	dropped		-2.080	1.067	dropped		0.1458

† Indicates variable was retained due to significance of SxTrA term.

Appendix 2: Supplementary materials for Chapter 5

Tables S1-S

Table S1 – Summary of relationships between best models for each type of variable and species abundance for the Glen Finglas field site. In all cases trapping effort variable was included.

	Topographic			**Temperature**			**Soil Moisture**			**Broad Habitat**		
Species	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2
Abax parallelepipedus	- TrA	273	0.44	- ANMAX + $ANMAX^2$	60	0.92	SWI	357	0.25	- NH	284	0.41
Agonum fuliginosum	TrA	130	0.13	- ANMAX	134	0.10	SWI	140	0.03	LOCH + NH	124	0.33
Amara lunicollis	- E - TrA + S	85	0.67	ANMEAN - $ANMEAN^2$ - MAMEAN + $MAMEAN^2$	89	0.09	SWI - SWI^2	164	0.05	LOCH	141	0.28
Carabus arvensis	S - E	347	0.37	ANMEAN - $ANMEAN^2$ - MAMEAN + $MAMEAN^2$ + ANMAX	297	0.52	- SWI	410	0.21	LOCH + NH	321	0.46
Carabus glabratus	E - E^2 + TrA - S + S^2 + TrA*S	208	0.76	ANMIN - ANMAX + $ANMAX^2$ + ANMEAN - $ANMEAN^2$	217	0.74	SWI	593	0.07	-NH + LOCH	571	0.13
Carabus problematicus	E + S + TrA - S*TrA	230	0.41	ANMEAN - MAMEAN	230	0.39	- SWI	277	0.12	LOCH	270	0.22
Carabus violaceus	TrA + E + S - TrA*S	247	0.35	- ANMIN - $ANMIN^2$ - MAMEAN + $MAMEAN^2$	243	0.37	- SWI	303	0.03	LOCH	273	0.24
Cychrus caraboides	E + S	62	0.25	- ANMIN + ANMAX	60	0.29	SWI	69	0.03	-NH	69	0.04
Loricera pilicornis	- E + E^2 - S	32	0.99	- MAMEAN + $MAMEAN^2$	42	0.97	- SWI + SWI^2	434	0.27	LOCH + NH	77	0.92
Patrobus assimilis	E	66	0.62	- MAMEAN	63	0.65	- SWI	128	0.05	LOCH	73	0.65
Pterostichus adstrictus	E - E^2 - TrA - TrA^2 - S + S^2 + TrA*S	234	0.45	ANMEAN - $ANMEAN^2$ + ANMAX	242	0.40	- SWI	355	0.05	LOCH	337	0.14
Pterostichus aethiops	S	64	0.19	ANMAX - MAMEAN	63	0.25	- SWI	74	0.01	LOCH	65	0.36
Pterostichus diligens	- E + E^2 + TrA - TrA^2 - S	125	0.42	ANMIN + $ANMIN^2$	137	0.27	SWI	166	0.00	LOCH	145	0.27
Pterostichus madidus	S - S^2 - E - TrA	684	0.68	ANMEAN - $ANMEAN^2$ - ANMIN - MAMEAN + $MAMEAN^2$	542	0.76	- SWI	1587	0.15	LOCH	1435	0.25
Pterostichus melanarius	S - S^2 - TrA	139	0.86	ANMAX + ANMIN + $ANMIN^2$ + ANMEAN - $ANMEAN^2$	246	0.72	- SWI + SWI^2	555	0.30	- NH + LOCH	540	0.34
Pterostichus niger	S - E - TrA - S*TrA	431	0.52	ANMAX + ANMEAN - MAMEAN	426	0.53	- SWI + SWI^2	619	0.16	LOCH	554	0.30

Pterostichus nigrita	E - E^2 - S - TrA - S*TrA	605	0.38	ANMEAN - ANMEAN^2 + ANMAX - ANMAX^2	629	0.35	SWI	740	0.17	LOCH	789	0.11
Poecilus versicolor	- E - TrA - S + S^2 + TrA*S	286	0.80	ANMEAN - ANMEAN^2 + ANMIN + ANMIN^2 + ANMAX	454	0.63	- SWI	925	0.15	LOCH	773	0.31

Table S2 – Summary of relationships between best models for each type of variable and species abundance for the Lake Vyrnwy field site. In all cases trapping effort variable was included.

	Topographic			**Temperature**			**Soil Moisture**			**Broad Habitat**		
Species	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2
Abax parallelepipedus	E - E^2 + S - TrA	50.83	0.9266	ANMEAN + ANMIN	56.19	0.8849	- SWI	228.83	0.1074	LOCH + NH	149.05	0.4982
Agonum fuliginosum	E - E^2 + TrA - TrA^2 + S - S^2	234.02	0.4123	ANMAX - $ANMAX^2$ - ANMIN - $ANMIN^2$	265.58	0.2897	- SWI - SWI^2	307.38	0.1317	LOCH	282.71	0.2306
Amara lunicollis	- TrA	53.80	0.1320	ANMAX	47.14	0.3115	- SWI	58.68	0.0005	- NH	57.42	0.0345
Carabus arvensis	- TrA - E	140.39	0.3379	ANMAX + ANMEAN - $ANMEAN^2$	127.85	0.4530	- SWI	172.42	0.0685	LOCH	137.53	0.3922
Carabus glabratus	TrA - TrA^2 - S + S*TrA + E	552.23	0.3581	ANMAX - $ANMAX^2$ + ANMIN - MAMEAN + ANMEAN	497.56	0.4403	SWI - SWI^2	680.66	0.1561	LOCH - NH	674.89	0.1738
Carabus problematicus	- E	61.06	0.5288	ANMIN + $ANMIN^2$ + ANMEAN - $ANMEAN^2$	52.16	0.7210	SWI - SWI^2	97.19	0.0885	NH + LOCH	78.73	0.4041
Carabus violaceus	E	190.33	0.2266	- ANMIN	192.83	0.2045	SWI - SWI^2	198.19	0.1750	NH	196.34	0.1736
Cychrus caraboides	- E + E^2	119.98	0.2530	ANMIN + $ANMIN^2$	123.03	0.1906	SWI	130.05	0.1084	- NH	130.11	0.1078
Notiophilus biguttatus	E	49.46	0.1852	- ANMEAN	48.44	0.2187	- SWI	52.00	0.1021	LOCH	51.73	0.3076
Pterostichus diligens	- TrA + TrA^2 - S + S^2 + E - E^2	325.55	0.3896	ANMEAN - $ANMEAN^2$ - MAMEAN + $MAMEAN^2$	405.49	0.1366	- SWI + SWI^2	386.72	0.1811	LOCH - NH	385.17	0.2038
Pterostichus madidus	- TrA + S - S^2 + S*TrA	187.20	0.5781	ANMEAN - $ANMEAN^2$ - ANMIN - MAMEAN + $MAMEAN^2$ + ANMAX - $ANMAX^2$	212.28	0.4962	SWI - SWI^2	321.30	0.0314	LOCH + NH	305.22	0.1188
Pterostichus niger	E - E^2 + TrA - TrA^2 + S - S^2	181.94	0.3896	ANMEAN - $ANMEAN^2$ - MAMEAN + $MAMEAN^2$	156.34	0.5070	- SWI	237.82	0.0314	- NH	236.38	0.0393
Pterostichus nigrita	E - E^2 - S + S^2 - TrA + TrA^2	2091.80	0.2067	- ANMIN - $ANMIN^2$ + MAMEAN - ANMAX - ANMEAN	2211.10	0.1563	- SWI + SWI^2	2144.20	0.1816	LOCH - NH	2345.50	0.1004
Poecilus versicolor	- E + TrA - TrA^2 + S	74.50	0.8515	ANMEAN + ANMAX - MAMEAN	73.36	0.8480	SWI	210.98	0.2638	- NH + LOCH	129.52	0.6329

Table S3 – Summary of relationships between best models for each type of variable and species abundance for the Peak District field site. In all cases trapping effort variable was included.

	Topographic			**Temperature**			**Soil Moisture**			**Broad Habitat**		
Species	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2	Model	AIC	R^2
Agonum fuliginosum	E - E^2 + S + TrA	50.17	0.6054	- ANMAX	43.72	0.6128	SWI	74.52	0.1063	LOCH	69.86	0.3475
Amara lunicollis	TrA + TrA^2 + S + S*TrA	44.64	0.7069	ANMAX	64.64	0.1967	SWI	68.78	0.1153	LOCH	60.51	0.4740
Carabus problematicus	S - S^2 + TrA - S*TrA	216.61	0.5316	ANMAX	283.71	0.2931	SWI	364.12	0.0309	NH	355.41	0.0593
Carabus violaceus	S - S^2 + TrA - TrA*S + E	149.13	0.4893	- ANMAX + $ANMAX^2$	162.47	0.3014	- SWI	179.21	0.1193	NH	184.58	0.0671
Cychrus caraboides	S - S^2	29.65	0.8454	ANMIN	41.72	0.4688	- SWI (ns)	42.93	0.4366	NH (ns)	43.49	0.4254
Nebria brevicollis	S - S^2 -TrA	100.71	0.2677	- ANMAX - ANMEAN + MAMEAN - ANMIN	75.26	0.5310	- SWI (ns)	117.99	0.0635	LOCH (all ns)	50.91	0.8030
Pterostichus adstrictus	E + S - S^2	130.41	0.6492	- ANMIN - $ANMIN^2$	200.19	0.3224	SWI - SWI^2 (ns)	240.23	0.1401	LOCH - NH	159.98	0.5510
Pterostichus diligens	- E + TrA	278.30	0.1886	ANMIN + ANMAX - $ANMAX^2$	272.56	0.2192	- SWI + SWI^2	283.07	0.1698	LOCH + NH	220.45	0.4570
Pterostichus nigrita	TrA + E + S - TrA*S	163.19	0.4900	AMAX - $ANMAX^2$ - ANMIN + MAMEAN + $MAMEAN^2$	189.58	0.3527	SWI	202.50	0.1698	LOCH - NH	220.87	0.2300

Table S4 – Variables retained in the best models as selected by AIC for each species at the Glen Finglas site. X denotes that the variable was retained in the model

Species	Slope	Elevation	Aspect	SWI	ANMAX	ANMEAN	MAMEAN	ANMIN	LOCH	NH
Abax parallelepipedus				x	x					x
Agonum fuliginosum					x				x	x
Amara lunicollis	x	x	x			x	x			
Carabus arvensis				x		x	x		x	x
Carabus glabratus	x	x	x		x		x		x	
Carabus problematicus						x	x			
Carabus violaceus	x						x	x	x	
Cychrus caraboides					x			x		
Loricera pilicornis	x	x								
Patrobus assimilis							x			
Poecilus versicolor	x		x		x	x		x		
Pterostichus adstrictus	x	x	x	x					x	
Pterostichus aethiops					x		x		x	
Pterostichus diligens	x	x	x							
Pterostichus madidus	x	x	x	x		x	x		x	
Pterostichus melanarius	x		x							x
Pterostichus niger	x	x	x			x	x		x	
Pterostichus nigrita agg.	x	x		x	x				x	

Table S5 - Variables retained in the best models as selected by AIC for each species at Lake Vyrnwy

Species	Slope	Elevation	Aspect	SWI	ANMAX	ANMEAN	MAMEAN	ANMIN	LOCH	NH
Abax parallelepipedus	x	x	x							x
Agonum fuliginosum	x	x	x						x	
Amara lunicollis					x					
Carabus arvensis					x	x			x	
Carabus glabratus	x	x	x		x	x	x		x	x
Carabus problematicus						x		x		
Carabus violaceus		x								x
Cychrus caraboides		x								
Notiophilus biguttatus						x				
Poecilus versicolor			x			x	x			
Pterostichus diligens	x	x	x			x	x		x	x
Pterostichus madidus	x		x		x	x	x	x		
Pterostichus niger	x	x	x			x	x			
Pterostichus nigrita agg.	x	x		x	x	x	x	x	x	

Table S6 - Variables retained in the best models as selected by AIC for each species at the Peak District

Species	Slope	Elevation	Aspect	SWI	ANMAX	ANMEAN	MAMEAN	ANMIN	LOCH	NH
Agonum fuliginosum					x					
Amara lunicollis	x		x							
Carabus problematicus	x		x		x					x
Carabus violaceus	x	x	x							x
Cychrus caraboides	x									
Nebria brevicollis									x	
Pterostichus adstrictus	x	x						x	x	
Pterostichus diligens					x			x	x	x
Pterostichus nigrita agg.	x	x	x		x		x	x		

Appendix 3 – Supplementary material for Chapter 6

Table S6.1: The different models produced by moving the 900m gridded temperatures across the landscape by the specified amount (both x and y co-ordinates at the same time). Presented are the β-coefficient of Annual Maximum temperature (βJulMax), with standard errors in brackets and associated p-value, as well as the β-coefficient of the log-offset variable Trap Days and associated p-value and the estimated intercept of the model. The amount of variation explained by βJulMax is presented as R^2JulMax.

Grid Change (m)	N	βJulmax	p	βTrap	p	intercept	R²JulMax
0	20	-0.8096 (0.2729)	0.0030	1.2081	0.0007	16.6539	0.2066
-100	20	-0.1381 (0.1739)	0.4271	0.7625	0.0518	1.646	0.0030
-200	20	-0.4305 (0.2100)	0.0404	0.7570	0.0298	9.5574	0.1472
-300	20	-0.4277 (0.2129)	0.0445	0.7618	0.0497	9.5512	0.1626
-400	19	-0.0289 (0.2608)	0.912	0.8817	0.121	-2.1291	0.0018
+100	25	-0.2755 (0.1518)	0.0695	1.2810	0.0028	1.7207	0.0804
+200	24	-0.2170 (0.1417)	0.1258	1.1060	0.0326	1.1355	0.0700
+300	22	-0.3372 (0.1778)	0.0579	0.8857	0.0091	6.1454	0.0594
+400	19	0.1136 (0.3044)	0.709	0.4655	0.310	-3.1344	0.0359
+450	19	-0.3169 (0.6066)	0.6013	0.7422	0.0798	4.3055	0.00002

Table S6.2: The different models produced by moving the 1000m gridded temperatures across the landscape by the specified amount (both x and y co-ordinates at the same time). Presented are the β-coefficient of Annual Maximum temperature (βJulMax), with standard errors in brackets and associated p-value, as well as the β-coefficient of the log-offset variable Trap Days and associated p-value and the estimated intercept of the model. The amount of variation explained by βJulMax is presented as R^2JulMax.

Grid Change (m)	N	βJulmax	p	βTrap	p	intercept	R²JulMax
0	21	-0.7385 (0.5253)	0.1597	1.1591	0.0007	15.1597	0.0131
-100	21	0.0995 (0.2215)	0.6531	0.9916	0.0073	-6.409	0.0486
-200	21	-0.3813 (0.1927)	0.0478	0.9576	0.0298	6.7063	0.2126
-300	19	-0.4504 (0.2018)	0.0256	1.0130	0.0100	8.2657	0.1429
-400	20	-0.3396 (0.1712)	0.0473	1.1115	0.0089	4.3833	0.2553
-500	19	-0.1630 (0.1587)	0.3043	0.9536	0.0206	0.9400	0.0568
+100	19	-0.3894 (0.2534)	0.1243	1.1190	0.0111	6.1382	0.0542
+200	19	-0.5303 (0.2509)	0.0345	1.1195	0.0080	9.7559	0.0832
+300	19	-0.2112 (0.2105)	0.3157	0.9597	0.0239	2.2717	0.0008
+400	18	-0.1696 (0.2048)	0.4075	1.3900	0.0165	-1.9657	<0.0001

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