Natural England Commissioned Report NECR162

# Climate change refugia for the flora and fauna of England

First published 21 November 2014

www.gov.uk/natural-england

# Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties.

## Background

A variety of evidence suggests that species have, in the past, been able to withstand the effects of climatic change in localised environments known as refugia, where specific environmental conditions acted as a buffer against broader-scale climatic changes.

Therefore, an important question for conservation is whether refugia might exist under current and future anthropogenic climate change. If there are areas that are likely to remain relatively climatically stable and so enable species to persist despite climate change making surrounding areas unsuitable, identifying and protecting these places will be an important part of future conservation strategies.

This report is part of a project that is investigating this question. The report was commissioned to identify the characteristics of potential refugia, to investigate evidence for the existence of contemporary refugia by analysing patterns of local persistence and disappearance of over 1000 species across a range of taxa, and to identify sites in England with the potential to function as refugia for different taxonomic groups at a range of spatial scales.

The results of this report and the related report *Palaeoecological evidence to inform identification of potential climatic change refugia and areas for ecological restoration* (NECR163) will be used by Natural England and others to advise on and help design conservation areas and ecological networks that will be resilient to climate change.

This report should be cited as:

SUGGITT, A.J., WILSON, R.J., AUGUST, T.A., BEALE, C.M., BENNIE, J.J., DORDOLO, A., FOX, R., HOPKINS, J.J., ISAAC, N.J.B., JORIEUX, P., MACGREGOR, N.A., MARCETTEAU, J., MASSIMINO, D., MORECROFT, M.D., PEARCE-HIGGINS, J.W., WALKER, K. & MACLEAN, I.M.D. 2014. *Climate change refugia for the flora and fauna of England*. Natural England Commissioned Reports, Number 162.

**Natural England Project Officer** - Nicholas Macgregor, Principal Specialist in Landscape Ecology
**nicholas macgregor@naturalengland.org.uk**

**Contractor** - Ilya Maclean, Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, TR10 9EZ **I.M.D.Maclean@exeter.ac.uk**

**Keywords** - Climate change, refugia, resilience, adaptation, biodiversity, ecological networks, conservation planning

**Further information**
This report can be downloaded from the Natural England website: **www.gov.uk/natural-england**. For information on Natural England publications contact the Natural England Enquiry Service on 0845 600 3078 or e-mail **enquiries@naturalengland.org.uk**.

ISBN 978-1-78354-146-1

A.J. Suggitt[1,2], R.J. Wilson[2], T.A. August[3], C.M. Beale[4], J.J. Bennie[1], A. Dordolo[5], R. Fox[6], J.J. Hopkins[1], N.J.B. Isaac[3], P. Jorieux[5], N. A. Macgregor[7], J. Marcetteau[1,8], D. Massimino[9], M.D. Morecroft[7], J.W. Pearce-Higgins[9], K. Walker[10] and I.M.D. Maclean[1].

[1] Environment and Sustainability Institute, University of Exeter.
[2] Department of Biosciences, University of Exeter.
[3] Centre for Ecology and Hydrology, Wallingford.
[4] Department of Biology, University of York.
[5] École Nationale Vétérinaire, Toulouse.
[6] Butterfly Conservation, East Lulworth.
[7] Natural England, London.
[8] Department of Life Sciences, Silwood Park, Imperial College London.
[9] British Trust for Ornithology, Thetford.
[10] Botanical Society of Britain and Ireland.

# Contents

# 1. Executive summary

1. A variety of evidence suggests that species may be able to withstand the effects of climate change in localised environments known as refugia, where specific environmental conditions act as a buffer against broader scale climatic changes. This report assesses the published evidence for such refugia, while also establishing novel empirical evidence for their existence in England, based on recent changes to the distributions of a wide range of taxa.

2. Properties of the landscape identified in the published literature as contributing to ‘refugium potential’ were modelled at 100 m resolution for England, and summarised at the scale of 10 x 10 km grid squares. Maps are presented showing variation in these properties, as well as variation in rates of change in temperature, precipitation and snow cover.

3. Using data from the Centre for Ecology and Hydrology’s Biological Records Centre, the persistence (or extinction) of 1,082 species that retracted their range over the past four decades was modelled against these environmental properties.

4. After controlling for the effects of recorder effort and agricultural intensity, there were strong indications that rates of population persistence were influenced both by rates of climate change, and by microclimatic variability.

5. There were consistent differences in the responses of different taxonomic groups to different properties of landscape and climate change. Hence a refugium for one particular group may not be suitable for another group.

6. Plant persistence tended to be reduced in regions of greater summer warming; however, this negative effect of warming was buffered by topographic variability in slope, aspect and elevation.

7. Beetles showed stronger responses than the other taxa to changes in rainfall, and to modelled topographic variability in moisture levels. Persistence in the other invertebrate groups (e.g. butterflies and moths) showed stronger relationships with changes in summer temperature, which were modified by regional topographic variability.

8. The models of species persistence were used to provide maps of refugium potential in England. Maps were created to represent: i) all modelled variables, including geology and agricultural intensity; ii) climate change and microclimate effects; iii) microclimate variables only.

9. There was a positive correlation between modelled refugium potential and designation as Sites of Special Scientific Interest (SSSIs). Thus, the English protected area network is generally well placed to take advantage of environmental characteristics that increase the potential of landscapes to act as refugia.

10. The patterns of persistence / extinction in animal groups were related to the distribution of SSSIs, especially in the butterflies and moths, where probability of persistence had a strong positive relationship with SSSI cover in 10 km grid squares. In contrast, higher plant persistence had a weakly negative relationship with SSSI cover.

11. Six 20 km x 20 km landscapes in three regions were selected for more detailed study at higher resolution. These landscapes were located in West Cumbria, Upper Teesdale, Dartmoor, Exmoor, South Brecks and the Norfolk Broads.

12. Responses to microclimate differed in each of these landscapes, and it was difficult to identify general patterns. Given the limited number of high resolution records available, it is

unsurprising that the statistical models have identified different microclimatic drivers of trends in persistence.

13. The reliability of the microclimate proxies used in this study was also assessed using field surveys of plants and butterflies in the Dartmoor landscape. We examined whether species with high moisture requirements were located in areas with high topographic wetness index values and whether those with high thermal requirements were located in areas with high solar index values.

14. In the field, species with high moisture requirements were significantly more likely to be recorded in areas with a high topographic wetness.

15. The majority of plant species with low temperature requirements occurred more frequently in areas with a low solar index, but this association with topographic features promoting cool temperatures was weaker at field locations with long vegetation. This suggests that reductions in grazing pressure could be used as a tool to offset the effects of climate change.

16. The literature review revealed few studies examining the influence of fine-scale climate on endothermic organisms. We therefore tested whether fine-scale microclimate heterogeneity affected the UK distribution of an exemplar endotherm: the meadow pipit (*Anthus pratensis*).

17. Meadow pipits were more likely to occur in areas with high variation in the topographic wetness index and low variation in the solar index. Response to wetness was stronger in regions where the macroclimate was less suitable. Therefore, the importance of microclimate to the English distribution of this species is likely to increase as the climate warms.

18. Overall, our results provide support for the hypothesis that refugia can be identified where the impacts of climate change on organisms have been less detrimental than elsewhere. This effect arises because of heterogeneity in both: a) the microclimate; and b) the rate of recent climate change across the landscape.

# 2. Introduction

Climate change is having numerous effects on English wildlife (Morecroft and Speakman, 2013), causing range shifts both northward (e.g. Hickling et al. 2006) and to high altitudes (Franco et al. 2006), phenological shifts (Thackeray et al. 2010) and changes in habitat association (Pateman et al. 2012). It is also postulated that a substantial number of species will be ‘committed to extinction’ by 2050 due to its effects (Thomas et al. 2004). Although these effects are well described, little is known about the landscape attributes that promote species persistence under climatic warming. Such areas are known as ‘refugia’ and are increasingly recognised by conservation agencies developing adaptation plans (Natural England 2012).

Based on studies of landscape effects on local climate (e.g. slope/aspects- Bennie et al. 2006), the locations of refugia can be hypothesised. A handful of studies have modelled the local climate effect of selected landscape properties (e.g. Ashcroft et al. 2012, Maclean et al. 2012). Yet to date there has not been a broad, multi-taxon assessment of the extent to which these properties have enhanced the persistence of biota in the context of modern climate change.

This study addresses this gap. Firstly, a literature review was conducted (Chapter 3), to determine the likely properties of refugia as reported in scientific journals. Secondly, quantitative variables were calculated to represent these properties, and tested for their ability to predict patterns of persistence in the English biota, using species records collected nationally over 40 years of modern climate change (Chapter 4). Thirdly, as there may be effects of scale on the relative importance of refugia variables, similar analyses were conducted for six landscapes containing suitable refugia (Chapter 5). Fourthly, to ground-truth the findings of the landscape-level analyses, field surveys were conducted within one selected landscape (Dartmoor, Chapter 6). Fifthly, as the literature review identified few studies on endotherms, we tested the refugia concept on an exemplar species: the meadow pipit (*Anthus pratensis*, Chapter 7). ‘Refugia maps’ were constructed from the relationships of species’ persistence to microclimate and other landscape features at the national and landscape levels. These maps will facilitate the consideration of climate change refugia in adaptation planning.

Despite the recent economic downturn, the concentrations of greenhouse gases in the atmosphere continue to rise in a manner consistent with the highest pathway estimates of the IPCC (Hansen and Sato 2013). Given the relative failure of mitigation efforts to date, and the high levels of climate change that will likely result, climate change adaptation will be increasingly prioritised by conservationists. Protecting or enhancing the locations of suitable refugia will ensure that limited funds are spent in sites or landscapes that give wildlife the best possible chance of adapting to climate change successfully.

# 3. Literature review: determining the characteristics of refugia

## 3.1 Preamble

There is a great need to determine the level of threat posed by climate change to biodiversity, and the most appropriate means of adapting conservation to this threat. Recent climate change has been accompanied by widespread shifts in species distributions from low to high latitudes and elevations (Chen et al. 2011). These rapid observed changes provide empirical support for model projections that many species will suffer reductions in geographic range as the climate warms (Maclean and Wilson 2011), with 15 - 37% of species potentially committed to extinction as their current or projected ranges become confined to areas of unsuitable climate (Thomas et al. 2004). However, many estimates of extinction risk are based on coarsely-resolved models of species' responses to climate (Pearson and Dawson 2003, Townsend Peterson et al. 2011), whereas the climatic conditions experienced by organisms vary over much finer spatial and temporal scales (Suggitt et al. 2011).

Furthermore, species often select microhabitats that offer a thermal or moisture resource closer to an optimal operative or developmental maximum than the wider environment (Andersen 1993). For many species it is the protection of these microhabitats, rather than more general conservation measures which is important to their survival in parts or all of their range. Such places are likely to be critical to future conservation strategy. Many species which were likely widespread in the Arctic tundra found across England at the end of the last glaciation, are today rarities restricted to refugial microhabitats maintaining analogous cold climatic conditions. Statutory protected areas include a number of these locations, including: Upper Teesdale, County Durham; The Lake District High Fells, Cumbria; and Ingleborough, North Yorkshire. That such refugia enabled the persistence of cold adapted species during past warming conditions suggests that analogous areas might be important for the future conservation of species under contemporary climatic change.

Correct usage of the term 'refugia' is still a matter of debate (Rull 2010); in particular, its use to describe all types of isolated populations/species or climates has received some criticism (Ashcroft 2010). In this report we will use the term in its general sense; that is, inclusive of all taxa, inclusive of both glacial (cold) and interglacial (warm) contexts, inclusive of all locations worldwide, yet exclusive of temporary or transient 'refuges' utilised by species.

Refugia can exist at a range of scales. There are a number of regions across Southern Europe that have been identified as important large-scale refugia during the Last Glacial Maximum (LGM). These include Turkey and the Caucasus, and the peninsulas of Iberia, Italy and the Balkans. To varying extents, all contributed to the post-glacial expansion of species into Northern, North-western and Central Europe. This is especially true for animals with a large range or body size, which are unlikely to have persisted in microrefugia (see below). However, not all refugia played a role in these expansions. For example, genetic fingerprinting has ruled out any contribution of Pyrenean refugia to the makeup of modern day Central European populations of alpine blue-sow-thistle (*Cicerbita alpina*, Michl et al. 2010). Refugia that do not act as a source of migrants during an improvement in conditions are known as *passive* refugia (Médail and Diadema 2009). Many studies on refugia stop at simply documenting the locations of LGM refugia, or perhaps postulating postglacial recolonisation routes. Recent advances in the detection and analysis of pollen and genetic material are increasingly identifying the presence of so-called 'microrefugia' outside of the large refugial areas referred to above.

## 3.2 Microclimate and its relevance for conservation

Microclimate differs in character from the wider atmospheric climate. In the wider atmosphere, pressure differences drive the movement of air masses, which ensures that the air is relatively well mixed over scales of many kilometres. Hence temperatures too can be homogenous at this scale and, averaged over many years, can be used to define the climate of a particular region. However, at ground level, vertical wind shear caused by surface roughness means that the effect of wind is much reduced, and the role of wind in chilling or warming a surface or organism is diminished (Figure 3.1). Therefore, the potential for fine-scale heterogeneity in surface or near-surface air temperature (or humidity) exists, and patches of warmer or cooler air can persist under stiller conditions. This thermal heterogeneity is driven by variation in the properties of the topography, soil, vegetation, or all three. Rudolf Geiger (1927) described microclimate as:

“Variations [in meteorological elements]... brought about by changes in the nature and the moisture of the soil, even by minute differences in surface slopes, and by the type and height of vegetation growing on it. All these climates found within a small space are grouped together under the general description of microclimate.”

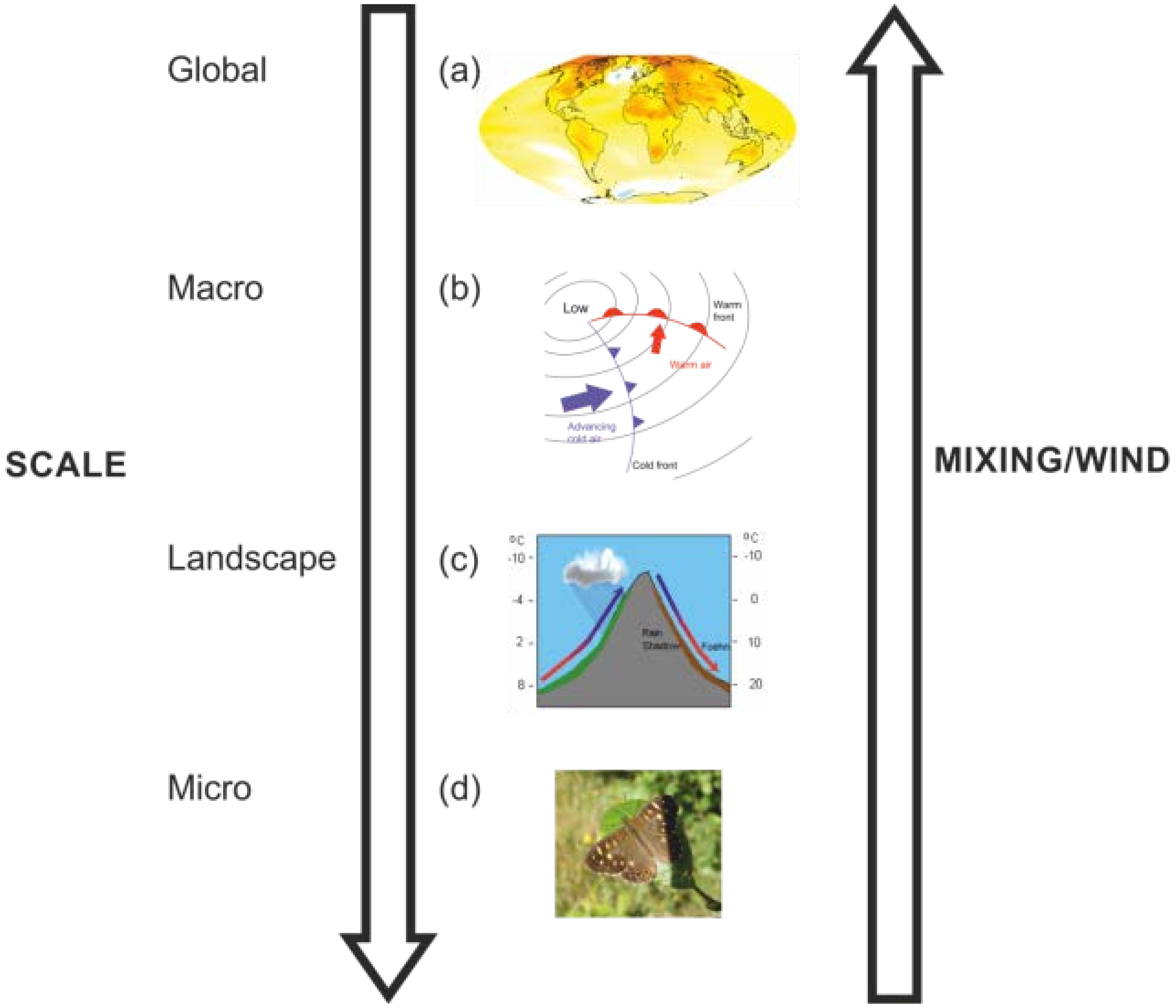

**Figure 3.1** Examples of climatic effects at various scales. (a) At the global scale, climate change acts alongside natural cycles and internal variability to define the world’s climate. (b) At the macro scale, differences in pressure drive the movement of air masses that can be classified into broad weather types (such as depressions). (c) At the landscape level, surface features can influence atmospheric conditions, creating substantial differences in temperature and moisture over a few kilometres, such as the Föhn effect in the European Alps. (d) At the micro level, surface microclimates form in areas of habitat heterogeneity, offering opportunities for species to adopt their preferred thermal regime. Here, a Speckled Wood butterfly (*Pararge aegeria*) heats up by occupying a sunfleck in an (otherwise cool) woodland (Photo credit: Martin Wainwright).

It is the effect of these landscape properties on the radiation balance that defines how they behave thermally. Specifically, incoming short wavelength infrared radiation from the sun contacts the surface, with varying proportions being reflected, absorbed or transmitted. The same applies for diffuse radiation incident upon the surface. Hence the more incoming radiation the land surface retains, the warmer the microclimate, and vice-versa. Norman J. Rosenberg (1974) offered a more biological definition: “The microclimate is the climate in which plants and animals live.”

The implications of this second definition are critical for conservation. All of the world's terrestrial biota (birds, insects or aerial microbiota with long flight periods aside) live in microclimates. The hypothesis that there exist patches of atypical microclimates that may harbour species less common in the wider landscape has existed for some time (e.g. Wolfe 1951). In a warming or cooling context, these small patches can become critical to the persistence of species unable to move and track their required (macro-) climatic niches. This is because such patches can offer local variation in temperature quantitatively similar to expected changes under climatic change, particularly for maximum temperatures (Figure 3.2).

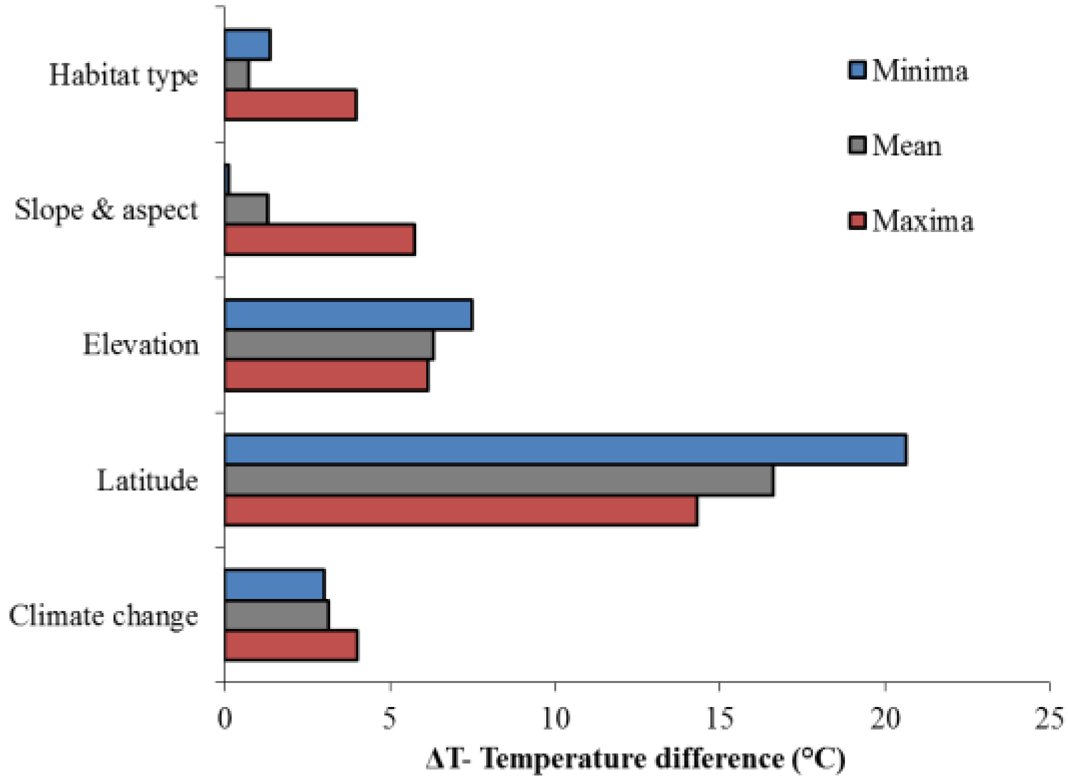

**Figure 3.2** The degree of variability in mean, minimum and maximum temperatures that habitat type, slope & aspect, elevation and latitude provide. Future changes to these variables under 21st century climatic change are also provided. Values for latitude were standardised for elevation by reduction to sea level using the international standardised atmosphere adiabatic lapse rate of a reduction in temperature of 6.5°C per km of elevation (ISO 1975). Monthly mean, maximum and minimum temperature differences for the slope & aspect and habitat microclimates were derived from Suggitt *et al.* (2011). These data represent local differences between north- and south- facing slopes, and between open and closed habitats, respectively. Data for elevation and latitude calculations were derived from the European Climate Assessment 1km dataset (Klein Tank et al. 2002). Climate change data were derived from ensemble mean projections conducted at 50 km resolution by the Prudence project, for 2100 relative to 2000 levels (Christensen et al. 2007).

## 3.3 Temporal aspects of microclimate and the effect of cloud cover

The degree to which microclimates differ from macroclimates is highly variable through time. For example, Figure 3.2 uses microclimatic data (for habitat, and slope/aspect) averaged over the period of one exemplar month. If however the period had been restricted to one cloud-free day, these site level differences can often reach 15°C (Bennie et al. 2008), and on occasion, over 30°C (Stoutjesdijk et al. 1977). With increasing cloud cover, however, locally heterogeneous climates become less likely, and the difference in temperature between the macroclimate and the microclimate decreases. The effect of clouds is also felt at night. A clear, cloud-free night allows more outgoing longwave radiation to escape, leading to large temperature differentials in the landscape, and warmer temperatures in closed habitat compared with open areas (Morecroft et al. 1998, Suggitt et al. 2011). Therefore, in a cloudy period such as the passage of a low pressure system, the effect of microclimate is diminished, and in a clear period such as the dominance of an anticyclonic high pressure system, it is enhanced.

Hence, the differences in the temperature across a landscape, and the difference in temperature between what an organism may experience and what is recorded at a nearby meteorological station (representing macroclimate), are both contingent on the cloudiness regime. They are also contingent on the selection of an averaging period in time, which will include periods with both cloudy and clear conditions. The greater the duration and thickness of cloud cover within this period, the lower the differential between macroclimate and microclimate will be. Hence the importance of microclimate as a driver of wildlife ecology will differ depending upon the cloudiness regime; with potential east-west and other regional variations within England. It will also depend on the climatic variables that most affect persistence and reproduction of species – mean values are often important, but one off extremes, such as minimum temperature, can also play a role.

## 3.4 Microclimates lead to microrefugia

Rull *et al.* (1988) first used the term *microrefugia* to describe patches of microclimate occupied by species atypical to a given area. Rull (2009) defines a microrefugium as:

“A small area with local favourable environmental features, in which small populations can survive outside their main distribution area (the macrorefugium), protected from the unfavourable regional environmental conditions.”

Evidence of such roles during the LGM and the period immediately thereafter has been reported only in the last 20 years or so. Because of difficulties in detecting such small populations, palaeoecologists have also coined the term ‘cryptic refugia’ to describe them (Stuart and Lister 2001). There have been numerous attempts to provide clarity on the scope of what is meant by ‘microrefugia’, and to broadly describe their properties (e.g. Provan and Bennett 2008, Holderegger and Thiel-Egenter 2009, Mosblech et al. 2011). In addition, several recent workshops on the subject have also recently reported on discussion points and knowledge gaps in this area (Hodgson et al. 2012, Hampe et al. 2013).

Recolonisation of the post-LGM warming environment often originated from surprisingly small populations of plants or animals, some of which survived the LGM in microrefugia. Modern genetic techniques have successfully identified glacial microrefugia in locations that would have seemed improbable to palaeoecologists working solely with pollen data (e.g. Huntley and Birks 1983). For example, highly-differentiated haplotypes of the shrub *Hippophae tibetana* in the Tibetan Plateau indicated refugial areas at over 4,000m (Wang et al. 2010). Similar evidence for juniper (*Juniperus tibetica*) at one of the highest present-day treelines in Tibet showed that small populations survived the LGM in deep river gorges above 3,500m (Opgenoorth et al. 2010). Palynological records of conifers found at Dozmary Pool on Bodmin Moor pointed to the presence of a microrefugium just beyond the hypothesised southern extent of the LGM ice sheet (Kelly et al. 2010). Other records within areas previously thought to be under ice, such as pollen data of pine trees in Northern Scotland (Birks 1989), and radiocarbon-dated evidence of Red Squirrel populations from as far north as Norway (Stewart and Lister 2001), lend weight to the idea that microrefugia were present in the immediate proximity of ice. Putative microrefugia for plants and animals have also been identified above the ice-sheet, on mountain tops or arêtes known as ‘Nunataks’. These ice-free patches may have been occupied by species such as the Alpine jumping bristletail *Machilis pallida* (Wachter et al. 2012). It must be stressed however that at present, definitive proof of Nunatak occupancy by such species does not exist; it is inferred by patterns of post-glacial recolonisation (Holderegger and Thiel-Egenter 2012).

Conventional wisdom has seen references to the range core (e.g. Lawton 1993), range margin (Travis and Dytham 2004), connectivity (Fahrig and Merriam 1985) or management (Mönkkönen & Reunanen 1999) of populations as the key to their continued survival. Yet evidence from the previous glacial episodes tells us that small, marginal populations within microrefugia can show high levels of persistence (Willis et al. 2010); this in addition to the merit of their genetically diverse (Feurdean et al. 2007) and phylogenetically divergent (Petit et al. 2003) properties. To identify where such refugia might be in the future however, we need to know what the specific properties are that lead to their formation. This was the subject of the literature review, described below.

## 3.5 The properties of refugia that promote species persistence: a literature review

We conducted various meta-searches in Web of Science (wok.mimas.ac.uk) using a search strategy designed to yield studies that determined the properties of refugia. Our search terms were tailored to the standard terminologies of the disciplines that cover the subject, such as palaeoecology, bioclimate modelling and global change ecology. Once the results were returned, they were filtered by title and abstract, before being prioritised based on the amount of useful information.

To obtain studies of past refugial locations, we used a title search for "glac* refug*", as well as the following topic searches: "glac* refug*" + species + climat*, "postglac* recolon*" + refug*, "glac* refug*" + biodivers* + climat*, "cryptic refug*", microrefug*, "glac* phylogeograph*", micro-refug*. These returned 967 studies, and eventually yielded 20 studies containing information on the properties of refugia.

To obtain studies of refugial areas in the present, we used a title search for microclimat* + species, and topic searches for: microclimat* + species + refug*, "climat* refug*", "topograph* refug*", micro-climat* + species, microclimat* + topograph*, micro-climat* + topograph*. These returned 930 studies, and eventually yielded 20 studies containing information on the properties of refugia.

To obtain studies of future refugial areas, we used a title search for "climat* change" + persist*, and topic searches for: "climat* change" + "species persist*", "global warming" + "species persist*", "climat* change" + "local persist*", "global warming" + "local persist*", "climat* change" + "bio* persist*", "global warming" + "bio* persist*". These returned 157 studies, and eventually yielded nine studies containing information on the properties of refugia.

We invited all lead authors with two or more papers returned in our metasearch to submit for inclusion in the review any further papers that had been accepted or were in press. We also contacted a number of our collaborators known to have worked on refugia with the same request. This generated a further seven useful studies, making 56 in total.

Of the final 56, ten were general discussions of refugia characteristics (e.g. Rull 2009) and, although they have contributed to this literature review, did not offer any information on the specific features or properties of refugia. The remaining 46 described refugial properties that can be classified into four main types: refugia arising from a particular temperature feature (e.g. low summer maximum temperatures), moisture feature (e.g. proximity to surface water features), geophysical feature (e.g. low soil phosphorous), or a biotic feature (e.g. absence of a fungal chytrid, *Batrachochytrium dendrobatidis*). These features are shown in Appendix 1 Tables 1, 2 and 3, corresponding to studies returned by search terms targeting past, present and future refugia, respectively. Appendix 1 Table 4 describes features leading to refugia revealed by studies suggested by collaborators and other authors of refugia articles.

**Box 3.1** Features of refugia investigated or reported in the literature.

**Temperature features**

- The extreme percentiles of temperature distributions;
- Particularly climatically stable or diverse areas;
- Areas that had experienced particularly spatially heterogeneous warming or a low climate change velocity;
- Mean temperatures in the warmest or coldest parts of the year;
- High numbers of, or late, frost days;
- Variation in growing day degrees.

**Moisture features**

- High annual rainfall;
- Seasonality or stability of rainfall;
- Mean precipitation in the warmest, wettest or driest quarters;
- Water balance or soil moisture;
- Proximity to surface water features or aquifers;
- Low potential evapotranspiration;
- High humidity;
- Low soil drainage;
- Low Palmer Drought Severity Index (Palmer 1965).

**Geophysical features**

- Soil pH, depth, type or mineral content;
- Absolute height or diversity of topography;
- Presence of valley bottoms or sinks/basins;
- Specific bedrock types;
- Slopes of a particular orientation or gradient;
- Presence of snow cover;
- Presence of other surface material such as boulders or stumps;
- Incoming solar radiation;
- Return period of fire events;
- Distance to the coast.

**Biotic features**

- Presence of particular habitat structure or type;
- Presence of a particular cushion plant facilitator;
- Food availability;
- Resistance to invasion;
- Absence of a fungal parasite;
- Large patch size;
- Presence of old growth forest.

These full tables are summarised in Table 3.1 (below), and a collated list of the features of refugia investigated or reported in the literature is in Box 3.1 (above). When features were described, many studies documented a particular species that had persisted in cooler or wetter refugial areas, i.e. interglacial refugia, in present day climate warming. This is despite the overwhelming weight of literature on LGM refugia (i.e. warm refugia in glacial environments). This discrepancy can be explained by the fact that, although traces of a species presence may remain in a refugial area, and the location reported, the specific climatic or other features that lead to its persistence at that site in the LGM were often left uninvestigated. The lack of studies indicating that certain landscape features are of no importance is likely to be the result of a file drawer problem (Rosenthal 1979), wherein researchers either a) have not published results which have failed to determine the process leading to a particular refugium, or b) have not included negative results of refugia analyses and simply published the positive results. The reported lack of information may also reflect the relative novelty or immaturity of the field.

## 3.6 The role of past refugia in the present day

The LGM had a substantial limiting effect on biodiversity in what we now call the temperate and boreal zones. Reaching its peak around 25 thousand years before present (kYBP, Clark et al. 2009), the advance of the ice sheets and onset of cooler conditions had substantial implications for wildlife, which either became extinct or persisted in unglaciated refugia or microrefugia within or outside the main glaciated area.

The present day composition of communities in temperate and boreal environments largely depends upon the locations of these past refugia, and the species that were contained therein (Stewart and Lister 2001). This is evident across all taxa for which reliable records exist. For example, patterns of genetic diversity in European mammals reflect their southern distributions in the LGM (Willis and Whittaker 2000). The English biota is a mix of multiple refugial source populations, and even individual species can have several refugial source populations (e.g. English oak, Ferris et al. 1995). In areas of southern Europe beyond the extent of the ice-sheet at the LGM, climatic conditions at the time of glaciation still explain variation in patterns of richness for many species with a present day restricted range (for 18 species, area < 400,000 km$^2$), indicating that these species are found in modern day locations where conditions were formerly warmer and wetter than the surrounding area (Svenning and Skov 2007). By contrast, species that are widespread today (n=19) are largely responsive to modern day climatic conditions. Continued isolation of refugial populations can also be enforced by other agents, such as mountain barriers: especially so for species with limited dispersal or thermal tolerances, such as reptiles (Joger et al. 2007).

For those species that survived the cold episode, the warming of the late glacial (13-10kYBP) and the onset of the Holocene brought newly available niche space in the mid-high latitudes, including England. Spreading north from southern refugia, and in multiple directions from microrefugia (Mosblech et al. 2011), species recolonised these areas at varying rates and to varying extents, in a manner that can often be established via DNA analysis (e.g. Qiu et al. 2011). Routes of recolonisation are often reflected in modern day distribution patterns. For example, post-glacial dispersal limitation is still the primary driver of the distributions of one in six plants, and the second most important driver for all plant species (after climate, Normand et al. 2011). Where a landscape has been colonised from multiple sources, routes of colonisation can have higher intraspecific diversity than the glacial refugia themselves. This explains the high-diversity Slovakian forests, which occupy the ‘corridor’ between the Alps and the Carpathians (Petit et al. 2003). In addition, many current hybridisation zones are artefacts of colonisation routes, physical barriers and commonalities in the locations of glacial refugia (Hewitt 2000).

**Table 3.1** Summary matrix detailing the importance of landscape refugia for various taxa, as reported in the literature. Refugia supporting warmer conditions during cold episodes (glacials) are coloured in blue, while refugia supporting cooler conditions during warm episodes (interglacials) are coloured in red.

**Key**

| Cold | Warm | |
|---|---|---|
| 🟦 | 🟥 | High importance |
| 🔵 | 🔴 | Medium importance |
| 🔹 | 🔺 | Some importance |
| | | No importance |
| ▨ | ▨ | No information |

| | | **Taxa** | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Snails and slugs | | Plants | | Trees | | Spiders, mites and ticks | | Insects | | Amphibians | | Reptiles | | Mammals | | Birds | |
| **Landscape Features** | Soil (pH, depth) | ▨ | ▨ | ▨ | 🟥 | ▨ | 🟥 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Topographic features (diversity, elevation, valley bottoms) | ▨ | ▨ | 🔵 | 🟥 | 🟦 | 🟥 | ▨ | ▨ | 🔵 | 🔴 | ▨ | 🟥 | ▨ | 🟥 | 🔹 | 🟥 | ▨ | 🟥 |
| | Absence of snow or permafrost | ▨ | ▨ | ▨ | ▨ | 🔵 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Presence of snow | ▨ | ▨ | 🔹 | 🟥 | 🔹 | 🔴 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | 🔵 | ▨ | ▨ | ▨ |
| | Vegetation (structure, cushion plants, grazing) | ▨ | 🔴 | ▨ | 🔺 | ▨ | ▨ | ▨ | 🔴 | 🔹 | 🔺 | ▨ | ▨ | ▨ | ▨ | 🔵 | 🔺 | ▨ | ▨ |
| | Geology | ▨ | 🟥 | 🟦 | 🟥 | ▨ | ▨ | ▨ | ▨ | 🔹 | ▨ | ▨ | ▨ | ▨ | ▨ | 🔹 | ▨ | ▨ | ▨ |
| | Proximity to surface water | ▨ | ▨ | ▨ | 🟥 | ▨ | 🟥 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | 🔴 | ▨ | ▨ | ▨ | ▨ |
| | Absence of a pathogen or competitor | ▨ | ▨ | ▨ | 🔴 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | 🔴 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Proximity to coast | ▨ | ▨ | ▨ | 🔴 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |

Past habitat management has also offered numerous species warm refugia during cold spells. Land management in Britain over the last 6,000 years has created a continuing presence of early successional habitats that would otherwise have matured into closed habitats. This shorter, more open vegetation provides a warmer microclimate (Rosenberg 1974) and hence more opportunity for development in insects such as butterflies. Existing in Britain after the closure of the Channel land bridge circa 7kYBP, butterflies are hypothesised to have moved into the warmer microclimates of anthropogenic downland and heathland as the climate cooled 5kYBP and several are now dependent upon these habitats for their survival (Thomas 1993). Supporting this idea, the cessation of land management practices such as grazing, which create and preserve open habitats, has been identified as the primary cause of declines in many open habitat butterflies, such as the large blue (*Maculinea arion*, Thomas 1980). Similar findings for plants add weight to this idea: Bennett and Provan (2008) report various herbs which are now commonplace in Britain, were patchy, scarce or even absent prior to the arrival of humans. A difficulty here is separating a direct effect of the temperature difference between open and closed habitat, from a direct effect of differing light regime. For example, some plants have physiological adaptations to low light regimes that may see them associated with low light conditions within a forest, rather than a preference for dampened temperature extremes. Nevertheless, Pigott and Walters (1954) point out the unusual preponderance of open habitat species for an island that is considered to have been widely covered by forest, although the Vera hypothesis of herbivore-driven succession from open to closed habitats and vice versa could explain this using a cyclic model of vegetation change (Vera 2000).

## 3.7 Future refugia

The species that are of most conservation concern in a warming world are those currently limited to interglacial refugia, or those that prefer cooler conditions and at present restricted to cooler microclimates to avoid warm temperatures, such as populations of ptarmigan and dwarf birch in the Alps (Stewart and Lister 2001, Ashcroft 2010). There is evidence to suggest that some landscapes that are already relatively cold have experienced less warming (Ashcroft et al. 2009), and are forecast to receive less warming (Christensen et al. 2007) than the average, meaning that refugia in these cooler areas could play a continuing role in the conservation of cold-adapted species: this trend is not repeated at a global scale however, with polar areas warming fastest (Ashcroft 2010, IPCC 2007). At a landscape scale, many species have a preference for different topographic or geographic locations and so (unless their habitat preferences change as the climate warms) will be exposed to varying levels of climate change (Ashcroft et al. 2009). This bias in habitat selection cannot be represented or detected with coarse-scale modelling, emphasising the need for fine-scale temperature surfaces to be developed to quantify thermally heterogeneous landscapes and identify potential refugia for species considered at risk. Conversely, species also show flexibility in their habitat associations, becoming more specific closer to their range edge (Oliver et al. 2009). Species considered to be associated with a specific habitat may also be found in other habitats (Varga 2010), opening up the possibility of species switching habitats and thereby avoiding a particular effect of climate change (Davies et al. 2006).

Very few studies have explicitly modelled microrefugia and predicted their locations under climatic warming, although there are notable exceptions (Ackerly et al. 2010, Dobrowski 2011, Ashcroft et al. 2012, Gillingham et al. 2012). Given the relative novelty of the field, definitive statements on changes to the distributions and importance of refugia cannot be made. Despite this, some broad conclusions from the early work on microrefugia can be offered.

Climatic microrefugia are likely to exhibit one or more of three properties: 1) relatively extreme conditions; 2) relatively stable climates; 3) distinct differences from their surroundings (Ashcroft et al. 2012). Areas exhibiting extremes of climate, particularly those associated with cold air drainage effects, can be more climatically unstable (Ashcroft et al. 2012): hence, such areas may not be able to satisfy all the potential requirements for climate change refugia. Omitting such local climate effects from microclimate models can modify the outputs substantially: for example, areas predicted as suitable when including cold air drainage effects can be predicted to be unsuitable when removing such processes from the model (Dobrowski 2011). Comparisons of coarsely resolved and finely resolved models find that coarsely resolved models tend to underestimate the actual range of temperatures in the landscape (Gillingham et al. 2012). The distances over which species must migrate to track their climatic niche (and the speeds at which they must do it) are generally lower for precipitation than for temperature, owing to greater spatial variation in the former, at most scales (Ackerly et al. 2010). This will mean that it will more likely be the thermally sensitive species facing larger migration distances to track their niche than moisture sensitive ones, although the latter can also be sensitive to soil moisture gradients. In a further complication, the directions of distribution change required to track temperature and precipitation niches do not always align: a warmer, drier scenario provides more alignment of these vectors than does a warmer, wetter scenario (Ackerly et al. 2010). The areas that remain notably stable or different from the prevailing climate over one particular length of time (e.g. one month) may not be the most stable areas in a landscape over other lengths of time (e.g. one season, or three months, Ashcroft et al. 2012). And finally, areas with the lowest minima and the highest maxima relative to the prevailing climate can also overlap, highlighting the need to include all ecologically relevant variables in any examination of landscape suitability (Ashcroft et al. 2012). The extent to which these rules of thumb can be applied universally depends upon the degree to which it is appropriate to extrapolate beyond the limited areas that have been the subject of study (including parts of: California, U.S.A., Sierra Nevada, U.S.A., Lake Vyrnwy, Wales, and New South Wales, Australia), something which will become clearer as more literature accrues.

There have been a number of studies that have investigated the effect of changing the spatial resolution of models on predictions of landscape suitability for species. These studies fail to reach a consensus as to whether coarsely resolved models overestimate, or underestimate, extinction risk, when compared with fine-scale models (Table 3.2). Studies that have tested the performance of models with and without fine-scale information included have tended to find that including such information increases estimates of persistence under climatic change.

**Table 3.2** Studies examining the effect of modelling at a finer resolution (grain size) or including fine-scale features (e.g. soil pH, topographic information) on predictions of species persistence under climatic change. The table was populated with studies revealed by the literature search described above, and a further topic search for: (resol*) + (extinct* OR persist*) + (climat*) + (spat*).

| **Treatment** | **Did the treatment decrease persistence or increase it?** | | |
|---|---|---|---|
| | **Decreased** | **Neutral** | **Increased** |
| **Modelling at a finer resolution** | Trivedi *et al.* (2008)<br>Martínez *et al.* (2012)<br>Shimazaki *et al.* (2011) | Guisan *et al.* (2007)<br>Joyner *et al.* (2010)<br>Kriticos & Leriche (2010) | Randin *et al.* (2009)<br>Scherrer *et al.* (2011)<br>Gillingham *et al.* (2012) |
| **Including fine-scale environmental features** | Trivedi *et al.* (2008) | Luoto & Heikkinen (2008) | Virkkala *et al.* (2010)<br>Dobrowski (2011)<br>Sears *et al.* (2011)<br>Bertrand *et al.* (2012) |

Trivedi *et al.* (2008) suggest that their result of coarse-scale models underestimating extinction risk could be due to coarse-scale climate surfaces dampening the actual range of temperatures experienced by species at the local level. In this study, the montane species in question were only found at higher elevations and therefore colder parts of each coarse-scale grid square. Averaging climate over increasingly larger sized grid cells biases the data towards those temperatures found in the more common areas (in the *Trivedi* et al. 2008 case: higher temperature, lower elevation areas), an effect known as regression dilution or attenuation bias (Frost and Thompson 2000).

When the niche was subsequently fitted to the presence of that species at a coarse-scale, the tolerance of that species to higher temperatures was overestimated, and hence, estimates of extinction risk via those higher temperatures were perhaps underestimated. This can also be an issue when averaging data over long periods of time, such as fitting a predictor variable of annual mean temperature, where considerable variation over shorter periods may occur, such as blocking high pressure weather systems over Britain in summer, or cyclonic depressions in autumn- both of which may influence species composition at a site more than a long term mean. The effects of such contrasting weather events on species will of course be quite different, yet the coarsely-resolved model is unable to capture this, and will (incorrectly) assign this uncertainty to error in the species response (McInerny and Purves 2011).

In other circumstances, potential escapes for species from higher temperatures provided by elevational range or topographic diversity are unlikely to be represented in coarse-scale models (Randin et al. 2009). If the model fit for a species' temperature niche reflects their tolerances in reality (c.f. the situation in Trivedi et al. 2008), modelled persistence under future warming scenarios is likely to be higher in contexts offering a greater range of temperatures, i.e. those generated by fine-scale models. Hence a comparison of coarse-scale and fine-scale model predictions would lead to higher expected persistence in the latter. Note also that the outcome of coarse vs. fine scale comparisons will also be sensitive to the study area selected (which differs in the above), and the degree to which the target species are or are not near their climatic limit.

That likelihood of occupancy does not scale with increasing resolution in a predictable manner across different species is well established (Hartley and Kunin 2003). Given this, and the lack of consistency reported in Table 2, it is clear that quantifying the effect of study scale on projections of persistence or extinction risk remains a priority for research. To our knowledge, there are two studies that have attempted to address this problem systematically. Guisan *et al.* (2007) tested the effect of a ten-fold coarsening of resolution on the outputs of ten species distribution models, across five study regions. They found that finer-resolution model runs can both improve and diminish model performance. Gillingham *et al.* (2012) tested resolution effects alone by using the same input data and the same study area/extent, and simply specifying numerous (11) model resolutions. But even here, for a northern species expected to decline under climatic change (the ground beetle *Carabus glabratus*), the proportion of the landscape projected to be suitable by each resolution of the model did not decline at the same rate with warming. Therefore, estimates of persistence are sensitive not only to model resolution, but also to an interaction between resolution and amount of warming. The results of modelling experiments conducted at varying resolutions lead to disparate findings. This suggests that a greater convergence and consensus on methodology and approach is required if research is to provide greater clarity to conservation practitioners at the landscape level. More ground-truthing may also be required to ensure models remain representative of reality when they are used at finer resolutions.

### 3.8 Are the locations or properties of refugia predictable, based on taxon or phylogeny?

As Table 3.1 suggests, there is often no information available as to the potential importance of refugia for the majority of taxa and the majority of refugial features. This is compounded by the lack of a multi-taxon analysis of refugia to date. That no studies indicate that a particular feature was unimportant for a particular taxon could be the result of a file drawer problem (see discussion of Table 3.1 above).

Despite these gaps in the knowledge, topographic features, such as topographic diversity, are relatively well tested, particularly for warm (interglacial) episodes, and their importance for many taxa is often highlighted in the literature. This may also be a reflection on the relative availability of finely-resolved models to represent these landscape characteristics, compared to other features for which our understanding is less well-developed (such as vegetation or snow cover, the dynamics of which presently preclude their inclusion within fine-scale climatic modelling). Plants, including trees, would appear to respond to a greater variety of refugia characteristics (Table 3.1): this may reflect the relative lack of mobility of many plants compared to most animals groups, which reduces the potential for them to occupy new locations in response to changing conditions.

Our understanding of the landscape features important to various taxa present during cold episodes is constrained by the weight and quality of evidence describing the locations of those taxa; therefore, more information on refugial properties for taxa that are easy to detect (plants, mammals) is to be expected, and indeed is borne out in Table 3.1. Interestingly, the landscape features that mammals respond to during warm and cold episodes differs somewhat, with authors citing presence of snow-free vegetation (e.g. Fløjgaard et al. 2009) as a limiting factor during cold episodes like the LGM. The greater abundance of such resources during warmer episodes such as the present presumably frees them of this constraint.

## 3.9 Other factors affecting suitable refugial areas

The success of areas protected as climatic refugia may be influenced by a multitude of factors that could act for or against the likely persistence of the target species. Other factors may include proximity to coastal areas (less extreme climates), changes in human land use and absence of a pathogen or competitor. As Table 3.1 shows, very few studies have considered these effects in tandem with investigations into refugia; however, in this section we will describe their findings.

Interspecific interactions (e.g. competition) are already known to drive a myriad of responses in wildlife, and are considered a major driver of patterns in diversity (Menge and Sutherland 1976). Despite it being well studied, however, even some of the more famous examples of its effects are more complex than initial analyses suggest. One example is the recent discovery of the effect of Squirrelpox disease on Red Squirrel populations, via contact with Greys (Rushton et al. 2000). Additionally, effects that could prove critical to the future survival of a species may not be apparent in the present day. For instance, climatically cooler areas that are potentially important to the local survival of the Northern Brown Argus (*Aricia artaxerxes*) are vulnerable to colonisations by its close relative, the Brown Argus (*Aricia agestis*); this is because the range of host plants of the latter species can use has broadened, possibly in response to climate change. This has speeded the northward expansion of the more southerly distributed Brown Argus (Pateman et al. 2012). Given the relative success of Brown Argus, and the potential for interbreeding between the two species (Ford 1945), the Northern Brown Argus therefore faces the threat of local extinction via introgression within 100 years, should current rates of expansion of Brown Argus under climatic change continue (~40km per decade, Mallet et al. 2011, Pateman et al. 2012). Although Northern Brown Argus also occurs on in continental Europe (e.g. in Scandinavia), this could result in the British subspecies *Aricia artaxerxes artaxerxes* going extinct. No matter how well potential refugia are managed on a climatic basis, this process may prove difficult to stop, as the two butterflies have very similar habitat requirements: hence, any attempt to facilitate the migration of (southern) Brown Argus with climate change will put Northern Brown Argus populations at risk (Mallet et al. 2011).

Identifying refugial areas that may provide relief from competition (and other negative interactions) might therefore prove difficult in at least some cases. Ashcroft *et al.* (2012) suggest an approach which identifies areas as being different or isolated from the matrix: that is, areas where species averse to competition are more likely to have locally adapted to a temperature regime that, in the wider landscape 'matrix', is unusual. They find that in mountainous terrain, there are more unusual cells for minimum temperatures than for maximum temperatures. This is due to cold air drainage effects causing cold air to pool in valley bottoms, leading to large differences from the surrounding landscape. For conservation practitioners there is however a trade-off between prioritising a landscape featuring occasional, isolated patches of microclimate, and a landscape offering a greater degree of heterogeneity (which will offer more instances of analogous climates, and by implication therefore, will be subject to higher rates of competition). A further trade-off concerns temporal heterogeneity: for example, temporal variation in microhydrological variables has been shown by Silvertown *et al.* (1999) to enhance species richness, as it prevents any one species with a particular hydrological niche from dominating the landscape. This contrasts with the assertions of Ashcroft *et al.* (2012), who suggest that temporal heterogeneity in temperature is associated with higher extinction rates and lower persistence of species, and indeed suggest climate stability is one of the three attributes that define microrefugia.

Identification of suitable climatic refugia may be confounded by additional factors other than the variables outlined above, and these may lead to false positive identifications of refugia if they are not properly understood, or measured. For example, slope angles of 18° or more prevent artificial mowing. As a result, a greater diversity of tree species is found on steeper slopes, where species can persist undisturbed (Hörsch 2003). In countries with a longer history of intensive agriculture, this effect may simply be caused by the extirpation of species adapted to flat, lowland areas before biological monitoring became widespread. However, areas of higher plant diversity in England are often mown upland and upland meadows. Hence care must be taken in the design and interpretation of spatial studies of refugia to ensure that any climatic basis for persistence is correctly identified, and where generalisations are not possible, careful interpretation of the local ecological context is required.

# 4. Identifying refugia at national scale

## 4.1 Introduction

Our literature review identified relatively few tests of the refugia hypothesis on present day biological data. Given roughly forty years of climate warming (IPCC 2007), and the excellent availability of species data for England, there existed potential to test for refugia in the English landscape: determining which, if any, locations were buffering the flora and/or fauna from climate change. This would have relevance for conservation organisations nationwide.

Specifically, the approach was to assemble national datasets of species persistence at a relatively coarse scale- the 10 km cell (or hectad) level- and test for associations with environmental variables that the literature review had identified as being indicative of refugia. Using statistical models, the variables that best identified areas of persistence over the last 40 years were established, both a) across the biota, in an ‘all species’ approach, and b) by taxon. Our statistical approach allowed the relative effect sizes of these variables to be compared, disentangling the drivers of species occurrence.

The statistical models also generated refugia maps, identifying the areas most likely to host refugial populations of species under climatic change. These maps are Geographical Information Systems (GIS) ready and hence can be easily included in national conservation planning exercises. Finally, we provided a preliminary assessment of the overlap between these refugia and the English protected area network (Sites of Specific Scientific Interest, National Nature Reserves, National Parks), to assess the extent to which refugia are protected by existing statutory legislation.

## 4.2 Methods

### Data collation and processing

Data were gathered to represent a) areas of persistence or extinction, b) potential predictors of refugia, and c) confounding effects, where a particular confounding factor (such as agricultural intensity) could be responsible for enhanced persistence and hence necessitated inclusion in our models as a control variable.

### *Areas of persistence or extinction*

To identify species at risk from climate change, data from the Biological Records Centre (BRC) at the Centre for Ecology and Hydrology (CEH), the Botanical Society of Britain & Ireland, and Butterfly Conservation were used to identify species that had suffered a recent range retraction (not necessarily a statistically significant decline). This species list was combined with a list of species for which a range retraction under a medium climate change scenario was predicted, as part of the analyses for the parallel Natural England research project: ‘Assessing the risks and opportunities for species in England as a result of climate change’. We opted for this quantitative approach (as opposed to a qualitative approach based on expert opinion) as this offers the fairest test of the refugia hypothesis across the English biota as a whole.

To establish the areas in which these species have either persisted or gone (locally) extinct, the BRC data were divided into two discrete time windows: 1970-89, and 1990-2009. These windows were applied to all taxa except plants, for which 1970-86 and 1987-2009 were used, to correspond to Plant Atlas recording periods. For all 10 km squares in which a species was recorded present in the first window, records in the second window were examined to establish either persistence (1) or extinction (0) in each square. Thus, a binary measure of geographic persistence was created for each species. Mean persistence across all taxa is mapped in Figure 4.1 (overleaf). Note that new colonisations were ignored.

To select suitable taxa, we chose groups that: 1) number at least a few tens of species, 2) are recorded as a group, rather than individually or idiosyncratically (e.g. mammals, particularly bats, are often recorded individually), and 3) had at least ten records per species per year. Of roughly 3,000 selected species, 2,430 declined between the two study periods. Of these, 1,082 were projected to retract further, and these formed the final species list. The taxa included in the study are listed in Table 4.1. These taxa were grouped into six broad groupings, based where possible on taxonomic association (tracheophytes, bryophytes, Lepidoptera, Coleoptera), but also in two broader taxonomic groupings where more loosely associated taxa were combined to ensure sufficiently large sample sizes (Other insects, comprising Diptera, Hymenoptera, Orthoptera and Odonata; Other arthropods, comprising Araneae, Chilopoda and Diplopoda).

**Table 4.1** Taxa included in national scale analyses.

| **Formal name** | **Common name (n)** | **Grouping (n)** |
|---|---|---|
| Tracheophytes | Higher plants (474) | Higher plants (474) |
| Bryophytes | Lower plants (204) | Lower plants (204) |
| Rhopalocera | Butterflies (27) | Butterflies and moths (153) |
| Heterocera | Moths (126) | |
| Carabidae | Ground beetles (53) | Beetles (65) |
| Cerambycidae | Longhorn beetles (1) | |
| Coccinellidae | Ladybirds (4) | |
| Cantharidae | Soldier beetles (7) | |
| Formicidae | Ants (1) | Other insects (91) |
| Anthophila | Bees (9) | |
| Tipulidae | Craneflies (12) | |
| Syrphidae | Hoverflies (40) | |
| Odonata | Dragonflies and damselflies (10) | |
| Orthoptera | Grasshoppers and crickets (6) | |
| Apocrita | Wasps (13) | |
| Araneae | Spiders (86) | Other arthropods (95) |
| Chilopoda | Centipedes (3) | |
| Diplopoda | Millipedes (6) | |

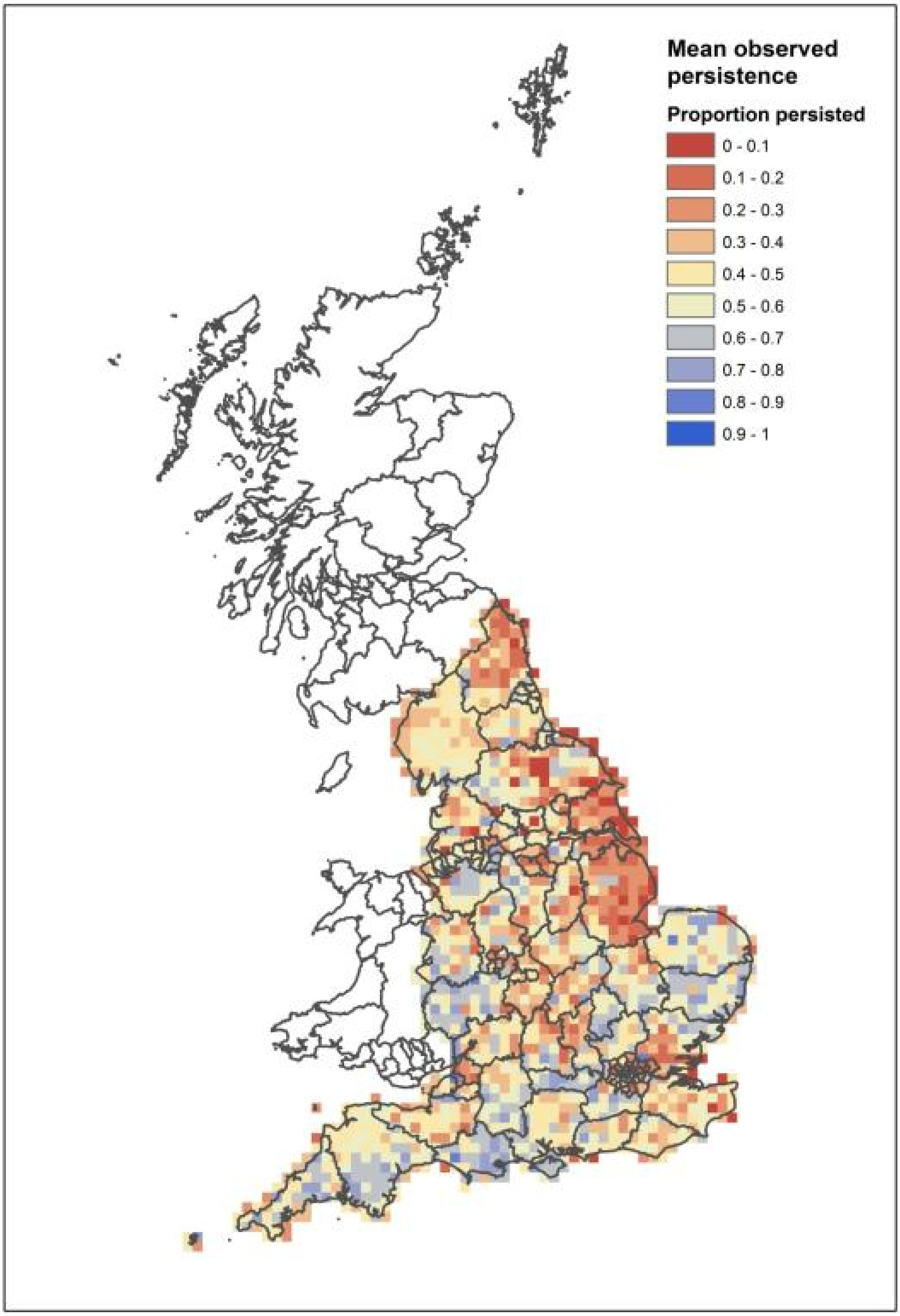

**Figure 4.1** Map showing a crude mean of persistence values across all taxa. Values can range between 0 and 1, and represent the proportion of species that persisted in each 10k (hectad) cell, from TP1 (1970-89; 1970-86 for higher plants) to TP2 (1990-2009; 1987-2009 for higher plants). Only cells in which species have persisted, or gone locally extinct, are included: hence colonisations are ignored.

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## Potential predictors of refugia

### *A) Geology*

A 1:625,000 vector map of bedrock geology (1979, 3rd edition) was obtained from the Natural England Geographical Information (GI) team and resampled at 100 m resolution. Using the British Geological Society Rock Classification Scheme (RCS) codes (Gillespie and Styles 1999), we calculated the proportions of each 10k square comprising of the following geological features:

**1) Felsic rock** - see Table 4.2.

**Table 4.2** Constituents of the felsic rock layer, with associated Rock Classification Scheme (RCS) codes.

| **Layers** | **RCS code** | **Description** |
|---|---|---|
| Felsic | FELS | Felsic rock (mainly granite) |
| | FLAV | Felsic lava |
| | LATF | Felsic lava and felsic tuff |
| | FTUF | Felsic tuff |

**2) Calcium carbonate rock** - see Table 4.3.

**Table 4.3** Constituents of the Calcium carbonate layer, with associated Rock Classification Scheme (RCS) codes.

| **Layers** | **RCS code** | **Description** |
|---|---|---|
| Chalk | CHLK | Chalk |
| Limestone | LMAS | Limestone, argillaceous rocks and subordinate sandstone, interbedded |
| | LMCM | Limestone, mudstone and calcareous mudstone |
| | LMCS | Limestone and calcareous sandstone |
| | LMST | Limestone |
| | LSMD | Limestone and mudstone, interbedded |
| | LSSA | Limestone with subordinate sandstone and argillaceous rocks |
| | LSSM | Limestone, sandstone, siltstone and mudstone |
| | SLAR | Sandstone, limestone and argillaceous rocks |
| | DLDO | Dolomitised limestone and dolomite |

**3) Mafic rock** - see Table 4.4.

**Table 4.4** Constituents of the Mafic rock layer, with associated Rock Classification Scheme (RCS) codes.

| **Layers** | **RCS code** | **Description** |
|---|---|---|
| Ultramafic | UMFT | Ultramafitite (The Lizard) |
| Mafic | LATM | Mafic lava and mafic tuff |
| | MAFI | Mafite |
| | GNS | Mafic gneiss |
| | MFIR | Mafic igneous rock (mainly gabbro) |
| | MFLA | Mafic lava |
| | MFTU | Mafic tuff |
| Dolerite and tholeiitic basalt | DBAT | Basalt (Teesdale) |
| Serpentinite | SMLP | Serpentine group minerals |

As the three geology variables were heavily zero-inflated (i.e. numerous grid cells of no occurrence), they were excluded from the correlation analyses used for variable screening (see below), and all three retained for the 'all species' model.

### *B) Elevation*

We obtained 90 m grid cell resolution digital elevation data from the Shuttle Radar Topography Mission (SRTM; Farr et al. 2007) to model topoclimatic variables. To ensure consistency with the UK national grid and species data, this was resampled to 100 m resolution using the bilinear interpolation algorithm in ArcGIS (ESRI, Redlands, CA). From this layer, a number of statistics were derived, summarising elevation data from the 100 m cells within each 10 km square:

1) Mean of the square;
2) Standard deviation of the square;
3) Maximum value in the square;
4) Minimum value in the square;
5) The difference between the maximum value and the mean value of the square;
6) The 5th percentile of the square;
7) The 95th percentile of the square.

Hence, seven elevation variables were included in the initial screening stage of analysis.

### *C) Flow accumulation*

To represent potential for cold air drainage effects, the 100 m resolution elevation data were used to calculate accumulated flow to each grid cell. The algorithm for calculating this is more usually applied in the context of water flow, but was thought to serve as a reasonable proxy of near-surface air flow. The method entailed first calculating the direction of flow, by determining the direction of the steepest descent from each cell of the digital elevation dataset. From this dataset, the number of uphill grid cells that would contribute cold air to each target grid cell was determined. These surfaces were calculated using the flow direction and flow accumulation tools in ArcGIS, which implements algorithms described in Jenson and Dominque (1988). Hence each 100 m square was assigned a discrete value of between 0 (no uphill cells contributing cold air) and a maximum (in Britain) of ~ 25,000. This flow accumulation layer at 100 m resolution was subsequently summarised at the 10 km level using statistics 1-7, as described in the methods for the elevation layer. Again, all seven variables were included in the initial screening stage of analysis.

### D) Water availability (topographic wetness index)

To provide a proxy of fine-scale variations in water availability, the 100 m flow accumulation layer was combined with information on slope angle to generate a topographic wetness index for each 100 m square. The index was calculated via the equations in Box 4.1 below (following Bevan and Kirkby 1979).

**Box 4.1** Calculating the topographic wetness index

Topographic wetness index = $\log_e ( a / \tan \beta)$

Where $\beta$ is the slope angle and $a$ is the contributing area, which can be derived from flow accumulation as follows:

$a$ = (flow accumulation + 1) x grid cell resolution$^2$

Using this approach, valley bottoms (which have a high contributing area) are considered to be wetter than mountain tops, and flat areas (which have low surface run-off) are considered to be wetter than areas with steep slopes. This topographic wetness index layer at 100 m resolution was again summarised at the 10 km level using statistics 1-7 detailed in the methods for the elevation layer, and all seven topographic wetness index layers included in initial screening.

### E) Surface temperature (solar index)

To provide a proxy of fine-scale variations in surface temperature due to topography, we calculated a solar index. This index measures the proportion of direct beam solar radiation (i.e. that which is not reflected or scattered – also termed insolation) that reaches a surface. Although differences between fine-scale surface and regional temperatures are also affected strongly by factors such as cloud cover and wind speed, it has been shown to serve as a useful proxy of fine-scale variations in surface temperatures (Bennie et al. 2008) and concomitant variations in biota (Bennie et al. 2006). Topography influences direct beam radiation by affecting the incidence angle between the sun and surface and can be calculated from the slope inclination and aspect and from the solar altitude and azimuth, which are themselves contingent on the time of day and year and geographic location of the surface. Our algorithm, based on that provided in Šúri and Hofierka (2004), also accounted for shading, whereby the direct radiation is obscured by topographic features.

This calculation was performed for three times of year: the longest day (21st June), the shortest day (21st December) and the vernal equinox (21st March). To account for within-day variations in the solar altitude and azimuth, we calculated the mean of hourly values over 24 hours. Only one equinox was included as solar index values at any given location on the 21st September are near identical to those on the 21st March (Pearsons's $r = 0.95$, $p<0.0005$, d.f.= 24349795), with differences arising purely due to the fact that equinoxes do not precisely match given days of the year. The three 100 m solar index layers were summarised at the 10 km level using the following statistics:

1) Mean of the square;
2) Standard deviation of the square;
3) Maximum value in the square;
4) Minimum value in the square;
5) The difference between the *minimum* value and the mean value of the square;
6) The 5th percentile of the square;
7) The 95th percentile of the square.

Note the emphasis on minimum value for statistic 5 (rather than the maximum value as used for some of the other predictors), as lower solar radiation is associated with potential refugia from the current warming episode, whereas with elevation and the moisture layers, higher values signify potential refugia. Thus, a total of 21 variables related to solar radiation were included in initial screening, since each of variables 1 to 7 were calculated for both solstices and the vernal equinox.

### *F) Climate change*

Two types of variable were calculated to represent climate change: trend variables, and differences in trend from the surrounding geographic matrix (Ashcroft et al. 2012), the latter of which highlights regionally atypical trends and coastal/continental differences. We used historic monthly mean 5 km gridded climate data available from the Met Office (UKCP09 data, Met Office, 2009). Linear models were then fitted to the data from each year, one for each 5 km square, spanning 1961-2006 (1971-2006 for snow lie). The slope values from these models were extracted and represented the trend in that square. This process was conducted for temperature and rainfall trends in all four seasons, and for the year as a whole. For snow lie, the annual trend and spring trend were calculated. A total of 12 trend variables were advanced to correlation analyses for screening. To produce seasonal values, data were averaged across the following months (spring: March, April, May; summer: June, July August; autumn: September, October, November; winter: December, January, February). The resulting 5 km gridded dataset was then resampled to a resolution of 10 km, by averaging the four 5 km grid cell values within each 10 km grid cell. To calculate difference in these trends from the matrix, a moving window approach was adopted, in which the trend was subtracted from the mean trend across the surrounding 100 km window. Hence areas of lower temperature trend were negative, and vice versa. This calculation was performed for all 12 trend variables, generating a further 12 difference variables for screening. Note that although warming in England has been ubiquitous, rainfall has both increased (~33% of 10 km squares) and decreased (~67% of 10 km squares) across the country (Appendix 3 Figure 11).

### *Screening potential predictors*

A total of 66 variables underwent screening. Screening involved the selection of a sensible number of predictor variables for the 'all species' model that both a) avoided overfitting the model (not too many predictors), and b) avoided the loss of predictors highlighted in the literature as important in identifying refugia (i.e. not too few). Inputs for the process included an assessment of the following:

**1) Does the variable come out as significant in an 'all species', single variable model?**

If the variable came out as significant as the sole predictor of species persistences, this made its inclusion in the final model more likely.

**2) Is the variable correlated with other variables?**

Pearson product-moment correlations were performed pairwise between each of the 66 variables. Removal of variables proceeded on the basis that no final model variables should be excessively correlated with each other (r > 0.8 or < -0.8) (Zar 1999).

**3) Is there a biological reason for retaining the variable?**

Based on the literature, is there a compelling biological reason for retaining the variable, despite 1) or 2)? This may be to ensure that at least one variable from each group of variables (e.g. elevation, or water availability) is in the final model.

This process reduced the 66 variables to 8. A summary table of these variables, and an intuitive description of what they represent, is presented in Table 4.5.

**Table 4.5** Environmental variables selected for the final, 'all species' model.

| **Type of variable** | | | | **Intuitive description** |
|---|---|---|---|---|
| **Trend** | **Local extreme** | **Local heterogeneity** | **Local stability** | |
| | Mean elevation | | | Cold, wet conditions. |
| | | Flow SD | | Availability of local escapes to cold/wet. |
| Summer rain change | | Topographic wetness SD | | Availability of local escapes from drought; Water stability. |
| Summer temp change | | Summer solar index SD | | Local escapes from heat and drought stress; Thermal stability. |
| Snow change | | | Spring temp diff from matrix | Stability in start of growing season, frost damage risk, stability in spring phenology. |

## Confounding effects

### *Agricultural intensity*

The Centre for Ecology and Hydrology's Land Cover Map 2007 (LCM2007, Morton et al. 2011) – vector version – was obtained from the Natural England GI team and resampled at 1 km resolution, and the proportion of each 10 km square attributed to the broad habitat category 'Arable and horticulture' was calculated.

### *Recorder effort*

The total number of visits per 10 km square was calculated for each taxon. This number represents, for each 10 km square, the total number of unique combinations of date and 1 km square in the record data, for the entire study period (i.e. including both windows, 1970-2009). Values were logarithmically transformed, as the distributions of the raw values were strongly non-normal.

## Statistical modelling

All statistical modelling was conducted using Generalised Linear Mixed Models (GLMMs) fitted to the data using the 'lme4' package in R. In order to assess the effects of the various potential predictors of refugia separately, GLMMs with three different assemblies of variables were constructed. These were a) an 'all refugia' model, b) a model with only climate change and microclimate variables, and c) a model containing only microclimate variables. Constructing these three model variants allows the inherent assumptions of the modelling to be tested separately. In a), all (quantifiable) potential predictors of persistence were included, allowing for the relative importance of climate-related predictors to be measured against other important (non-climatic) predictors of persistence, such as geology. In b), non-climatic predictors were removed, to examine the sensitivity of the model outcomes (as quantified by the refugia maps) to these non-climatic predictors. In c), the predictors representing (past) climate change were removed, as the spatial pattern of future warming will not necessarily be similar to the spatial pattern of past warming. These three model types are described in turn below:

### *All refugia model*

This model included all the variables described in 1b) and 1c) above, and had the following structure:

#### Response variable

10 km squares of persistence (1) or extinction (0) for all range declining species in England, that are predicted to experience further retraction under climatic change. A logit link function, with a binomial error distribution was used.

Species ID was included in the model as a random (intercept) effect. In practice, this allows the probability of persistence of each species to exhibit different sensitivities to predictor variables (see below), while ensuring that the directional effect of predictor variables is constant across species. The final model provides a (weighted by number of records) mean across species estimate of the effects of each predictor variable on probability of persistence.

#### Predictor variables

All calculated for each 10 km square, these were:

-Proportion of chalk or limestone rock;
-Proportion of felsic rock;
-Proportion of mafic rock;
-Mean elevation;
-Standard deviation of flow accumulation;
-Summer trend in rainfall;
-Standard deviation in topographic wetness index.
-Summer trend in temperature;
-Standard deviation in summer solar index;
-Spring trend in snow lie;
-Difference in spring temperature trend from the matrix;

#### Control (confounding) variables

All calculated for each 10 km square, these were:

-Log (total number of visits);
-Proportion of arable land.

#### Interaction terms

The model had the following interaction terms:

-Summer trend in temperature * Standard deviation of flow accumulation;
-Summer trend in temperature * Mean elevation;
-Summer trend in temperature * Standard deviation in summer solar index;
-Summer trend in rainfall * Standard deviation in topographic wetness index.

These terms investigated potential interactive effects, wherein a particular microclimatic property may only become important in areas suffering from higher rates of climate change. For example, variability in solar index may help to buffer populations against increases in summer temperature.

### *Climate change and microclimate model*

This model excluded the geological and agricultural intensity variables. It had the following structure:

#### Response variable

As per the ‘all refugia’ model in a) above.

#### Predictor variables
All calculated for each 10k square, these were:

-Mean elevation;
-Standard deviation of flow accumulation;
-Summer trend in rainfall;
-Standard deviation in topographic wetness index.
-Summer trend in temperature;
-Standard deviation in summer solar index;
-Spring trend in snow lie;
-Difference in spring temperature trend from the matrix;

#### Control (confounding) variable
Calculated for each 10 km square, this was:

-Log (total number of visits).

#### Interaction terms
The model had the following interaction terms:

-Summer trend in temperature * Standard deviation of flow accumulation;
-Summer trend in temperature * Mean elevation;
-Summer trend in temperature * Standard deviation in summer solar index;
-Summer trend in rainfall * Standard deviation in topographic wetness index.

### *Microclimate only model*
This model excluded both the geological and agricultural intensity variables, and the climate change variables. Hence, associated refugia maps do not assume that the areas of high (or low) climate change in the past will be subject to high (or low) climate change in the future. It had the following structure:

#### Response variable
As per the ‘all refugia’ model in a) above.

#### Predictor variables
All calculated for each 10 km square, these were:

-Mean elevation;
-Standard deviation of flow accumulation;
-Standard deviation in topographic wetness index;
-Standard deviation in summer solar index;
-Difference in spring temperature trend from the matrix;

#### Control (confounding) variable
Calculated for each 10 km square, this was:

-Log (total number of visits).

### *Analyses at the taxon level*
The three types of model were applied to all the species data as a unit, but also to the six groupings of species (detailed in Table 4.1 above) individually. Hence 3 x 7 = 21 models were constructed.

### *Computing effect sizes*
Because the datasets of local persistence and extinction are very large sample size, almost all the terms in the model are likely to appear significant. Moreover, biological importance can be

assessed using the magnitude of an effect included as model term, but cannot be assessed using statistical significances (Nakagawa and Cuthill 2007). Statistical significance is a measure of the probability that the observed data would occur by chance and does not in itself measure the importance of each individual variable: the probability is reduced by both the quantity of data and the size an effect and these factors cannot be distinguished from one another. The model coefficients (i.e. the parameter estimates) provide a measure of the strength of the relationship between the dependent variable and each dependent variable, but are sensitive to units of measurement: variables, such as altitude, with a large range of values will tend to have large model coefficients. To provide an independent measure of effect size, we used Cohen's $f^2$ statistic (Cohen 1988). This is a measure of the relative contribution that a single variable included as a term in a model has to the overall model results within the context of a multivariate model. Values of c. 0.01 are considered small, c. 0.15 medium and c. 0.35 large (Cohen 1988). Using this approach, Cohen's $f^2$ can be obtained as follows (Selya et al. 2012):

$$f^2 = \frac{R_{AB}^2 - R_A^2}{1 - R_{AB}^2}$$

Where $B$ is the variable of interest, $A$ is the set of all other variables $R^2_{AB}$ is the proportion of variance accounted for by A and B together (relative to a model with no terms included) and $R^2_A$ is the proportion of variance accounted for by A (relative to a model with no terms included). However, to account for inter-species differences in our multi-species models, we used a generalized linear-mixed model (GLMM) approach. Obtaining $R^2$ from GLMMs turns out to be a difficult task, although a number of ways have been proposed (see Nakagawa and Schielzeth 2012 for a review). These proposed methods, however, share some theoretical problems or practical difficulties and consequently, no consensus for a definition of $R^2$ for mixed-effects models has emerged in the statistical literature. Therefore, it is not surprising that $R^2$ values and effect sizes are very rarely reported when mixed models are used. We use the approach suggested by Nakagawa and Schielzeth (2012), the most general and widely adopted method developed to date. The tables (5.1 to 5.3) in which model results are reported thus include a valid measure of the contribution that each variable makes to the overall results. Positive effects are denoted by a plus symbol, negative effects by a minus symbol and the number of symbols denotes the magnitude of the effect: (large ($f^2 > 0.25$): +++ or ---, medium ($f^2 > 0.08$): ++ or --, small ($f^2 < 0.08$): + or -).

### Generating refugia maps

The outputs of the three types of statistical model were used to generate 'refugia maps' for England, illustrating the potential of locations to act as refugia. The refugium potential of each 10 km square was calculated by multiplying the model parameter (slope) estimate of predictor variables by the value of that predictor, in each square. Note that the recorder effort parameter estimate was multiplied by the average recorder effort for the whole country, as it is not a landscape property, nor a property of refugia. The resultant total was added to the intercept value for the model, and subsequently logit transformed to derive a refugia score, based on probability of persistence, for each model type. Maps were generated for each model type and species grouping combination (n=21 maps). A worked example of this calculation is provided (Box 4.2).

### Comparison with protected areas (SSSIs, NNRs and National Parks)

To visually assess the degree to which current protected areas adequately encompass areas of high refugium potential, locations of protected areas were added to the maps of refugia outlined above. In addition, refugium potential scores were plotted against the proportion of each 10 km square designated as SSSI and NNR (three graphs for each designation), with correlation analyses establishing the extent to which areas of high potential also had more protection. Proportion of each 10 km square designated as protected was calculated by resampling the Natural England vector layer representing the locations of protected sites at 100m resolution, before calculating the proportion of each 10 km square these sites occupied (generating three data layers). These layers and the refugium potential scores were logit transformed to account for heteroscedasticity violating the assumptions of the Pearson's r correlation test.

Because at 10km resolution each square is essentially either 'inside' or 'outside' a National Park, boxplots were provided to contrast scores 'inside' or 'outside' National Parks. Simple t-tests examined the statistical significance of these differences.

Establishing the extent to which protection genuinely enhances species persistence, as opposed to simply being coincident with such areas, requires a different approach however. To test this, the three protection layers were added into the all refugia statistical model (in turn). Hence the effect of different types of protection could be discerned, while controlling for the other potential predictors of persistence (climate change, geology, and microclimate).

**Box 4.2** Generating refugia maps: a hypothetical worked example.

1) Models establish the relationship between the species group and each predictor variable.

2) The intercept from the model (0.05) serves as a basis for the calculation. The slope of the relationship between persistence and each predictor is multiplied by the grid cell value in each grid cell (see table below). These values are then added to the intercept value. In the hypothesised example above, the calculation begins thusly: 0.05 + (0.15 x 0.04) + (-0.01 x 0).

| Variable | Relationship | | Grid cell value |
|---|---|---|---|
| | Slope | P value | |
| Agricultural intensity | 0.15 | <0.0005 | 0.04 |
| Chalk or limestone geology | -0.01 | <0.0005 | 0 |
| Felsic geology | 0.05 | 0.0025 | 0.1 |
| Mafic geology | 0.005 | 0.0099 | 0 |
| Summer trend in temperature | 0.9 | 0.0034 | 0.65 |
| Summer trend in rainfall | -0.15 | 0.4594 | 0.13 |
| Spring trend in snow lie | 0.001 | <0.0005 | 0.005 |
| Standard deviation of flow accumulation | 0.0065 | <0.0005 | 25 |
| Standard deviation in topographic wetness index | 0.0005 | <0.0005 | 457 |
| Mean elevation | 0.025 | <0.0005 | 85 |
| Standard deviation in summer solar index | 0.267 | <0.0005 | 0.12 |
| Difference in spring temperature trend from the matrix | 0.5684 | <0.0005 | 0.02 |
| Standard deviation of flow accumulation * Summer trend in temperature | 0.05478 | <0.0005 | 16.25 |
| Standard deviation in topographic wetness index * Summer trend in rainfall | 0.00054 | 0.2546 | 59.41 |
| Mean elevation * Summer trend in temperature | 0.0012 | <0.0005 | 55.25 |
| Standard deviation in summer solar index * Summer trend in temperature | 0.458 | <0.0005 | 0.078 |
| Log (total visits) | 0.01 | <0.0005 | 5.62 |

3) As recorder effort is not a property of refugia, the mean effort across the entire country is used, as opposed to cell-specific values. Hence (0.01 * 4.68) would be added to the score, even though the grid cell value in our example (5.62) is different.

4) The total score of 4.62 is logit transformed to a final score of 0.986, indicating that this grid cell is an area of high refugium potential.

## 4.3 Results

### Statistical modelling results

Results are presented for statistical models using all refugia (Table 4.6), climate change and microclimate (Table 4.7), and microclimate only (Table 4.8). The first column in each table show the slope of the relationship between probability of persistence over the past four decades for all species (n = 1,082) and the variable concerned; cells shaded blue represent variables for which higher values increased chances of persistence, and cells shaded red represent variables for which higher values decreased chances of persistence. The significance of these variables in the model is shown in the following column. Eight pairs of columns are then presented showing the same data for individual taxonomic groups. Note that for some variables in models, a quantitative estimate of effect size could not be calculated via Cohen's $f^2$. This is likely due to the effect sizes in these cases being very small. In these cases we have bracketed the slope symbols and simply stated the direction of the effect (i.e. positive or negative).

### Control variables

*Recorder Effort:* The number of recorder visits per 10 km square was positively and significantly related to persistence in all species groups and for all types of model. Including this variable in all three types of model thus provides a control for the increased likelihood of inferred extinction in poorly recorded regions of England.

*Agricultural Intensity:* Overall, there was a negative effect of agricultural intensity in the all-species model. However, this negative model appears to reflect the negative effect of agricultural intensity on the most species-rich group (Higher Plants), the only taxon showing a significant negative effect of agricultural intensity. Agricultural intensity was positively related to persistence in lower plants, and did not show clear effects on any of the other taxonomic groups. This variable is not included in the climate change or microclimate models. Note that including the broad habitat type 'Improved grassland' did not alter the statistical significance of results (data not shown).

### Predictor variables

#### *Geology (Table 4.6):*

*Chalk and limestone:* Calcareous geology had positive effects on both higher plant and lepidopteran persistence, and this positive significant effect was carried over to the all-species model. Many habitat specialist plants and Lepidoptera are associated with calcareous geology, and the natural and semi-natural habitats that remain in these locations are likely to have favoured the persistence of species, given adverse changes to the wider environment since the middle part of the twentieth century. However, changes to the favourability of calcareous grassland habitats owing to abandonment of low-intensity livestock grazing, agricultural intensification and fluctuations in numbers of wild grazers (e.g. rabbit) mean that many calcareous habitat specialists have experienced habitat loss and declines. Hence it is encouraging that we have identified positive effects of calcareous geology on persistence. For plants, limited soil depth or limited mineral availability could reduce levels of competition from climate-related colonists. Higher frequency of extremes (e.g. drought) in these areas may also favour stress-tolerant incumbents (Hopkins 1978, Grime et al. 2000), while steepness and/or orientation of slopes may enhance this effect further (Bennie et al. 2006).

Conservation management has also been introduced widely in chalk and limestone areas to conserve specialist plants and invertebrates. There were marginally significant negative effects of chalk and limestone geology on persistence in beetles and the other arthropod (spiders, centipedes and millipedes) group, but no significant effects on Lower plants or other insects (Hymenoptera, Diptera, Orthoptera and Odonata).

*Felsic geology:* The negative effect of Felsic geology on all-species persistence appears to reflect a negative effect on climate-threatened higher plants. In contrast, there were positive effects on persistence in lower plants, Lepidoptera, and (weakly) other arthropods.

*Mafic geology:* The only taxon to show a clear significant effect of Mafic geology on persistence was the Coleoptera, for which there was a negative effect. There were also marginal negative effects in the Higher plants and Lepidoptera, and the negative relationship carried over to the all-species model. For the wider group of species considered here, there is no strong evidence that mafic geology is positively associated with locations of enhanced persistence, although there are likely to be individual species for which areas of serpentine or related geology are key habitats.

### *Climate change and microclimate (Tables 4.6 and 4.7):*

*Summer trend in temperature:* There was strong evidence that persistence in several taxonomic groups was influenced by the trend in summer temperature, but that these effects of climate warming were modified by topographic variability.

Some caution is required in interpreting the signs of the individual effect of summer trend in temperature, since the models included interaction terms between this variable and three topographic features: standard deviation of flow accumulation (related to spatial variation in water flow and cold air pooling); mean elevation (which influences average temperature and rainfall); and standard deviation in solar index (related to variability in insolation owing to variation in slope and aspect). Where these interaction terms are statistically significant, the warming response of a group is modified by the topographic feature included in the interaction variable (see results for these features below, and also the Discussion subsection).

Spatial differences in the warming trend in summer temperature had apparently contrasting effects on persistence in plants and animals. Higher increases in summer temperature had a negative effect on both Higher and Lower plants (and in the all-species model), but a positive effect on persistence in all the animal groups except beetles. These patterns are consistent between the “All variables” and “Climate change and microclimate” models: in other words, they do not depend on the inclusion / exclusion of agricultural intensity and geology variables.

*Standard deviation in flow accumulation:* Higher plants and Lepidoptera both showed positive individual effects of variability in flow accumulation. However, both of these groups showed significant negative interactions of temperature trend with variability in flow accumulation. Thus, more topographically variable environments may have favoured persistence, but do not buffer wildlife sufficiently to avoid declines in the biota associated with higher rates of warming.

*Mean elevation:* Individual effects of mean elevation on persistence differed between Higher plants (positive) and Lepidoptera (negative), but these groups also showed contrasting interaction terms between elevation and summer temperature trend (negative for Higher plants; positive for Lepidoptera). Thus, both groups show evidence that mean elevation can modify the effects of warming on persistence. For Lepidoptera, high elevations appear to increase chances of persistence in regions with the most rapidly warming summer temperatures. For Higher plants, warming temperatures appear to have reduced persistence: plants appear to have shown higher persistence at higher elevations, but not to the extent that a higher elevation has buffered populations in regions where summer temperatures are increasing the most.

*Standard deviation in summer solar index:* Again there was an apparent contrast between plants and animals. The individual effect of variability in solar index was negative in plants, and positive in animals; yet the interactions terms with summer warming were positive in plants but negative in animals. The results suggest that for plants, a wide range of slopes and aspects may not directly increase persistence at all rates of warming, but may do so where temperatures are increasing most: in other words, solar variability might buffer plants against higher levels of climate warming. In contrast, taken individually, both warming temperatures and a variable solar index appear to favour persistence of most animal groups. However, the interaction term for these variables is negative, hence persistence in animals declined in areas with both a high warming trend and a summer solar index that is more variable.

Interpretation of the effects of the summer warming trend and its interactions with solar variability is not straightforward. However, there does seem to be good evidence that solar variability may have buffered plants against negative effects of summer warming. For the invertebrate groups considered, populations of a number of species may have shown positive responses to the levels of warming experienced to date: but again, there is good evidence that persistence is also influenced by topographic variability.

*Summer trend in rainfall* and *standard deviation in topographic wetness index:* The effects of summer trend in rainfall and its interactions with the topographic wetness index were generally less consistent across the species groups than the effects of summer trend in temperature. However, for beetles both the all-variables model and the climate change / microclimate model showed a negative individual effect of summer rainfall trend, a positive effect of variation in topographic wetness index, and a positive interaction term between these two variables. In contrast to most other groups, beetles appear to be more sensitive to moisture levels than to temperature (see also Morecroft et al. 2002). Regional variability in topographic drainage appears to favour persistence in this taxonomic group. There was also some evidence that more variable topographic wetness values within 10 km squares increased chances of persistence for plants.

*Spring trend in snow lie* and *Difference in spring temperature trend from the matrix*: Where the reduction in the number of spring snow days has been less (or there has been an increase in snow days), persistence was higher for Lepidoptera and lower plants. For higher plants, the opposite was true (i.e. greater reductions in the period of spring snow lie are associated with increased persistence). Only the higher plants showed strong evidence of an effect (positive) of difference in spring temperature trend from the matrix: hence, where spring temperatures were warming to a greater extent than in surrounding grid cells, plants had increased chances of persistence. Both of these results suggest increased chances of persistence for higher plants under warmer spring conditions- this is likely to be more applicable to species with a northern range limit in England.

Given the relative lack of snow days in the south of the country compared with the north, interpretation of the snow lie effects is difficult and conclusions may be unsafe. However, spring snow days have declined notably in Cumbria and on the Yorkshire limestone (see Appendix 3), both are areas which for other reasons (e.g. conservation interventions, protection status) may have promoted persistence in higher plants, hence a negative relationship for this species group in models which don't take these reasons into account. Snow lie may also interact with climate change in numerous ways, some of them counter-intuitive. Areas of snow lie can in some circumstances support warmer temperatures under the snow, and hence reduce exposure to cold, which may therefore enhance the persistence of species exposed to such risks during sensitive life-cycle stages in spring. In England, climate change is reducing snow lie on the whole, and may perversely be exposing species to higher levels of winter/spring cold. Species (in this case, possibly lower plants and lepidopterans) may therefore be protected from this effect in areas where snow lie has not reduced as much relative to the average. However, these effects too may be the result of false positives (Type I errors), where other factors (e.g. beneficial climate change elsewhere) may be responsible. Whilst the ecology of arctic and alpine snowbeds has been relatively well studied, the wider effect of trends in snow lie on wildlife is less well understood. Unlike for variables such as solar index, a landscape scale, fine-resolution model of snow lie has not yet been developed. Consequently, the effects on species persistence, of fine-resolution heterogeneity in snow lie cannot yet be examined.

### *Microclimate models (Table 4.8):*

A positive response of persistence to *Mean elevation* was evident across the taxa, but given that responses to variables were largely taxon-specific, results for these models are summarised by taxonomic group. The statements below offer generalisations on the responses of species at the taxon level. (It is also worth noting that some species within groups will have responded differently to the wider trend across the taxon):

*Higher plants:* Two variables (*Standard deviation in topographic wetness index*, *Mean elevation*) had significant positive effects on persistence, consistent with their effects in the models in which climate change effects were included. These suggest robust positive relationships between plant persistence and high elevations and topographic variation in moisture levels. The effects of two variables on persistence were highly significant, but in the opposite direction to their effects in models in which climate change was also incorporated. This is likely to be due to the strong microclimate * climate change interaction identified above. *Standard deviation of flow accumulation* showed a negative effect, suggesting greater persistence of higher plants in regions with relatively smooth / flat relief. *Standard deviation of summer solar index* showed a strong positive effect, suggesting higher persistence in regions with greater variation in slope and aspect.

*Lower plants:* The only two variables with significant effects in the microclimate model were *Standard deviation in topographic wetness* (negative) and *Mean elevation* (positive).These variables did not have strong effects in the models in which climate change terms were included, suggesting that the greater persistence of Bryophytes in sites with spatial variation in wetness, and at high altitudes, may have been masked by the negative relationship of Bryophyte persistence with summer warming, and a positive relationship of persistence with remaining snow lie in spring. The importance of moisture conditions, and the positive effect of elevation on persistence, is consistent with the association of many bryophytes with relatively cool, damp conditions.

*Beetles:* As in the climate change model, there was a strong positive effect of *Standard deviation in topographic wetness*, suggesting an association of beetle persistence with spatial variation in moisture conditions. There was also evidence of a positive effect on persistence of *mean elevation*, and a negative effect of *Standard Deviation in summer solar index*. Neither of these variables nor their interactions terms had particularly strong effects in the climate change model, suggesting that they may have been masked by effects of *regional trends in summer rainfall*.

*Butterflies and moths*: Lepidoptera persistence was weakly positively associated with *Standard deviation in summer solar index* and *Difference in spring temperature trend from the matrix*. The critical effects of spring and summer temperatures are generally consistent with those in Tables 4.6 and 4.7, although neither of the specific relationships found in the microclimate model emerged clearly in the models including climate change. There was an indication of a marginally non-significant positive effect of *mean elevation*.

*Other insects (Hymenoptera, Orthoptera, Diptera, Odonata):* The only clearly significant relationship was a positive effect of *mean elevation* on persistence, but all other variables had significance levels between $P = 0.01$ and $P = 0.07$. There is some indication of a positive overall effect of topographic variability (positive effects of *Standard deviation in topographic wetness*, *Standard deviation in summer solar index*). There were weak negative associations of persistence with *Standard deviation of flow accumulation* and *Difference in spring temperature trend from the matrix*.

*Other arthropods (Spiders, Centipedes, Millipedes):* Species in this group showed no significant relationships of persistence with the microclimate variables in models which did not include climate change.

**Table 4.6** Summary of results from statistical models with all refugia variables included. The direction of the relationship is indicated by positive (+) and negative (-) symbols, and the number of symbols corresponds to the size of the effect (see methods). Bracketed values indicate that quantitative effect size could not be calculated (see text).

| Variable | All species (n = 1082) | | Higher plants (n = 474) | | Lower plants (n = 204) | | Beetles (n = 65) | | Butterflies and moths (n = 153) | | Other insects (n = 91) | | Other arthropods (n = 95) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value |
| Log (total visits) | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | + | <0.0005 | + | <0.0005 |
| Agricultural intensity | - | <0.0005 | - | <0.0005 | ++ | <0.0005 | + | 0.7716 | - | 0.1122 | + | 0.0024 | + | 0.0456 |
| Chalk or limestone geology | + | <0.0005 | + | <0.0005 | ++ | 0.8773 | - | 0.0205 | + | <0.0005 | - | 0.3480 | - | 0.0129 |
| Felsic geology | - | 0.0025 | - | <0.0005 | ++ | 0.0043 | + | 0.6135 | + | 0.0078 | ( + ) | 0.9028 | ++ | 0.0216 |
| Mafic geology | - | 0.0099 | - | 0.0185 | -- | 0.1161 | - | 0.0074 | - | 0.0104 | ( - ) | 0.9728 | + | 0.2490 |
| Summer trend in temperature | - | 0.0034 | - | 0.0047 | -- | <0.0005 | + | 0.3957 | + | 0.0074 | + | 0.0374 | + | 0.0267 |
| Summer trend in rainfall | + | 0.4594 | + | 0.7546 | ++ | 0.2306 | - | 0.0069 | + | 0.3598 | + | 0.0256 | + | 0.8263 |
| Spring trend in snow lie | - | <0.0005 | - | <0.0005 | ++ | <0.0005 | + | 0.4653 | + | <0.0005 | ( - ) | 0.6061 | - | 0.5528 |
| Standard deviation of flow accumulation | + | <0.0005 | + | <0.0005 | ++ | 0.9406 | + | 0.4595 | + | 0.0011 | + | 0.0115 | + | 0.0813 |
| Standard deviation in topographic wetness index | + | <0.0005 | + | <0.0005 | -- | 0.0133 | + | <0.0005 | - | 0.2721 | + | 0.4393 | - | 0.1679 |
| Mean elevation | + | <0.0005 | + | <0.0005 | ++ | 0.2825 | + | 0.7654 | - | <0.0005 | - | 0.8425 | - | <0.0005 |
| Standard deviation in summer solar index | - | <0.0005 | - | <0.0005 | -- | <0.0005 | + | 0.0816 | + | <0.0005 | + | 0.1306 | + | <0.0005 |
| Difference in spring temperature trend from the matrix | + | <0.0005 | + | <0.0005 | ++ | 0.0230 | + | 0.4274 | + | 0.2007 | ( - ) | 0.1898 | - | 0.0018 |
| Standard of flow accumulation * Summer trend in temperature | - | <0.0005 | - | <0.0005 | -- | 0.8446 | - | 0.4144 | - | 0.0005 | - | 0.0064 | - | 0.0825 |
| Standard deviation in topographic wetness index * Summer trend in rainfall | - | 0.2546 | - | 0.3888 | -- | 0.3270 | + | 0.0069 | - | 0.3535 | - | 0.0316 | - | 0.8452 |
| Mean elevation * Summer trend in temperature | - | <0.0005 | - | <0.0005 | ++ | 0.8686 | + | 0.7835 | + | <0.0005 | ++ | 0.3409 | ++ | <0.0005 |
| Standard deviation in summer solar index * Summer trend in temperature | + | <0.0005 | + | <0.0005 | ++ | <0.0005 | - | 0.0217 | - | <0.0005 | ( - ) | 0.2083 | - | <0.0005 |

**Table 4.7** Summary of results from statistical models with only climate change and microclimate refugia variables included. The direction of the relationship is indication by + and -, and the number of symbols corresponds to the size of the effect (see methods).

| Variable | All species (n = 1082) | | Higher plants (n = 474) | | Lower plants (n = 204) | | Beetles (n = 65) | | Butterflies and moths (n = 153) | | Other insects (n = 91) | | Other arthropods (n = 95) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value |
| Log (total visits) | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | + | <0.0005 |
| Summer trend in temperature | - | 0.0007 | - | <0.0005 | - | <0.0005 | - | 0.9797 | + | 0.0030 | + | 0.0189 | + | 0.0129 |
| Summer trend in rainfall | + | 0.0641 | + | 0.1304 | + | 0.5347 | - | 0.0100 | + | 0.0751 | + | 0.0496 | - | 0.8603 |
| Spring trend in snow lie | - | <0.0005 | - | <0.0005 | ++ | <0.0005 | + | 0.5003 | + | <0.0005 | - | 0.6611 | - | 0.8961 |
| Standard deviation of flow accumulation | + | <0.0005 | + | <0.0005 | - | 0.1220 | + | 0.9003 | + | 0.0064 | + | 0.0137 | + | 0.0509 |
| Standard deviation in topographic wetness index | + | 0.0105 | + | 0.0007 | - | 0.0408 | + | <0.0005 | - | 0.0996 | + | 0.3520 | - | 0.2801 |
| Mean elevation | + | <0.0005 | + | <0.0005 | + | 0.1103 | + | 0.5950 | - | 0.0648 | - | 0.9747 | - | <0.0005 |
| Standard deviation in summer solar index | - | <0.0005 | - | <0.0005 | - | 0.0219 | + | 0.2111 | + | 0.0042 | + | 0.1695 | + | <0.0005 |
| Difference in spring temperature trend from the matrix | + | <0.0005 | + | <0.0005 | + | 0.0578 | + | 0.2410 | + | 0.5118 | - | 0.0817 | -- | 0.0025 |
| Standard deviation of flow accumulation * Summer trend in temperature | - | <0.0005 | - | <0.0005 | + | 0.1656 | - | 0.8062 | - | 0.0039 | - | 0.0076 | - | 0.0537 |
| Standard deviation in topographic wetness index * Summer trend in rainfall | - | 0.0175 | - | 0.0237 | - | 0.7426 | + | 0.0095 | - | 0.0695 | - | 0.0646 | + | 0.8256 |
| Mean elevation * Summer trend in temperature | - | <0.0005 | - | <0.0005 | - | 0.5486 | + | 0.9718 | + | 0.0163 | + | 0.4745 | + | <0.0005 |
| Standard deviation in summer solar index * Summer trend in temperature | + | <0.0005 | + | <0.0005 | + | 0.0201 | - | 0.0502 | - | 0.0151 | - | 0.2601 | -- | <0.0005 |

**Table 4.8** Summary of results from statistical models with only microclimate refugia variables included. The direction of the relationship is indication by + and -, and the number of symbols corresponds to the size of the effect (see methods). Bracketed values indicate that quantitative effect size could not be calculated (see text).

| Variable | All species (n = 1082) | | Higher plants (n = 474) | | Lower plants (n = 204) | | Beetles (n = 65) | | Butterflies and moths (n = 153) | | Other insects (n = 91) | | Other arthropods (n = 95) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value |
| Log (total visits) | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | +++ | <0.0005 | + | <0.0005 |
| Standard deviation of flow accumulation | - | <0.0005 | - | <0.0005 | - | 0.0945 | - | 0.2545 | - | 0.2278 | - | 0.0673 | - | 0.9871 |
| Standard deviation in topographic wetness index | + | <0.0005 | + | <0.0005 | - | <0.0005 | + | 0.0006 | - | 0.3101 | + | 0.0228 | - | 0.4773 |
| Mean elevation | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | 0.0019 | ( + ) | 0.0608 | + | <0.0005 | + | 0.3144 |
| Standard deviation in summer solar index | + | <0.0005 | + | <0.0005 | - | 0.7602 | - | <0.0005 | + | 0.0126 | + | 0.0421 | -- | 0.9075 |
| Difference in spring temperature trend from the matrix | - | 0.9611 | - | 0.9083 | + | 0.1437 | - | 0.7652 | ( + ) | 0.0346 | ( - ) | 0.0136 | - | 0.2774 |

### Refugia maps

Based on the model parameter estimates and relationships reported above (Tables 4.6 – 4.8), maps were compiled to illustrate refugium potential across England (see Methods and Box 4.3). These maps are presented for suites of variables representing all refugia types (Figure 4.2), climate change and microclimate (Figure 4.3), and microclimate only (Figure 4.4) characteristics. These figures represent the mean modelled probability of persistence over the last 40 years, which can be interpreted as a score of refugium potential (Box 4.3). Appendix 2 Figures 1, 2 and 3 show the locations featuring the top 10% of refugium scores for each model type. Maps for each species group are also presented (see Methods Table 4.1 and Appendix 2 Figures 4-9). The maps were plotted by using a national average for the number of recorder visits per 10 km square, to control for recorder effort (hence values on the maps do not reflect patterns of recorder effort). Note that all maps are derived from the statistical models described above, rather than raw persistence data, and hence may not reflect areas known areas of biological diversity or conservation.

**Box 4.3** Mapping refugia: understanding the refugium potential of the English landscape.

Rates of persistence in the English biota have varied across the country (Figure 4.1) due to a number of drivers of distributional change. Statistical modelling of persistence in response to these drivers can help determine *why* these rates have varied nationwide. But to determine *where* in the landscape persistence has been highest (i.e. in refugia) requires mapping. In this section (and in Chapter 5), we used the relationships between persistence and various explanatory variables to generate maps of persistence probability, which can be interpreted as a refugium potential 'score', where a higher score represents high refugium potential, and *vice versa*. Hence, for the first time, the potential of various regions and landscapes to buffer species from climate change can be compared.

We have generated three types of refugia map. The first type, representing all types of refugia (Figure 4.2), represents refugia that arise from microclimatic and geological diversity, and protection from intensive agriculture. Because patterns of agricultural intensity may change, and geology in the immediate future is immutable, we provide a type of map with these variables removed (Figure 4.3), termed a 'climate change and microclimate' map as only these variables were involved in its construction. Finally, because areas of past climate change may not correspond to future climate change (Murphy et al. 2009), we produce a third and final variant of map, with climate change also removed (Figure 4.4). This map represents solely the influence of microclimate on persistence.

No one type of map is superior, or more 'reliable' than the others, and indeed, the usefulness of each map type will depend on the specific conservation question.

The map illustrating all refugia types (Figure 4.2) highlights areas of topographic and/or geological diversity. Examples with high scores include the North Pennines, the White Peak, and the Shropshire Hills. Other large expanses of high quality habitat in the lowlands are also identified, including: the western part of Salisbury Plain, the south-east fringes of Northumberland and southern Breckland. An important 20 km x 20 km area to the south-east of the North York Moors, including the Wykeham and Langdale Forests, was scored highly, as was the south of Exmoor, Kielder Forest and parts of the South Downs chalk. Note that the areas identified as being most important do not always correspond to upland areas, or classical, high quality areas of suitable geology. Many of the areas outside the North Pennines could perhaps be characterised as peripheral: offering a degree of topographic diversity, unusual geologies, and local 'escapes' both for lowland species requiring cooler climates, or upland species moving downslope in cooler years. The paucity of suitable refugia in the East Midlands and northern Home Counties is striking, and it is here that more intensive habitat management may be required to conserve species in the future, given the lack of 'natural' refugium potential, especially as these areas are already known for their lack of semi-natural habitats.

The map of climate change and microclimate score (Figure 4.3) identifies areas of the South-West peninsula and East Anglia that have experienced notably differing levels of climate change from their surroundings. It is important to stress here that the South West has experienced relatively less temperature change than the country average, while East Anglia has experienced relatively more (Appendix 3 Figure 10). Both are likely to have enhanced persistence, but in different species groups: given that persistence in higher plants was negatively related to warming, the South West has been an important refugium from change for this group. However, the Lepidoptera, the ‘other insects’ and ‘other arthropods’ groups all responded positively to past warming (Table 4.6, also cf. Warren et al. 2001 for butterflies), and hence relatively higher levels of warming in East Anglia may have been beneficial for these groups. Note that this does not necessarily mean future warming will also prove beneficial, and future temperatures will likely be too hot for some current English species, e.g. Northern Brown Argus (*Aricia artaxerxes*, Settele et al. 2008). The extent to which these areas will continue to experience similar levels of relative change cannot be established with certainty; however, 25 x 25 km projections for both the East of England and the South West are fairly typical for the country as a whole (Murphy et al. 2009). It should however be noted that the South West is in fact more likely to experience higher levels of summer temperature change under current higher emissions scenarios (Murphy et al. 2009).

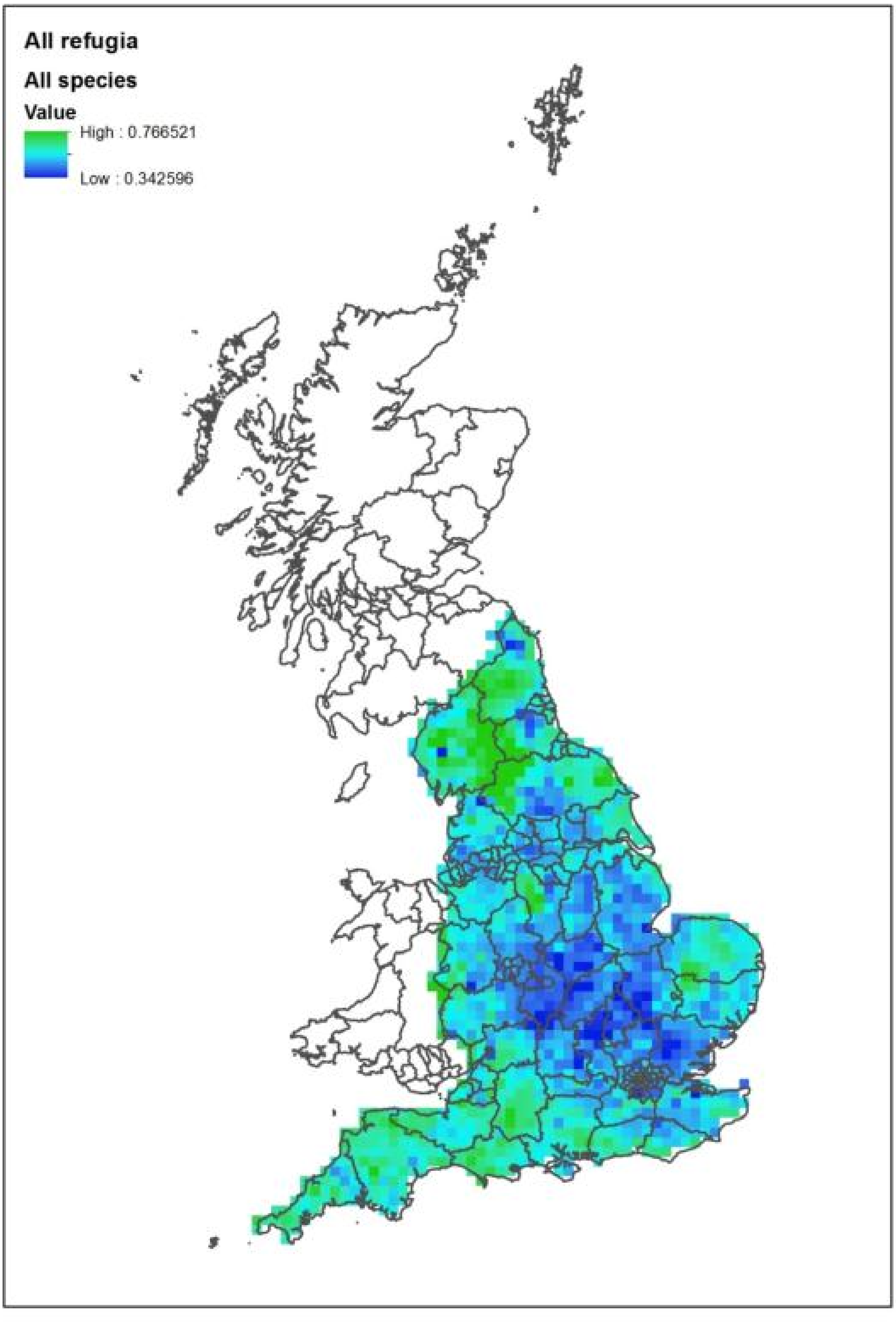

**Figure 4.2** Map showing refugial areas calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.

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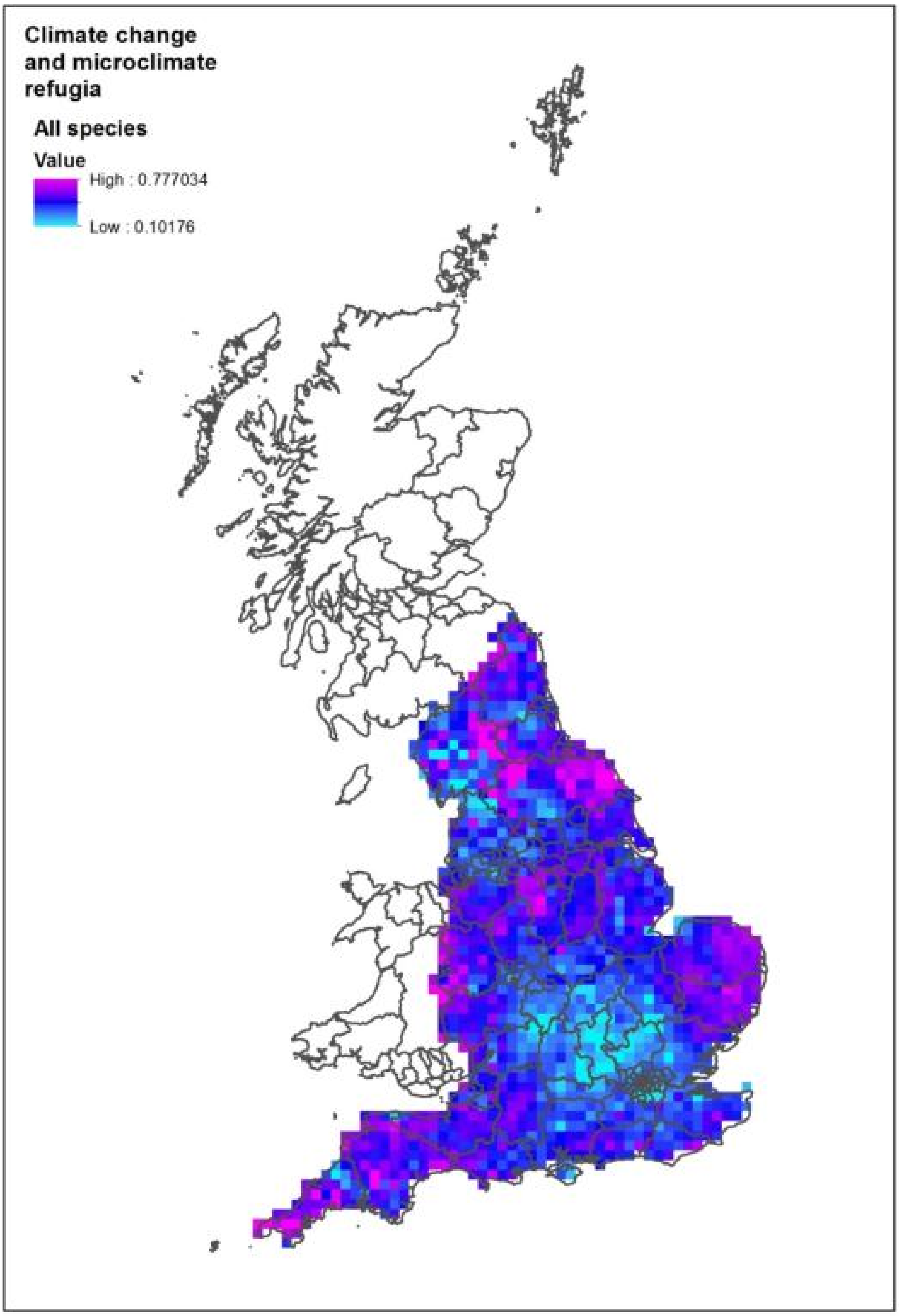

**Figure 4.3** Map showing climate refugial areas. In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.

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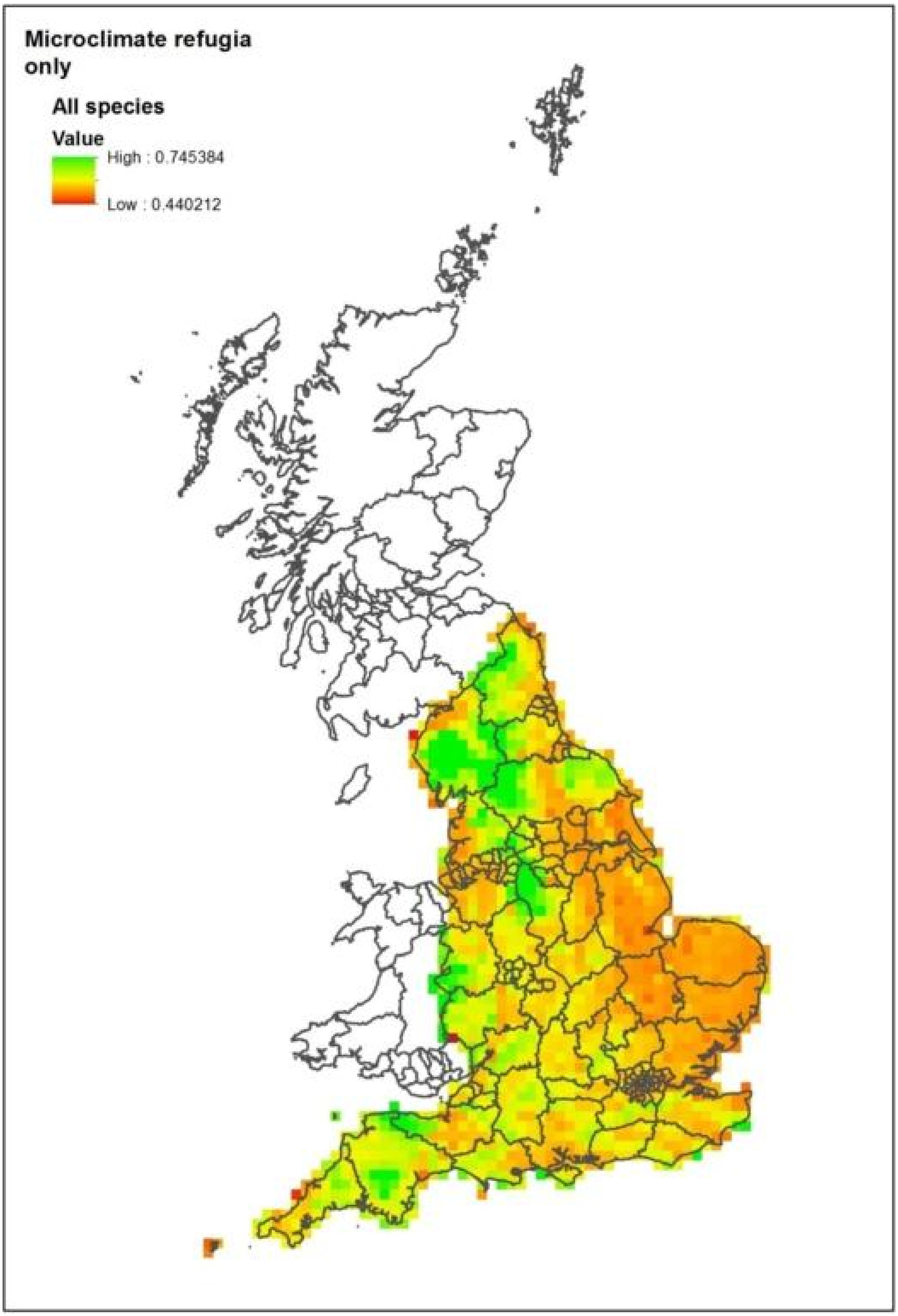


**Figure 4.4** Map showing microclimate refugial areas. In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.

On the map of climate change and microclimate refugia (Figure 4.3), as in the map of microclimatic refugia (Figure 4.4), large parts of the North York Moors and Hambleton Hills are identified as having high refugium potential. This is in sharp regional contrast to the relative lack of modelled refugia in the Vale of York and East Yorkshire. The North York Moors and Hambleton Hills are also atypical in light of wider agricultural intensity in the region (Appendix 3 Figure 1), leaving this area isolated both in climate and habitat terms. Conservation at the landscape scale is already underway to increase the number and stability of sensitive species in the area (Ellis et al. 2012), with initial success. The degree to which these populations, and others in similar northern 'outposts' can be made resilient to climate change will be critical for the conservation of some species, which may have a national distribution under the present climate, but could find large parts of the south inhospitable by 2100.

Areas identified as important on the microclimate only map (Figure 4.4) tend to be upland areas or areas of topographic diversity, with large parts of Cumbria, the North Pennines, the Cheviots, the Peak District, the Shropshire Hills, Dartmoor, and Exmoor scoring highly. Pockets of the coastal south, such as the Dover chalk and Folkestone Warren, are also identified as areas of high refugium potential. Outside of the larger, more predictable areas, these smaller patches of high scores tend to have high variability in solar index (Appendix 3 Figure 9), and contain high topographic variability. That many are situated on the coast may indicate that disturbance acts to maintain topographic variability and hence preserve important habitat in these areas, making persistence more likely (e.g. rockfalls on cliffs, Ravenscroft and Young 1996). Bodmin Moor, Lundy, the Malverns, the Forest of Dean, the Forest of Bowland, the Hambleton Hills, the Cleveland Hills, the Oswestry Uplands, the Black Mountains and other parts of the Welsh Marches also appear in the top 10% of sites.

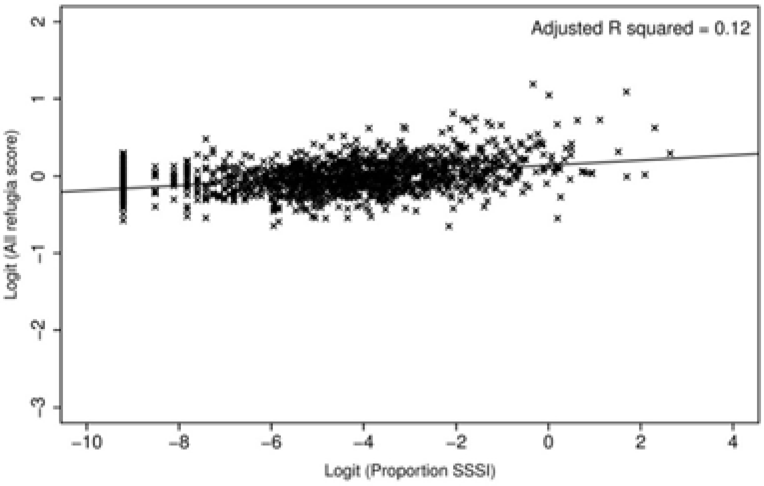
### Protected areas comparison

Areas of high refugial potential were correlated with protected areas in almost all cases (Table 4.9, Figures 4.5, 4.6, 4.7). Note that the correlations with the NNR network (Figure 4.6) were weaker than those for SSSIs (Figure 4.7). Bonferroni correction for multiple comparisons would give a critical value of 0.0056 (to 4 decimal places). Degrees of freedom for the all refugia and climate refugia scores were constrained by the limited spatial extent of the UKCP09 climate data, calculated at 5 km resolution. Microclimate surfaces were initially calculated at 100 m resolution; hence, microclimate layers covered more of the coastline squares, which was subsequently reflected in the greater spatial coverage of models (and derived maps) constructed using only these variables.

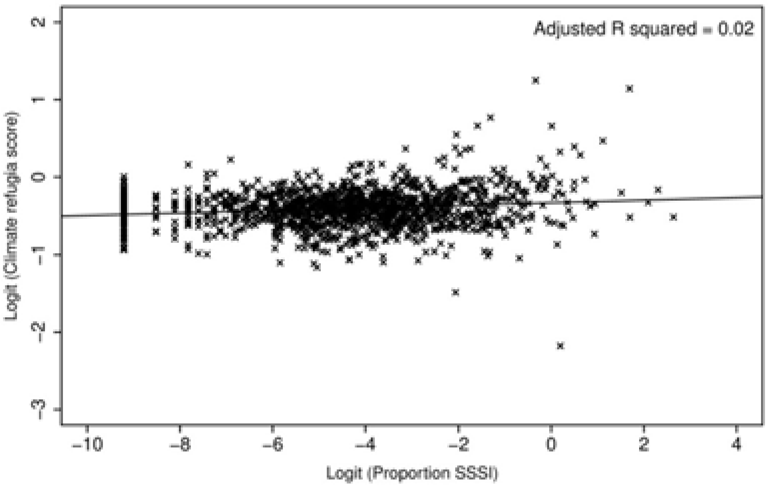
**Table 4.9** Results of correlations between SSSI or NNR protection status and refugium potential.

| Protection type | Refugium potential map | Pearson's r | d.f. | p-value |
|---|---|---|---|---|
| **SSSI** | All refugia | 0.2771 | 1355 | <0.0005 |
| | Climate change and microclimate | 0.1174 | 1355 | <0.0005 |
| | Microclimate only | 0.2849 | 1470 | <0.0005 |
| **NNR** | All refugia | 0.1254 | 1355 | <0.0005 |
| | Climate change and microclimate | 0.0609 | 1355 | 0.0249 |
| | Microclimate only | 0.0943 | 1470 | <0.0005 |

(a) All refugia score



(b) Climate change and microclimate score



(c) Microclimate only score

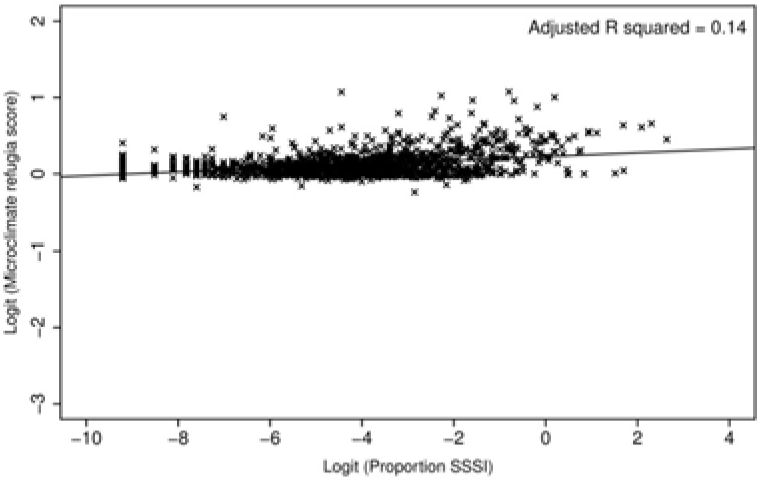
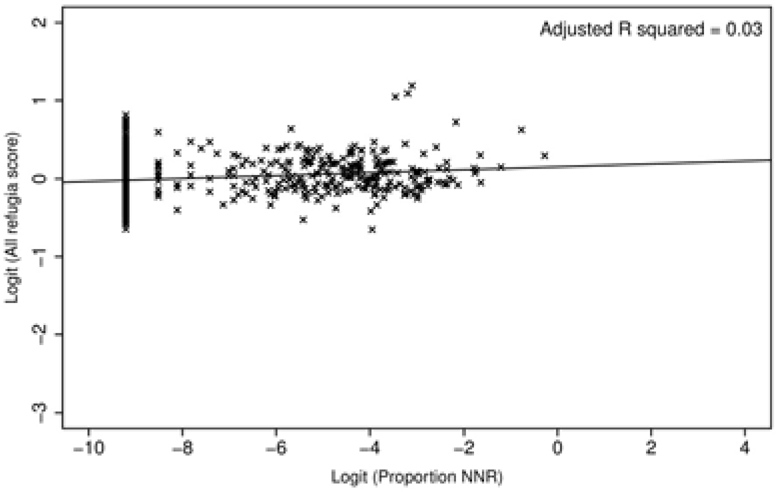
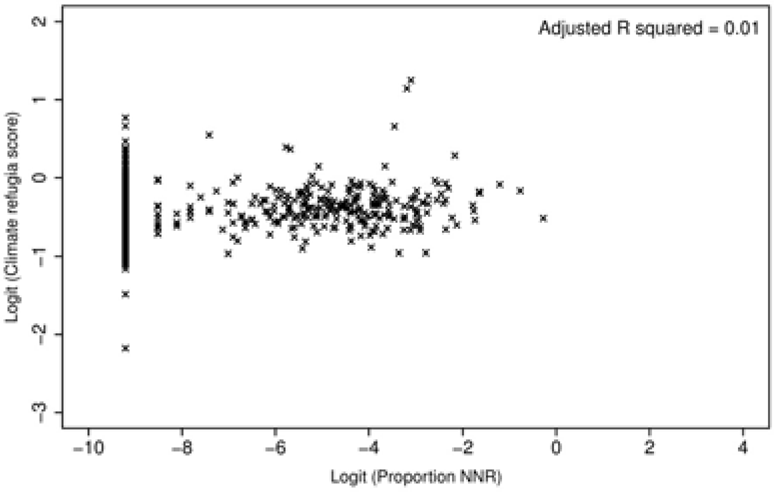


**Figure 4.5** Refugia scores (persistence probability) for each 10km square plotted against the proportion of that square designated SSSI. Note that both variables have been Logit transformed (see Methods).

(a) All refugia score



(b) Climate change and microclimate score



(c) Microclimate only score

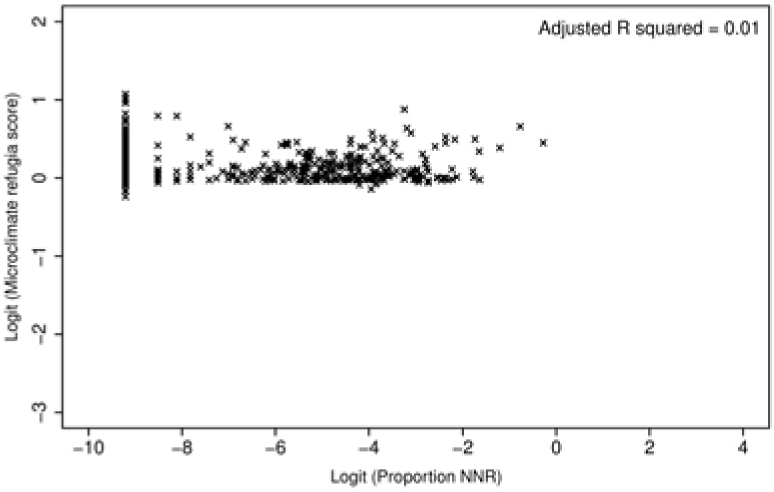
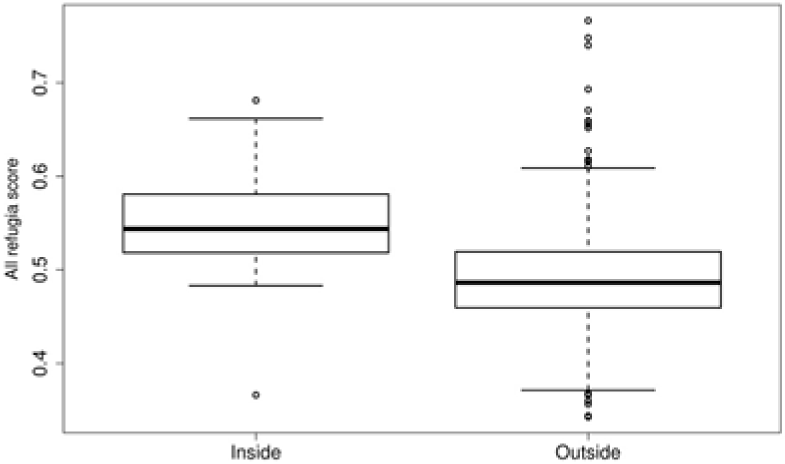
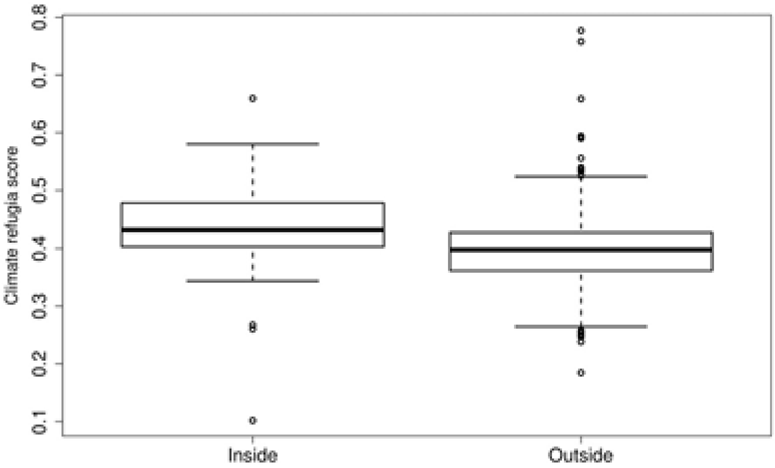


**Figure 4.6** Refugia scores (persistence probability) for each 10km square plotted against the proportion of that square designated NNR. Note that both variables have been Logit transformed (see Methods).

(a) All refugia score



(b) Climate change and microclimate score



(c) Microclimate only score

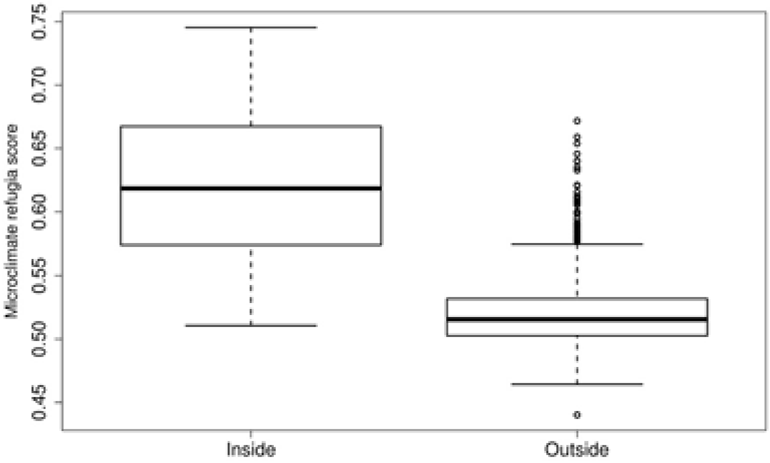


**Figure 4.7** Refugia scores (persistence probability) for each 10km square both inside and outside National Parks.

Maps of the English protected area network, and how this corresponds to the refugia maps in Figures 4.2, 4.3 and 4.4 above, are presented below (Figure 4.8, 4.9, 4.10, Appendix 3 Figures 14-16). Areas of high refugium potential and National Parks/SSSIs largely overlap, with notably important areas in Cumbria, Dartmoor, Exmoor, the North York Moors, The Fens, the Yorkshire Limestone and The Cheviots all protected. However, there are some notable areas of high potential that are unprotected. These include the Welsh Marches and the (England/Scotland) Borders, and areas in the periphery of Exmoor, Dartmoor and the Pennines.

Adding the proportion of each 10 km square with one of the three types of protection status into the all refugia statistical model showed that areas with protection were also areas of higher persistence (Table 4.10): however the opposite was true for higher plants. The positive effect of protection was strongest for butterflies and moths. Because the all refugia model includes the effects of geology, climate change and microclimate, one can conclude that there is a (marginally non-significant) positive effect of SSSI protection on species persistence regardless of these site properties. The extent to which this is solely a result of the protection status, or that SSSIs were designated at sites with the best quality habitat and highest population levels, cannot be established from these analyses, and could be the subject of further work.

**Table 4.10** The relationships of species' persistence to conservation status, when included (separately) in the all refugia statistical model (see Methods 2a).

| Species group | | Proportion SSSI | Proportion NNR | Proportion National Park |
|---|---|---|---|---|
| All species | Slope | + | + | + |
| | P value | 0.0525 | 0.4015 | 0.1964 |
| Higher plants | Slope | - | - | - |
| | P value | 0.0622 | 0.0237 | 0.7788 |
| Lower plants | Slope | + | - | - |
| | P value | 0.0303 | 0.9517 | 0.0134 |
| Beetles | Slope | + | + | - |
| | P value | 0.3857 | 0.0310 | 0.9899 |
| Butterflies and moths | Slope | + | + | + |
| | P value | <0.0005 | <0.0005 | <0.0005 |
| Other insects | Slope | + | + | + |
| | P value | 0.0011 | 0.0287 | 0.3886 |
| Other arthropods | Slope | + | + | - |
| | P value | 0.0144 | 0.0044 | 0.0067 |

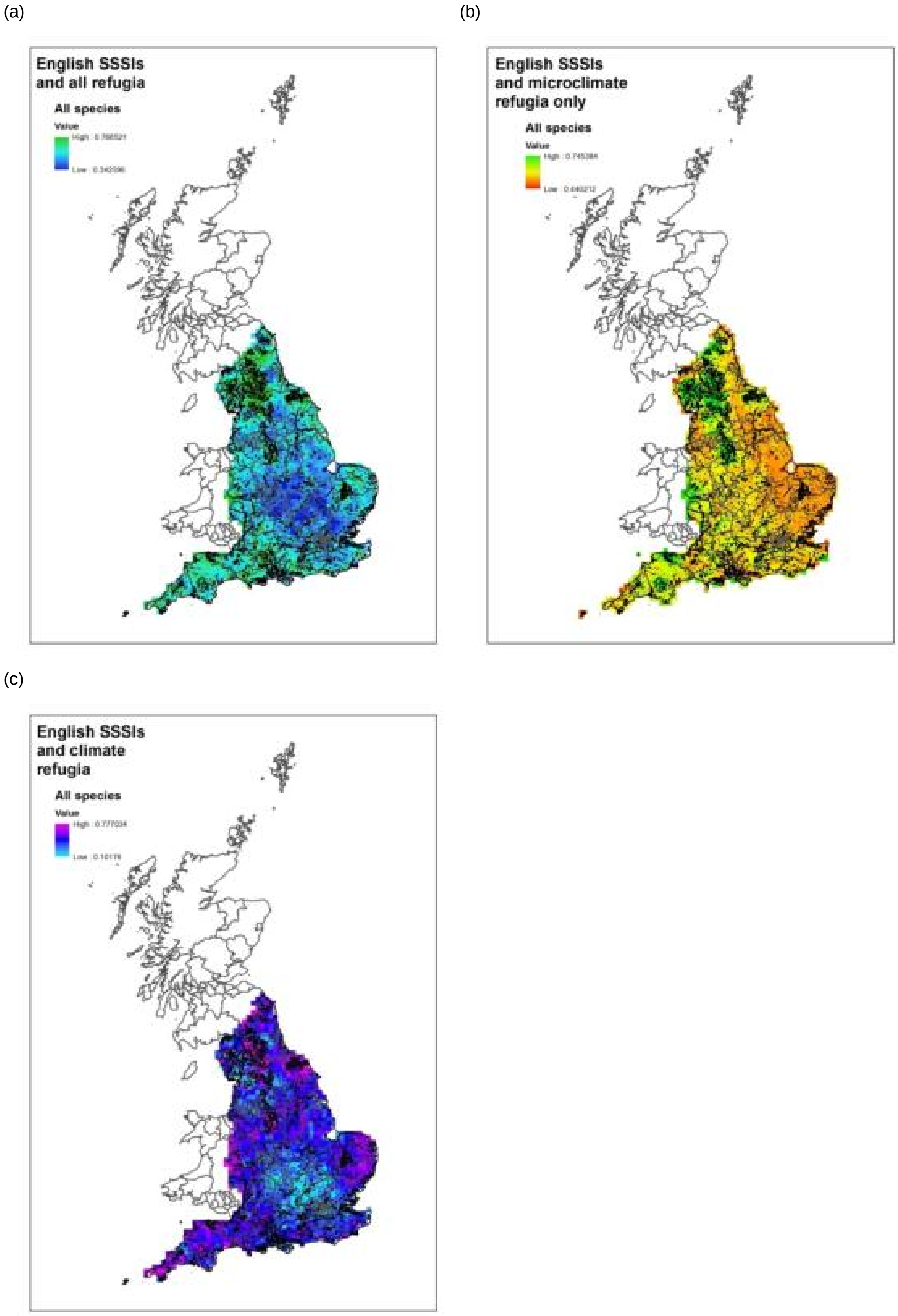


**Figure 4.8** Maps showing the English protected area network overlying the maps of refugium potential. Maps show the SSSI (Site of Specific Scientific Interest) network overlying potential maps for (a) all refugia types; (b) climate change and microclimate refugia; and (c) microclimate refugia only.

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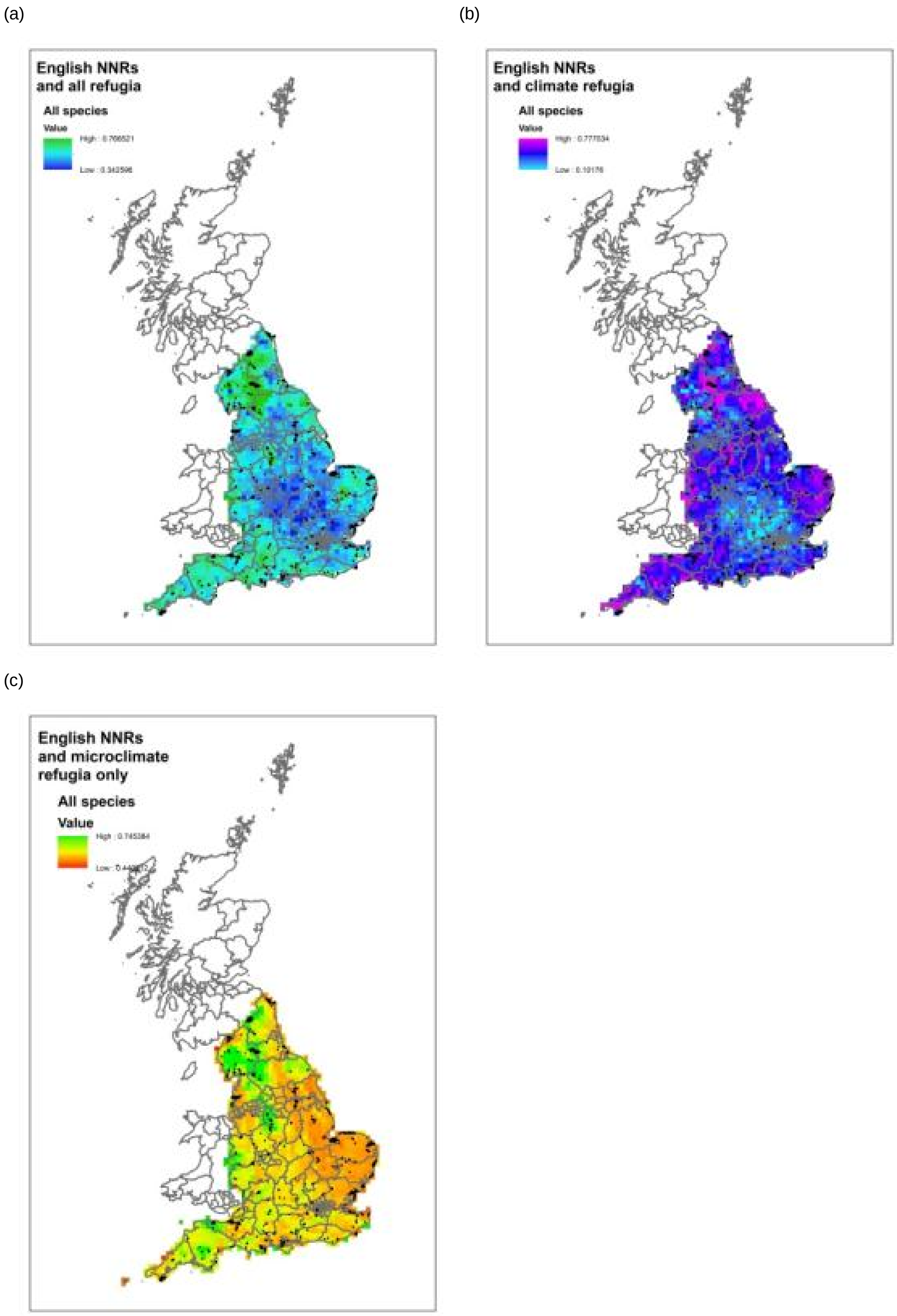

**Figure 4.9** Maps showing the English protected area network overlying the maps of refugium potential. Panels show the NNR (National Nature Reserve) network overlying potential maps for (a) all refugia types; (b) climate change and microclimate refugia; and (c) microclimate refugia only.
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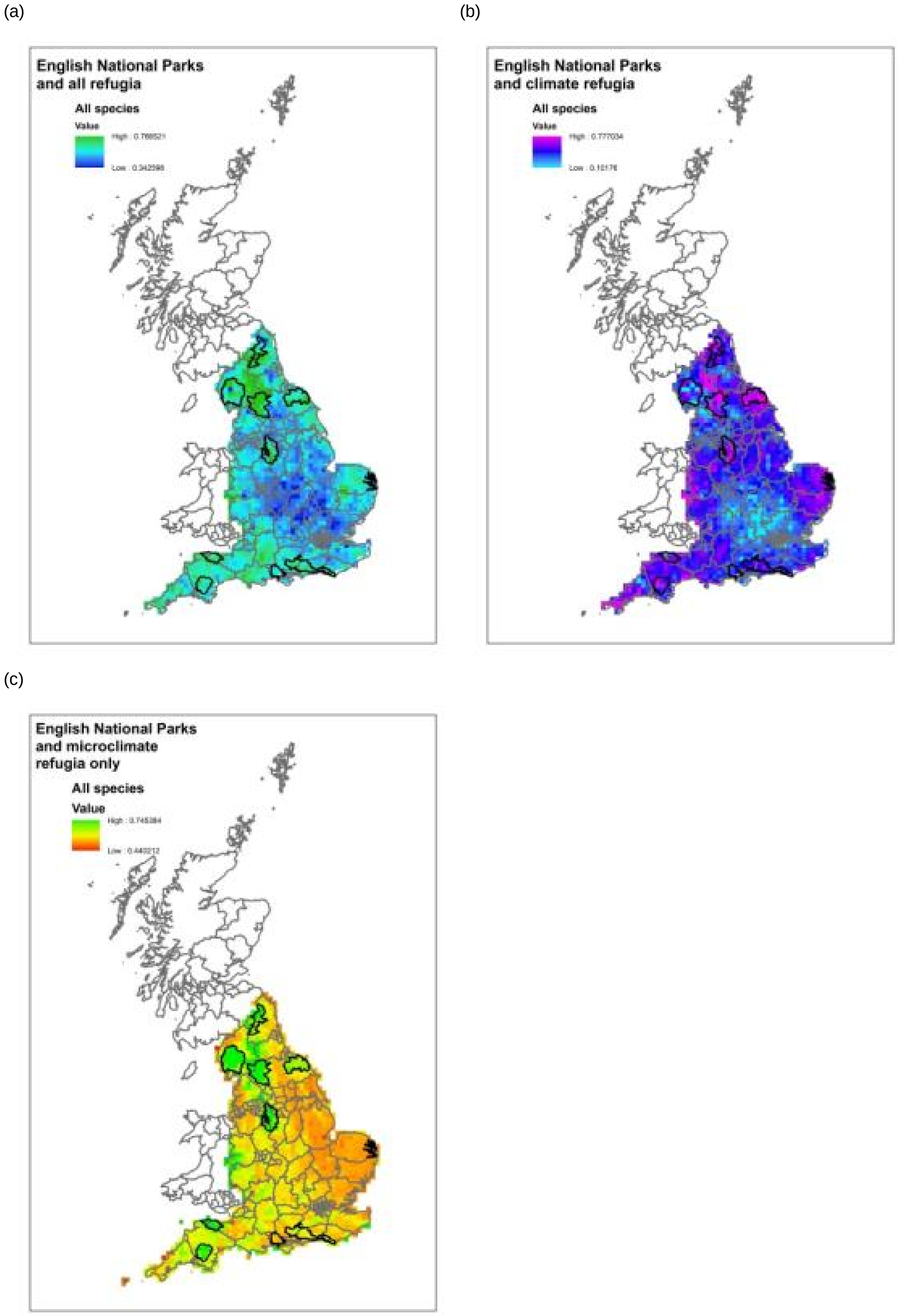

**Figure 4.10** Maps showing the English protected area network overlying the maps of refugium potential. Panels show National Parks overlying potential maps for (a) all refugia types; (b) climate change and microclimate refugia; and (c) microclimate refugia only.

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## 4.4 Discussion

The results above indicate strong effects of microclimate in buffering species from climate change. Given that these effects are interactive, and therefore somewhat complex, we provide a more intuitive description of their operation in the following subsection.

### Interpreting the interactions between microclimate and climate change

The interaction terms between climate change variables and microclimate (included in Tables 4.6 & 4.7) provide insight as to the types of microclimate important for each species group. A larger summer trend in temperature means more summer warming. As mentioned above, both plant groups have responded negatively to this, whereas the insect and arthropod groups have responded positively. Notice that for each of these groups, the sign of the interaction between standard deviation in summer solar index and summer trend in temperature (last row, both Table 4.6 & Table 4.7) *opposes* the sign of their response to summer temperature trend, on its own (6th row Table 4.6, 2nd row Table 4.7). For every unit increase in warming, therefore, the effect of having higher variability in summer solar index is positive for plants, and negative for insects and other arthropods. This is what we would expect: given increasing levels of warming, species harmed by this trend were therefore more likely to persist in areas where there exists variability in the solar regime, and by extension local escapes from hotter conditions. Species that benefitted from warming were less likely to persist in areas where solar variability was higher, because it is warmer conditions *per se* that enhance their persistence.

Note that the signs of the relationships of each group to standard deviation in summer solar index are always opposite to the signs of the relationships to the standard deviation in summer solar index * summer trend in temperature interaction. Unlike models without interaction terms, in which the sign reflects the relationship of persistence to this single variable (holding other variables constant), this sign actually represents the effect of the single variable – in this case standard deviation in summer solar index – when its companion interaction term – in this case summer trend in temperature – is zero. Hence, the signs for standard deviation in summer solar index can be interpreted as follows: given no trend in summer warming, plants respond negatively to local variability in summer solar index, and insects and arthropods respond positively. This is possibly due to the ability of animals to move around the landscape and seek out their optimal thermal habitat. In plants, given no climate change, if they are located in their optimal thermal habitat already, then that population is more likely to persist if it is larger, as would be the case in a more homogeneous (i.e. less variable) landscape. But given warming, plants were more likely to persist in landscapes with variable solar regimes, as alternative, cooler habitats are closer to hand.

Higher elevation populations in topographically diverse areas are often reported to be less vulnerable to climate warming, due to there being less distance to travel to reach to the nearest analogous climates (Ackerly et al. 2010, Bertrand et al. 2012). For England, this was true in animals, as their positive signs for the mean elevation * summer trend in temperature interactions show (Tables 4.6 & 4.7, although these relationships were only significant for Lepidoptera and 'Other arthropods'). However, the sign for this interaction in higher plants was negative, which means that upland higher plants in England are more vulnerable to climate change effects. The difference between this result and those in the wider literature could be due to the relatively lower elevations available to English species (similar to Trivedi et al. 2008), and therefore, a lower chance of finding suitable habitat at higher elevations, particularly for low dispersal species that are already constrained to upland plateaus. Note that, in the absence of climate change, higher mean elevation had a positive effect on persistence in higher plants, as the single variable sign was positive (this is also reflected in the microclimate only model results in Table 4.8). Nevertheless, the sign of the interaction term indicates that upland populations are vulnerable to warming, and hence should be the subject of conservation attention.

The third interaction term including the summer warming trend was standard deviation of flow accumulation * summer trend in temperature. The hypothesis here was that any harmful effects of warming would be buffered by cold air drainage effects, often responsible for the lowest temperatures in a landscape, yet commonly omitted from species distribution modelling (Dobrowski 2011). This proved not to be the case however: all the standard deviation of flow accumulation * summer trend in temperature coefficients were negative. This suggests that the landscape properties that lead to cold air drainage do not enhance persistence in a warming context, although this type of effect may simply be too difficult to detect at relatively coarse resolutions.

The final interaction term included in the models explored the extent to which local variability in moisture buffered species from a drop in summer rainfall (standard deviation in topographic wetness index * summer trend in rainfall). Important here is the fact that rainfall has both increased and decreased in different parts of England (Appendix 3 Figure 11, whereas all of England has warmed, to varying degrees, Appendix 3 Figure 10). The results for beetles show that this group is highly sensitive to local variability in moisture, responding positively to local heterogeneity in wetness both with and without a concurrent change in rainfall, as the interaction illustrates (Tables 4.6 & 4.7). This effect was also discernible in the microclimate only model (Table 4.8).

The difference in spring warming trend from the 'matrix', i.e. a wider, 100 km$^2$ window, promoted the persistence of plants on the whole (Tables 4.6 & 4.7). Higher values of this variable indicate a 10 km square that has a higher warming trend than the average for the surrounding 100 km$^2$ window, whereas lower values indicate a lower warming trend than the 'local' average. The behaviour of relationships to this variable was unpredictable: for example, given the overall positive response of the Lepidoptera to warming, one might hypothesise that this group would respond positively to this variable, and the results support this (Tables 4.6, 4.7 & 4.8). However, given the negative response of plants to warming, the prediction would be that the relationships of the plant groups to this variable would be negative, which in fact is only true for the microclimate only model (and even here, these relationships are non-significant). As shown in Tables 4.6 & 4.7, both higher and lower plants respond positively to areas with relatively higher spring warming trends than the matrix. This is despite the groups responding negatively to higher spring warming in single variable models (data not shown). To achieve a higher value- a larger difference- compared with the matrix, a square must feature both a relatively high warming trend, and the surroundings must be relatively cooler. Given the degree to which warming is aggregated across large parts of England (summer warming in Appendix 3 Figure 10 illustrates this), areas of high warming do not always achieve a high value for their difference score (Appendix 3 Figure 13).

### Concluding remarks on national refugia

Climate is one of several drivers of distributional change in England in the latter half of the 20th century, and not all these drivers are captured in our analyses. Others include nitrogen deposition, agricultural intensification and broader land use change. On the first of these, nitrogen deposition has been shown to negatively affect species richness, particularly in plants (Stevens et al. 2004). On the whole, the cumulative volume of nitrogen deposition has been highest in the north and west of England (Stevens et al. 2004, RoTAP 2012), hence, a negative effect of nitrogen deposition would lead to *lower* persistence in these areas, and thus, would be acting contrary to our hypothesis: greater microclimatic availability in the north and west leads to *higher* persistence in these areas. On agricultural *intensification*, as opposed to *intensity per se*, there exists a digitised GI layer of land use compiled from the Dudley Stamp surveys of the 1930s (Brown 2013), which, if compared to modern CEH Land Cover data, could be used to construct a data layer useful for analysing agricultural intensification and wider land use change. Although CEH are in the process of formulating a robust methodology for conducting this comparison, the layer was not in a form ready for use at the time of this project.

It is worth noting that the 'all species' results are heavily influenced by the higher plants results, unsurprising given that higher plants numbered 474 species of the 1,082 total, and 225,562 records of the 545,770 total. The relative numbers of species were 678 for plants and 404 animals, and reflect the relative (measurable) species richness of both kingdoms. Hence, although the effect of the plant response on the total is quite striking, pooling the animal species and running models on the group as a whole might have a similar effect. Given the differences in response across the animal groups, however, such analyses would contain far less information useful to conservation, particularly for organisations concerned with particular species groups (e.g. Butterfly Conservation, BSBI, Buglife). The fates of the various species will also depend on their capacity to acclimate to future changes in the longer term, while also adapting to higher levels of heat or drought stress that may only affect them during certain times of the day and/or year (Angilletta 2009). For example, it may be that some species will be able to endure longer spells of adverse temperatures during summer days, providing they have a cooler microclimate to retreat to. This could also have effects on competitive ability.

In conclusion, we have demonstrated that both: a) rates of persistence in the English biota have been higher in areas with less climate change; and b) that (local) extinctions have been ameliorated in areas of microclimatic diversity, i.e. refugia. These developments have real relevance for national conservation planning, as they show that a strategy for promoting adaptation to climate change *in situ* has merit, at least for the levels of climate change experienced thus far. Given the variant responses to climate change and microclimate across the taxa however, a ‘one size fits all’ policy may not be appropriate, and instead the design would have to be tailored to the species group of priority.

# 5. Identifying refugia at the landscape scale

## 5.1 Introduction

The national scale analysis (Chapter 4) determined that persistence in the English biota over the last 40 years was higher in refugia: areas with particular landscape characteristics (e.g. heterogeneity in solar index) that buffer species from adverse changes to the climate. The broad scope of this countrywide analysis meant that that, although microclimatic availability and other predictors were calculated at a relatively fine scale (100 m grid square), the size of grid square to denote a presence or absence was necessarily coarse (10 km grid square).

A growing volume of species records are collected at resolutions finer than this, however, and thus there existed the possibility to test these records of species presence/absence for selected regions at a finer scale. Based on the findings from the national scale analysis (Chapter 4), areas of high refugium potential were identified for further study via landscape scale analyses at the finer scale. Six study areas (20 km across) were selected to represent different types of refugia: both upland and lowland, and locations of both microclimate and climate change refugia. In an analogous approach to Chapter 4, patterns of persistence at a finer scale (1 km grid square) were tested for association with the same geophysical refugia variables described in Chapter 4, for consistency. Here again, the resultant statistical models were used to generate maps of refugium potential for the six study areas.

## 5.2 Methods

### Selecting landscapes

Using the refugia maps described in Chapter 4, a longlist of 34 grid squares (each square of width 10 km, i.e. hectads) was prepared. The ‘all refugia’ maps (including geological refugia, i.e. non-climatic) were disregarded. Squares were selected based on:

1) Refugial potential score, for both: a) microclimate and climate change refugia, and b) microclimate only refugia- (see Chapter 4 Methods for descriptions).

2) Complementarity: squares that offered a unique rock type, soil type, topography, regional context or some biological or physical attribute.

Data from the Biological Records Centre were examined for the availability of fine-scale species records, i.e. at resolutions of 1 km, 100 m, 10 m, or 1 m, for the locations on the longlist. There were insufficient records of 100 m (or finer) grid squares in both time periods to build statistical models in any of the longlist of study areas, so all records at a resolution of 1 km or finer were used to establish species persistence/extinction. Given the paucity of records at even 1 km resolution or finer, species data were gathered from a broader spatial extent of 20 km x 20 km for each study area. Due to the difficulty of building statistical models where data are zero-inflated, the following inclusion criterion was applied: a species must have persisted in a minimum of ten squares in the landscape to be included in models.

Based on the criteria described above, and the availability of species data at a fine resolution, a final list of study areas was prepared. Areas were chosen to reflect the diversity of English regions, and were also paired with respect to location, to provide contrasts within regions. These study areas are described in Table 5.1, and mapped in Figure 5.1.

**Table 5.1** The six areas selected for landscape-level study.

| Pair no. | Location | Relief | Refugia type | 10k hectad codes (grid squares) |
|---|---|---|---|---|
| 1 | West Cumbria | Upland | Microclimate and climate change | NY10, NY11, NY20 & NY21 |
|  | Upper Teesdale |  |  | NY72, NY73, NY82 & NY83 |
| 2 | Dartmoor | Upland (periphery) | Microclimate and climate change | SX67, SX68, SX77 & SX78 |
|  | Exmoor |  |  | SS62, SS63, SS72 & SS73 |
| 3 | South Brecks | Lowland | Climate change only | TL78, TL79, TL88 & TL89 |
|  | Broads |  |  | TG31, TG32, TG41 & TG42 |

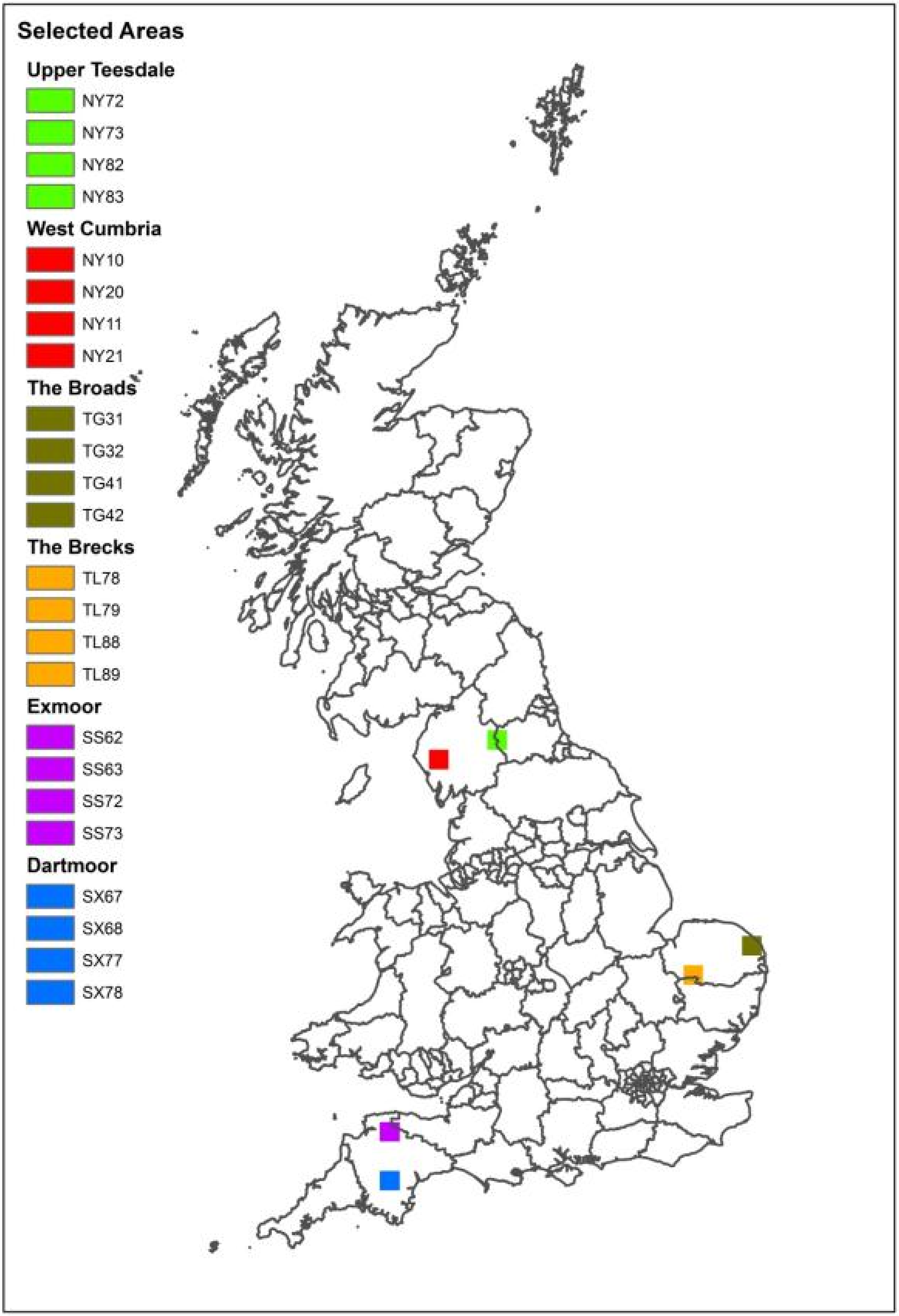

**Figure 5.1** Areas selected for landscape-level analyses, and their associated OSGB hectad codes (10km grid squares). Contains, or is derived from, information supplied by Ordnance Survey. © Crown copyright and database right 2014. All rights reserved. Ordnance Survey Licence number 100022021.

## Data collation and processing

As in Chapter 4, data were gathered to represent a) areas of persistence or extinction (this time for 1k squares), b) potential predictors of refugia, and c) confounding effects, where a particular confounding factor (such as agricultural intensity) could be responsible for enhanced persistence and hence necessitated inclusion in our models as a control variable. For consistency, the same variables used in statistical analyses at the national level (Table 4.5) were also calculated at the landscape level.

### *Areas of persistence or extinction*

Data at 1km resolution or finer were collected from the Biological Records Centre at the Centre for Ecology and Hydrology (CEH), for each study area. The low number of records at fine resolution meant that no further species selection criteria (e.g. range retracting, or sensitivity to climate change) could be applied. Data were grouped into the same two time periods and species groups as per Chapter 4 (see Chapter 4 Methods and Table 4.1), with each species noted as having either persisted or gone extinct in each 1k square. As before, colonisations were disregarded.

### *Potential predictors of refugia*

#### A) Geology

A 1:50,000 vector map of bedrock geology (2004, 2nd edition) was obtained from the Natural England Geographical Information (GI) team and resampled at 5 m resolution. Using the British Geological Society Rock Classification Scheme (RCS) codes, we calculated the proportions of each 1 km square comprising of the following geological features:

1) **Felsic rock** - Present in Cumbria, Dartmoor and Upper Teesdale. See Table 5.2.

2) **Calcium carbonate rock** - Present in The Brecks, The Broads, Dartmoor, Exmoor and Upper Teesdale. See Table 5.3.

3) **Mafic rock** - Present in Cumbria, Dartmoor and Upper Teesdale. See Table 5.4.

**Table 5.2** Constituents of the felsic rock layer, with associated Rock Classification Scheme (RCS) codes.

| Layers | RCS code | Description |
|---|---|---|
| | AND | Andesite |
| | ANDCLA | Andesitic lava |
| | ANDGB | Garnet bearing andesite |
| | ANDTFF | Andesitic tuff |
| | ANDVST | Andesitic volcaniclastic-sandstone |
| | ANLTUF | Andesitic lapilli-tuff |
| | BAANDT | Basaltic andesite |
| | DA | Dacite |
| | DALTUF | Dacitic lapilli-tuff |
| | DCLAV | Dacitic lava |
| | FTUFF | Felsic tuff |
| | GN | Granite |
| | GNGP | Granophyric granite |
| | MCGDP | Porphyritic microgranodiorite |
| | MCGN | Microgranite |
| | MCGNA | Microgranite with aplitic veins |
| | MCGNP | Porphyritic microgranite |
| | RHFT | Rhyolite and felsic tuff |
| | RY | Rhyolite |
| | RYLTUF | Rhyolitic lapilli-tuff |
| | RYTUF | Rhyolitic tuff |

**Table 5.3** Constituents of the Calcium carbonate layer, with associated Rock Classification Scheme (RCS) codes.

| **Layers** | **RCS code** | **Description** |
|---|---|---|
| Chalk | CHLK | Chalk |
| Limestone | LMAS | Limestone, argillaceous rocks and subordinate sandstone, interbedded |
| | LMST | Limestone |
| | LSSM | Limestone, sandstone, siltstone and mudstone |
| | MDSL | Mudstone, sandstone and limestone |

**Table 5.4** Constituents of the Mafic rock layer, with associated Rock Classification Scheme (RCS) codes.

| **Layers** | **RCS code** | **Description** |
|---|---|---|
| Ultramafic | LMPY | Lamprophyres |
| Mafic | DI | Diorite |
| | GB | Gabbro |
| | MCGB | Microgabbro |
| | MCQGB | Quartz microgabbro |
| | MFTUF | Mafic tuff |
| | MMCGB | Metamicrogabbro |

### B) Elevation

For each study area, 5 m resolution Bluesky Digitial Terrain Models (DTMs) were obtained. From these, the mean elevation of each 1k square was calculated for inclusion in the statistical analyses.

### C) Flow accumulation

Using the 5 m DTMs, flow accumulation was calculated for each 20 km x 20 km study area, plus a surrounding 5 km buffer, to ensure drainage basins were represented properly. Following the calculation, the outer 5 km buffer was removed from this larger (30 km x 30 km) layer to make a 20 km x 20 km layer, before the standard deviation in flow accumulation within each 1 km square was calculated for inclusion in the statistical analyses.

### D) Water availability (topographic wetness index)

The 5 m flow accumulation layer was combined with information on slope angle to generate a topographic wetness index for each 5 m square. The standard deviation of this layer was calculated at the 1 km level for inclusion in the statistical analyses.

### E) Surface temperature (solar index)

The summer (21st June) solar index for each 5 m grid cell was calculated across the six landscapes, again allowing a 5 km buffer, this time to account for shading from nearby mountains outside the 20 km window. The standard deviation of this layer was calculated at the 1 km level for inclusion in the statistical analyses.

## *Confounding effects*

### Agricultural intensity

The raw Centre for Ecology and Hydrology LCM2007 raster grid (25 m resolution) was used to calculate, for each 1 km square, the proportion of land cover classified as ‘Arable and horticulture’.

#### Recorder effort

The number of records for each 1 km square was calculated for each species group. Values were again logarithmically transformed, as the distributions of the raw values were strongly non-normal.

## Statistical modelling

As in Chapter 4, all statistical modelling was conducted using Generalised Linear Mixed Models (GLMMs) fitted to the data using the ‘lme4’ package in R. Models were constructed with two different assemblies of variables: a) An all refugia model, and b) A microclimate only refugia model.

### *All refugia model*

This model had the following structure:

#### Response variable

1 km squares of persistence (1) or extinction (0) for all range declining species in England, that are predicted to experience further retraction under climatic change. A logit link function, with a binomial error distribution was used.

Species ID was included in the model as a random (intercept) effect.

#### Predictor variables

All calculated for each 1 km square, these were:

-Proportion of chalk or limestone rock (where present);
-Proportion of felsic rock (where present);
-Proportion of mafic rock (where present);
-Mean elevation;
-Standard deviation of flow accumulation;
-Standard deviation in topographic wetness index;
-Standard deviation in summer solar index.

#### Control (confounding) variables

All calculated for each 1 km square, these were:

-Log (total number of records);
-Proportion of arable land.

### *Microclimate only model*

This model excluded the geological and agricultural intensity variables. It had the following structure:

#### Response variable

As per the ‘all refugia’ model in a) above.

#### Predictor variables

All calculated for each 1 km square, these were:

-Mean elevation;
-Standard deviation of flow accumulation;
-Standard deviation in topographic wetness index.
-Standard deviation in summer solar index.

#### Control (confounding) variable

Calculated for each 1 km square, this was:

-Log (total number of records).

### Generating refugia maps

The outputs of the three types of statistical model were used to generate 'refugia maps', as in Chapter 4. Maps were generated using all species data, for each model type, in each study area (n=12 maps). As before, maps of the top 10% of sites were also generated (n=12; 24 maps total).

## 5.3 Results

Results are presented for statistical models of 20 km x 20 km landscapes using all refugia variables and microclimate variables only. The columns in each table show, for each landscape, the slope of the relationship between probability of persistence over the past four decades (for all species) and the variable concerned: cells shaded blue represent variables for which more positive values increased chances of persistence, and cells shaded red represent variables for which more positive values decreased chances of persistence. The significance of these variables in the model is shown in the following column. Table 5.7 documents the availability of high resolution species records at the taxon level. Where these records were sufficient to construct statistical models, the tabulated model results are also available (Tables 5.5-5.10).

### All species models

#### *Control variables*

*Recorder Effort*: As at the national level, recorder effort was positively and significantly related to persistence in all species groups and for all types of model, except for the microclimate only model for Cumbria (Table 5.6).

*Agricultural Intensity*: Overall, there was a negative effect of agricultural intensity across the landscapes, although there were no statistically significant effects in either The Broads or Upper Teesdale. This variable is not included in the microclimate only models.

#### *Predictor variables*

##### Geology (Table 5.5)

Note that not all the rock types included in the national scale analyses were present in every study landscape. Where a particular geology was absent, this is denoted by a 'Not present' entry.

*Chalk and limestone*: Testing for the effect of chalk bedrock presence/absence on persistence was not possible in The Brecks or the Broads, owing to the near ubiquity of this rock in these landscapes. There was a negative effect of the Chercombe Bridge limestone in the Dartmoor landscape. This relatively small area is dominated by the A38 corridor and Linhay Hill Quarry (active prior to the earliest records from this study), thus, any interpretation of the limestone's negative effects must be put into this wider context. An abandonment of the quarry would likely lead to biodiversity gains, but with a recent (2010) upgrade to the plant on site, this is unlikely in the near term.

*Felsic geology*: Felsic rock (granite and microgranite) had a positive effect on persistence in the Dartmoor landscape: perhaps a surprising result given that all these records were made up of butterfly and moth species. This is not simply an artefact of a wider relationship to higher ground either, as species responded negatively to upland areas in this square.

*Mafic geology*: Persistence in the Upper Teesdale species records (consisting entirely of higher plants) was negatively related to mafic rock, mostly present in the valley below Cow Green Reservoir. This area has seen substantial alterations in microclimate due to the construction of Cow Green Reservoir (c. 1971), including dampened winter minima, which have resulted in changes to vegetation composition (Huntley et al. 1998). Therefore, given this potential confounding effect, it is unsafe to conclude that declines in this locality are due to any other particular factor.

### Microclimate (Tables 5.5 and 5.6)

Overall, responses to microclimate at the sub-landscape level differed in each of the landscapes. Given the dominance of stochastic population processes at this local level, and the paucity of high resolution records available to quantify them, it is perhaps unsurprising that the statistical models have identified different microclimatic drivers of these trends.

*Standard deviation in flow accumulation*: Species' responses to this variable were mixed across the landscapes; with persistence enhanced in The Brecks and Upper Teesdale, yet reduced in The Broads and in Dartmoor.

*Standard deviation in topographic wetness index*: Persistence was lower with higher values in this variable in The Brecks and The Broads, while in Cumbria and Exmoor it was higher.

*Mean elevation*: Mean elevation had marginally positive and negative effects on persistence in The Broads and The Brecks, respectively. As described above, rates of persistence were higher at lower elevations for the species (lepidopterans) on Dartmoor. In Exmoor, Cumbria and Upper Teesdale, there was a higher chance of persistence at higher elevations, although this effect was non-significant in Cumbria.

*Standard deviation in summer solar index*: In Dartmoor and Upper Teesdale, persistence was higher in areas with a greater standard deviation in summer solar index. However, this variable had a negative effect on persistence in the remaining four landscapes.

## Taxon-specific models

The lack of high resolution records means that not all taxon-landscape combinations could be modelled (Table 5.7), and that the results for models that were constructed are not always likely to be a full reflection for that taxon as a whole. Therefore descriptions of their results have been kept intentionally brief.

### *Higher plant models (Tables 5.8 and 5.9)*

For plants in Exmoor and Cumbria, persistence was higher in wetter areas with a higher elevation, and lower in areas of high variation in summer solar index and flow accumulation. Response to microclimate variables was mostly positive in the Upper Teesdale plants, whereas in The Broads no microclimate variable had a significant effect on plant persistence.

### *Butterfly and moth models (Tables 5.10 and 5.11)*

Lepidopterans responded similarly in Exmoor and The Brecks: positively to standard deviation in flow accumulation and negatively to the other microclimate variables. This is despite differing assemblies of species (n=9 and n=22, respectively). In The Broads, persistence was higher in areas of higher ground, yet lower in response to the other microclimate variables. In Dartmoor, the response of persistence to microclimate was sensitive to the inclusion of geology in the model (i.e. different between Tables 5.10 and 5.11).

### *Other taxa (Tables 5.12 and 5.13)*

Availability of high resolution records in The Broads meant that construction of models for the 'Other insects' and 'Other arthropods' groups was possible, although the low quantity of these records meant that few explanatory variables were found to be significant. Persistence in the other arthropods group (in this case made up entirely of spiders) responded consistently and positively to standard deviation in topographic wetness; other effects were either non-significant or inconsistent.

**Table 5.5** Summary of results from landscape statistical models with all species data and refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks (n = 25) | | Broads (n = 167) | | Dartmoor[1] (n = 30) | | Exmoor (n = 30) | | Cumbria (n = 7) | | Upper Teesdale[2] (n = 8) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value |
| Log (total records) | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 |
| Agricultural Intensity | - | 0.0037 | - | 0.1390 | - | <0.0005 | - | <0.0005 | - | 0.1256 | + | 0.9964 |
| Chalk or limestone geology | Not applicable[3] | | Not applicable[3] | | - | 0.0036 | - | 0.6290 | Not present | | + | 0.6048 |
| Felsic geology | Not present | | Not present | | + | 0.0285 | Not present | | - | 0.6382 | + | 0.7463 |
| Mafic geology | Not present | | Not present | | + | 0.4558 | Not present | | - | 0.7223 | - | <0.0005 |
| Log (standard deviation of flow accumulation) | + | <0.0005 | - | 0.0008 | - | 0.0220 | - | 0.1093 | - | 0.3001 | + | 0.0499 |
| Standard deviation in topographic wetness index | - | 0.0010 | - | 0.0380 | + | 0.7588 | + | 0.0482 | + | 0.0042 | + | 0.0029 |
| Mean elevation | - | 0.0614 | + | 0.0391 | - | <0.0005 | + | <0.0005 | + | 0.3803 | + | 0.0035 |
| Standard deviation in summer solar index | - | 0.1066 | - | 0.0049 | + | 0.1279 | - | 0.0118 | - | 0.0097 | + | 0.5325 |

1 The Dartmoor high-resolution data meeting the inclusion criteria consist entirely of butterfly or moth records.
2 The Upper Teesdale high-resolution data meeting the inclusion criteria consist entirely of higher plant records.
3 As chalk geology is almost ubiquitous in these locations, it would not explain patterns of persistence/extinction in particular locations. Therefore geology was omitted as an explanatory variable.

**Table 5.6** Summary of results from landscape statistical models with all species data and only microclimate refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks (n = 25) | | Broads (n = 167) | | Dartmoor[1] (n = 30) | | Exmoor (n = 30) | | Cumbria (n = 7) | | Upper Teesdale[2] (n = 8) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value | Slope | P value |
| Log (total records) | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | 0.4958 | + | <0.0005 |
| Log (standard deviation of flow accumulation) | + | <0.0005 | - | 0.0011 | - | 0.1330 | - | 0.2258 | - | 0.3122 | + | 0.0455 |
| Standard deviation in topographic wetness index | - | <0.0005 | - | 0.0773 | + | 0.5819 | + | 0.0750 | + | 0.0008 | - | 0.9478 |
| Mean elevation | - | 0.0712 | + | 0.1190 | - | 0.9850 | + | <0.0005 | + | 0.0948 | + | <0.0005 |
| Standard deviation in summer solar index | - | 0.2896 | - | 0.0042 | + | 0.0018 | - | 0.0226 | - | 0.0082 | + | 0.2655 |

[1] The Dartmoor high-resolution data meeting the inclusion criteria consist entirely of butterfly or moth records.

[2] The Upper Teesdale high-resolution data meeting the inclusion criteria consist entirely of higher plant records.

**Table 5.7** The availability of fine-scale records for each landscape-species grouping combination. ‘No data’ indicates that there were no records meeting modelling criteria for that species group in that landscape (n=22 combinations). ‘Insufficient data’ indicates that records existed, but were too few to build a statistical model with (n=4).

| **Species group** | **Brecks** | **Broads** | **Dartmoor** | **Exmoor** | **Cumbria** | **Upper Teesdale** |
|---|---|---|---|---|---|---|
| Higher plants | Insufficient data | See Tables 5.9 & 5.10 | No data | See Tables 5.9 & 5.10 | See Tables 5.9 & 5.10 | See Tables 5.9 & 5.10 |
| Lower plants | No data | No data | No data | No data | No data | No data |
| Beetles | No data | Insufficient data | No data | No data | No data | No data |
| Butterflies and moths | See Tables 5.11 & 5.12 | See Tables 5.11 & 5.12 | See Tables 5.11 & 5.12 | See Tables 5.11 & 5.12 | Insufficient data | No data |
| Other insects | Insufficient data | See Tables 5.13 & 5.14 | No data | No data | No data | No data |
| Other arthropods | No data | See Tables 5.13 & 5.14 | No data | No data | No data | No data |

**Table 5.8** Summary of results from landscape statistical models with plant species data and all refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks | Broads (n = 54) | | Dartmoor | Exmoor (n = 21) | | Cumbria (n = 6) | | Upper Teesdale (n = 8) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Slope | P value | | Slope | P value | Slope | P value | Slope | P value |
| Log (total records) | Insufficient data | + | <0.0005 | No data | + | 0.0782 | - | 0.2758 | + | <0.0005 |
| Agricultural Intensity | | - | 0.3129 | | - | 0.9931 | - | 0.0708 | + | 0.9964 |
| Chalk or limestone geology | | Not applicable | | | - | 0.0289 | Not applicable | | + | 0.6048 |
| Felsic geology | | Not applicable | | | Not applicable | | - | 0.5126 | + | 0.7463 |
| Mafic geology | | Not applicable | | | Not applicable | | - | 0.7085 | - | <0.0005 |
| Log (standard deviation of flow accumulation) | | - | 0.3389 | | - | <0.0005 | - | 0.3037 | + | 0.0499 |
| Standard deviation in topographic wetness index | | - | 0.7053 | | + | <0.0005 | + | 0.0068 | + | 0.0029 |
| Mean elevation | | + | 0.6355 | | + | <0.0005 | + | 0.6729 | + | 0.0035 |
| Standard deviation in summer solar index | | - | 0.4052 | | - | 0.0084 | - | 0.0113 | + | 0.5325 |

**Table 5.9** Summary of results from landscape statistical models with plant species data and microclimate refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks | Broads (n = 54) | | Dartmoor | Exmoor (n = 21) | | Cumbria (n = 6) | | Upper Teesdale (n = 8) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Slope | P value | | Slope | P value | Slope | P value | Slope | P value |
| Log (total records) | Insufficient data | + | <0.0005 | No data | + | 0.0059 | - | 0.4574 | + | <0.0005 |
| Log (standard deviation of flow accumulation) | | - | 0.4519 | | - | <0.0005 | - | 0.3430 | + | 0.0455 |
| Standard deviation in topographic wetness index | | - | 0.9069 | | + | <0.0005 | + | 0.0010 | - | 0.9478 |
| Mean elevation | | - | 0.9632 | | + | <0.0005 | + | 0.1873 | + | <0.0005 |
| Standard deviation in summer solar index | | - | 0.3345 | | - | 0.0397 | - | 0.0081 | + | 0.2655 |

**Table 5.10** Summary of results from landscape statistical models with butterfly and moth species data and all refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks (n = 22) | | Broads (n = 88) | | Dartmoor (n = 30) | | Exmoor (n = 9) | | Cumbria | Upper Teesdale |
|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | | |
| Log (total records) | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 | Insufficient data | No data |
| Agricultural Intensity | - | 0.0037 | - | 0.1751 | - | <0.0005 | + | 0.1744 | | |
| Chalk or limestone geology | Not applicable | | Not applicable | | - | 0.0036 | + | 0.1414 | | |
| Felsic geology | Not applicable | | Not applicable | | + | 0.0285 | Not applicable | | | |
| Mafic geology | Not applicable | | Not applicable | | + | 0.4558 | Not applicable | | | |
| Log (standard deviation of flow accumulation) | + | <0.0005 | - | 0.0172 | - | 0.0220 | + | 0.1919 | | |
| Standard deviation in topographic wetness index | - | 0.0010 | - | 0.0078 | + | 0.7588 | - | 0.3654 | | |
| Mean elevation | - | 0.0614 | + | 0.0048 | - | <0.0005 | - | 0.6506 | | |
| Standard deviation in summer solar index | - | 0.1066 | - | 0.0300 | + | 0.1279 | - | 0.1222 | | |

**Table 5.11** Summary of results from landscape statistical models with butterfly and moth species data and microclimate refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Brecks (n = 22) | | Broads (n = 88) | | Dartmoor (n = 30) | | Exmoor (n = 9) | | Cumbria | Upper Teesdale |
|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | P value | Slope | P value | Slope | P value | Slope | P value | | |
| Log (total records) | + | <0.0005 | + | <0.0005 | + | <0.0005 | + | <0.0005 | Insufficient data | No data |
| Log (standard deviation of flow accumulation) | + | <0.0005 | - | 0.0166 | - | 0.1330 | + | 0.2651 | | |
| Standard deviation in topographic wetness index | - | <0.0005 | - | 0.0185 | + | 0.5819 | - | 0.4844 | | |
| Mean elevation | - | 0.0701 | + | 0.0136 | - | 0.9850 | - | 0.2187 | | |
| Standard deviation in summer solar index | - | 0.1807 | - | 0.0253 | + | 0.0018 | - | 0.0385 | | |

**Table 5.12** Summary of results from statistical models of the Broads landscape with ('other') insect and arthropod species data and all refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Other insects (n = 18) | | Other arthropods (n = 6) | |
|---|---|---|---|---|
| | Slope | P value | Slope | P value |
| Log (total records) | + | <0.0005 | + | 0.0023 |
| Agricultural Intensity | + | 0.1305 | + | 0.1066 |
| Chalk or limestone geology | Not applicable | | Not applicable | |
| Felsic geology | Not applicable | | Not applicable | |
| Mafic geology | Not applicable | | Not applicable | |
| Log (standard deviation of flow accumulation) | - | 0.2994 | - | 0.9924 |
| Standard deviation in topographic wetness index | + | 0.0979 | + | 0.0196 |
| Mean elevation | - | 0.4581 | + | 0.2603 |
| Standard deviation in summer solar index | - | 0.5315 | - | 0.1892 |

**Table 5.13** Summary of results from statistical models of the Broads landscape with ('other') insect and arthropod species data and microclimate refugia variables included. The number of species represented in each landscape is indicated in brackets.

| Variable | Other insects (n = 18) | | Other arthropods (n = 6) | |
|---|---|---|---|---|
| | Slope | P value | Slope | P value |
| Log (total records) | + | <0.0005 | + | <0.0005 |
| Log (standard deviation of flow accumulation) | - | 0.2527 | - | 0.9301 |
| Standard deviation in topographic wetness index | + | 0.2336 | + | 0.0106 |
| Mean elevation | - | 0.9334 | + | 0.0116 |
| Standard deviation in summer solar index | - | 0.4589 | - | 0.0246 |

### Refugia maps (landscape level)

Using the relationships determined by the all species statistical models, landscape level refugia maps are presented (Figures 5.2 - 5.13). For each landscape, these maps quantify refugium potential based on all types of refugia (Figures 5.2 - 5.7), and based solely on microclimatic refugia (Figures 5.8 – 5.13). Each figure includes: a) a panel indicating the raw score of refugium potential, b) a panel indicating the top scoring 10% of 1 km squares of highest potential, underlain by a digital elevation model to improve readability, and c) an Ordnance Survey 1:250,000 map of the area for comparison.

In *The Brecks* (Figures 5.2 and 5.8), both maps prioritise the western periphery of Thetford Forest, close to Lakenheath. Other high scoring areas on both maps include the forested area to the north of Brandon and east of Weeting (Emily's Wood); 1km squares either side of Barnham Camp; and in Thetford Forest, north of Forest Drive. Overall the highest scoring areas on both maps are widely dispersed, particularly in the case of the microclimate only map.

The maps of refugium potential for *The Broads* are near identical (Figures 5.3 and 5.9). Areas identified as being of the highest potential coincide with 'higher' ground, particularly in the south-west of the 20 km x 20 km study square. This south-western area lies between Blofield Heath and Salhouse, extending to just west of Acle. A similarly large area of high refugia scores was identified between Hoveton and Worstead, in the north-west of the landscape. These areas of high potential largely reflect the positive association to mean elevation in the models.

For *Dartmoor* (Figures 5.4 and 5.10), 'all refugia' and 'microclimate only' maps were also similar. In this landscape, the areas of high score corresponded to steep, forested NW-SE valleys of the Rivers Dart, Webburn, Bovey and Teign, and at Wray Brook. These areas represent sites of high topographic variability that are relatively undisturbed, owing to the poor quality of the granite. The ancient woodlands that have flourished here have fostered high diversity (e.g. fritillary butterflies).

In *Exmoor* (Figures 5.5 and 5.11), both maps are again similar. Highest scoring areas are in the north-east corner of the square, representing the south-west of Exmoor National Park. This area is bounded by the River Barle to the north, and the southern fringe of the Exmoor hills (Shoulsbarrow Common, Western Common and Fyldon Common) to Sandyway Cross.

The variant *Cumbrian* maps (Figures 5.6 and 5.12) are also similar; with areas of high potential identified near Wast Water, Buttermere, Crummock Water, Derwent water, the Central Fells[1], the Langdale Pikes, Copeland Forest and the southern aspect of Sca Fell. Neither the highest nor the lowest areas, these squares represent wetter[1] areas of high variation in summer solar index.

The maps of refugium potential in *Upper Teesdale* (Figures 5.7 and 5.13) do differ in their 'all refugia' and 'microclimate only' forms. The maps based on the relationships established in the 'all refugia' models score the limestone escarpment and the fringes of the Vale of Eden highly, together with the edges of Burn Hope and Cow Green Reservoirs. The sequence of Tarns atop Blackstone Edge is also identified. Contrastingly, the 'microclimate only' maps present four aggregated groups of high scoring squares, namely: the slopes and summit of Burnhope Seat (747 m); Mickle Fell (788 m); Little Fell (748 m); and a large, upland ridge/plateau to the west of the landscape. This area extends from Meldon Hill in the east to Green Fell in the west, then north along the limestone escarpment to Cross Fell (893 m). This area broadly corresponds to the Moor House & Cross Fell SSSI.

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[1] Wainwright (1958) once described the summit cairn on High Tove, Central Fells as: "a seat for travellers who wish to pour the water out of their boots".

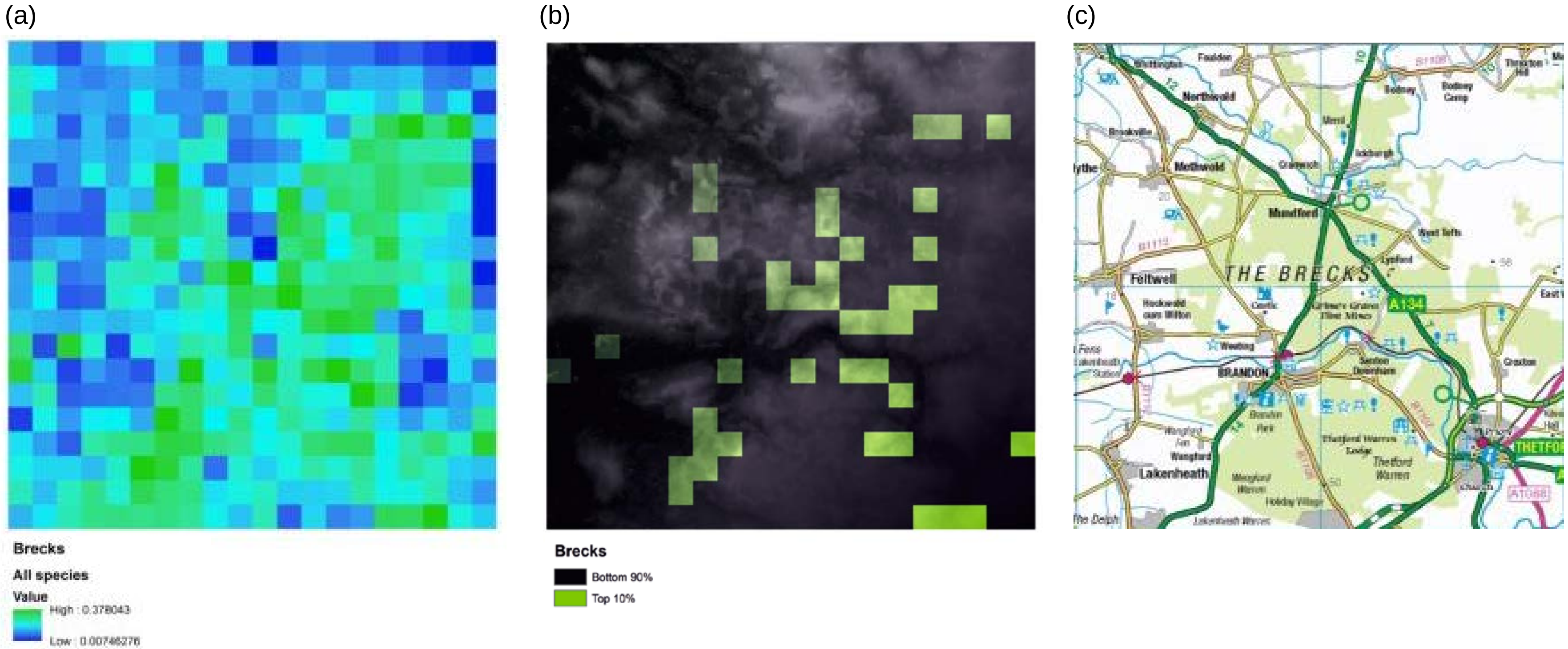

**Figure 5.2** Maps showing refugial areas (panels a and b) in The Brecks study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

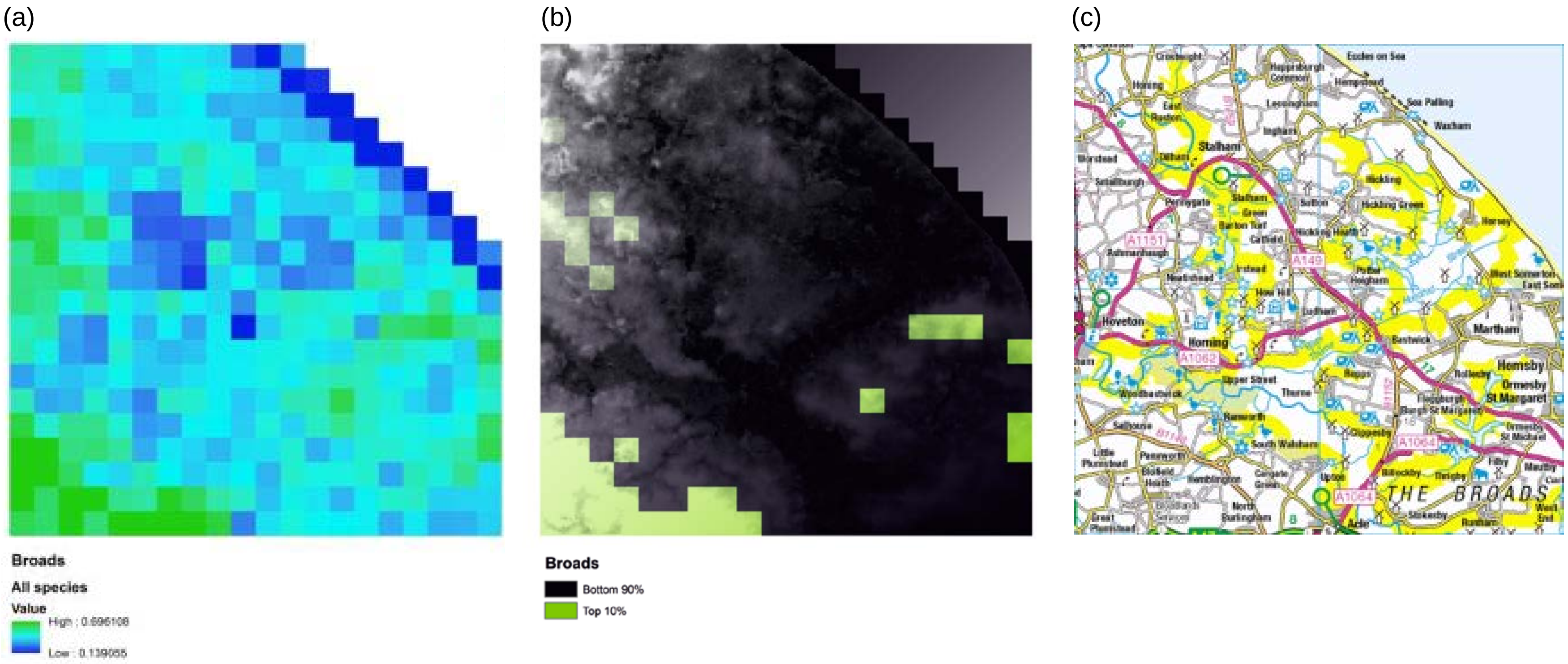

**Figure 5.3** Maps showing refugial areas (panels a and b) in The Broads study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).
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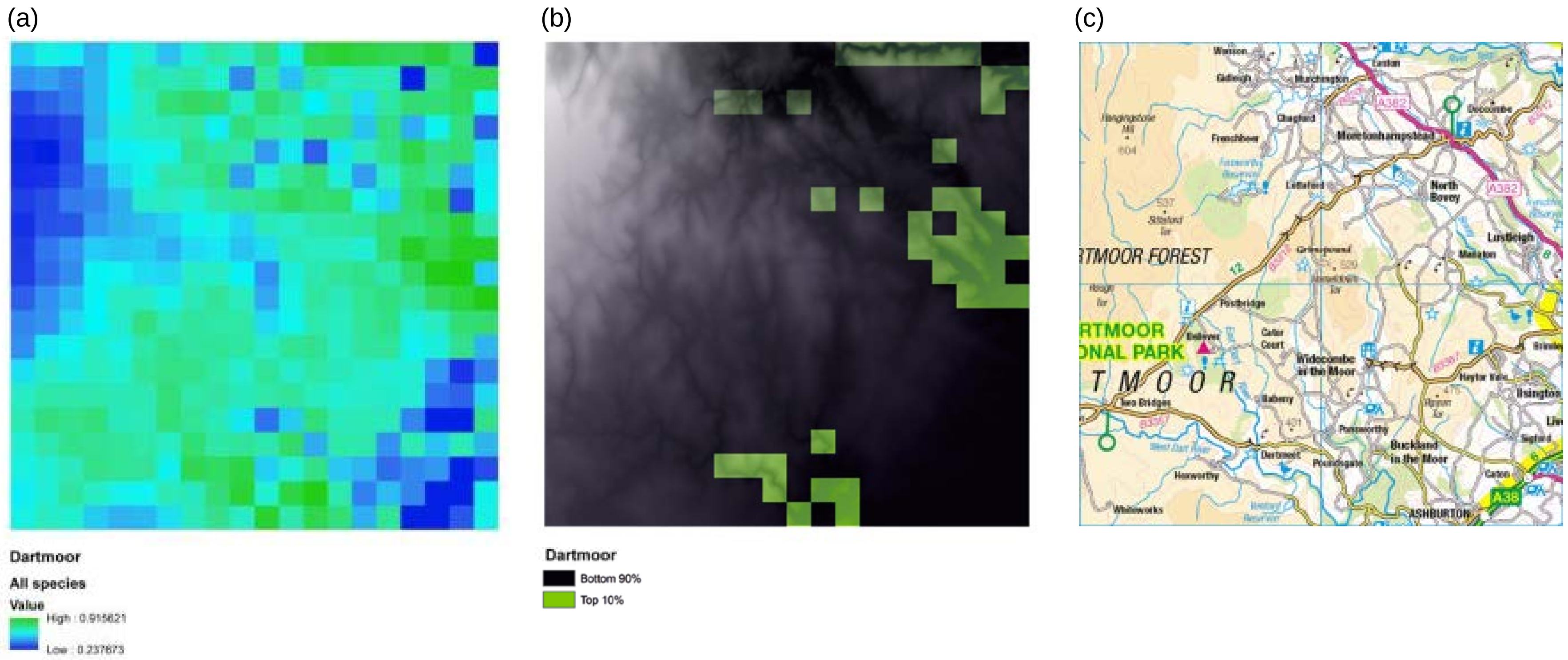

**Figure 5.4** Maps showing refugial areas (panels a and b) in the Dartmoor study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

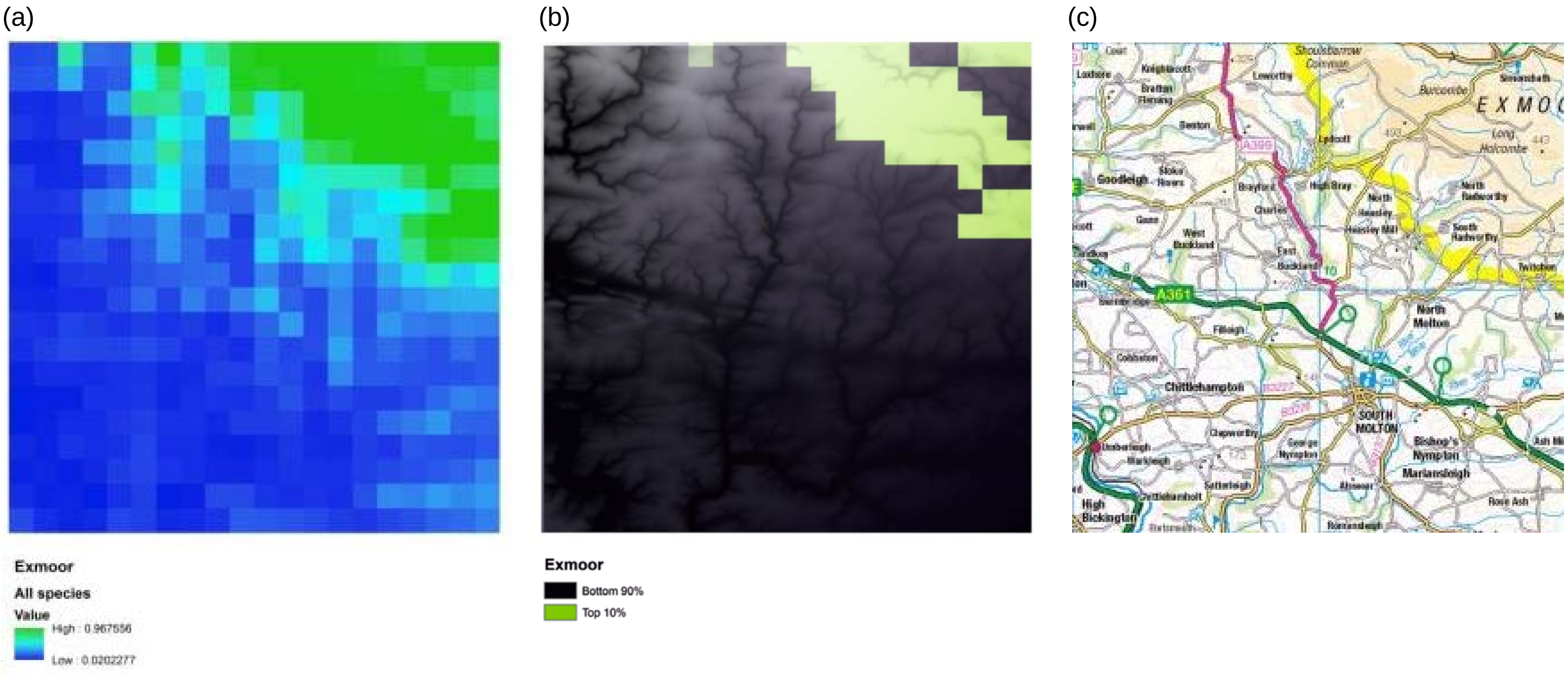

**Figure 5.5** Maps showing refugial areas (panels a and b) in the Exmoor study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

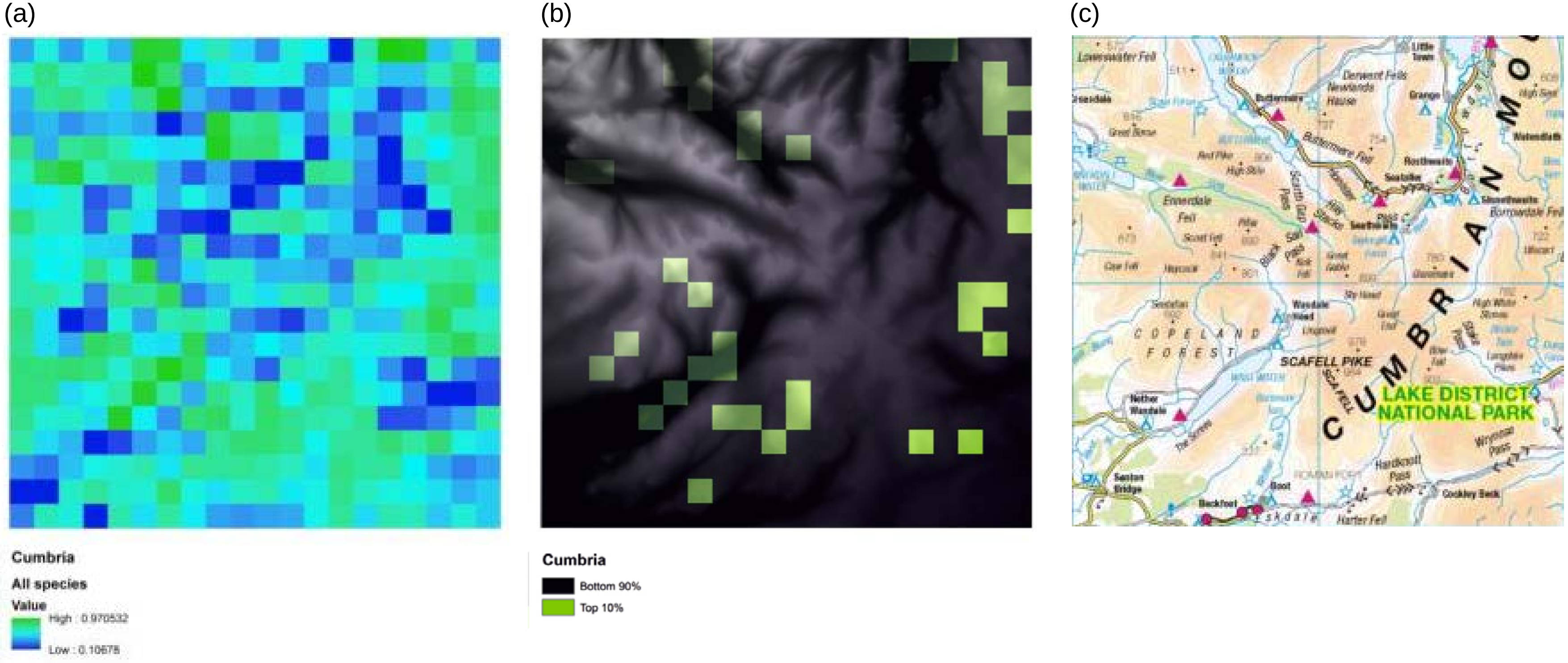

**Figure 5.6** Maps showing refugial areas (panels a and b) in the Cumbria study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

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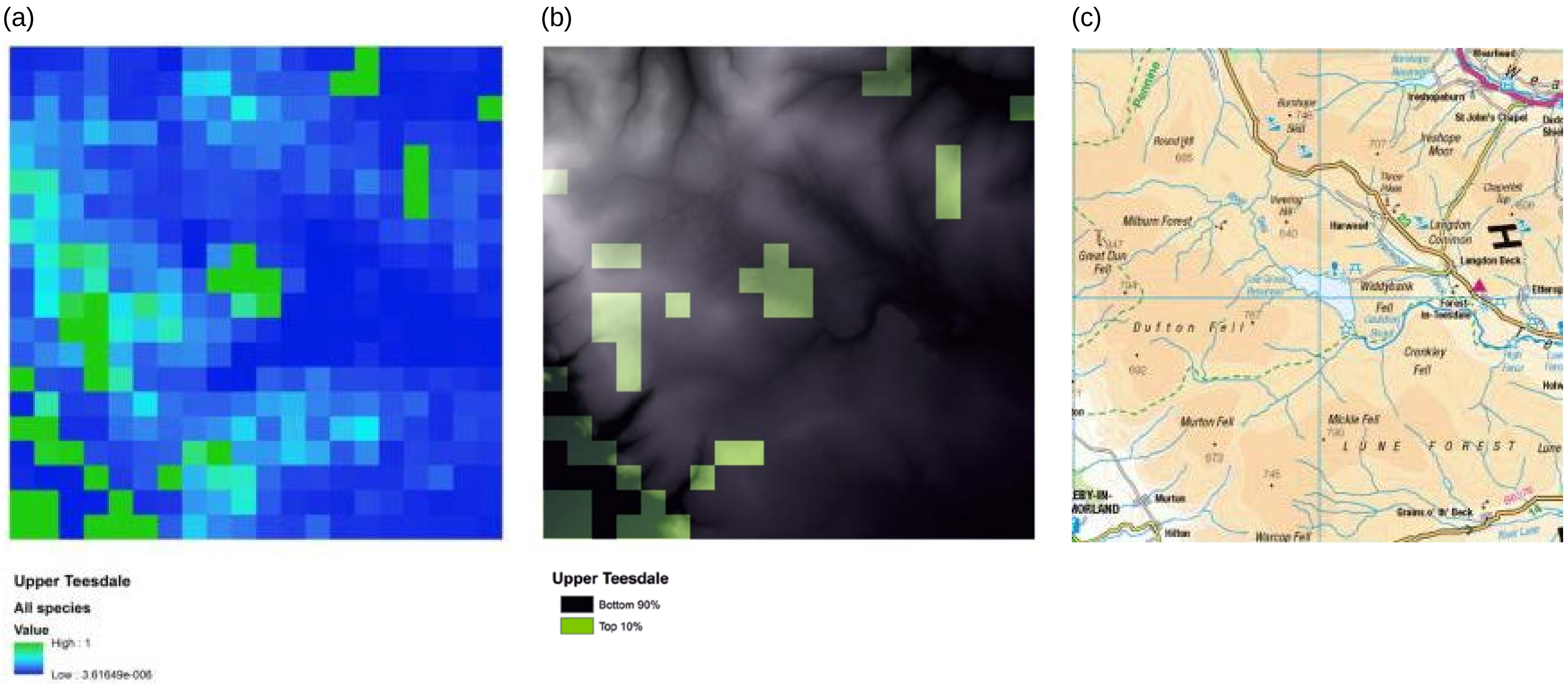

**Figure 5.7** Maps showing refugial areas (panels a and b) in the Upper Teesdale study region calculated using all relevant variables, not just those related to microclimate. In these maps, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The green areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

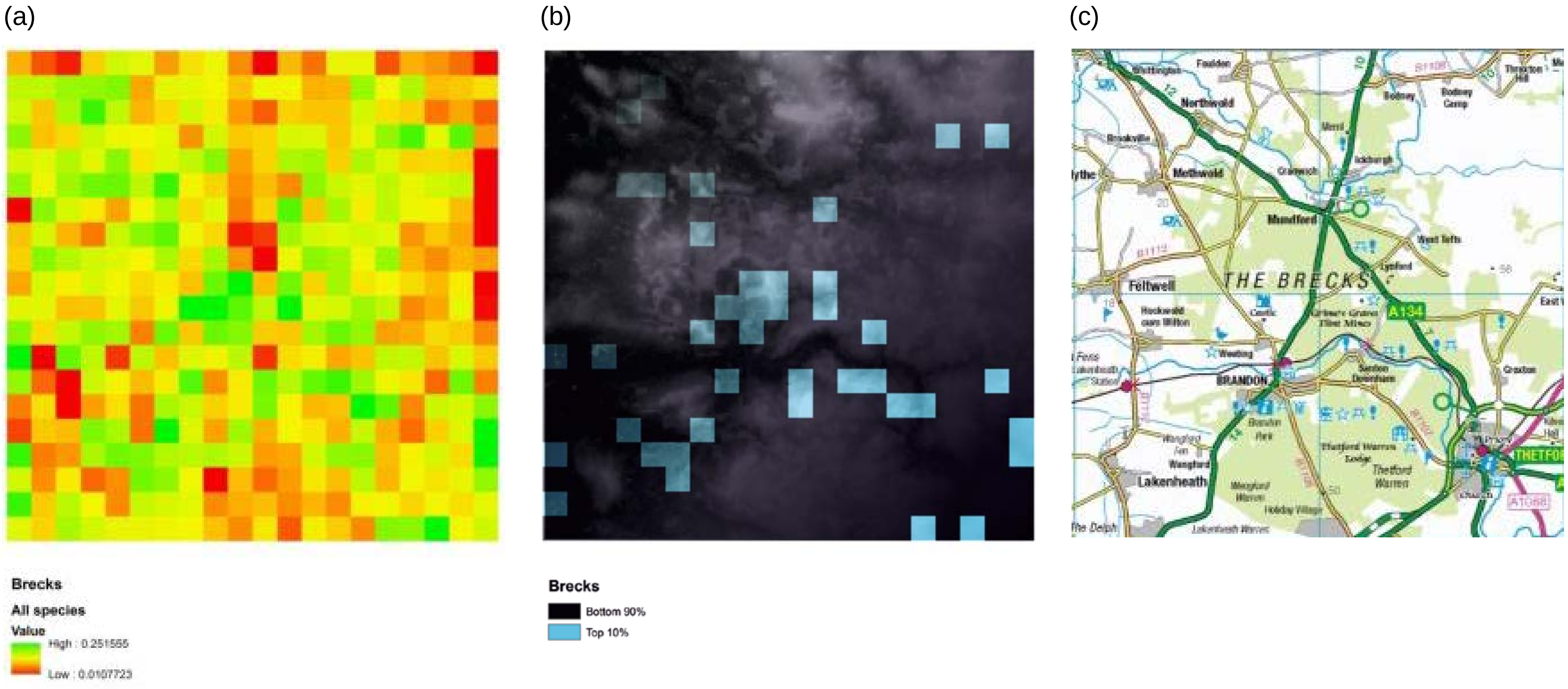

**Figure 5.8** Maps showing microclimate refugial areas (panels a and b) in The Brecks study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

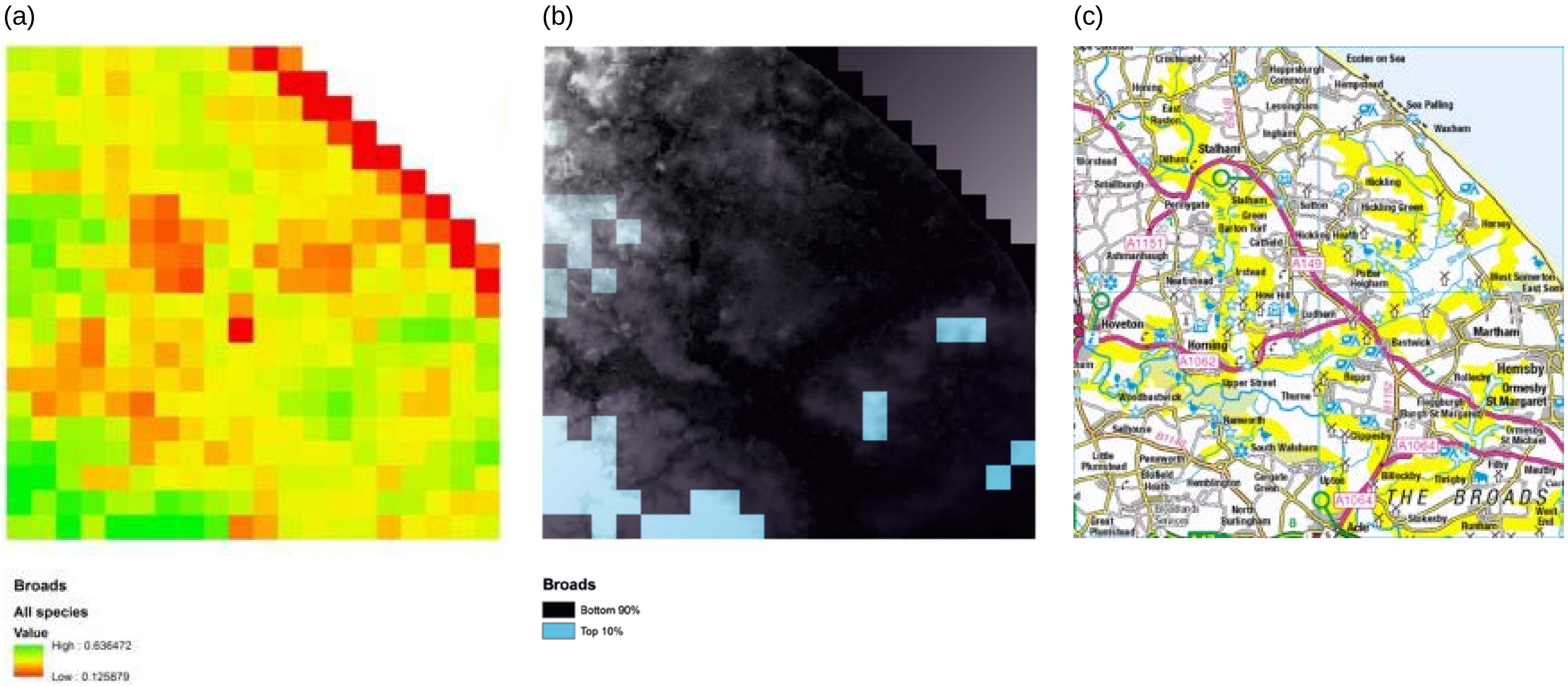

**Figure 5.9** Maps showing microclimate refugial areas (panels a and b) in The Broads study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).
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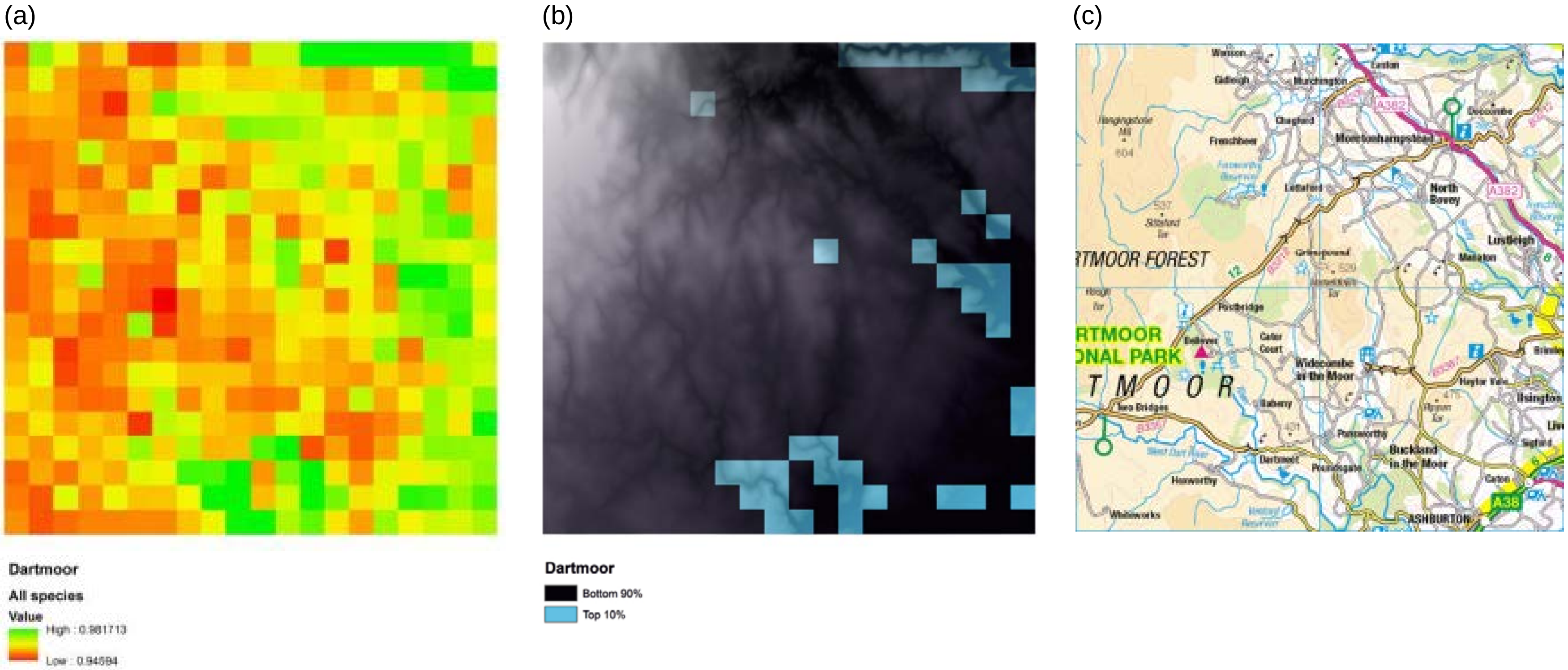

**Figure 5.10** Maps showing microclimate refugial areas (panels a and b) in the Dartmoor study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

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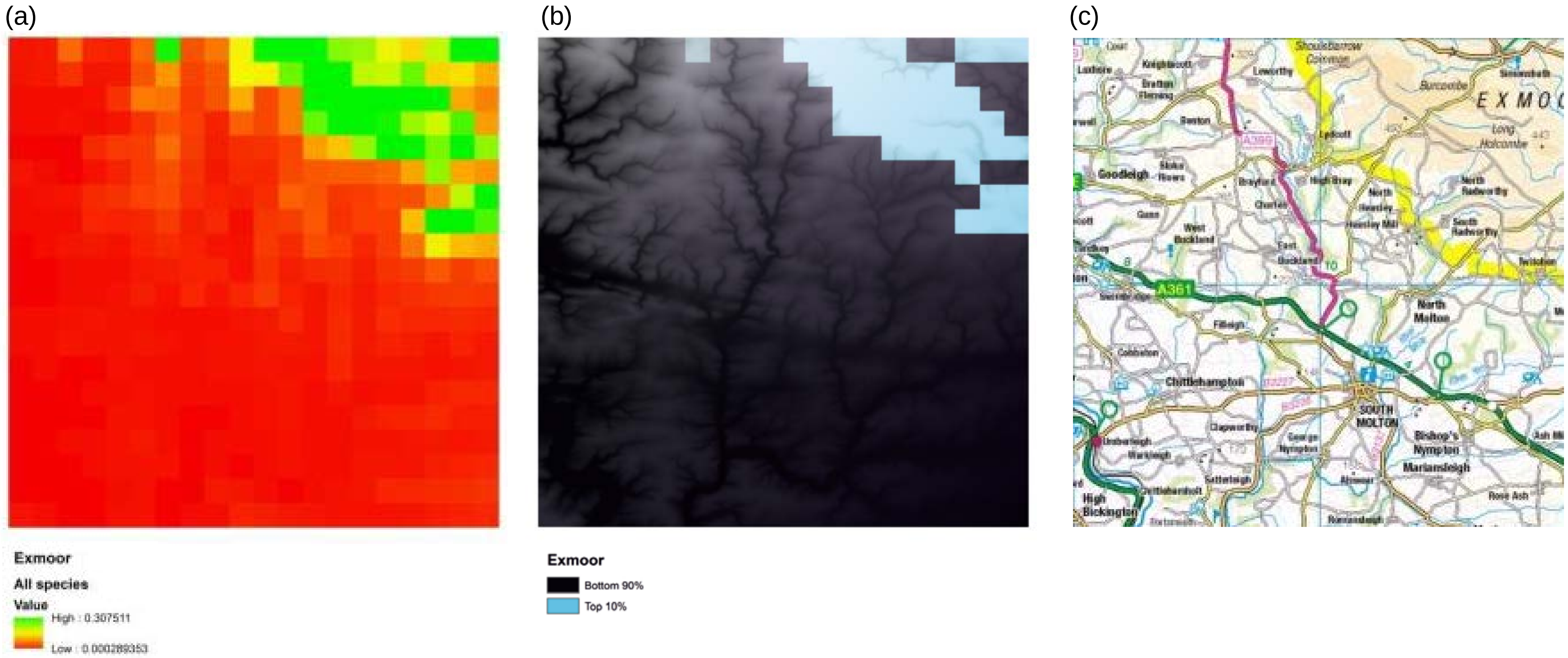

**Figure 5.11** Maps showing microclimate refugial areas (panels a and b) in the Exmoor study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).
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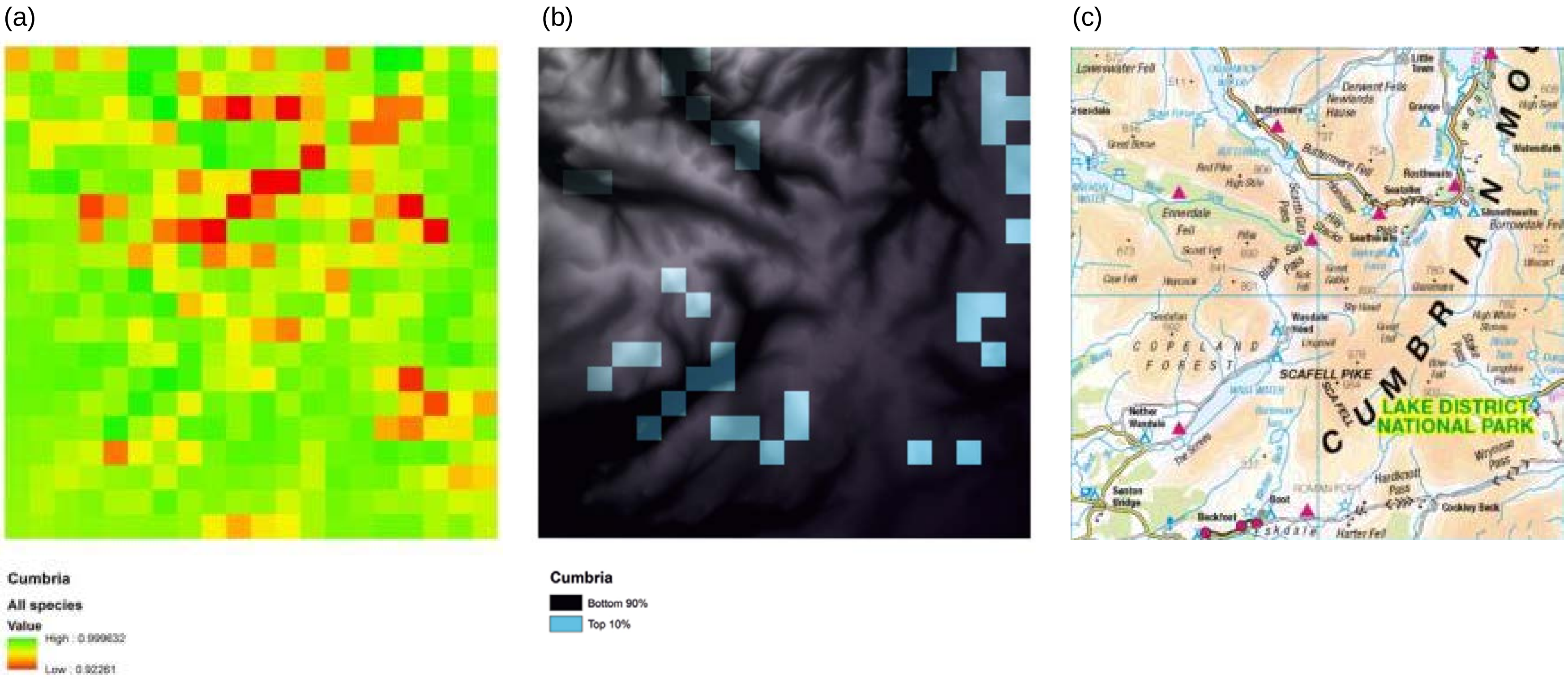

**Figure 5.12** Maps showing microclimate refugial areas (panels a and b) in the Cumbria study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).

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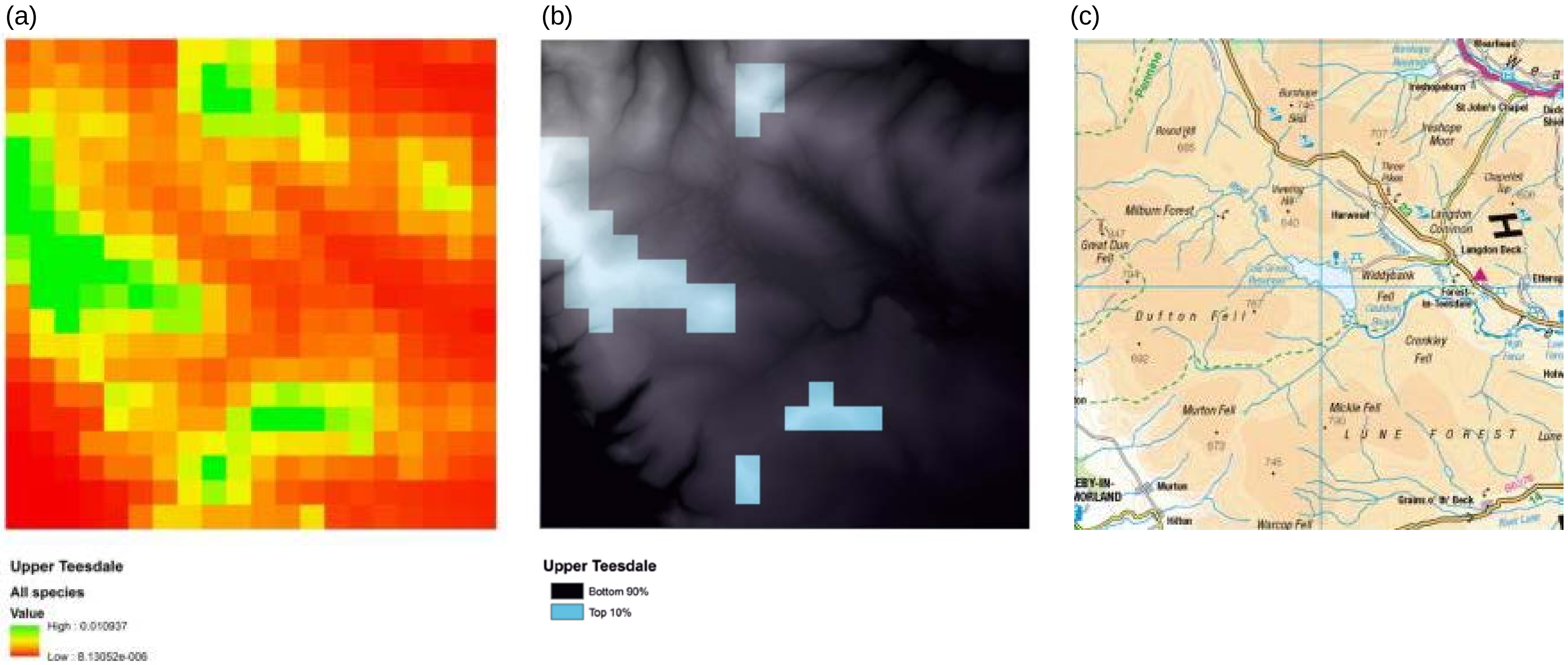

**Figure 5.13** Maps showing microclimate refugial areas (panels a and b) in the Upper Teesdale study region. In these maps, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors- agricultural intensity and geology- are ignored. The values in (a) correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential. The blue areas in (b) indicate 1 km squares that scored in the top 10%. A 1:250,000 Ordnance Survey map of the landscape is provided alongside for comparison (panel c).
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## 5.4 Discussion

In this Chapter, using six study areas identified by the national level analyses (Chapter 4) as being nationally important for refugia, we quantified the effects of refugia characteristics at the landscape scale. Aside from a consistent negative response to agricultural intensity nationally, the drivers of persistence at this scale differed across the study areas. There was a positive effect of elevation on persistence in areas with a larger elevational range (Exmoor, Upper Teesdale & Cumbria), although this effect was reversed for Dartmoor, possibly because the fine scale species records in this landscape were all lepidopteran records: a group which responded negatively to elevation in three of the four landscapes (Tables 5.10, 5.11).

Analyses were limited by the paucity of records at resolutions below 10 km grid square level. As the use of GPS and possibly species recording ‘Apps’ (Smartphone applications) increases, so should the availability of high resolution records, improving our understanding of refugia at the landscape level. An alternative approach would be to identify particularly rich datasets to apply the microclimate models to. In many cases, however, higher quality datasets with high recording intensity are more likely to be collected in areas of high diversity or biological interest. Thus they may not represent a fair test of the refugium potential of the landscape as a whole.

To surmise, a thorough testing for refugia at the landscape level was limited by the relative lack of records with a sufficiently fine resolution (sub 10 km grid square). Interestingly, this is a case where relative availability of techniques to compute microclimate variables has actually exceeded the availability of well-resolved biological data to test the import of these variables. Nevertheless, we show consistent responses of the biota to agricultural intensity (negative) and possibly mean elevation (positive). It could also be that the other drivers of ‘local’ persistence patterns within these broader areas do actually depend on the regional context, i.e. the statistical models presented above are a fair reflection of a complex reality at landscape level. Further testing of refugia at this level would help determine this.

# 6. Identifying refugia in the field: Dartmoor case study

## 6.1 Introduction

The previous chapters describe the development of a suite of microclimate indictors and demonstrate that areas with high microclimate heterogeneity have promoted species persistence. Thus far, however, the analyses have been conducted at a relatively coarse resolution, and questions remain as to whether, (a) the indicators of microclimate do indeed serve as reasonable proxies of temperature and moisture availability and (b) whether at fine-scales, areas with cool and damp microclimate promote species persistence and thus act as climate refugia. The former question is particularly pertinent for our proxy of water availability: the topographic wetness index and our proxy of temperature: the solar index.

With regards to temperature, although solar radiation is the most important element of the earth's heat budget (Geiger 1927, Bennie et al. 2008), the solar index does not act as a perfect proxy of surface temperatures for a number of reasons. It is a measure of the proportion of direct beam radiation and does not therefore account for diffuse radiation or outgoing long-wave radiation. While it serves as a useful proxy of daytime temperatures on clear, sunny days, on cloudy days diffuse radiation makes up a significant component of the radiation budget. On such cloudy days, temperatures are fairly uniform across the land's surface irrespective of the angle of incidence of the surface to the sun. Furthermore, at night, a lot of heat is lost as outgoing longwave radiation, which can also be a key determinant of microclimate (Bennie et al. 2008). The amount of energy received at the earth's surface is also a function of shading by the vegetation. Vegetation characteristics exert a strong influence on temperatures irrespective of solar radiation (Suggitt et al. 2011). Moreover, the relationship between surface temperatures and net solar radiation is affected by convective processes. This in itself is affected by surface roughness, wind speed and near-surface lapse rates (Geiger 1927, Bennie et al. 2008). Finally, latent heat exchange, namely evaporative cooling when surface water evaporates and warming when water condenses as dew, also makes up a significant component of the earth's heat budget (Geiger 1927).

With regards to wetness, while it is well known that steep slopes tend to be drier than flat areas and valley bottoms often wetter than hilltops, and the topographic wetness index developed by Bevan and Kirkby (1979) is very widely used in hydrological contexts, a number of other landscape factors also influence water availability. Firstly, soil properties exert an influence on water availability. Water is generally assumed to run-off from saturated areas and infiltrate into the soil at rates determined by soil particle size (Dunne and Leopold 1978, USDA 1986, Pyke 2004). In clay rich soils, infiltration rates are generally low increasing surface and near-surface water availability (Maclean et al. 2012). Secondly, vegetation characteristics also have an influence on water availability, albeit a rather complex one. With the lower temperatures and solar radiation associated with vegetative shading, evaporation is typically reduced. The lower wind speeds associated with dense vegetation also reduce evaporative losses. However, the presence of vegetation leads to transpiration: the vaporization of liquid water contained in plant tissues and the vapour removal to the atmosphere. Water losses from vegetated surfaces by evapotranspiration are typically much higher than from bare ground (Allen et al. 1998). Plants predominately lose their water through stomata: small openings in the leaves through which gases and water vapour can pass. Because of difference in leaf area and the shape and size of stomatal apertures, different vegetation types have different transpiration rates and the transpiration rate can also change as a function of a plant's development phase (Kozlowski 1983, Allen et al. 1998).

Fine-scale analysis of species distribution change is constrained by the rather patchy availability of high-resolution species distribution records through time, which hampers an assessment of whether and where species have persisted in the face of recent climate change. While it was not possible to test directly whether species have persisted through time as fieldwork was conducted in one time period, the aim of field surveys was to test whether types of species that occur in particular areas provide useful clues as to whether cool and damp microclimates do act as micro-refugia. One potential means by which this could be assessed is to determine whether there is a relationship between known macro-scale temperature and moisture requirements of species and our microclimate indicators. We set out to do this for two taxa: higher plants and butterflies.

Ellenberg *et al.* (1999) defined scales representing the temperature and moisture requirements of European higher plant species, and these indices have been extended to quantify the moisture requirements of species in Great Britain (Hill et al. 2004). However, the temperature index defined by Ellenberg is unreliable in oceanic climates (Hill et al. 2004) and for that reason is rarely applied in Great Britain. However, the mean July temperature of all 10-km squares in which each species of higher plant occurs in Britain, Ireland and the Channel Islands is readily available in the PlantAtt dataset accompanying Hill *et al.* (2004), and we used this to investigate relationships between temperature and our solar index. For butterflies, a similar temperature index is available, but derived from the mean March-September temperature of all occupied grid cells in Europe (see Van Swaay et al. 2008, Kudrna et al. 2011 and Devictor et al. 2012 for further details). Using the indices for temperature we explored whether species with high index values were more likely to occur in areas with a high solar index. Using Ellenberg indicator values for moisture, we explored whether plant species with high index values were more likely to occur in areas with a high topographic wetness index. An additional question is whether it is possible to manage habitats to promote their refugium potential. Reduced grazing pressure results in longer, and thus generally cooler and damper vegetation. We thus set out to test whether the relationships between temperature and moisture indices and the solar and topographic wetness indices were affected by the height of vegetation present at survey locations.

## 6.2 Methods

### Study location

The site for field survey was selected on the basis that (a) it was one of the landscapes analysed in Chapter 5, (b) a good range of variation in potential predictors of refugia was present in the study site and (c) it was logistically straightforward to carry-out fieldwork at the site. For this reason, field survey was conducted on southern Dartmoor. The site is a Special Area for Conservation (92/43/EEC) covering c. 23,000 ha and includes a range of habitats listed on Annex 1 of the EU Habitats Directive, such as: Northern Atlantic wet heaths with *Erica tetralix*; European dry heaths; blanket bogs; and ancient sessile oak woods with *Ilex* and *Blechnum*. The elevation ranges from 50m to 620m. Relative to other upland areas of the UK, the climate is comparatively mild, especially in winter: mean January temperatures typically range between 1-6 ºC, and higher areas receive notable snowfall in winter. Over the last 35 years, the mean annual and spring temperatures have increased by approximately 2 ºC (Jenkins et al. 2008).

### Survey methods

Between 18th June and 12th July 2013, the presence or absence of a subset of higher plant species (see selection criteria below) and all positively identified butterfly species was recorded in 184 plots 20m x 20 m in size (Figure 6.1). The study was restricted to heathland, grassland and blanket bog and a semi-subjective sampling strategy was adopted with the aim of ensuring that fairly widely spaced plots encompassing a range of altitudes, vegetation heights, slopes, aspects, valley bottoms and hilltops were sampled. Each plot was systematically recorded for 20-40 minutes to note the presence or absence of plant species, and an additional 15 minutes to note butterfly occurrences. Butterfly sampling was restricted to sunny periods (defined as shadows being visible) with low wind speed (<3 on the Beaufort scale). Only those butterflies that could be positively identified either by brief capture in butterfly nets, or by direct observation were included. In each plot, nine vegetation height measurements were taken (from the soil surface to the mean maximum height of vegetation, ignoring individual extremes). The location of the centre of each plot was also recorded using a Global Positioning System (GPS).

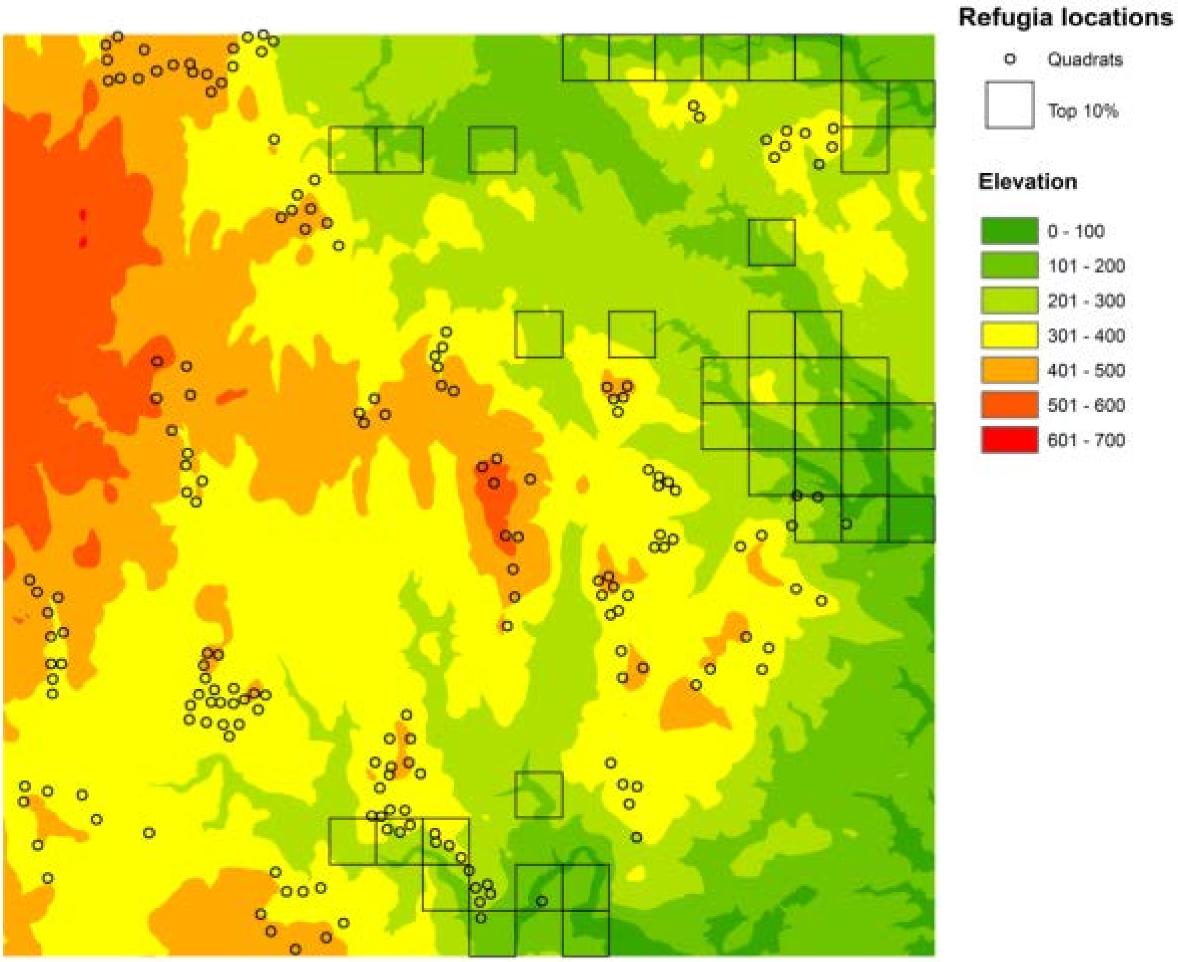


**Figure 6.1** Map showing elevation and location of survey plots (n=184) in the Dartmoor study area, together with the 1km squares on Dartmoor identified as having particularly high refugia scores (top 10%, see Chapter 5). Landscape is 20km across.

## Species selection

### *Plant species*

Prior to visiting the study site, we compiled a long list of higher plant species likely to be recorded using data provided by the Biological Records Centre at the Centre for Ecology and Hydrology. For each species on the longlist, using the Hill *et al.* 2004 dataset, we extracted the mean July temperature of the grid squares comprising its range (hereafter the species temperature index), and the Ellenberg Indicator value for moisture in these same squares (Ellenberg et al. 1991, hereafter referred to as the Ellenberg moisture index). Our final list of plant species was compiled using the following criteria:

(1) All species were relatively common and easy to locate and identify, thus permitting more sites to be surveyed and sufficient replicates for analysis.
(2) The full suite of species encompassed a wide range of Ellenberg Indicator values for moisture.
(3) The full suite of species encompassed a wide a range of July temperature index values as possible.

It should be noted however, that because of the need to fulfil criterion (1), the range of July temperature index values is relatively narrow (as by definition, ‘common’ indicates that the species is probably distributed widely). Those with extreme values were relatively rare and thus not or only very rarely encountered during field survey. The full list of species selected for analyses is shown in Table 6.1 (overleaf).

**Table 6.1** Plant species included in the study together with their Ellenberg Indicator value for moisture and July temperature index values. For ease of interpretation, rows are colour-coded according to Ellenberg Indicator value.

| English name | Scientific name | Ellenberg moisture index | July temperature index |
|---|---|---|---|
| Bracken | *Pteridium aquilinum* | 5 | 14.5 |
| Bilberry | *Vaccinium myrtillus* | 6 | 13.9 |
| Heath Bedstraw | *Galium saxatile* | 6 | 14.3 |
| Common Cotton-grass | *Eriophorum angustifolium* | 9 | 14.1 |
| Wood Sorrel | *Oxalis acetosella* | 6 | 14.4 |
| Bluebell | *Hyacinthoides non-scripta* | 5 | 14.6 |
| English Stonecrop | *Sedum anglicum* | 3 | 14.3 |
| Rowan | *Sorbus aucuparia* | 6 | 14.4 |
| Common Cow-wheat | *Melampyrum pratense* | 5 | 14.3 |
| Lousewort | *Pedicularis sylvatica* | 8 | 14.1 |
| Foxglove | *Digitalis purpurea* | 6 | 14.5 |
| Round -leaved Sundew | *Drosera rotundifolia* | 9 | 13.9 |
| Oblong -leaved Sundew | *Drosera intermedia* | 9 | 14.1 |
| Heath Spotted-orchid | *Dactylorhiza maculata* | 7 | 14.1 |
| Hawthorn | *Crataegus monogyna* | 5 | 14.7 |
| Blackthorn | *Prunus spinosa* | 5 | 14.8 |
| Common Heather | *Calluna vulgaris* | 6 | 14.3 |
| Cross-leaved Heath | *Erica tetralix* | 8 | 14.0 |
| Cow Parsley | *Anthriscus sylvestris* | 5 | 14.6 |
| Bell Heather | *Erica cinerea* | 5 | 14.0 |
| European Gorse | *Ulex europaeus* | 5 | 14.6 |
| Western Gorse | *Ulex gallii* | 6 | 15.0 |
| Wood Sage | *Teucrium scorodonia* | 4 | 14.5 |
| Bramble | *Rubus fruticosa* | 6 | 14.6 |
| Tormentil | *Potentilla erecta* | 7 | 14.4 |
| Soft Rush | *Juncus effusus* | 7 | 14.4 |
| Sheep Sorrel | *Rumex acetosella* | 5 | 14.4 |
| Common Sorrel | *Rumex acetosa* | 5 | 14.4 |
| Water Forget-me-not | *Myosotis scorpioides* | 9 | 14.7 |
| Holly | *Ilex aquifolium* | 5 | 14.7 |
| Slender St John's-wort | *Hypericum pulchrum* | 5 | 14.3 |
| Marsh Thistle | *Cirsium palustre* | 8 | 14.5 |
| Marsh Violet | *Viola palustris* | 9 | 13.9 |
| Marsh Bedstraw | *Galium palustre* | 9 | 14.5 |
| Marsh St John's-wort | *Hypericum elodes* | 10 | 14.8 |
| Pale Butterwort | *Pinguicula lusitanica* | 8 | 13.7 |
| Common Water-crowfoot | *Ranunculus aquatilis* | 11 | 15.2 |
| Lesser Spearwort | *Ranunculus flammula* | 9 | 14.4 |
| Bog Pondweed | *Potamogeton polygonifolius* | 10 | 13.9 |
| Marsh Pennywort | *Hydrocotyle vulgaris* | 8 | 14.4 |
| Dodder | *Cuscuta epithymum* | 6 | 15.9 |
| Eyebright | *Euphrasia spp.* | 5 | 14.4 |
| Bird's-foot Trefoil | *Lotus corniculatus* | 4 | 14.5 |
| Common Dog-violet | *Viola riviniana* | 5 | 14.5 |
| Common Speedwell | *Veronica persica* | 5 | 14.8 |
| Germander Speedwell | *Veronica chamaedrys* | 5 | 14.5 |
| Lesser Stitchwort | *Stellaria graminea* | 6 | 14.6 |
| Common Mouse-ear | *Cerastium fontanum* | 5 | 14.4 |
| Bog Asphodel | *Narthecium ossifragum* | 9 | 13.8 |
| Rosebay Willowherb | *Chamerion angustifolium* | 5 | 14.5 |
| Dove's-foot Cranesbill | *Geranium molle* | 5 | 14.8 |
| Woolly Thistle | *Cirsium eriophorum* | 4 | 16.0 |
| Selfheal | *Prunella vulgaris* | 5 | 14.4 |

### *Butterfly species*

All species identified were selected for analyses. The full list of species is shown in Table 6.2. For each species we calculated a summer temperature index, based on the mean March-September temperature of all grid cells in butterfly was recorded in Europe (see Van Swaay et al. 2008, Kudrna et al. 2011 and Devictor et al. 2012 for further details).

**Table 6.2** Butterfly species included in the study together with their temperature index values. For ease of interpretation, rows are colour-coded according to temperature index values.

| English name | Scientific name | Summer temperature index |
|---|---|---|
| Small Heath | *Coenonympha pamphilus* | 8.96 |
| Green Hairstreak | *Callophrys rubi* | 8.57 |
| Small Copper | *Lycaena phlaeas* | 9.29 |
| Small Tortoiseshell | *Aglais urticae* | 7.87 |
| Small White | *Pieris rapae* | 9.63 |
| Meadow Brown | *Maniola jurtina* | 9.85 |
| Large White | *Pieris brassicae* | 9.29 |
| Ringlet | *Aphantopus hyperantus* | 7.90 |

### Analyses

To investigate relationships between the temperature and moisture requirements of species and landscape predictors of refugia, the sampled plots were overlaid on 5m resolution surfaces of topographic wetness and received solar radiation (see Methods B2) and the mean topographic wetness and summer solar index values in each 20m x 20m plot were calculated. We used generalized linear models with a binomial error structure (presence / absence) and logit link function to test whether the occurrence of species was related to vegetation height, solar index, topographic wetness index and interactions between solar index and vegetation height and topographic wetness index and vegetation height. We used two general approaches. First we tested each term individually and examined the significance of results using the conventional frequentist (hypothesis-based) approach (Fisher 1922). Where interaction terms were assessed the two terms comprising the interaction were also included individually following recommendations in Zuur (2009). Secondly, we used models with combinations of predictor variables and selected the most parsimonious (i.e. most plausible) model using Akaike's Information Criterion (Akaike 1979). For butterflies, for which fewer species and individuals were recorded, we also report the results of plausible models (those for which $\Delta AIC < 4$). Analyses were performed using R statistical software (R core Development Team 2013) using the MuMIN package (Bartoń 2013) to automatically generate models with all combinations of predictor variables. Separate analyses were performed for each species.

## 6.3 Results

### Plants

### *Topographic wetness*

In the individual species models of presence-absence in which topographic wetness was included as the only term, 11 of 53 species were significantly related to this variable. Of these, five were more likely to occur in topographically dry areas and six in topographically wet areas (Table 6.3). The relatively low number is perhaps to be expected given the small number of presences recorded for some species, and the fact that many species would not be expected to be influenced strongly by topographic wetness given their intermediate Ellenberg moisture index values. Note here that some of the counts (i.e. presences) were low. However, it was necessary to construct these models to obtain model slopes for the subsequent analyses of climatic requirements (described below, and in Figure 6.2).

In the analyses of the most plausible models, topographic wetness added explanatory power for 18 species (Table 6.4). Of these, nine were found more frequently in topographically wetter areas and nine found more frequently in topographically drier areas. Most importantly, plotting the slopes (or betas) of the wetness relationships for each species (derived from the single variable models of species presence/absence with topographic wetness) against their respective Ellenberg indicator values derived a *positive* slope that was statistically significant ($F_{5,51} = 59.94$, $R^2 = 0.54$, $P<0.0001$), suggesting that species with high moisture requirements tended to be associated with high topographic wetness (Figure 6.2).

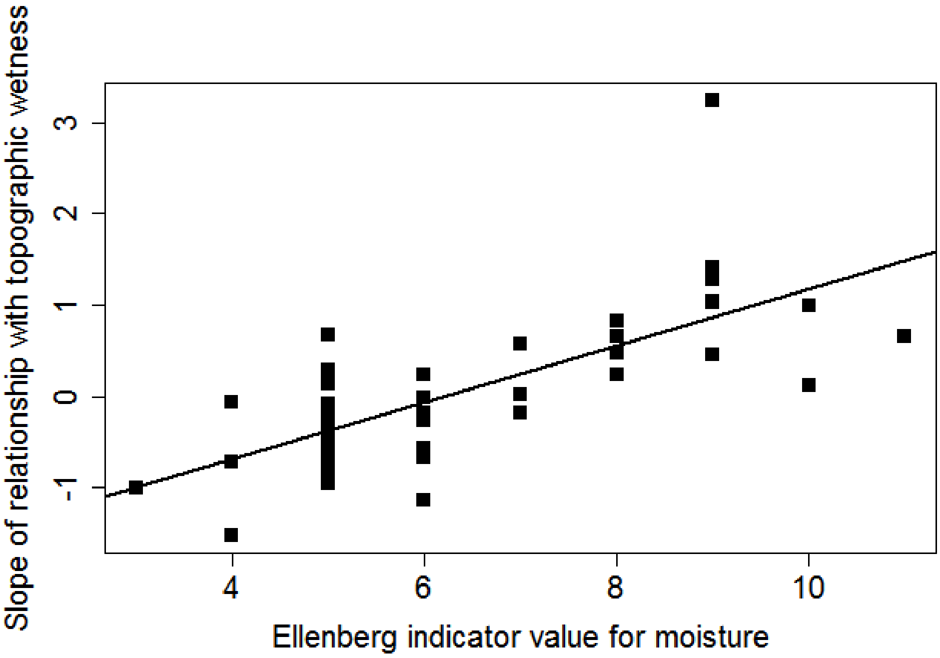


**Figure 6.2** Relationship between the slope of each species' relationship to topographic wetness, and its associated Ellenberg moisture index value. Each square represents the data for one species. The positive relationship indicates that species with high moisture requirements tended to be associated with areas of high topographic wetness.

### Solar index

In the individual species models of presence/absence in which solar index was included as the only term, only seven of 53 species exhibited a significant relationship. Of these, four (Bell Heather *Erica cinerea*, European Gorse *Ulex europaeus*, Sheep Sorrell *Rumex acetosella* and Lesser Stitchwort *Stellaria graminea*) occurred in areas receiving more solar radiation and three (Bracken *Pteridium aquilinum*, Wood Sorrel *Oxalis acetosella*, Slender St John's-wort *Hypericum pulchrum*) occurred in areas receiving less solar radiation. In the full models of the presence and absence of each species, the solar index added explanatory power for 24 species (Table 6.4). Of these, 8 occurred in areas receiving more solar radiation and 16 in areas with less solar radiation. The significance of solar index, where it was retained as a term in the most parsimonious models, is shown in Table 6.4. Plotting the slopes (betas) of the relationships between species presence/absence and the solar index against the Ellenberg July temperature index values for each species did not reveal a (significant) trend, suggesting that species with higher temperature requirements were not necessarily associated with areas receiving more solar radiation and *vice versa*. As highlighted earlier, the range of temperature index values was narrow, and it is possible a relationship might have been found if species with more extreme index values had occurred more frequently.

### Vegetation height

In the individual species models of presence/absence in which vegetation height was included as the only term, 11 of 53 species exhibited a significant relationship. Of these, nine (Bracken *Pteridium aquilinum*, Heath Bedstraw *Galium saxatile*, Wood Sorrell *Oxalis acetosella*, English Stonecrop *Sedum anglicum*, Hawthorn *Crataegus monogyna*, Cow Parsley *Anthriscus sylvestris*, Sheep Sorrel *Rumex acetosella*, Common Sorrel *Rumex acetosa* and Germander Speedwell

*Veronica chamaedrys*) had a preference for shorter vegetation and two (Ling *Calluna vulgaris* and Bell Heather *Erica cinerea*) for longer vegetation. In the analyses of the most plausible models, vegetation height added explanatory power for 28 species (Table 6.4). Of these, 24 had a preference for shorter vegetation and only four for longer vegetation. The significance of vegetation height, where retained as a term in most parsimonious models, is shown in Table 6.4.

### Interactions with vegetation height

In the individual models of the presence/absence in which vegetation height, solar index and interactions between these terms were included, the interaction was significant for four species. These species, namely Bilberry *Vaccinium myrtillus*, Heath Bedstraw *Galium saxatile*, Rowan *Sorbus aucuparia*, and Sheep Sorrel *Rumex acetosella*, were all found in areas with less solar radiation, but the strength of the relationship was weakened in longer vegetation. The analyses of the most plausible models yielded very similar results: an interaction between vegetation height and the solar index added explanatory power to the models for the same four species and again the models suggested that all were more frequently found in areas with less solar radiation, but the strength of the relationship was weakened in longer vegetation. Adding an interaction term for vegetation height and topographic wetness did not add explanatory power or yield significant results in any model type.

**Table 6.3** Logistic regression results showing the Slope (i.e. strength) and P value (significance) of the relationship between the presence of each species and topographic wetness index values. A negative relationship index shows the plant has a preference for areas with a low wetness index and a positive relationship indicates a preference for high wetness. For ease of interpretation, results are colour-coded according to values.

| Common name | Scientific name | Ellenberg moisture value | Number of presences | Slope | P value |
|---|---|---|---|---|---|
| English Stonecrop | *Sedum anglicum* | 3 | 37 | --- | <0.001 |
| Wood Sage | *Teucrium scorodonia* | 4 | 9 | --- | 0.095 |
| Bird's-foot Trefoil | *Lotus corniculatus* | 4 | 1 | --- | 0.282 |
| Woolly Thistle | *Cirsium eriophorum* | 4 | 1 | - | 0.958 |
| Bracken | *Pteridium aquilinum* | 5 | 94 | -- | 0.080 |
| Bluebell | *Hyacinthoides non-scripta* | 5 | 14 | - | 0.448 |
| Common Cow-wheat | *Melampyrum pratense* | 5 | 1 | +++ | 0.533 |
| Hawthorn | *Crataegus monogyna* | 5 | 15 | ++ | 0.343 |
| Blackthorn | *Prunus spinosa* | 5 | 2 | -- | 0.597 |
| Cow Parsley | *Anthriscus sylvestris* | 5 | 8 | --- | 0.235 |
| Bell Heather | *Erica cinerea* | 5 | 65 | - | 0.662 |
| European Gorse | *Ulex europaeus* | 5 | 44 | + | 0.519 |
| Sheep Sorrel | *Rumex acetosella* | 5 | 25 | --- | 0.018 |
| Common Sorrel | *Rumex acetosa* | 5 | 23 | -- | 0.140 |
| Holly | *Ilex aquifolium* | 5 | 6 | - | 0.815 |
| Slender St John's-wort | *Hypericum pulchrum* | 5 | 5 | - | 0.841 |
| Eyebright | *Euphrasia spp.* | 5 | 2 | -- | 0.702 |
| Common Dog-violet | *Viola riviniana* | 5 | 1 | --- | 0.634 |
| Common Speedwell | *Veronica persica* | 5 | 9 | --- | 0.064 |
| Germander Speedwell | *Veronica chamaedrys* | 5 | 3 | --- | 0.345 |
| Common Mouse-ear | *Cerastium fontanum* | 5 | 5 | -- | 0.450 |
| Rosebay Willowherb | *Chamerion angustifolium* | 5 | 3 | - | 0.756 |
| Dove's-foot Cranesbill | *Geranium molle* | 5 | 1 | --- | 0.626 |
| Selfheal | *Prunella vulgaris* | 5 | 2 | --- | 0.292 |
| Bilberry | *Vaccinium myrtillus* | 6 | 141 | + | 0.252 |
| Heath Bedstraw | *Galium saxatile* | 6 | 140 | -- | 0.198 |
| Wood Sorrel | *Oxalis acetosella* | 6 | 7 | - | 0.695 |
| Rowan | *Sorbus aucuparia* | 6 | 27 | - | 0.952 |
| Foxglove | *Digitalis purpurea* | 6 | 25 | --- | 0.014 |
| Common Heather | *Calluna vulgaris* | 6 | 105 | + | 0.168 |
| Western Gorse | *Ulex gallii* | 6 | 119 | - | 0.960 |
| Bramble | *Rubus fruticosa* | 6 | 47 | --- | 0.007 |
| Dodder | *Cuscuta epithymum* | 6 | 1 | -- | 0.822 |
| Lesser Stitchwort | *Stellaria graminea* | 6 | 11 | --- | 0.007 |
| Heath Spotted-orchid | *Dactylorhiza maculata* | 7 | 13 | + | 0.952 |
| Tormentil | *Potentilla erecta* | 7 | 183 | - | 0.877 |
| Soft Rush | *Juncus effusus* | 7 | 56 | +++ | 0.003 |
| Lousewort | *Pedicularis sylvatica* | 8 | 17 | + | 0.397 |
| Cross-leaved Heath | *Erica tetralix* | 8 | 62 | +++ | 0.000 |
| Marsh Thistle | *Cirsium palustre* | 8 | 10 | +++ | 0.198 |
| Pale Butterwort | *Pinguicula lusitanica* | 8 | 1 | +++ | 0.548 |
| Marsh Pennywort | *Hydrocotyle vulgaris* | 8 | 1 | +++ | 0.548 |
| Common Cotton-grass | *Eriophorum angustifolium* | 9 | 22 | +++ | 0.000 |
| Round -leaved Sundew | *Drosera rotundifolia* | 9 | 15 | +++ | 0.000 |
| Oblong -leaved Sundew | *Drosera intermedia* | 9 | 1 | +++ | 0.111 |
| Water Forget-me-not | *Myosotis scorpioides* | 9 | 2 | +++ | 0.564 |
| Marsh Violet | *Viola palustris* | 9 | 8 | +++ | 0.015 |
| Marsh Bedstraw | *Galium palustre* | 9 | 2 | ++ | 0.564 |
| Lesser Spearwort | *Ranunculus flammula* | 9 | 6 | +++ | 0.009 |
| Bog Asphodel | *Narthecium ossifragum* | 9 | 1 | +++ | 0.341 |
| Marsh St John's-wort | *Hypericum elodes* | 10 | 4 | +++ | 0.080 |
| Bog Pondweed | *Potamogeton polygonifolius* | 10 | 3 | + | 0.855 |
| Common Water-crowfoot | *Ranunculus aquatilis* | 11 | 1 | +++ | 0.548 |

**Table 6.4** Logistic regression results showing the terms included in the best model for each species. Negative relationships are indicated by (-) and positive relationships by (+). Results are colour-coded according to values and the significance of terms is denoted as follows: * P<0.05, **P<0.01, ***P<0.001.

| **Common name** | **Ellenberg Moisture index** | **July temperature index** | **Vegetation height** | **Solar index** | **Topographic wetness index** | **Vegetation height x solar index** |
|---|---|---|---|---|---|---|
| Bracken | 5 | 14.5 | (-) *** | (-) * | | |
| Bilberry | 6 | 13.9 | (-) ** | (-) ** | | (+) ** |
| Heath Bedstraw | 6 | 14.3 | (-) ** | (-) ** | | (+) ** |
| Common Cotton-grass | 9 | 14.1 | | | (+)*** | |
| Wood Sorrel | 6 | 14.4 | (-) * | (-) ** | | |
| Bluebell | 5 | 14.6 | (-) NS | | | |
| English Stonecrop | 3 | 14.3 | (-) ** | | (-) *** | |
| Rowan | 6 | 14.4 | (-) * | (-) * | | (+) * |
| Common Cow-wheat | 5 | 14.3 | (-) NS | | | |
| Lousewort | 8 | 14.1 | (+) NS | | | |
| Foxglove | 6 | 14.5 | | (-) * | (-) ** | |
| Round -leaved Sundew | 9 | 13.9 | | | (+) *** | |
| Oblong -leaved Sundew | 9 | 14.1 | | | | |
| Heath Spotted-orchid | 7 | 14.1 | (+) NS | (-) NS | | |
| Hawthorn | 5 | 14.7 | (-) *** | | (+) NS | |
| Blackthorn | 5 | 14.8 | | (+) NS | | |
| Common Heather | 6 | 14.3 | (+) *** | | | |
| Cross-leaved Heath | 8 | 14.0 | (+) *** | | (+) *** | |
| Cow Parsley | 5 | 14.6 | (-) * | | | |
| Bell Heather | 5 | 14.0 | | (+) * | | |
| European Gorse | 5 | 14.6 | (-) NS | (+) * | | |
| Western Gorse | 6 | 15.0 | | (+) NS | | |
| Wood Sage | 4 | 14.5 | | | (-) NS | |
| Bramble | 6 | 14.6 | | | (-) ** | |
| Tormentil | 7 | 14.4 | (-) NS | | | |
| Soft Rush | 7 | 14.4 | | | (+) ** | |
| Sheep Sorrel | 5 | 14.4 | (-) * | (-) NS | (-) NS | (+) * |
| Common Sorrel | 5 | 14.4 | (-) ** | | | |
| Water Forget-me-not | 9 | 14.7 | | (-) NS | | |
| Holly | 5 | 14.7 | | (-) NS | | |
| Slender St John's-wort | 5 | 14.3 | | (-) * | | |
| Marsh Thistle | 8 | 14.5 | | | (+) NS | |
| Marsh Violet | 9 | 13.9 | | | (+) * | |
| Marsh Bedstraw | 9 | 14.5 | | (-) NS | | |
| Marsh St John's-wort | 10 | 14.8 | | | (+) NS | |
| Pale Butterwort | 8 | 13.7 | | (-) NS | | |
| Common Water-crowfoot | 11 | 15.2 | | (-) NS | | |
| Lesser Spearwort | 9 | 14.4 | (-) NS | | (+) ** | |
| Bog Pondweed | 10 | 13.9 | (+) NS | | | |
| Marsh Pennywort | 8 | 14.4 | | (-) NS | | |
| Dodder | 6 | 15.9 | (-) NS | (+) NS | (-) NS | |
| Eyebright | 5 | 14.4 | (-) NS | | | |
| Bird's-foot Trefoil | 4 | 14.5 | (-) NS | | | |
| Common Dog-violet | 5 | 14.5 | (-) NS | | | |
| Common Speedwell | 5 | 14.8 | (-) NS | | | |
| Germander Speedwell | 5 | 14.5 | | | (-) NS | |
| Lesser Stitchwort | 6 | 14.6 | | (+) * | (-) * | |
| Common Mouse-ear | 5 | 14.4 | (-) NS | | | |
| Bog Asphodel | 9 | 13.8 | (-) NS | | | |
| Rosebay Willowherb | 5 | 14.5 | | (+) NS | | |
| Dove's-foot Cranesbill | 5 | 14.8 | | (+) NS | | |
| Woolly Thistle | 4 | 16.0 | (-) NS | | | |
| Selfheal | 5 | 14.4 | (-) *** | (-) * | (-) NS | |

## Butterflies

### *Topographic wetness*

In the individual species models of presence/absence in which the topographic wetness index was included as the only term, both Small Tortoiseshell *Aglais urticae* ($p < 0.05$) and Meadow Brown *Maniola jurtina* ($p < 0.001$) had significant relationships to topographic wetness, occurring more frequently in wetter areas (Table 6.5). In the analyses of the most plausible models, topographic wetness also added explanatory power to the models for these two species, again suggesting preference for drier areas. The topographic wetness index was also a plausible predictor ($\Delta AIC<4$) of the occurrence of all other species, providing some evidence of a preference for dry areas for all species with the exception of Small Copper *Lycaena phlaeas* (Table 6.5).

### *Solar index*

In the individual species models of presence-absence in which the solar index was included as the only term, a significant relationship was evident for Meadow Brown ($p < 0.05$), which was found more frequently in areas with a higher solar index (Table 6.5). In the analyses of the most plausible models, the solar index added explanatory power to the models for Meadow Brown and Large White *Pieris brassicae*, both species occurring more frequently in areas with a higher solar index. Solar index was also a plausible predictor ($\Delta AIC<4$) of the occurrence of all other species: negatively for all species with the exception of Small Heath *Coenonympha pamphilus* and Small Tortoiseshell *Aglais urticae* for which there was some evidence to suggest both species were more likely to occur in areas receiving higher solar radiation. Plotting the slopes (betas) of the relationships between presence/absence and solar index against the Ellenberg temperature indicator values for each species revealed a positive, non-significant trend ($p > 0.05$). Hence there was only weak evidence that species associations with solar index were related to their thermal requirements (Table 6.5).

### *Vegetation height*

In the individual species models of presence/absence in which vegetation height was included as the only term, vegetation height was not a significant predictor for any species (Table 6.5). In the analyses of the most plausible models, vegetation height added explanatory power to the models for Small Heath and Ringlet *Aphantopus hyperantus*. In both instances, presences were more likely in areas with shorter vegetation. Vegetation height was also a plausible predictor ($\Delta AIC<4$) of the occurrence of all other species: negatively for all species with the exception of Green Hairstreak *Callophrys rubi* for which there was some evidence to suggest it was more likely to occur in longer vegetation (Table 6.5).

### *Interactions with vegetation height*

In the individual models of presence/absence in which vegetation height, the solar index and interactions between these terms were included, the interaction was not significant for any species and did not add explanatory power in the analyses of the most parsimonious models. It was, however, retained as a plausible predictor ($\Delta AIC<4$) in the models for Green Hairstreak and Meadow Brown. In the case of Green Hairstreak, which occurred more frequently in areas with low solar radiation and long vegetation, the strength of the association with low solar radiation is strengthened in long vegetation. In the case of Meadow Brown, which occurred more frequently in areas receiving more solar radiation and in short vegetation, the dependence on areas with short vegetation is strengthened in areas with high solar radiation (Table 6.5).

In the individual models of presence/absence in which vegetation height, the topographic wetness index and interactions between these terms were included, the interaction was not significant for any species. In the individual models of the presence/absence in which vegetation height, the solar index and interactions between these terms were included, the interaction added explanatory power to the model for Small Heath and was also plausibly retained in the models for Small Tortoiseshell, Meadow Brown and Ringlet. All species appeared to occur more frequently in drier areas with shorter vegetation. For Small Heath and Small Tortoiseshell, the direction of the interaction suggests that preference for drier areas is not as strong in areas with longer vegetation.

For Meadow Brown and Ringlet, the direction of the interaction suggests that preference for drier areas increases where vegetation is longer (Table 6.5).

**Table 6.5.** Logistic regression results showing the terms included in the best model for each species. Negative relationships are indicated by (-) and positive relationships by (+). Results in grey are those for which the term was not retained in the most parsimonious model, but is nevertheless a plausible predictor ($\Delta AIC<4$). Results are colour-coded according to values and the significance of terms is denoted as follows: * P<0.05, **P<0.01, ***P<0.001.

| **Common name** | **Temperature index** | **Number of presences** | **Vegetation height** | **Solar index** | **Topographic wetness index** | **Vegetation height x solar index** | **Vegetation height x topographic wetness index** |
|---|---|---|---|---|---|---|---|
| Small Heath | 8.96 | 64 | (-)NS | (+)NS | (-)NS |  | (+)NS |
| Green Hairstreak | 8.57 | 2 | (+)NS | (-)NS | (-)NS | (-)NS |  |
| Small Copper | 9.29 | 1 | (-)NS | (-)NS | (+)NS |  |  |
| Small Tortoiseshell | 7.87 | 19 | (-)NS | (+)NS | (-)* |  | (+)NS |
| Small White | 9.63 | 1 | (-)NS | (-)NS | (-)NS |  |  |
| Meadow Brown | 9.85 | 24 | (-)NS | (+)* | (-)*** | (-)NS | (-)NS |
| Large White | 9.29 | 2 | (-)NS | (+)NS | (-)NS |  |  |
| Ringlet | 7.90 | 2 | (-)NS | (-)NS | (-)NS |  | (-)NS |

## 6.4 Discussion

This was a small scale study intended to explore the concept of microclimatic refugia at a local level. It provides indications of the role of microclimate in maintaining local refugia as well as some of the practical difficulties in assessing what constitutes a refugium at this scale. A wider study would be needed to fully test the concept, including more taxa at (or close to) their range margin.

### Solar index

Our results provide limited evidence of a relationship between the macro-requirements of species and the proportion of direct beam solar radiation received at the locations in which they were found to be present. The solar index helped to explain the fine-scale distributions of just under half of the plant species recorded, and while many species found in areas with a high solar index also had high macro-temperature requirements, the all species relationship between macro-temperature requirements and preference for areas with a solar index, was not significant. For butterflies, the solar index helped to explain the fine-scale distribution of only two species, and while both of these species had high temperature requirements, and were also more likely to occur in areas with a high solar index, the results for other species are less compelling. However, we attribute the lack of relationships to limitations in the selection of study species and the quantity of data rather than failure in the index *per se.* The July temperature index values of higher plant species in Great Britain varies from 10.4 to 16.9, but index values for the species included as part of this study varied from only 13.7 to 16.0. Moreover, the vast majority of species recorded frequently were those with a widespread distribution in the UK, which therefore had a mid-range temperature index value. This is to be expected given that species common at a particular spatial scale (e.g. widespread throughout Great Britain) are typically also more common at other scales (i.e. abundant within the study area, Hartley 1998; Gaston et al. 2000). This is a serious limitation of our study. For butterflies, only three species were recorded more than 10 times and it is thus not possible to infer meaningful patterns across species.

### Topographic wetness index

In contrast to the solar index, there is evidence of relationships between the moisture requirements of plant species and topographic wetness (Table 6.4). Most importantly, those species with high moisture requirements were almost always found in locations with a high topographic wetness, while those with low moisture requirements were typically confined to areas with low topographic wetness (Figure 6.2). Whilst it is not surprising that plants adapted to wet places were found in wet places (and *vice versa*), this is strong evidence that calculated topographic wetness is a good indicator of site suitability for species and that it is possible to identify potential refugia across large areas.

For butterflies, no moisture index is available, but interestingly, topographic wetness plausibly helped to explain the distribution of all species, and the species with the highest macro-temperature requirement (Meadow Brown) showed a strong preference for areas with low topographic wetness. In contrast to macro-temperature requirements, our study species here had a wide range of moisture requirements, making the process of inferring cross-taxon patterns much more robust.

### Vegetation height

Vegetation height helped to explain the distributions of half of the plant species and was also a plausible explanatory term in all of the species models explaining the fine-scale distributions of butterflies. It should be noted, however, that the direction of the causal relationship between the presence of some plant species and vegetation height is not entirely straightforward. The heathers, for example, in many instances are likely to have been the tallest species in the plots and therefore determinants of vegetation height, rather than being affected by it. The positive relationship between their occurrence and vegetation height is thus not that surprising.

For several plant species with requirements for lower temperature, the dependence on areas receiving less solar radiation was weakened in the presence of longer vegetation - the cooling effect of vegetation perhaps offsetting the effects of solar radiation. Our results thus provide at least some evidence that plant communities in longer vegetation could be more resilient to the effects of climate change. While any change in management should proceed with caution, not least because the presence of long vegetation could also result in higher levels of competition, it may be possible to partially offset the effects of climate change by manipulating grazing regimes. Broadly, there are two potential courses of action for helping species cope with climate change: (i) facilitate species' dispersal towards areas where the climate is becoming more suitable (including increases to connectivity); or (ii) improve species' abilities to cope with climate change in habitats within the existing range (Hodgson et al. 2009, Lawson et al. 2012, Morecroft et al. 2012). Manipulating microclimates by modifying sward height offers a promising means of allowing species to persist *in situ*.

# 7. Identifying refugia for an endothermic animal: Meadow pipit case study

## 7.1 Introduction

Climate change is regarded as a long-term threat to biodiversity (Thomas et al. 2004, Jetz et al. 2007, Bellard et al. 2012). The shift of climatic zones will force species to move and track their climatic niche or adapt to the new climatic conditions (Maggini et al. 2011). Poleward and, to lesser extent, upward range shifts in species' distributions have already been observed (Parmesan et al. 1999, Thomas and Lennon 1999, Hickling et al. 2006, Hitch and Leberg 2007, Devictor et al. 2008, Zuckerberg et al. 2009, Chen et al. 2011). These shifts, and projected future impacts, pose a significant challenge to conservationists, particularly as they may impact upon the future effectiveness of protected areas, a key tenet of conservation practice. As a result, it has been suggested that areas of environmental heterogeneity should be prioritised for protection, as they will be locations where species are most able to persist in a changing climate (Hannah et al. 2007, Hodgson et al. 2009).

Upland species are particularly threatened by warming, because, amongst other things, they are likely to suffer a dramatic reduction in the available land simply because of the smaller area of the landscape existing at higher elevations (Wilson et al. 2005). However, uplands can also be extremely heterogeneous environments where topography has a strong impact on microclimate, notably on the distribution of temperature and moisture availability, where spatial variation is often much greater than in lowland, and of similar magnitude to the amount of temperature change predicted from anthropogenic climate change (Suggitt et al. 2011). The wider range of available microclimates can provide opportunities for species to survive changes in macroclimate by shifting towards more suitable areas without moving over huge distances (Davies et al. 2006, Hodgson et al. 2009). Therefore, prioritising the protection of topographically heterogeneous regions has the advantage of focussing on areas where species are both likely to be threatened by global warming and may find more opportunities to persist thanks to the greater environmental and microclimatic heterogeneity (Hodgson et al. 2009).

Thus, in topographically heterogeneous environments, species may be able to track changes in climate by moving only relatively small distances. This has been best studied in ectothermic insects (e.g. Davies et al. 2006), and plants (e.g. Scherrer and Körner 2011), but it is unclear how important considerations of microclimate are for larger, endothermic taxa. For example, there is mixed evidence regarding the importance of microclimate in determining the distribution or range expansion of birds (Bradbury et al. 2011, Calladine and Bray 2012). Further, it is unclear where microclimate may be important. For ectotherms, microclimate is a more important driver of habitat availability towards the edge of their range (Thomas et al. 1999), but this has not been tested in endothermic species.

Here, we use extensive fine-grained data on the distribution of an exemplar bird species: the meadow pipit (*Anthus pratensis)*. We test firstly the extent to which microclimate is an important determinant of its distribution, and secondly, whether microclimate becomes an increasingly important determinant of distribution towards the edge of the species' range, as assessed from a bioclimate model of range extent. The meadow pipit is widespread across the British uplands where it is often the commonest breeding species, with only localised populations in the English lowlands (Gibbons et al. 1993, Pearce-Higgins and Grant 2006). In the last two decades, it has undergone a population decline throughout Europe (EBCC 2013), including the UK (Risely et al. 2012), where it is projected to further decline in response to future warming (Renwick et al. 2012).

The aim of this chapter was to model the occurrence of meadow pipits as a function of both macroclimate (as a measure of large-scale climate suitability and proximity to the species' range edge) and microclimate variables. This would identify the extent to which microclimate may affect the distribution of meadow pipits across the UK. Specifically, because craneflies (Tipulidae) are an important component of meadow pipit diet, we anticipate that their distribution is negatively affected by drought (Carroll et al. 2011, Pearce-Higgins 2010), and is consequently affected by elevation, solar radiation and topographic wetness indices. Secondly, we expect microclimate effects to be most pronounced towards the margin of the meadow pipit's range, and therefore expect an interacting effect of macroclimate and microclimate on the distribution of meadow pipits, such that microclimate effects are more pronounced in marginal macroclimates. Specifically we test the following hypotheses:

1. Meadow pipit occurrence is positively correlated with variation in the topographical wetness index and altitude and negatively with variation in the solar index.

2. The effect of these microclimate variables is strongest in areas of low macroclimatic suitability.

## 7.2 Methods

### Bird data

This study used data from the BTO/JNCC/RSPB Breeding Bird Survey (BBS), an extensive volunteer survey used to monitor bird populations in the United Kingdom. The BBS is undertaken on a stratified random sample of grid squares, each of width 1 km. Each 1 km square is visited twice between April and July, and birds are recorded along two 1 km line transects, each one divided into five 200 m sections. Each section is also classified according to habitat using a hierarchical coding system of nine classes (Crick 1992). For the purposes of this analysis, we considered the transect sections surveyed in each year (2007-2012) and we considered only sections where the main habitat was likely to be suitable for meadow pipits; specifically comprising semi-natural grassland/marsh, heathland and bogs, or inland rock. All other habitats were excluded. By combining data across years and filtering to exclude unsuitable transects, we reduce the degree of stochasticity in the data, whilst also ensuring that the findings are not simply a function of the weather in one particular year.

### Macroclimate model

Meadow pipit distribution was modelled using the two-step approach of Beale *et al.* (2013). This applies a Bayesian, spatially explicit (Conditional Autoregressive) Generalised Additive Model (GAM) to species distribution data in order to separate climatic, spatial and random components in determining the distribution of each species, and thus accounts for potential spatial autocorrelation in the data (Beale et al. 2013). During the first step, the European meadow pipit distribution (Hagemeijer and Blair 1997) was modelled as function of four bioclimate variables from the CRU TS 1.2 dataset for 1961-90, namely: mean temperature of the coldest month (henceforth referred to as MTCO), growing degree days (GDD5), the coefficient of variation of temperature (CVTemp), and soil moisture (soilWater). MTCO was calculated by simply finding the lowest mean monthly temperature for each cell. GDD5 was calculated by fitting a spline to mean monthly temperatures for each cell to convert monthly data to daily estimates, and then summing the accumulated daily temperature above 5°C. CVTemp was calculated by converting mean monthly temperatures to °K, and then dividing the standard deviation by the mean for each cell. Finally, soilWater was calculated following the bucket model described by Prentice *et al.* (1993), which takes inputs of temperature, rainfall, % sun/cloud and soil water capacities, then calculates the soil water balance over the year for each cell. This European scale model was initially constructed using uninformative priors to describe the relationship between occurrence and climate, which were described by the flexible GAM relationships. Once converged, a second model was fitted to 10x10km meadow pipit distribution data from Great Britain (Gibbons et al. 1993) using the UKCP09 climate data for the same 1961-1990 period. For these models, informative priors were applied from the European scale model so that any strong climatic signal based on the European distribution would remain essentially unchanged when modelled using British data only, unless the evidence for a different climatic signal within the UK is strong. Due to the spatial component in the modelling process, modelled distributions tend to closely match observed distributions (Beale et al. 2013).

## Microclimate data

Directly observed microclimatic data were not available at the required spatial resolution across the whole UK, so we used topographical information to calculate microclimate proxies. This is possible for open, upland environments where topography is the most important factor contributing to microclimate. Given their insectivorous diet, meadow pipits are potentially vulnerable to negative effects of summer temperature or drought upon prey abundance (Pearce-Higgins 2010), as well as more general effects of climate upon vegetation structure and composition (Pearce-Higgins and Grant 2006). We therefore summarised microclimate using two variables describing variation in temperature and variation in moisture availability. Firstly, we used the summer solar index as a proxy of summer maximum temperature, likely to reflect the period when temperature may be limiting (Pearce-Higgins et al. 2010). This was calculated as the proportion of direct full beam radiation that reaches the ground, which is a function of slope, aspect, topographic shading and sun position (itself a function of latitude, longitude, date and time), and was summarised as mean hourly solar radiation on the summer solstice (see Chapter 4). Secondly, we calculated a measure of soil moisture (the topographic wetness index) from estimated surface run-off and topographic situation. This measure has a lower value on flat areas and valley bottoms and a higher value on slopes and mountain tops (see Chapter 4). Thirdly, we also consider variation with elevation, likely to be strongly correlated with fine-scale variation in mean temperature, by including the difference between the elevation of each 100 x 100 m cell and the mean of the surrounding cells within 10 km (see Chapter 4). Microclimate values for each 100 m square were averaged for each 200 m transect section.

## Analysis

To test our first hypothesis we modelled the probability $P$ of each meadow pipit being recorded in each square as a function of the macroclimatic model ($Pm$), elevation ($h$); summer solar index ($s$) and the topographic wetness index ($w$). As the data are structured in three hierarchical levels (transect sections nested within 1 km squares nested within 10 x 10 km squares), we used a generalised mixed model approach in which each transect $T_i$ 1-km square $g_j$ and 10 x 10 km square $G_k$ were modelled as random effects. The full model is thus given as follows:

$$\text{logit}(P_{ijkl}) = \alpha + \beta_1 \times T_i + \beta_2 \times g_j + \beta_3 G_k + \beta_4 \times Pm_{ijkl} + \beta_5 \times h_{ijkl} + \beta_6 \times s_{ijkl} + \beta_7 w_{ijkl} + \varepsilon_{ijkl} \qquad (1)$$

Where $\alpha$ is the constant, $\beta_{1.-n}$ are model coefficients associated with random (1-3) and fixed (4-7) factors and $\varepsilon_{ijkl}$ are the random errors.

In order to examine the relative importance of macroclimate and microclimate suitability in determining meadow pipit occurrence at different scales, we documented changes to residual covariance at the 10 km, 1 km and transect level upon the insertion of firstly the macroclimate variable $P_m$, and then the inclusion of the microclimate variables ($h$, $s$ & $w$). Thus, we first described covariance in a null model with no fixed effect:

$$\text{logit}(P_{ijkl}) = \alpha + \beta_1 \times T_i + \beta_2 \times g_j + \beta_3 \times G_k + \varepsilon_{ijkl} \qquad (2)$$

Macroclimatic suitability was then included as the sole fixed effect:

$$\text{logit}(P_{ijkl}) = \alpha + \beta_1 \times T_i + \beta_2 \times g_j + \beta_3 \times G_k + \beta_4 \times Pm_{ijkl} + \varepsilon_{ijkl} \qquad (3)$$

Finally, this was compared to the full model (1).

The second hypothesis was tested by additionally testing the significance of interactions between macroclimate suitability $P_M$ and each of the microclimate variables as follows:

$$\text{logit}(P_{ijkl}) = \alpha + \beta_1 \times T_i + \beta_2 \times g_j + \beta_3 G_k + \beta_4 \times Pm_{ijkl} + \beta_5 \times h_{ijkl} + \beta_6 \times s_{ijkl} + \beta_7 \times w_{ijkl} + \beta_8 \times Pm \times h_{ijkl} + \beta_9 \times Pm \times s_{ijkl} + \beta_{10} \times Pm \times w_{ijkl} + \varepsilon_{ijkl} \qquad (4)$$

Where $\beta_{8..10}$ are the model coefficients associated with interactions between microclimate and macroclimate. This allowed us to describe the importance of variation in microclimate importance with increasing macroclimate suitability in driving additional variation in meadow pipit occurrence at the three spatial scales considered of 10 km, 1 km and transect level. A final model was simplified by backwards selection of non-significant ($p > 0.05$) variables from model (4). Individual relationships between variables and meadow pipit occurrence were plotted by fixing the values of the other explanatory variables to their median values.

## 7.3 Results

### Microclimate importance

The probability of meadow pipit occurrence in a transect section was significantly affected by both macroclimate and each of the microclimate variables (Model 1). As expected, occurrence was positively correlated with variation in the topographical wetness index and negatively correlated with variation in the solar radiation index, which confirm our hypotheses, although the former relationship was relatively weak. Meadow pipit occurrence was also positively correlated with elevation (the difference between the elevation of the 100 x 100 m cell and the surrounding cells within 10 km), confirming the association of this species to cooler locations at higher elevation (Table 7.1).

Examination of the variance components of the random effects indicates that $P_M$ (Model 3) accounts for 6.8% of the variation in meadow pipit occurrence at the 10 km level. The inclusion of the microclimate terms accounts for a further 28%, 37% and 31% of additional variance in meadow pipit presence, at the 10-km, 1-km and transect section levels respectively (Table 7.2). Thus, microclimate and topography have a significant impact on meadow pipit occurrence in the UK, in addition to the large-scale impacts of macroclimate suitability.

### Interactions between microclimate and macroclimate.

The model with interactions between microclimatic variables and macroclimate suitability (Model 4) showed that the importance of both elevation and summer solar index varied in relation to macroclimate suitability (Table 7.3). The full spread of these relationships is presented in Figure 7.1a-c, indicating not only the direction and importance of the relationships, but the spread of the data used to parameterise the models.

The positive interaction between elevation ($h$) and macroclimate suitability ($P_m$) was opposite to that expected; Meadow pipits were more likely to occur at cooler, higher elevation locations in the core of their range with maximum macroclimatic suitability (Figure 7.1a, 7.2a-c). The interaction therefore does not indicate that the importance of elevation decreases with increasing macroclimate suitability (high elevations are always preferred). This may reflect the underlying topographical variation around the country, in this case the relative lack of elevational range in areas of low macroclimatic suitability (the south and south-east).

The negative interaction between summer solar index and macroclimate suitability (Figure 7.1b, 7.2d-f) does match with expectation. The probability of meadow pipits being found on transect sections with the lowest summer solar index was greatest at sites with low macroclimate suitability, whilst when macroclimate suitability was high, this effect was somewhat less pronounced. Thus, meadow pipits occur more frequently on cooler slopes, particularly where macroclimate suitability is low, whilst this effect is less apparent where macroclimate suitability is high. The interaction between the topographic wetness index and macroclimate was non-significant ($p = 0.091$), and deleted from the final model (Figure 7.1c, 7.2g-i).

Combined, the effect of these interactions between macroclimatic suitability and measures of microclimate explained a relatively small proportion of the residual variation in meadow pipit occurrence at either the 10km, 1km or transect section scale, accounting for additional 3.5%, 0.8% and 0.3% of the variation in occurrence respectively.

**Table 7.1** Parameter estimates for the final model (1) without interactions. $P_m$: estimated probability of detecting the species from the macroclimatic model; $h$: difference between the elevation of the centroid of the transect section and the average elevation of the 10km grid square; $s$ midsummer insolation index; $w$ is the topographic wetness index.

| Variable | Coefficient | Std. error | p-value |
|---|---|---|---|
| $h$ | 0.009 | 0.001 | <0.001 |
| $s$ | -12.345 | 1.688 | <0.001 |
| $w$ | 0.019 | 0.009 | 0.035 |
| $P_m$ | 1.944 | 0.514 | <0.001 |
| Intercept | 1.702 | 0.643 | 0.008 |

**Table 7.2** Variance components of random effects.

| **Fixed effects** | **Random effects** | | |
|---|---|---|---|
| | **10-km square** | **1-km square** | **Transect section** |
| Model (2) None | 5.126 | 2.275 | 1.726 |
| *Model (3)* $P_m$ | 4.774 | 2.305 | 1.734 |
| *Model (1)* $P_m + h + s + w$ | 3.435 | 1.465 | 1.193 |
| *Model (4)* $P_m + h + s + w + P_m \times h + P_M \times s + P_M \times w$ | 3.254 | 1.446 | 1.187 |

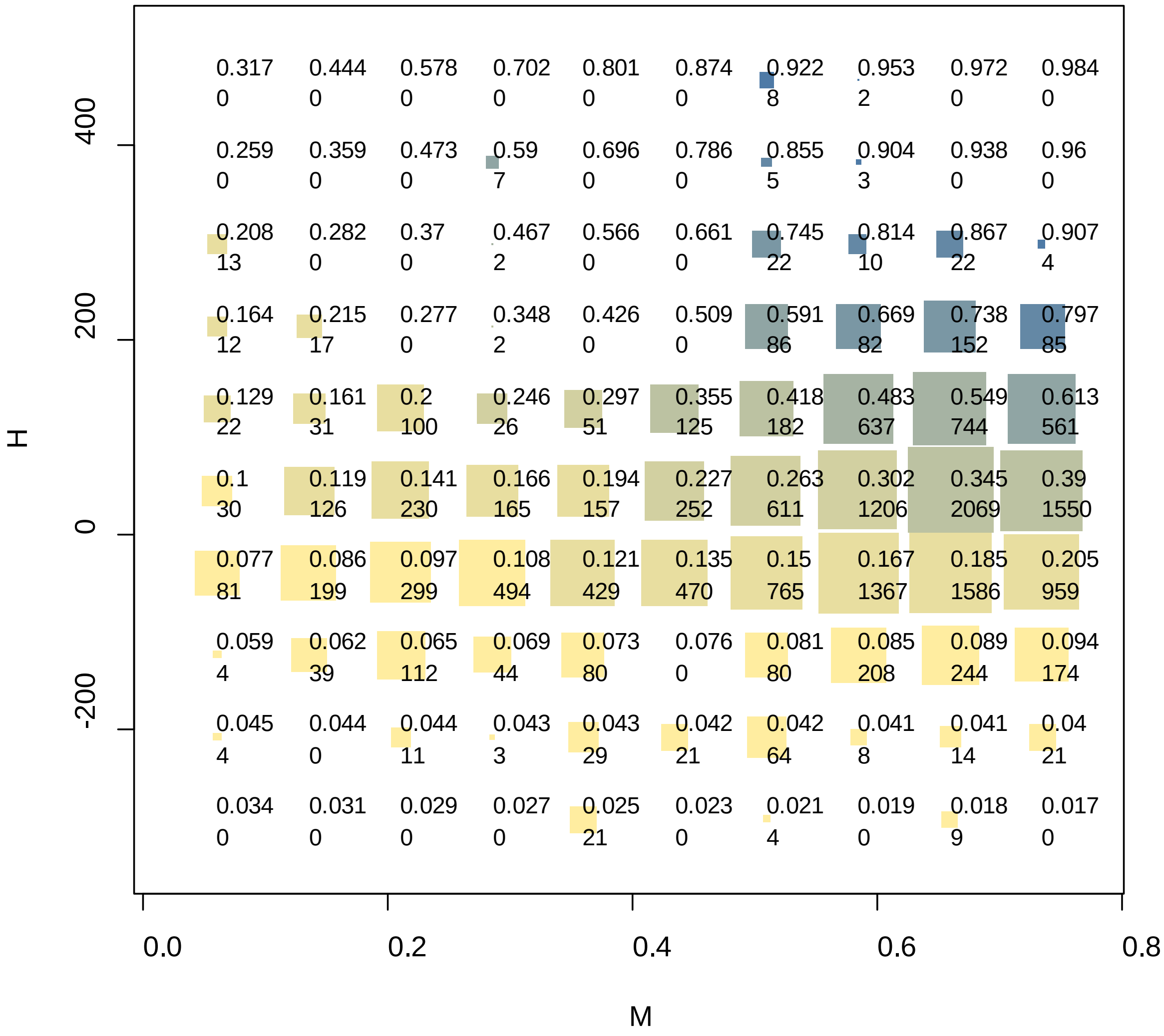


**Figure 7.1a.** Graphical representation of the effects of *M* (estimated probability of detecting the species from the macroclimatic model) and *H* (difference between the elevation of the centroid of the transect section and the average elevation of the 10km-square) and their interactions on the probability of finding the species in a transect section. For each combination of *M* and *H*, we present the results in two complementary ways, numerically (pair of numbers) and visually (square), for ease of interpretation. The upper number and the colour of the square indicate the estimated probability of detecting a meadow pipit (dark blue: high probability; light yellow: low probability). The lower number and the size (logarithm of the area) of the square indicate the number of transect sections with the given combination of *M* and *H*. When fitting the model to produce the graph, *S* and *W* were kept fixed to their median values across all data.

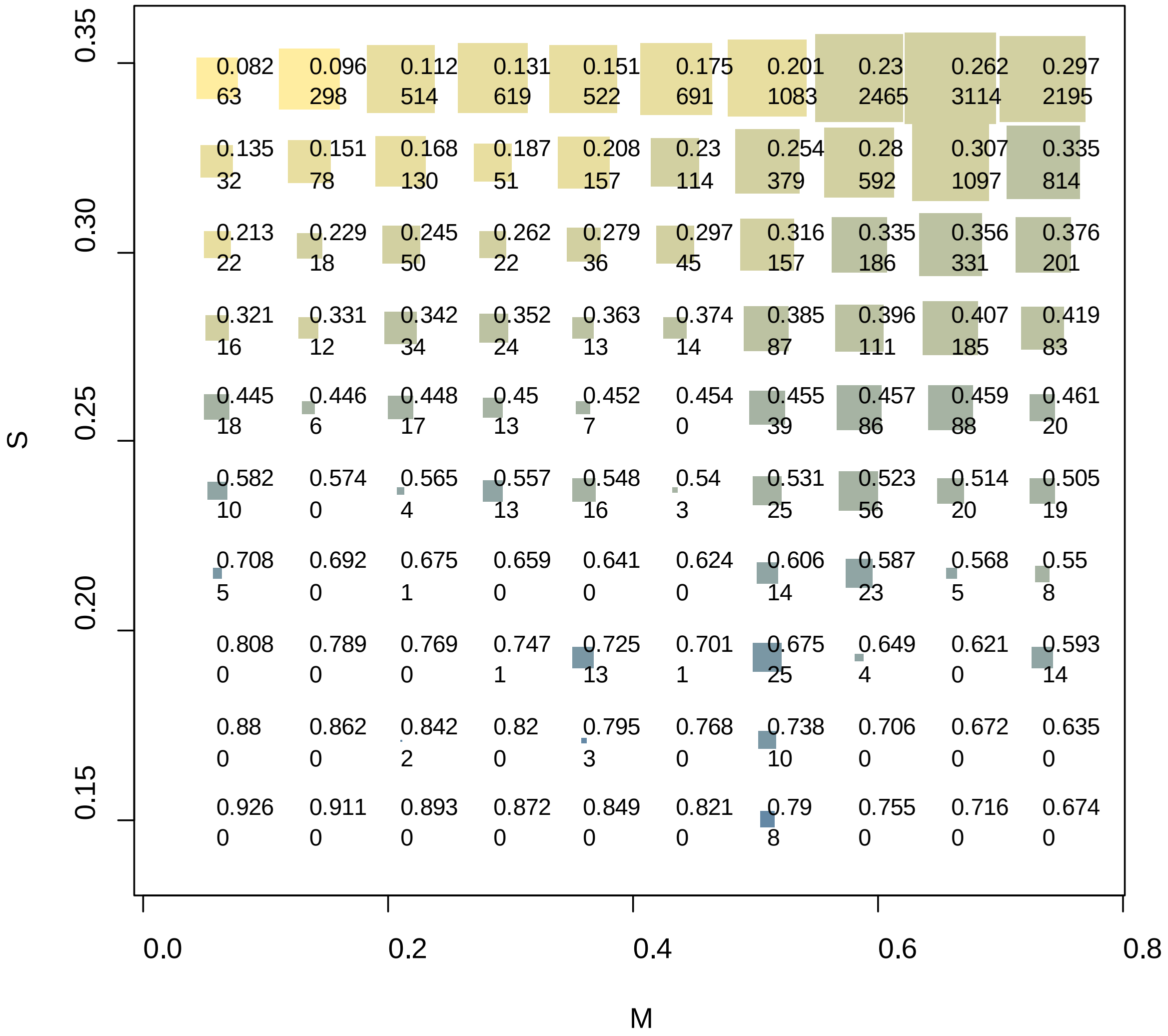


**Figure 7.1b.** Graphical representation of the effects of *M* (estimated probability of detecting the species from the macroclimatic model) and *S* (midsummer insolation index) and their interactions on the probability of finding the species in a transect section. For each combination of *M* and *S*, we present the results in two complementary ways, numerically (pair of numbers) and visually (square), for ease of interpretation. The upper number and the colour of the square indicate the estimated probability of detecting a meadow pipit (dark blue: high probability; light yellow: low probability). The lower number and the size (logarithm of the area) of the square indicate the number of transect sections with the given combination of *M* and *S*. When fitting the model to produce the graph, *H* and *W* were kept fixed to their median values across all data.

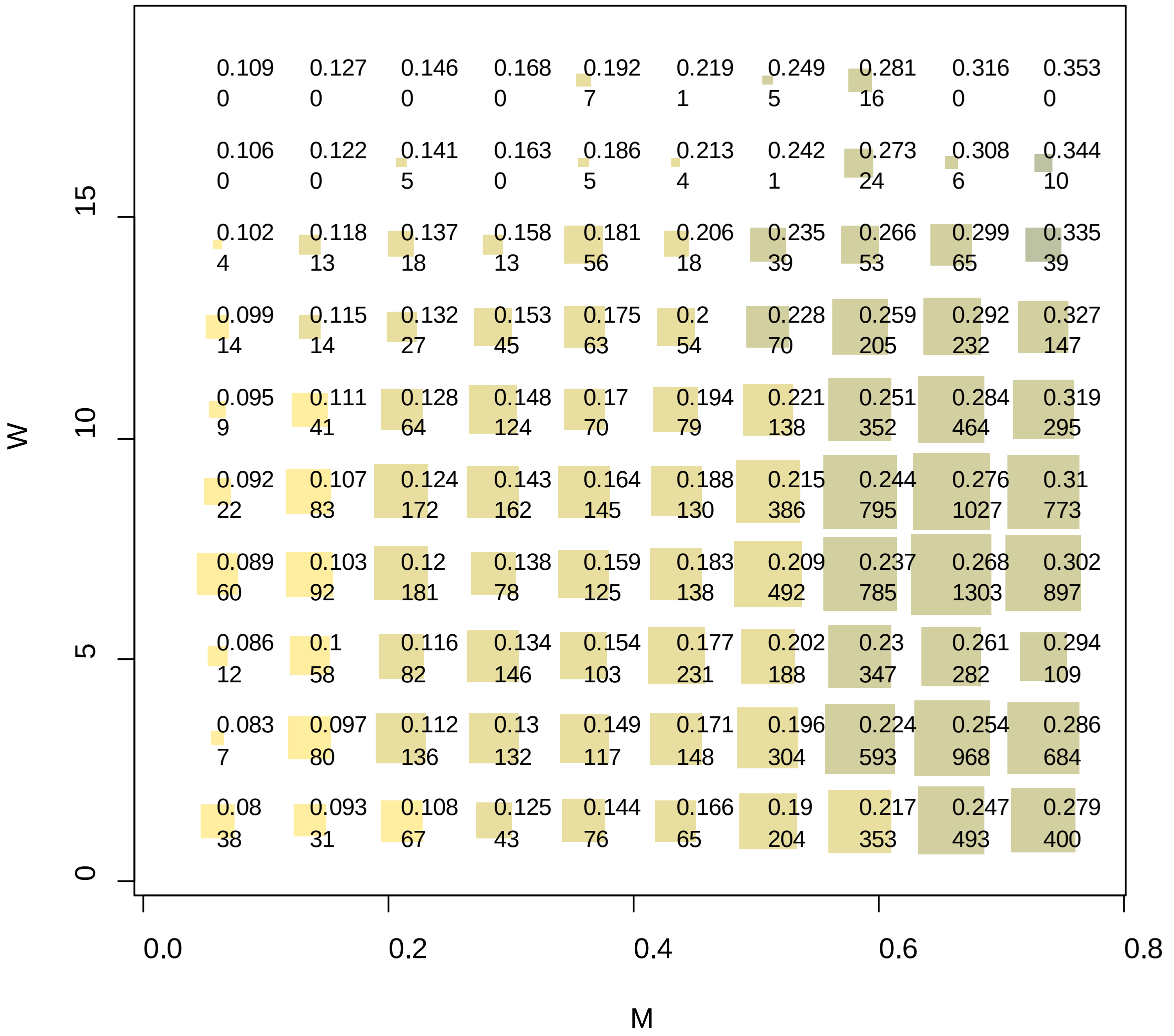
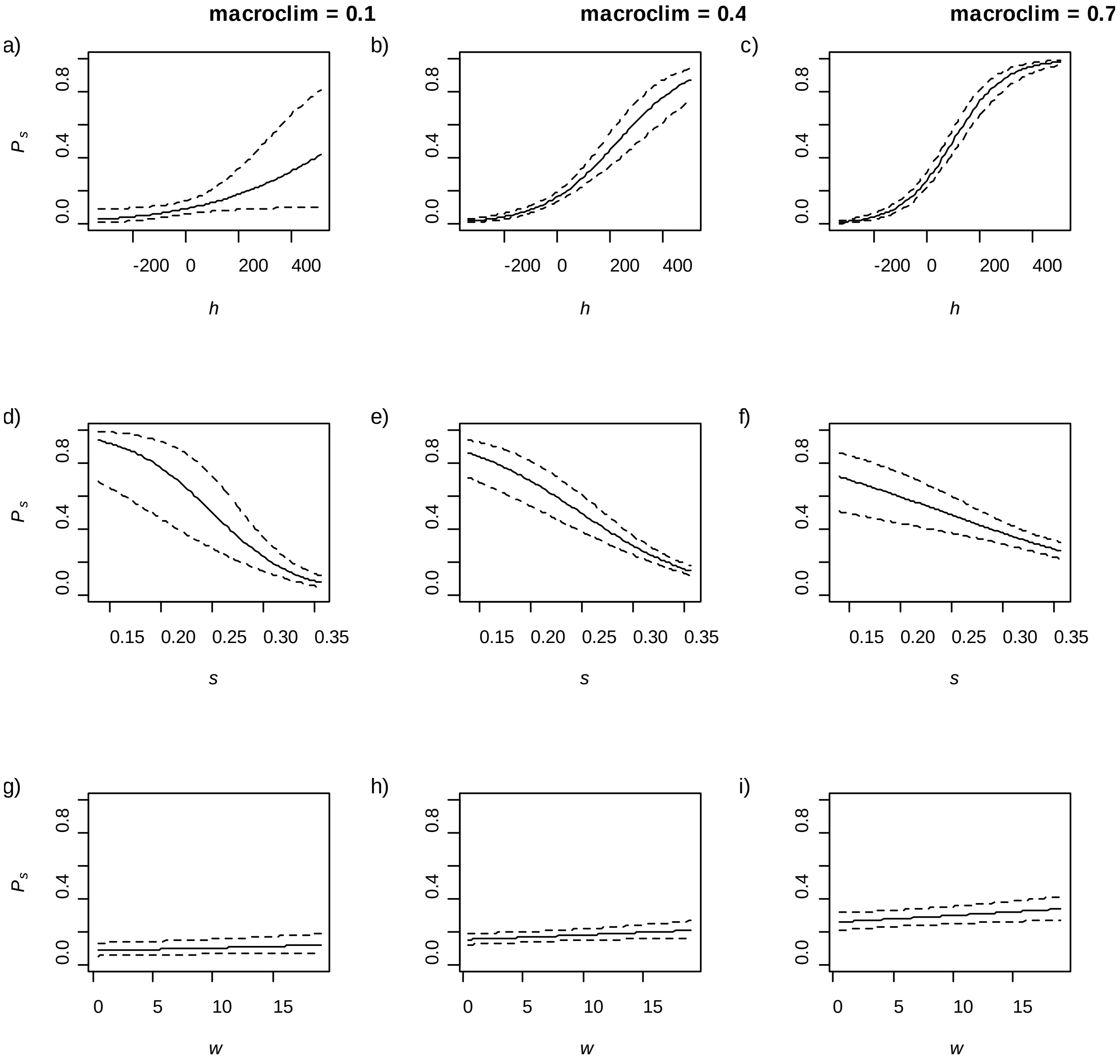


**Figure 7.1c.** Graphical representation of the effects of *M* (estimated probability of detecting the species from the macroclimatic model) and *W* (topographic wetness index) on the probability of finding the species in a transect section. For each combination of *M* and *W*, we present the results in two complementary ways, numerically (pair of numbers) and visually (square), for ease of interpretation. The upper number and the colour of the square indicate the estimated probability of detecting a meadow pipit (dark blue: high probability; light yellow: low probability). The lower number and the size (logarithm of the area) of the square indicate the number of transect sections with the given combination of *M* and *W*. When fitting the model to produce the graph, *H* and *S* were kept fixed to their median values across all data.

**Table 7.3** Parameter estimates for the final model with interactions. $P_m$*:* estimated probability of detecting the species from the macroclimatic model; *h:* difference between the elevation of the centroid of the transect section and the average elevation of the 10km grid square; *s*: summer insolation index; and *w:* the topographic wetness index.

| Variable | Coefficient | Std. error | p-value |
|---|---|---|---|
| $h$ | 0.003 | 0.002 | 0.177 |
| $s$ | -26.726 | 5.600 | <0.001 |
| $w$ | 0.021 | 0.009 | 0.024 |
| $P_m$ | -6.57 | 3.295 | 0.046 |
| $P_{m\times}h$ | 0.011 | 0.004 | 0.002 |
| $P_{m\times}s$ | 25.339 | 9.705 | 0.009 |
| Intercept | 6.523 | 1.905 | 0.001 |

**Figure 7.2** Plots of the partial effects of elevation difference (*h*, panels a, b, c), summer insolation index (*s*, panels d, e, f) and topographic wetness index (*w*, panels g, h, i) on the probability of finding a meadow pipit in a transect section, for three different levels of macroclimatic suitability ($P_m$, calculated by Beale *et al.* 2013). A value of 0.1 corresponds to low macroclimate suitability, 0.4 to medium suitability, and 0.7 to high suitability. Dashed lines show 95% confidence intervals. $P_s$ is the probability of detecting meadow pipit derived from Model 4.



## 7.4 Discussion

There have been relatively few studies of the impact of microclimate on birds. Whilst a number of studies have examined the effects of microclimatic variation of nest sites upon measures of the condition of chicks or productivity of those nests (e.g. Dawson et al. 2005, Rockweit et al. 2012), relatively few have considered the importance of these effects in determining the distribution of breeding birds. Our first conclusion is that for meadow pipit, fine-scale variation in topography, as measured by elevation, solar index and topographic wetness, influences both: a) where meadow pipits are located in the landscape (explaining about 1/3 of the variation in the probability of occurrence between transect sections within individual 1 km squares), b) variation in the distributions of meadow pipits measured at the 1 km square level and at the 10 km square level. Previous work has shown that elevation alone can explain almost a quarter of the variation in meadow pipit abundance between 200 ha plots (Pearce-Higgins and Grant 2006), some of which, our results suggest, may be directly attributable to microclimatic associations. As outlined in the introduction, these apparent associations of meadow pipits for high elevations, cool slopes and wet locations, can be explained by reference to their ecology and that of their prey (Pearce-Higgins 2010, Pearce-Higgins et al. 2010, Carroll et al. 2011). Given the importance of topography in determining the abundance or occurrence of a wide range of upland bird species (e.g. Sim et al. 2007, Pearce-Higgins et al. 2007), these findings may be widely applicable. Certainly the elevational distribution of Whinchat *Saxicola rubetra* varies significantly between north- and south-facing slopes in a manner consistent with temperature limiting their occurrence (Calladine and Bray 2012).

Secondly, we considered the extent to which the importance of microclimate varied with proximity to the species range margin, as assessed by the outputs from the macroclimate suitability model of Beale *et al.* (2013, in review). Previous work has shown how microclimate may be an increasingly important driver of occurrence towards a species range edge in some invertebrate groups (Thomas et al. 1999, Davies et al. 2006, Oliver et al. 2009), but not others (Gillingham et al. 2012). Here, in what is to our knowledge the first test of this in birds, we find evidence that statistically, this is the case. However, it appears to be a relatively weak effect in terms of actually influencing the occurrence of meadow pipits on the ground. At the range margin of a species, the importance may be greater than this figure suggests. Thus, we find that meadow pipits are increasingly found on cool slopes with a lower solar index in areas of decreasing macroclimate suitability in southern England. This suggests that when it is warm, birds are increasingly found on cool slopes (Figure 7.1b, Figure 7.2 panels d-f), but when macroclimate suitability is high, solar index has a rather weaker effect on occurrence. Further modelling work should be conducted to consider the potential for microclimate to actually prevent localised population declines and extinctions as a result of climate change, for example extending the modelling work of Renwick *et al*. (2012). We found no evidence for the same relationship with wetness or elevation, with in fact the opposite interaction than expected for the latter (Figure 7.1a, 7.2 panels a-c).

To conclude, these results suggest that in a changing climate, where warming may reduce large-scale climatic suitability for meadow pipits in the UK (Renwick et al. 2012), topography and microclimate may influence their distribution. Thus, areas of potentially suitable habitat on cool slopes with a low solar index should be particularly protected as they will become increasingly utilised, and potentially may remain the only locations occupied in conditions of unsuitable climate (Figure 7.1b). Given the statistical strength of our interactions, but their relatively limited impact on occurrence across the entire dataset, it remains unclear precisely what degree of warming birds occupying areas of low solar index would be resilient to. Although our results suggest that the extent of cool slopes may influence occurrence and therefore probably meadow pipit density at both 1 km and 10 km resolutions, more work examining the relationships between macro- and micro-climate and abundance is required to test this fully. Thus, as a study of an example upland bird likely to be threatened by climate change in ways relevant to other species (cf. Pearce-Higgins 2010), this work supports the suggestion that areas of high topographical complexity, which are likely to contain cool slopes and high altitudes, should be protected (Hodgson et al. 2009). Thus, although there was little evidence that the range expansion of Dartford Warbler *Sylvia undata* had resulted in significant changes to the microclimatic association of the species, apart from warmer temperatures facilitating an altitudinal expansion in range (Bradbury et al. 2011), there may be more potential for microclimatic variation to provide refugia for cold-adapted species. We recommend that this work be extended, using the same BBS data, to a wider range of species to test this more fully, and particularly to compare the responses of northerly- and southerly-distributed species.

# 8. General discussion

## Evidence for the existence and role of refugia from climate change

Given limits on resources, existing pressures on the natural environment and competing demands for land use, the adaptation of conservation to climate change will need to be prioritised and targeted carefully. We have assessed evidence for the existence of *refugia* from climate change, areas where species are more likely to persist, despite climate change making the wider landscape less suitable. We have found evidence that refugia exist in England, and have likely buffered both plant and animal species from the adverse effects of recent climate change. Therefore, the identification of refugia, and the prioritisation of action to protect and enhance them, could both play an important role in adapting conservation to climate change.

An ever-broadening literature on the subject of refugia from climate change (Chapter 3) has united the otherwise disparate fields of biogeography, ecology, palaeoecology and phylogeography. This literature suggests that a range of particular landscape characteristics may have contributed to the ability of species to withstand past changes to the climate *in situ*. These characteristics included various atypical temperature or moisture regimes. The evidence for the relative importance of such characteristics varies greatly among taxa (Table 3.1).

Nevertheless, information from our literature review enabled us to construct proxies for microclimatic features of the landscape that are likely to contribute to refugium potential across England. National trends in the distributions of 1,082 declining species, drawn from a range of taxa that are expected to be threatened by climate change, provided evidence that such features of the landscape may indeed have enhanced recent persistence (Chapter 4). Most tellingly, although local extinctions are higher in areas of England that have experienced greater climatic change, regional variation in topographic features influencing microclimate appears to have enhanced the persistence of a broad range of species in these areas.

Finding clear and consistent evidence of refugia acting at the landscape level proved more challenging (Chapter 5), because of a paucity of fine resolution species distribution records. However, we did find evidence that lower agricultural intensity and (to a lesser extent) higher elevations have protected species from climate change. We selected one study area (Dartmoor) for testing these results with field surveys (Chapter 6), finding that our proxies of the availability of microclimatic conditions expected to favour persistence explained the fine-scale distributions of species with reasonable success. Finally, we found that populations of an exemplar species with a high moisture requirement, the meadow pipit (Chapter 7), responded to microclimate. This species occurred on cooler, wetter slopes at higher elevations more frequently, especially where the wider climate is less suitable.

Taken together, these lines of evidence offer real support for the hypothesis that refugia exist in England and have already buffered species from climate change. At national level (Chapter 4), microclimatic diversity in regions like Cumbria and the North Pennines is relatively high. Levels of persistence in these areas were high enough for them to be considered interglacial refugia for cold-adapted species (parts of these areas, such as Upper Teesdale NNR, already are). The identification of microclimatically diverse areas *within* these landscapes (Chapters 5, 6, 7), at finer resolutions, again led to the discovery of associations with high persistence in areas that could be termed *micro*refugia (Rull 2009). As in the previous glacial episode, these microrefugia are more likely to buffer smaller species (with smaller territories, if the species has one) from the effects of climate change, while larger species (and particularly larger animals) will require macrorefugia to persist at a particular location.

Persistence in different taxa was associated with different environmental drivers. This was apparent across all scales and in all elements of the project. Therefore, although the maps in Figures 4.2-4.4 provide an indication of the sorts of areas that are important in the climate response of the biota as a whole, a ‘one size fits all’ approach may not be appropriate. Specifically, managing the landscape for floral refugia may require a different set of interventions or measures to management targeted at insects, other invertebrates or birds. There may still be commonalities, however: in particular, the protection of upland, hilly areas may lead to positive outcomes for many taxa. It is worth noting that, although some taxonomic groups have benefitted from recent climate warming on the whole (e.g. butterflies, Chapter 4, see also Warren et al. 2001, Hickling et al. 2006), the level of future climate change will be such that more species will be adversely affected by 2050 (IPCC 2007). Apparent benefits must therefore be interpreted carefully, and actions to enhance persistence in cold-adapted taxa may be of benefit to a wider range of species in future. We discuss what some of these actions might be below.

## Relevance for conservation

Do refugia matter for conservation? Of course, this question depends on the context, taxonomic group and landscape(s) in question, but we hope this report provides some useful information on where and how adapting conservation to climate change *could* take advantage of microclimate, instead of merely saying that it *should*. The refugia maps provide a clear starting point for action on the ground. Integrating refugia into approaches to prioritise conservation management (for example in the targeting of new Agri-Environment Schemes) could prove fruitful. As we have shown, proxies of microclimate are relatively easy to compute at the scale required for this. A robust integration of methods for prioritisation, including refugium potential, would likely require more detailed testing of the microclimate proxies at the fine scale. The analyses presented in Chapter 5 showed that more finely-resolved species distribution data are needed for this; although these data are not available nationally, there are a number of well-understood, data-rich study areas where fine-scale analyses would be possible (e.g. The Lizard NNR, Cornwall). Further detail on applying microclimate at this scale may also emerge from a subsequent NERC Knowledge Exchange Project currently being conducted by the authors.

Our identification of areas of high refugium potential (based on rates of persistence) also allowed a cross-comparison with the current protected area network, and an assessment of the overlap between them. It is encouraging that: a) persistence has been higher within protected areas (except in higher plants), and b) areas of higher refugium potential do largely overlap with the protected area network. This is consistent with similar work on other, independent datasets (for birds, Johnston et al. 2013). Including the locations of protected areas within the models showed that protection was a significant predictor of persistence, independent of the refugia properties of these areas. So we cannot conclude that it is solely these landscape properties that drive persistence patterns (i.e. irrespective of protection). There may therefore be additional benefits to expanding the network of protected areas to include important refugia areas uncaptured by current sites. Further analysis would be required to identify these locations.

There may also be opportunities to integrate refugia within wider, less formal conservation initiatives, such as landscape scale conservation approaches (e.g. Wildlife Trusts ‘Living Landscapes’, RSPB ‘Futurescapes’, and ‘Nature Improvement Areas’). These initiatives aim to go beyond site-based conservation to expand, buffer and link up existing reserves and extend conservation management into the wider countryside, where populations interact and respond to change (Macgregor et al. 2012). Although this is a relatively recent move, some projects are well-established, and have reported a number of successes (Ellis et al. 2012). As well as an understanding of metapopulation dynamics, such schemes rely on a wider assessment of landscape resources, and require careful spatial prioritisation of conservation effort. The buffering effect of refugia, and its benefit to species undergoing climatic shifts (quantified above), should be considered within these assessments (Dennis 2010, Van Dijk et al. 2013). As with the targeting of the new Agri-Environment Scheme, such assessments will provide the best information if they are updated regularly; this applies even more so when considering the role of refugia in protecting populations of species against the effects of climate change, as patterns of climate change will be spatially variable. These updates would also add value by ground-truthing model outputs, and giving an indication of which refugia are most effective.

## Questions for further research

Our report provides a useful, ‘first pass’ assessment of the role of refugia across selected English taxa in the context of climate change. There remains however a great deal to learn about contemporary refugia, especially in comparison to the relatively mature literatures on glacial refugia or species range shifts at the macro scale. Rates of persistence vary substantially across England, and we have shown that some of this variation can be explained by modelling the landscape features that lead to refugia. There are, however, other landscape features that lead to climate refugia that were not captured by our datasets that will undoubtedly interact with the landscape features we modelled, notably habitat type. For example, taller vegetation provides a cooler daytime microclimate that could provide relief from hot conditions (Thomas et al. 1999). Availability of such habitat may be important for species already occupying the warmest microsites, i.e., south-facing slopes. Testing for the importance of such interactions beyond the field scale will tell us more about which particular habitat patches are critical to species’ climate responses. Moreover, we use proxies of microclimate heterogeneity. It would be useful to explicitly model the climate itself at the fine scales that better match those experienced by organism. This would also allow an assessment of whether there are local differences in the rates of climate change, and a subsequent test to determine whether species exploit microclimates that expose them to lower rates of change.

Whilst autecology may be out of vogue in ecology (Huntley 2012), our case study of the meadow pipit illustrates that, for a species of conservation priority, where the biology is well understood, there is value in bespoke analyses of responses to microclimate. As we have emphasised above, computing power now permits the calculation of microclimate for large spatial extents. Testing these predictive data against large biological datasets (‘big data’), which are also increasingly available, would likely reveal further associations between microclimate and the distributions of many more taxa. The need to understand these associations is made pressing by climate change, and improvement here would lead to conservation practices more targeted and tailored to the species of interest (potentially saving money in the process).

## Concluding remarks

Refugia are a well-established feature of the last glaciation, harbouring many of the warm-adapted species occupying England today. Anthropogenic climate change now means that our present biota will struggle to track its (macro) climatic niche; this has led to a drive to understand how wildlife may adapt to warming *in situ*. Here, we offered evidence that contemporary refugia have buffered English species from adverse climate changes, in a similar manner to the last glacial episode. The buffering effect of microclimate was apparent across all spatial scales and in all environments we tested. Where they exist outside of current conservation networks, these refugia should be protected to ensure that English wildlife has the best possible opportunity to persist in the warmer world.

# 9. Acknowledgements

Funding for this project was provided by Natural England (Contract reference 24799). Many thanks to the Centre for Ecology and Hydrology Biological Records Centre, Butterfly Conservation, Botanical Society of Britain and Ireland, Natural England GI team (Hannah Ross, Nigel Brown), Met Office Hadley Centre, British Geological Survey, National Aeronautics and Space Administration, and British Trust for Ornithology for data access. Robin Shail (Camborne School of Mines) provided support on the creation and interpretation of geological layers.

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# Appendix 1: Literature search results

Supplementary tables from the literature review.

**Appendix 1 Table 1** Studies revealed by literature search with ‘past’ refugia search terms.

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Ashcroft | A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix | Global Change Biology | Not applicable | Rainforests, alpine grasslands and swamps | | 2 years (2009-10) | 5th percentile TMIN, 95th percentile TMAX, difference from the matrix (5km radius), intra-seasonal, intra-annual and interannual stability | | | | Warm |
| | **One sentence summary**<br>Retracting rainforests and Alpine grasses occupy microrefugia that are more extreme, stable or isolated than the landscape average. | | | | | **Why is it a refugium?**<br>Sites that were extremely cold, colder than the matrix, or climatically very stable. Input variables to topoclimate models were elevation, distance to coast, canopy cover, latitude, cold-air drainage, and topographic exposure to the northwest, northeast, and south. | | | | | |
| 2010 Ashcroft | Identifying refugia from climate change | Journal of Biogeography | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>More care needs to be taken in how we use the term 'refugia'. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Bertrand | Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: the case of *Quercus pubescens* in France | Global Change Biology | Downy oak (*Quercus pubescens*) | Trees | France | Present and future | | | High soil pH | | Warm |
| | **One sentence summary**<br>Potential refugia for a tree species were unidentified if soil data were omitted from an analysis of future range patterns. | | | | | **Why is it a refugium?**<br>Areas of high pH facilitated persistence under climatic change. | | | | | |
| 2008 Birks (entry on LGM trees) | Alpines, trees, and refugia in Europe | Plant Ecology and Diversity | Various | (Temperate deciduous) Trees | Europe | Present | Absence of permafrost | | Mid elevation, diverse topography, valley bottoms | | Cold |
| | **One sentence summary**<br>Trees survived in LGM refugia that were in mid-elevational bands in southerly refugia, but also in local microrefugia in the north (mostly in Central Europe). | | | | | **Why is it a refugium?**<br>Adequate soil moisture, temperatures warm enough to permit tree growth, shelter from strong winds, and an absence of permafrost and periglacial activity. | | | | | |

| Year and lead author | | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2008 | Birks (entry on Arctic-Alpines in present day) | Alpines, trees, and refugia in Europe | Plant Ecology and Diversity | Various | (Arctic-Alpine) plants | Europe | | | | Steep slopes with base-rich soils, such as sea cliffs, other coastal habitats, inland cliffs and screes, open river shingle and alluvium, river gorges and eroded river banks, lake shores, and shallow soils on steep limestone slopes | Open habitat, absence of (larger) competitors | Warm |
| | | **One sentence summary**<br>Arctic-Alpine plants survived interglacials in areas of naturally open habitat that were not beyond or above the forest limit. | | | | | **Why is it a refugium?**<br>Steep terrain, shallow soils, and/or exposure prevents competition by larger shrubs or trees. | | | | | |
| 2008 | Depraz | Postglacial recolonization at a snail's pace (*Trochulus villosus*): confronting competing refugia hypotheses using model selection | Molecular Ecology | Hairy land snail *(Trochulus villosus)* | Gastropods | The French Jura and Central Switzerland | LGM and present | Mean temperature in the warmest quarter, mean maximum temperature of the warmest month | Mean precipitation in the warmest quarter, mean annual precipitation, mean precipitation in the wettest month | | | Cold |
| | | **One sentence summary**<br>Hairy land snails occupied warm ice-free refugia in the French Jura and Central Switzerland during the LGM. | | | | | **Why is it a refugium?**<br>Ice-free patches within the ice sheet that offer sufficient moisture. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2011 Dobrowski | A climatic basis for microrefugia: the influence of terrain on climate | Global Change Biology | *Abies magnifica* | Trees | Sierra Nevada, USA | Present and future | Minimum temperature | Climatic water deficit | Valley bottoms (cold air drainage) | | Warm |
| | **One sentence summary**<br>A better understanding of topographic climate effects, and the microrefugia they can generate, alters predictions of species persistence. | | | | | **Why is it a refugium?**<br>Cold air drainage provides the necessary minimum temperatures in valley bottoms. | | | | | |
| 2009 Fløjgaard | Ice age distributions of European small mammals: insights from species distribution modelling | Journal of Biogeography | Various rodents | Mammals | Eurasia | LGM and present | Growing day degrees, annual mean temp | Water balance, annual precipitation | | Habitat structure and food availability provided by vegetation (indirect climate effect) | Cold |
| | **One sentence summary**<br>Rodents with higher latitude distributions in the present day are more likely to have occupied higher latitude refugia in the LGM. | | | | | **Why is it a refugium?**<br>Refugial locations provided the requisite growth potential and water availability for the vegetation that the rodents require for food and as habitat. | | | | | |
| 2009 Holderegger | A discussion of different types of glacial refugia used in mountain biogeography and phylogeography | Journal of Biogeography | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>The terms nunatak, peripheral, lowland, in situ and ex situ are described and their meanings clarified. | | | | | **Why is it a refugium?**<br>(Non-quantitative study) | | | | | |

<table>
<tr><th>Year and lead author</th><th>Title</th><th>Journal</th><th>Species</th><th>Taxon</th><th>Location</th><th>Period of reference (eg LGM, present)</th><th>Temp feature of the refugium</th><th>Moisture feature of the refugium</th><th>Geophysical feature of the refugium (eg frost hollow, topo diversity)</th><th>Biotic feature of the refugium</th><th>Is it a refugium for a warm episode or a cold episode?</th></tr>
<tr><td rowspan="2">2012 Keppel</td><td>Refugia: identifying and understanding safe havens for biodiversity under climate change</td><td>Global Ecology and Biogeography</td><td colspan="8">(General discussion of refugia characteristics- include only in text)</td><td>Not applicable</td></tr>
<tr><td colspan="5">**One sentence summary**<br>Refugia are reviewed and a conceptual framework for refugia is presented, which is hoped will facilitate more integrative studies.</td><td colspan="6">**Why is it a refugium?**<br>Review paper, covering a number of processes that lead to refugia, including climatic (meteorological, geographical, vegetation effects), resource availability (hydrology, pedology, vegetation cover), and disturbance (disturbance mapping, geology).</td></tr>
<tr><td rowspan="2">2012 McLaughlin</td><td>Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*)</td><td>Global Change Biology</td><td>California valley oak (*Quercus lobata*)</td><td>Trees</td><td>California, U.S.</td><td>Present and future</td><td>Low summer MAX temperature</td><td>Proximity to surface water features (streams, lakes, etc), high average annual rainfall, also proximity to groundwater aquifers</td><td></td><td></td><td>Warm</td></tr>
<tr><td colspan="5">**One sentence summary**<br>A Californian tree species has begun a retraction to microrefugia in response to climate warming.</td><td colspan="6">**Why is it a refugium?**<br>Water bodies provide necessary groundwater for saplings more vulnerable to drought stress under climate warming, while the species also requires maximum August temperatures of below 35°C.</td></tr>
<tr><td rowspan="2">2011 Mosblech</td><td>On metapopulations and microrefugia: palaeoecological insights</td><td>Journal of Biogeography</td><td colspan="8">(General discussion of refugia characteristics- include only in text)</td><td>Not applicable</td></tr>
<tr><td colspan="5">**One sentence summary**<br>Microrefugia are more likely to have preserved species with life history traits such as small body size, the capacity for asexual reproduction, and species with light genetic loads.</td><td colspan="6">**Why is it a refugium?**<br>(Non-quantitative study)</td></tr>
</table>

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Ohlemüller | Potential source and sink locations for climate-driven species range shifts in Europe since the Last Glacial Maximum | Global Ecology and Biogeography | Not applicable | Not applicable | Europe | LGM and present | Absolute minimum temperature, Mean summer temperature, Growing degree days above 5°C | Annual precipitation, Mean summer precipitation, winter precipitation | | | Cold |
| | **One sentence summary**<br>Southern refugia and patches of Central Europe acted as refugia, or source areas for species expansions following the LGM, because they were climatically analogous to modern conditions. | | | | | **Why is it a refugium?**<br>(No process-based explanation attempted). | | | | | |
| 2008 Provan | Phylogeographic insights into cryptic glacial refugia | Trends in Ecology & Evolution | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>Novel phylogeographic techniques have facilitated the identification of microrefugial areas during the LGM. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |
| 2009 Rull | Microrefugia | Journal of Biogeography | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>A microrefugium is defined as: 'a small area with local favourable environmental features, in which small populations can survive outside their main distribution area (the macrorefugium), protected from the unfavourable regional environmental conditions. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |
| 2010 Rull | On microrefugia and cryptic refugia | Journal of Biogeography | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>The descriptor 'cryptic refugia' should be replaced by the more precise term 'microrefugia', except for larger (e.g. mountain ranges) areas of cryptic locations, where they can be termed 'macrorefugia'. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2005 Schönswetter | Molecular evidence for glacial refugia of mountain plants in the European Alps | Molecular Ecology | 10 montane species | (Mountain) plants | European Alps | LGM and present | | | Siliceous bedrock | | Cold |
| | **One sentence summary**<br>Montane plants persisted in the LGM in the Alps, both on mountain tops and in various peripheral refugia. | | | | | **Why is it a refugium?**<br>Absence of ice and presence of siliceous bedrock. | | | | | |
| 2001 Stewart | Cryptic northern refugia and the origins of the modern biota | Trends in Ecology & Evolution | | Mammals | Europe | LGM | | | "deeply incised valleys in limestone massifs" | | Cold |
| | **One sentence summary**<br>Well documented southern refugia for species during the LGM were supplemented by cryptic refugia (microrefugia) north of the postulated ice sheet extent. | | | | | **Why is it a refugium?**<br>The sheltered, stable habitats of deeply incised valleys in limestone massifs could have provided microclimates that encouraged the survival of thermophilous biotas. | | | | | |
| 2010 Stewart | Refugia revisited: individualistic responses of species in space and time | Proceedings of the Royal Society B-Biological Sciences | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>Refugia are reviewed and the hypothesis of cryptic northern and southern refugia (microrefugia) is described. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2008 Svenning | Glacial refugia of temperate trees in Europe: insights from species distribution modelling | Journal of Ecology | 22 species: 7 boreal, 15 nemoral | Trees | Europe | Present and LGM | GDD, Absolute min temperature | Water balance: yearly sum of the monthly differences between precipitation and potential evapotranspiration following Skov & Svenning (2004). | | | Cold |
| | **One sentence summary**<br>Boreal trees took advantage of microrefugia in Russia, Central and Eastern Europe during the LGM, while nemoral trees were restricted to the Mediterranean basin and Black Sea regions. | | | | | **Why is it a refugium?**<br>Moisture enhanced persistence in the cold, low $CO_2$ conditions. | | | | | |
| 2011 Svenning | Applications of species distribution modelling to paleobiology | Quaternary Science Reviews | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>Species distribution modelling provides a quantitative basis for investigating ecological questions concerning refugia. | | | | | **Why is it a refugium?**<br>(Non-quantitative study). | | | | | |

**Appendix 1 Table 2** Studies revealed by literature search with ‘present’ refugia search terms.

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2006 Bennie | Influence of slope and aspect on long-term vegetation change in British chalk grasslands | Journal of Ecology | 153 species of vascular plant on chalk grassland | Plants | England | 1950-present | | low moisture content | low soil phosphorous, (steep) south facing slopes | (Indirect- resistance to invasion) | Warm |
| | **One sentence summary**<br>Habitat fragmentation and/or nutrient enrichment have facilitated a shift away from calcareous towards mesotrophic communities in chalk grasslands; however, calcareous species are more resistant to invasion in phosphorous limited areas, or steep south-facing slopes. | | | | | **Why is it a refugium?**<br>Steep, south-facing slopes provide the necessary droughting to exclude invasive mesotrophic species that are outcompeting calcareous incumbents in other areas. | | | | | |
| 1986 Calvert | The location of monarch butterfly (*Danaus plexippus* L.) overwintering colonies in Mexico in relation to topography and climate | Journal of the Lepidopterists' Society | Monarch Butterfly (*Danaus plexippus*) | Butterflies and moths | Trans-volcanic Belt, Central Mexico | Present | Dampened temperature extremes when overwintering | Proximity to surface water feature, Moisture availability | Warm SW facing slopes | | Not applicable |
| | **One sentence summary**<br>Monarch butterflies overwinter at sites providing temperatures low enough to keep activity, metabolism, and lipid expenditure to a minimum, but not so cold as to cause freezing. | | | | | **Why is it a refugium?**<br>The forests of the Trans-volcanic Belt in Mexico provide the necessary moisture and dampened temperature extremes to allow the Monarchs to overwinter. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2007 Fickert | Did debris-covered glaciers serve as pleistocene refugia for plants? A new hypothesis derived from observations of recent plant growth on glacier surfaces | Arctic Antarctic and Alpine Research | 50 species | Plants, mosses, lichens | Mount Rainier, Alaska, U.S. | LGM and present | Cooler subsurface soil temperature | | Surface of the glacier (debris covering), presence of ice | | Warm |
| | **One sentence summary**<br>Debris-covered glaciers provide atypical environmental conditions that can allow species to survive outside their usual climate envelope. | | | | | **Why is it a refugium?**<br>Cooler subsurface soil temperatures found on glacial debris with ice underneath facilitated plant growth at altitudes below their typical niche. | | | | | |
| 2011 Game | Incorporating climate change adaptation into national conservation assessments | Global Change Biology | Not applicable | Representative vegetation types | Papua New Guinea | Present | Mean temperature coldest quarter, mean temperature warmest quarter, average monthly temperature | Profile available water capacity, potential evapo-transpiration, precipitation/ potential evapo-transpiration, precipitation coldest quarter, precipitation warmest quarter | Potential solar radiation, elevation, compound topographic index, soil bulk density, soil carbon density, and total soil nitrogen | | Warm |
| | **One sentence summary**<br>Designing conservation networks to incorporate climate change refugia can substantially reduce expected levels of climate change within those areas. | | | | | **Why is it a refugium?**<br>Approach involved simulating where conditions analogous to the present day exist in the future (variables listed to the left). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Gillingham | The effect of spatial resolution on projected responses to climate warming | Diversity and Distributions | *Carabus glabratus* (northerly distributed) and *Poecilus versicolor* (southerly distributed) | (Ground) beetles | Lake Vyrnwy RSPB Reserve, Wales | Present (2008) and future | Maximum temperature in July, minimum temperature in December, annual mean temperature | | | | Warm |
| | **One sentence summary**<br>Resolution strongly affects the proportion of the landscape projected to be suitable for a northerly distributed species under climatic warming. | | | | | **Why is it a refugium?**<br>Heterogeneous topography provided areas with low mean temperatures and low summer (July) maximum temperatures for the northerly distributed species. | | | | | |
| 2008 Hancock | An exceptional *Calluna vulgaris* winter die-back event, Abernethy Forest, Scottish Highlands | Plant Ecology & Diversity | *Calluna vulgaris* | Plants | Abernethy Forest, Scottish Highlands | 2003-2005 | High mean ground temperature, Small mean daily temperature range, low proportion of days with frost | High winter humidity, moisture content | Steep % slope, south-facing (sic!) slopes, presence of snow cover | | Cold |
| | **One sentence summary**<br>Exceptional cold and low humidity caused substantial dieback in populations of heather in the Central Scottish Highlands during winter 2002-03. | | | | | **Why is it a refugium?**<br>Warm, south-facing slopes reduced mortality during a winter dieback event (combined drought and cold effect). | | | | | |
| 2012 Hennon | Shifting Climate, Altered Niche, and a Dynamic Conservation Strategy for Yellow-Cedar in the North Pacific Coastal Rainforest | Bioscience | Yellow-cedar (*Callitropsis nootkatensis*) | Trees | North Pacific Coast, British Columbia, Canada | Present | | Poor to moderate soil drainage | Greater soil depth, presence of snow cover, north-facing slopes | | Warm |
| | **One sentence summary**<br>Climate warming has driven decline in Yellow-cedar by reducing snow cover and exposing the species to increased freezing injury. | | | | | **Why is it a refugium?**<br>Patches of snow cover reduce susceptibility to freezing injury. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2010 Horsack | Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe | Journal of Biogeography | 7 species | Snails | Altai Mountains, Russia | Present | Mean January temperatures (below -17°C), low mean July temperature, low mean annual temperature | | Loess sediments | Presence of woody or scrub habitat (Indirect effect of moisture, or small temp range?) | Warm |
| | **One sentence summary**<br>Glacial relict snails require habitats with low mean temperatures, but are normally found in sheltered, warm microclimates within them, such as scrub or open woodland. | | | | | **Why is it a refugium?**<br>The southern Russian Altai provides annual mean temperatures cold enough for glacial relict snails to persist. | | | | | |
| 2003 Hörsch | Modelling the spatial distribution of montane and subalpine forests in the central Alps using digital elevation models | Ecological Modelling | Two assemblages of Subalpine coniferous forest | Trees | Switzerland | Present | | Profile curvature, plan curvature, low accumulation, water distribution model output | Elevation, slope, cos-transformed aspect, sine-transformed aspect | | Not applicable |
| | **One sentence summary**<br>Subalpines are limited to higher elevations and steep slopes as these are unfavourable for agricultural use; Montanes are limited to high radiation sites, lower elevations and steep slopes for the same reason as Subalpines. | | | | | **Why is it a refugium?**<br>Slope angles of 18°< prevent mechanised agriculture. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Molenda | The Alpine Cushion Plant *Silene acaulis* as Foundation Species: A Bug's-Eye View to Facilitation and Microclimate | Plos One | Various | Arthropods, plants | Whistler Mountain, British Columbia, Canada | Present | | | | Presence of *Silene acaulis*, a facilitating cushion plant | Not applicable |
| | **One sentence summary**<br>*Silene acaulis*, an Alpine cushion plant, facilitates the presence of arthropods and other plants by providing a dampened microclimate. | | | | | **Why is it a refugium?**<br>The cushion plant creates a micro-environment in which variation in humidity and temperature is dampened, particularly maximum temperatures. | | | | | |
| 2002 Motzkin | Frost pockets on a level sand plain: Does variation in microclimate help maintain persistent vegetation patterns? | Journal of the Torrey Botanical Society | Various | Scrub oak stands | Montague Plain, Massachusetts, U.S. | Present | "Frost pockets" - frequent late-spring frosts, low mean minimum temperature | Xeric soil | Level topography | Open forest clearings | Warm |
| | **One sentence summary**<br>Open habitat microclimates create and maintain an unusual vegetation community in so-called 'frost pockets'. | | | | | **Why is it a refugium?**<br>Open habitats on level, xeric soil lead to frequent late spring frosts and shorter frost-free periods, allowing slower growing, frost resistant scrub vegetation to dominate. | | | | | |
| 2009 Puschendorf | Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica: proposing climatic refuges as a conservation tool | Diversity and Distributions | 35 species | Amphibians | Costa Rica | Present | High annual mean temperature | Low rainfall during driest part of year | | Absence of chytrid *Batrachochytrium dendrobatidis* | Not applicable |
| | **One sentence summary**<br>The fungal chytrid *Batrachochytrium dendrobatidis* is constrained by climate: hence, conservation measures for amphibians could be targeted in these refugial areas (e.g. Santa Elena Peninsula or Central Valley, Costa Rica). | | | | | **Why is it a refugium?**<br>Areas of low rainfall and high (mean) temperature prevent a chytrid fungus from establishing on amphibians. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1996 Ravenscroft | Habitat specificity, restricted range and metapopulation persistence of the slender scotch burnet moth *Zygaena loti* in western Scotland | Journal of Applied Ecology | Slender Scotch Burnet Moth (*Zygaena loti*) | Moths | West Scotland | Present | | | Basaltic rock/soil, steep slope, south-facing cliffs | Disturbance regime, grazing | Cold |
| | **One sentence summary**<br>The slender scotch burnet moth, like many other isolated, warm dwelling species in Western Scotland, spread into Britain in a warm episode following the LGM, and was subsequently isolated as temperatures cooled slightly. | | | | | **Why is it a refugium?**<br>Short early-successional vegetation on sheltered, steep, south-facing slopes create the necessary microclimate for the slender scotch burnet moth to exist in isolated refugial populations far north of its poleward range boundary. | | | | | |
| 2011 Scherrer | Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming | Journal of Biogeography | 174 vascular plants | Plants | Swiss Central Alps | Present | Seasonal mean temperature, mean temp 12-6am (night hours) | | Presence of snow | | Warm |
| | **One sentence summary**<br>Topographic heterogeneity and associated thermal heterogeneity explains the local distributions of Alpine plant species well. | | | | | **Why is it a refugium?**<br>Cold-dwelling species were found at sites with high snow cover and low seasonal (June - September) mean temperature, where the surface temperature was substantially lower than the air temperature. | | | | | |
| 2011 Schmalholz | Microtopography creates small-scale refugia for boreal forest floor bryophytes during clear-cut logging | Ecography | Various | Boreal forest floor bryophytes | Gävleborgs county, Sweden | Present | | | Sheltered microtopography, presence of boulders and stumps | | Warm |
| | **One sentence summary**<br>Microtopography and surface features can create small-scale refugia for forest floor species following logging. | | | | | **Why is it a refugium?**<br>Following logging, forest floor bryophytes are more likely to survive in areas with sheltered microtopography or in which boulders and stumps are present. | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2011 Sears | The World Is not Flat: Defining Relevant Thermal Landscapes in the Context of Climate Change | Integrative and Comparative Biology | Not applicable (theoretical study) | Lizards (Sceloporus) | (Simulated landscape, climate data from New Mexico, U.S.) | Present, future | | | Elevational range, topographic heterogeneity | | Warm |
| | **One sentence summary**<br>Variation in topography can attenuate the effects of climate change. | | | | | **Why is it a refugium?**<br>Hilly topography increases the range of temperatures available to species in the landscape, meaning that the movement cost of finding a microsite with a suitable temperature is decreased. | | | | | |
| 2012 Serra-Diaz | Coexistence of *Abies alba* (Mill.) - *Fagus sylvatica* (L.) and climate change impact in the Iberian Peninsula: A climatic-niche perspective approach | Flora | *Abies alba* (European silver fir) and *Fagus sylvatica* (beech) | Trees | Iberia, Europe | Present, future | | | High elevation, North-facing slopes | | Warm |
| | **One sentence summary**<br>*Abies alba* and *Fagus sylvatica* will retract to refugia in the Pyrenees. | | | | | **Why is it a refugium?**<br>North-facing slopes of high elevation will allow *Abies alba* and *Fagus sylvatica* to persist in northern Spain. | | | | | |
| 2008 Trivedi | Spatial scale affects bioclimate model projections of climate change impacts on mountain plants | Global Change Biology | 10 species | (Mountain) plants | Grampians, Scotland, U.K. | Future | Absolute minimum temperature, maximum annual temperature, GDD. | Soil moisture surplus, soil moisture deficit | High elevation, North-facing slopes | | Not applicable |
| | **One sentence summary**<br>Coarse-scale models may have overestimated the potential for montane species to survive climatic warming. | | | | | **Why is it a refugium?**<br>(Contrary findings: Fine-scale models predicted a total loss of 7-8 of 10 montane species from a topographically diverse site due to climate warming). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2010 Turlure | Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change | Global Change Biology | Cranberry fritillary (*Boloria aquilonaris*) | Butterflies and moths | Belgium | Present | 12°C stable daytime temperature under direct sun (see biotic feature) | High humidity |  | Presence of Sphagnum hummocks in early- to mid-successional peat bogs (i.e. not late). | Warm |
|  | **One sentence summary**<br>A glacial relict butterfly (*Boloria aquilonaris*) is dependent on humid zones in its peat bog habitat, in which Sphagnum hummocks act to dampen elevated air temperatures. |  |  |  |  | **Why is it a refugium?**<br>Sphagnum hummocks enhance the persistence of larvae by dampening warm temperatures, especially in areas of high humidity. |  |  |  |  |  |
| 2012 Vegas-Vilarrúbia | Global warming, habitat shifts and potential refugia for biodiversity conservation in the neotropical Guayana Highlands | Biological Conservation | 618 species | (Vascular) plants | Guayanan Highlands (Pantepui) | Future | Low annual average temperature | High annual average precipitation | High elevation (>1500m, tepui summits). Elevational niche was used as a proxy for climatic niche |  | Warm |
|  | **One sentence summary**<br>High elevation table mountains (tepui) in South America harbour numerous endemic species and may act as refugia from climate change. |  |  |  |  | **Why is it a refugium?**<br>The combination of high elevation, low average temperatures and high rainfall is unusual for the geographic region and may provide suitable habitat for species migrating from lower areas. |  |  |  |  |  |

**Appendix 1 Table 3** Studies revealed by literature search with ‘future’ refugia search terms.

<table>
<tr><th>Year and lead author</th><th>Title</th><th>Journal</th><th>Species</th><th>Taxon</th><th>Location</th><th>Period of reference (eg LGM, present)</th><th>Temp feature of the refugium</th><th>Moisture feature of the refugium</th><th>Geophysical feature of the refugium (eg frost hollow, topo diversity)</th><th>Biotic feature of the refugium</th><th>Is it a refugium for a warm episode or a cold episode?</th></tr>
<tr><td rowspan="2">2012 Bertrand</td><td>Changes in plant community composition lag behind climate warming in lowland forests</td><td>Nature</td><td>760 species</td><td>Forest plants</td><td>France</td><td>1965-2008</td><td>Temperature heterogeneity arising from topographic heterogeneity at 500-2,600m a.s.l.</td><td></td><td></td><td></td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>Lowland plants are responding to climate change slower than those in the uplands, because in the lowlands habitats are more fragmented, provide fewer opportunities for short distance escapes, and contain more species with wider thermal tolerances, on average.</td><td colspan="6"><b>Why is it a refugium?</b><br>Topographically-derived temperature heterogeneity gives species a higher chance of short distance migrations in response to climate change.</td></tr>
<tr><td rowspan="2">2006 Chamaillé-Jammes</td><td>Global warming and positive fitness response in mountain populations of common lizards <i>Lacerta vivipara</i></td><td>Global Change Biology</td><td>Common lizard (<i>Lacerta vivipara</i>)</td><td>Lizards</td><td>Mont Lozère, Southern France</td><td>1981-2001</td><td>Mean temperature in May</td><td>Presence of running water, medium to high precipitation and humidity</td><td></td><td></td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>Outlying southern populations of the common lizard in France have responded positively to warmer spring and summer temperatures, both in terms of fitness and survival.</td><td colspan="6"><b>Why is it a refugium?</b><br>Elevation over 1000m, presence of running water and med to high humidity/precipitation facilitates the persistence of <i>Lacerta vivipara</i> south of its equatorward range margin.</td></tr>
</table>

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2010 Graham | Dynamic refugia and species persistence: tracking spatial shifts in habitat through time | Ecography | 72 upland rainforest species | Plants | Australian Wet Tropics | Past (18000YBP - Present) | Mean of annual temperature, temperature of the warmest and coldest quarters (where quarter is defined by e.g. 3 consecutive wettest months). | Mean of annual precipitation, precipitation of the wettest quarter (where quarter is defined by e.g. 3 consecutive wettest months) |  |  | Warm |
|  | **One sentence summary**<br>Refugial areas for upland rainforest are likely to have been spatially dynamic through time, as species tracked their required climatic niches. |  |  |  |  | **Why is it a refugium?**<br>Areas offering climatically stable conditions, or conditions analogous to species' niche requirements. |  |  |  |  |  |
| 2007 Hilderbrand | Evaluating population persistence of Delmarva fox squirrels and potential impacts of climate change | Biological Conservation | Delmarva fox squirrel (*Sciurus niger cinereus*) | Mammals | Delmarva Peninsula, U.S. | Present, future | Monthly mean, max, min temperatures | Monthly mean, max, min precipitation, Palmer Drought Severity Index |  | Large forest patch size (>400ha) | Warm |
|  | **One sentence summary**<br>Refugial populations of the Delmarva fox squirrel is likely to be vulnerable to extinction from climate change, especially in drought affected areas with variable climates. |  |  |  |  | **Why is it a refugium?**<br>Areas of less climatic variability could reduce the Delmarva fox squirrel's susceptibility to drought. |  |  |  |  |  |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2012 Larsen | Upslope Range Shifts of Andean Dung Beetles in Response to Deforestation: Compounding and Confounding Effects of Microclimatic Change | Biotropica | Various | Beetles | South-eastern Peru | 1999-2000 | Low temperature | High relative humidity | High(er) elevation sites, for alternative temp and humidity regimes in deforested landscapes | | |
| | **One sentence summary**<br>In deforested landscapes, dung beetles have shifted upslope to counteract the microclimatic effect (warmer, drier) of newly open habitat. | | | | | **Why is it a refugium?**<br>Closed habitat microclimates provide cooler and wetter conditions, facilitating dung beetle persistence. | | | | | |
| 2010 Lawson | Cumulative effects of land use, altered fire regime and climate change on persistence of Ceanothus verrucosus, a rare, fire-dependent plant species | Global Change Biology | *Ceanothus verrucosus* | Plants | Southern California, U.S. | Present, future | Mean January min temperature, mean July max temperature | Available water holding capacity | Soil type, (Topographic) slope, Return period of fire events of 35-40 years | | Warm |
| | **One sentence summary**<br>Interactions between habitat loss, climate change and fire intervals will require careful management for the fire dependent Mediterranean shrub *Ceanothus verrucosus*. | | | | | **Why is it a refugium?**<br>The shrub *Ceanothus verrucosus* requires low January minimum temperatures (to prevent competition) and low July maximum temperatures (physiological/drought stress), both of which are expected to increase in California. | | | | | |

<table>
<tr><th>Year and lead author</th><th>Title</th><th>Journal</th><th>Species</th><th>Taxon</th><th>Location</th><th>Period of reference (eg LGM, present)</th><th>Temp feature of the refugium</th><th>Moisture feature of the refugium</th><th>Geophysical feature of the refugium (eg frost hollow, topo diversity)</th><th>Biotic feature of the refugium</th><th>Is it a refugium for a warm episode or a cold episode?</th></tr>
<tr><td rowspan="2">2007 Mejías</td><td>Ecology and biogeography of plant communities associated with the post Plio-Pleistocene <i>relict Rhododendron ponticum</i> subsp <i>baeticum</i> in southern Spain</td><td>Journal of Biogeography</td><td>Target species was <i>Rhododendron ponticum baeticum</i>, but all woody plants and ferns sampled</td><td>Plants</td><td>Southern Spain</td><td>1997</td><td></td><td>Proximity to inclined, running streams with steep, narrow banks</td><td>Mid elevation sites 140-730m, Nutrient poor, acidic soil (mean pH ~ 5)</td><td>Closed canopy (84% cover)</td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>A southern refugial population of <i>Rhododendron ponticum baeticum</i> in the Sierra del Aljibe is restricted to the coolest, wettest conditions and is likely to be in decline.</td><td colspan="6"><b>Why is it a refugium?</b><br>The banks of inclined and enclosed streams in acidic, Riparian forests with a closed canopy provide the necessary cool, wet conditions for <i>Rhododendron ponticum baeticum</i> to persist at its southern range boundary.</td></tr>
<tr><td rowspan="2">2009 Randin</td><td>Climate change and plant distribution: local models predict high-elevation persistence</td><td>Global Change Biology</td><td>78 species</td><td>Plants</td><td>Swiss Alps</td><td>Present</td><td></td><td></td><td>Elevational range within a 10' x 10' cell</td><td></td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>Changing the resolution of plant distribution models affects predicted extinctions; the inclusion of elevational range in fine-scale models results in 100% predicted persistence, vis-à-vis predictions of total loss of habitat by coarse-scale models.</td><td colspan="6"><b>Why is it a refugium?</b><br>(Fine-scale models predicted up to 100% persistence of alpine plants despite coarse-scale models predicting total loss of suitable habitat, due to a better representation of elevational range in the former models).</td></tr>
<tr><td rowspan="2">2003 Wichmann</td><td>Implication of climate change for the persistence of raptors in arid savanna</td><td>Oikos</td><td>Tawny eagle (<i>Aquila rapax</i>)</td><td>Birds (Raptors)</td><td>Southern Kalahari, Africa</td><td>Present, future (simulated)</td><td></td><td>Annual precipitation at least 250mm, stability of precipitation regime</td><td></td><td></td><td></td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>In arid savannas, changes to rainfall dynamics may be a bigger driver of extinctions than temperature change; for the tawny eagle, projected increases in rainfall variability will likely drive population declines.</td><td colspan="6"><b>Why is it a refugium?</b><br>Increased interannual variability in rainfall will limit the tawny eagle to areas of stable rainfall at medium to high levels.</td></tr>
</table>

**Appendix 1 Table 4** Studies of refugia suggested by collaborators or authors of refugia articles.

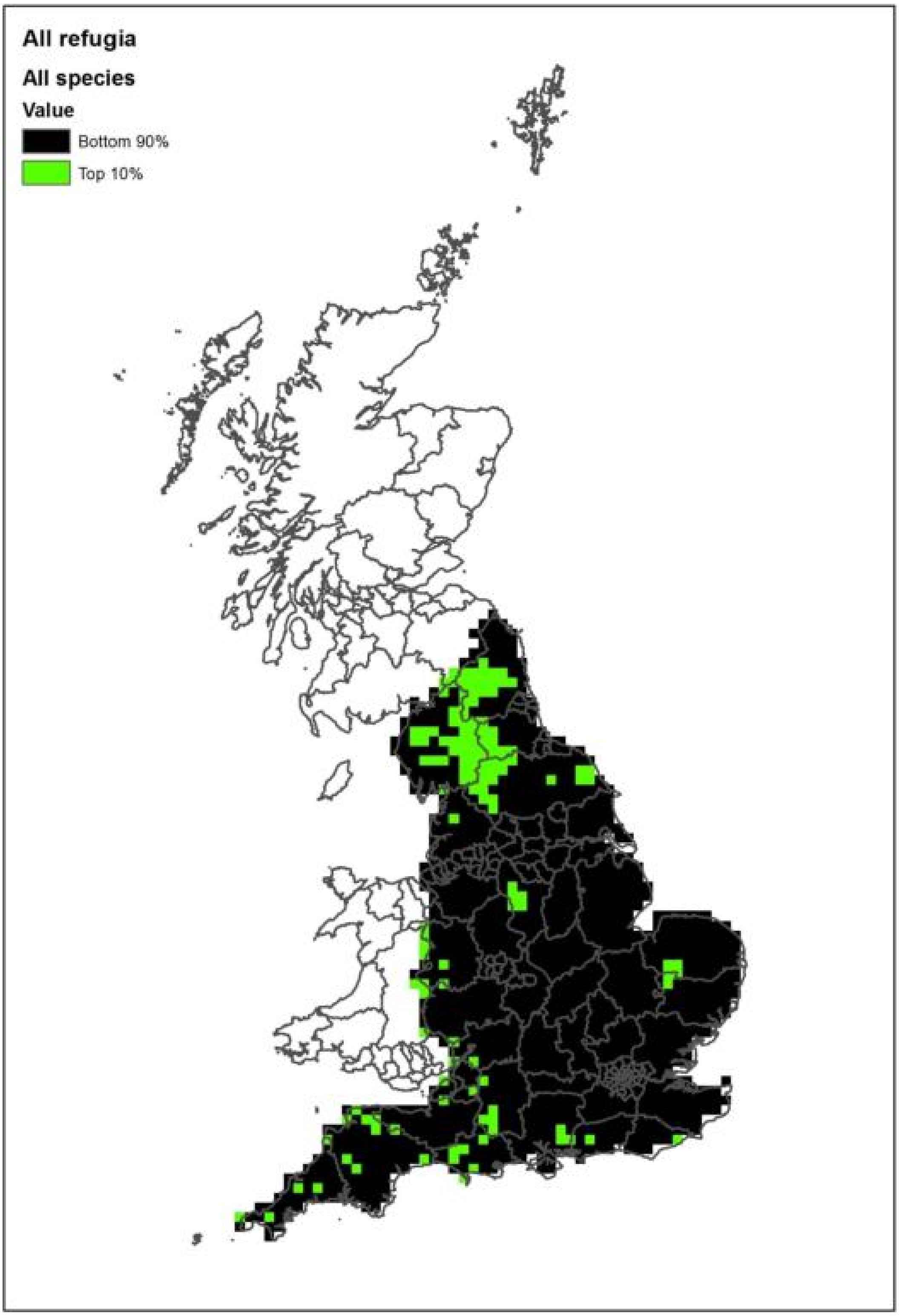
| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2010 Ackerly | The geography of climate change: implications for conservation biogeography | Diversity and Distributions | NA | WWF Ecoregions | California and Nevada, U.S. | Present, future | Rao's quadratic entropy, a measure of climatic diversity (see paper for equation) - for summer temperatures (JJA). | | | | Warm |
| | **One sentence summary**<br>The vast majority (492 of 500) of protected areas will experience temperatures entirely outside their current climatic range by 2100, with climate change velocity higher in flat areas, as topographic heterogeneity shortens the distance species will have to migrate to find analogous climates. | | | | | **Why is it a refugium?**<br>Climate heterogeneity arising from topographic heterogeneity will lower climate change velocities and buffer species from warming by providing the coldest habitats in the future. | | | | | |
| 2009 Ashcroft | Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation | Global Change Biology | 37 common species of plant | Plants | The Illawarra Escarpment and Woronora Plateau, NSW, Australia | 1972-2007 | Heterogeneity in climatic warming of seasonal average minimum and maximum temperatures (see paper for method). | Distance from streams | Elevation, distance from coast, exposure | | Warm |
| | **One sentence summary**<br>The distribution of climatic warming has varied according to season and is influenced by various features (see Why? Box on right) that will provide refugia in the future. | | | | | **Why is it a refugium?**<br>Sites with less climatic warming were: at mid to high elevations (lower increases in winter minimum temperatures); proximate to streams (lower warming year-round); and closer to the coast (depressing increases in summer maximum and winter minimum temperatures). | | | | | |

| Year and lead author | Title | Journal | Species | Taxon | Location | Period of reference (eg LGM, present) | Temp feature of the refugium | Moisture feature of the refugium | Geophysical feature of the refugium (eg frost hollow, topo diversity) | Biotic feature of the refugium | Is it a refugium for a warm episode or a cold episode? |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2005 Bannister | Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? | Oecologia | 7 species of Alpine plant | Plants | Southern New Zealand | 2003-2004 | | | Presence of snow cover (for species that were not frost-resistant) | | Warm |
| | **One sentence summary**<br>Because the development of temporary frost resistance is linked to day length, and not temperature per se, species should be resistant to increased spring temperatures and maintain frost resistance where there remains a risk of frost. | | | | | **Why is it a refugium?**<br>For species with limited frost resistance, presence of snow cover reduces exposure to frost and prevents competition from more vigorous species intolerant of snow cover. | | | | | |
| 2012 Crossman | Identifying priority areas for reducing species vulnerability to climate change | Diversity and Distributions | 171 native plants | Plants | Mount Lofty Ranges region, South Australia | Present, future | Low annual mean temperature | High annual mean precipitation | | | Warm |
| | **One sentence summary**<br>An exercise in prioritising areas for conservation across a taxon (plants) revealed that cooler, wetter climates are of high priority, particularly under no/low dispersal and high climate change scenarios. | | | | | **Why is it a refugium?**<br>Priority areas for reducing species vulnerability to climate change were cold and wet. | | | | | |
| 2013 Hampe | Climate refugia: from the Last Glacial Maximum to the twenty-first century | New Phytologist | (General discussion of refugia characteristics- include only in text) | | | | | | | | Not applicable |
| | **One sentence summary**<br>Quantitative, mechanistic approaches are required if we are to define the characteristics of refugia from climate change. | | | | | **Why is it a refugium?**<br>(Non-quantitative study) | | | | | |

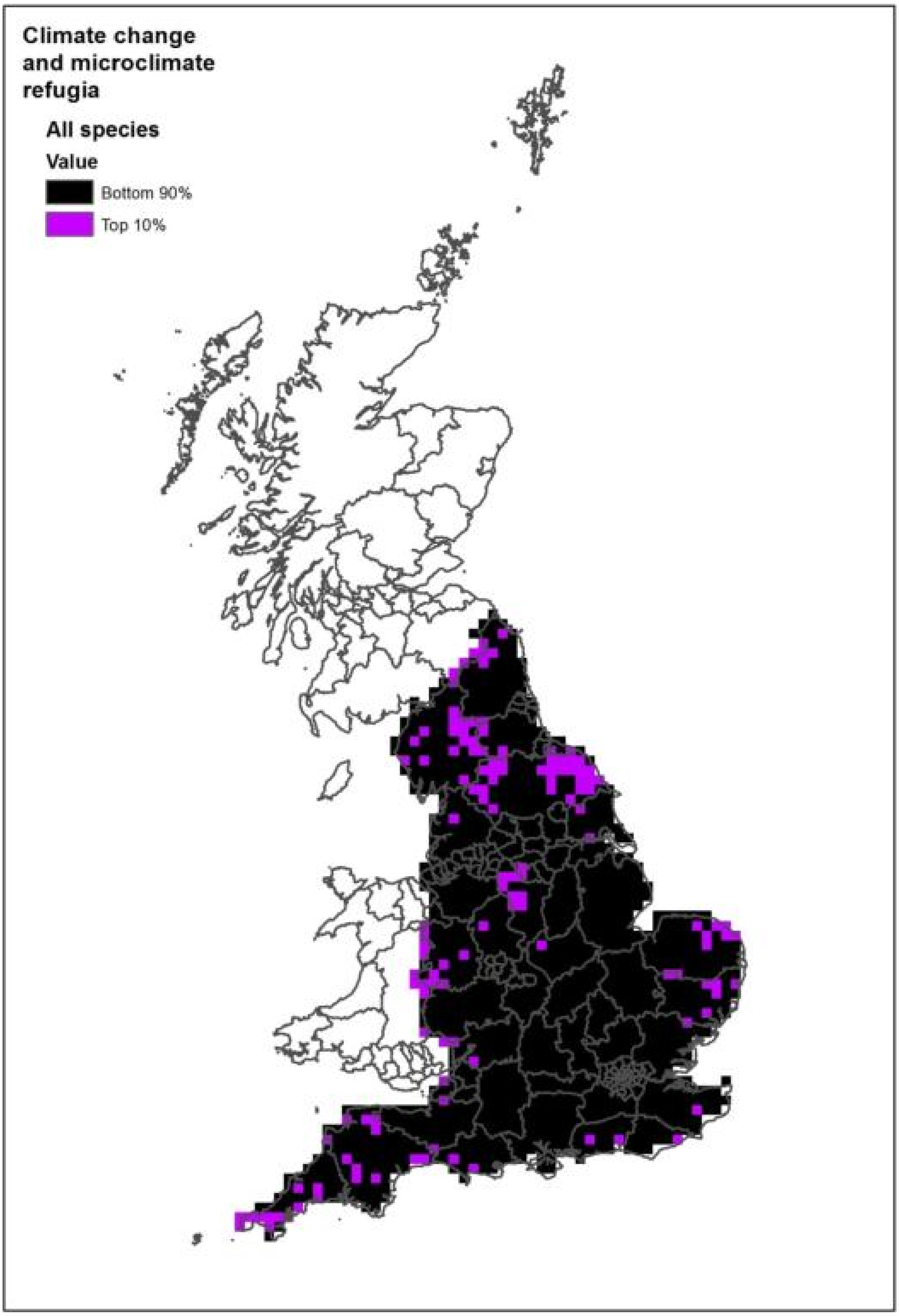
<table>
<tr><th>Year and lead author</th><th>Title</th><th>Journal</th><th>Species</th><th>Taxon</th><th>Location</th><th>Period of reference (eg LGM, present)</th><th>Temp feature of the refugium</th><th>Moisture feature of the refugium</th><th>Geophysical feature of the refugium (eg frost hollow, topo diversity)</th><th>Biotic feature of the refugium</th><th>Is it a refugium for a warm episode or a cold episode?</th></tr>
<tr><td rowspan="2">2012 Olson</td><td>Climate Change Refugia for Biodiversity in the Klamath-Siskiyou Ecoregion</td><td>Natural Areas Journal</td><td>Various</td><td>Multi-taxon (qualitative) approach</td><td>Klamath-Siskiyou Ecoregion, Southwest Oregon & Northern California, U.S.</td><td>Present</td><td></td><td>High precipitation</td><td>North-and northeast-facing slopes, valley bottoms and steep canyons, and sinks and basins</td><td>Old growth forests</td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>A total of 62 highest and high priority refugia were identified for a region in the Western U.S.: these sites featured old growth and intact forests on north-facing slopes and in canyon bottoms, lower- and middle-elevations, wetter coastal mountains, and elevational gradients.</td><td colspan="6"><b>Why is it a refugium?</b><br>The features of the refugia listed above were prioritised because the species of greatest concern in the region are invertebrates, non-vascular plants, and fungi that are largely restricted to persistently cool and moist late-successional forests. These features provide the necessary cool, wet conditions to enable their persistence.</td></tr>
<tr><td rowspan="2">2011 Sandel</td><td>The Influence of Late Quaternary Climate-Change Velocity on Species Endemism</td><td>Science</td><td>Various</td><td>Amphibians, mammals, birds</td><td>Global</td><td>Past, present</td><td colspan="2">Low climate change velocity (units- m/year, divide the rate of climate change through time by the local rate of climate change across space), analogous climates (total area of land within a 1000-km radius that had a mean annual temperature (MAT) within 1°C and mean annual precipitation (MAP) within 100 mm of that focal cell).</td><td>Topographic heterogeneity</td><td></td><td>Warm</td></tr>
<tr><td colspan="5"><b>One sentence summary</b><br>Areas of low past (21000 YBP to present) climate change velocity harbour higher levels of endemism.</td><td colspan="6"><b>Why is it a refugium?</b><br>Topographic heterogeneity buffers the effects of climate change, which lowers the expected climate change velocity in these areas.</td></tr>
</table>

## Appendix 2: Additional refugia maps

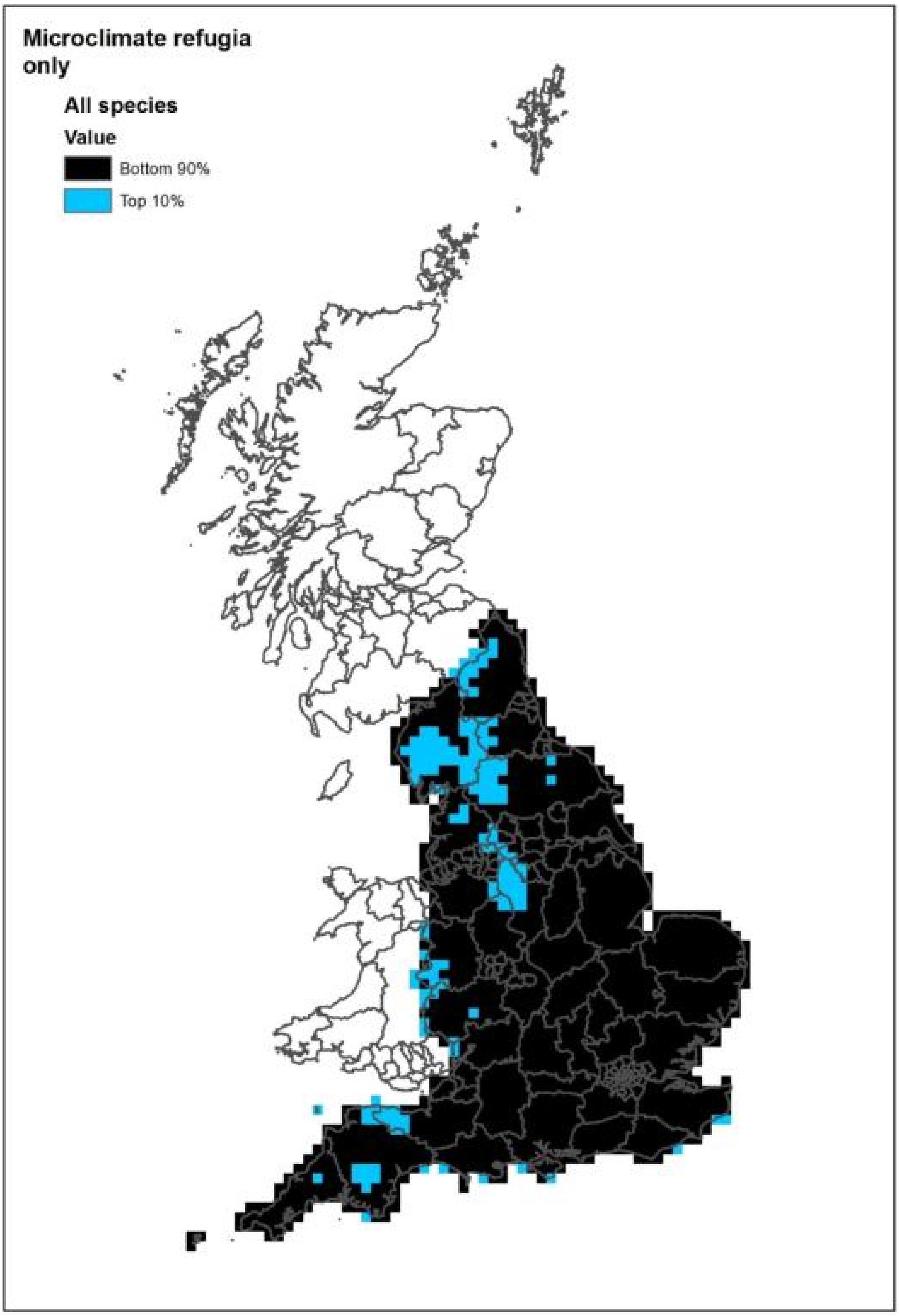
See overleaf for Appendix 2 maps showing the top 10% of refugia areas for each model type, followed by maps of refugium potential for each species group.



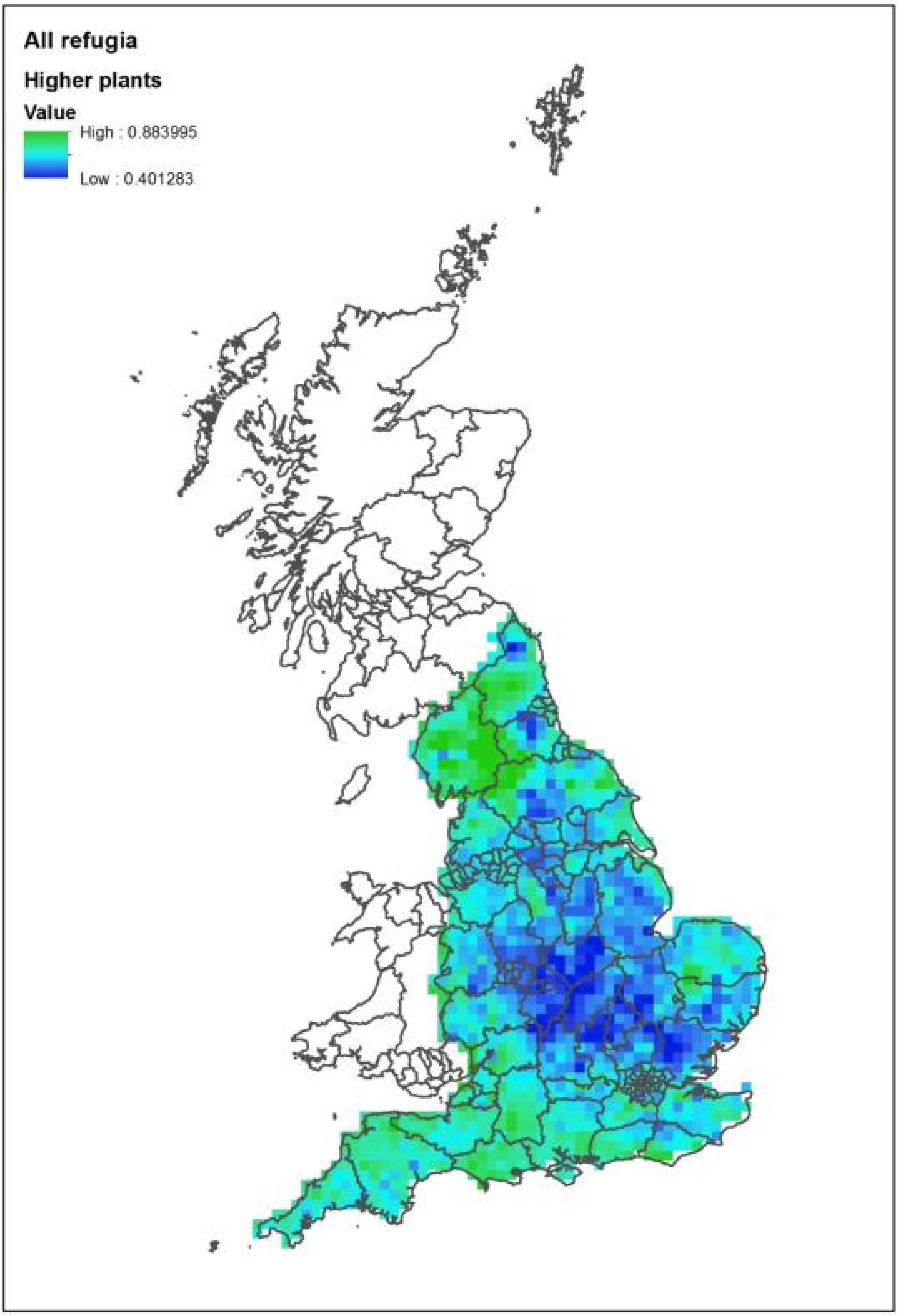
**Appendix 2 Figure 1** Map showing the location of the top 10% of refugial areas calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



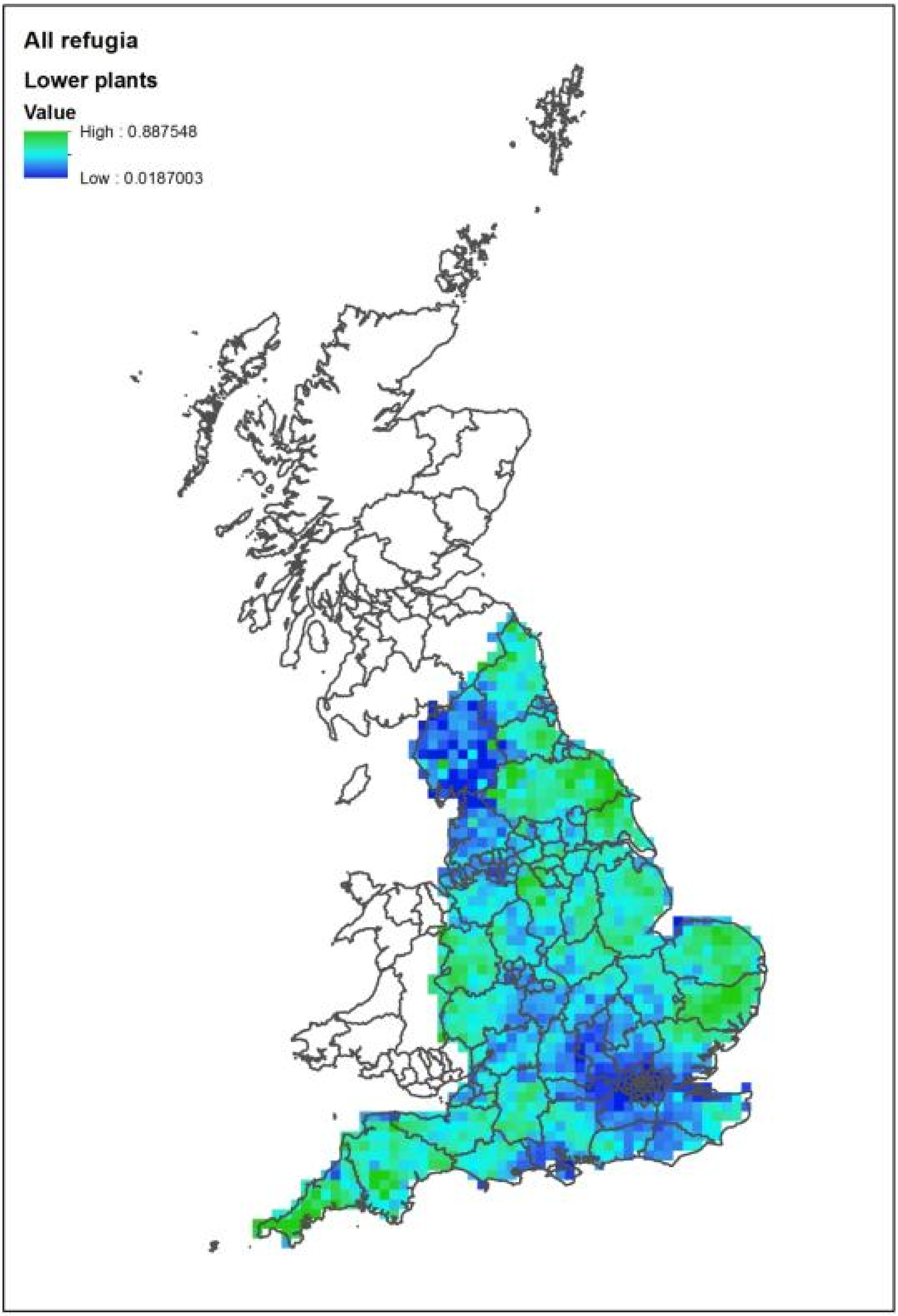
**Appendix 2 Figure 2** Map showing the location of the top 10% of climate refugial areas. In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



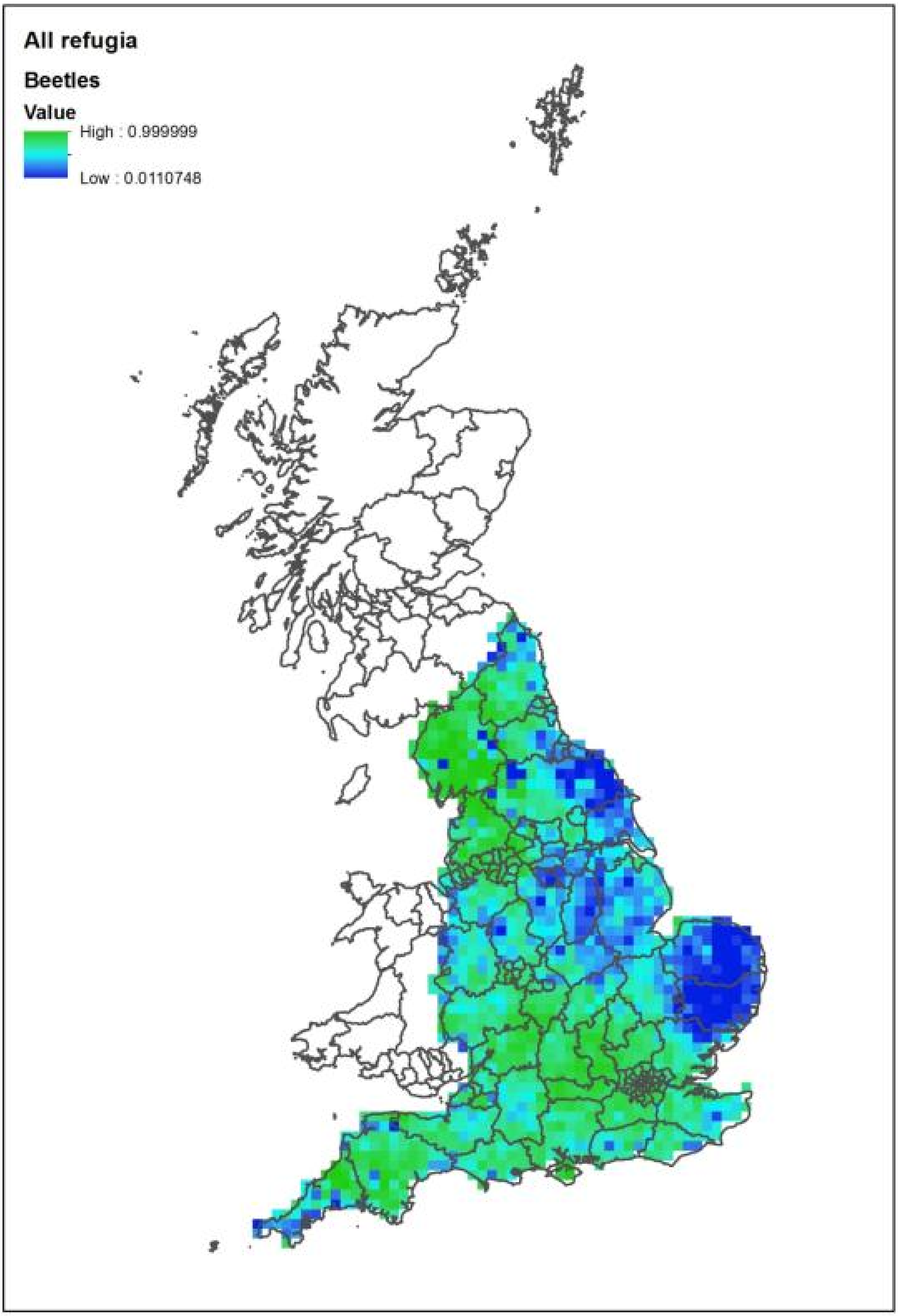
**Appendix 2 Figure 3** Map showing the location of the top 10% of microclimate refugial areas. In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



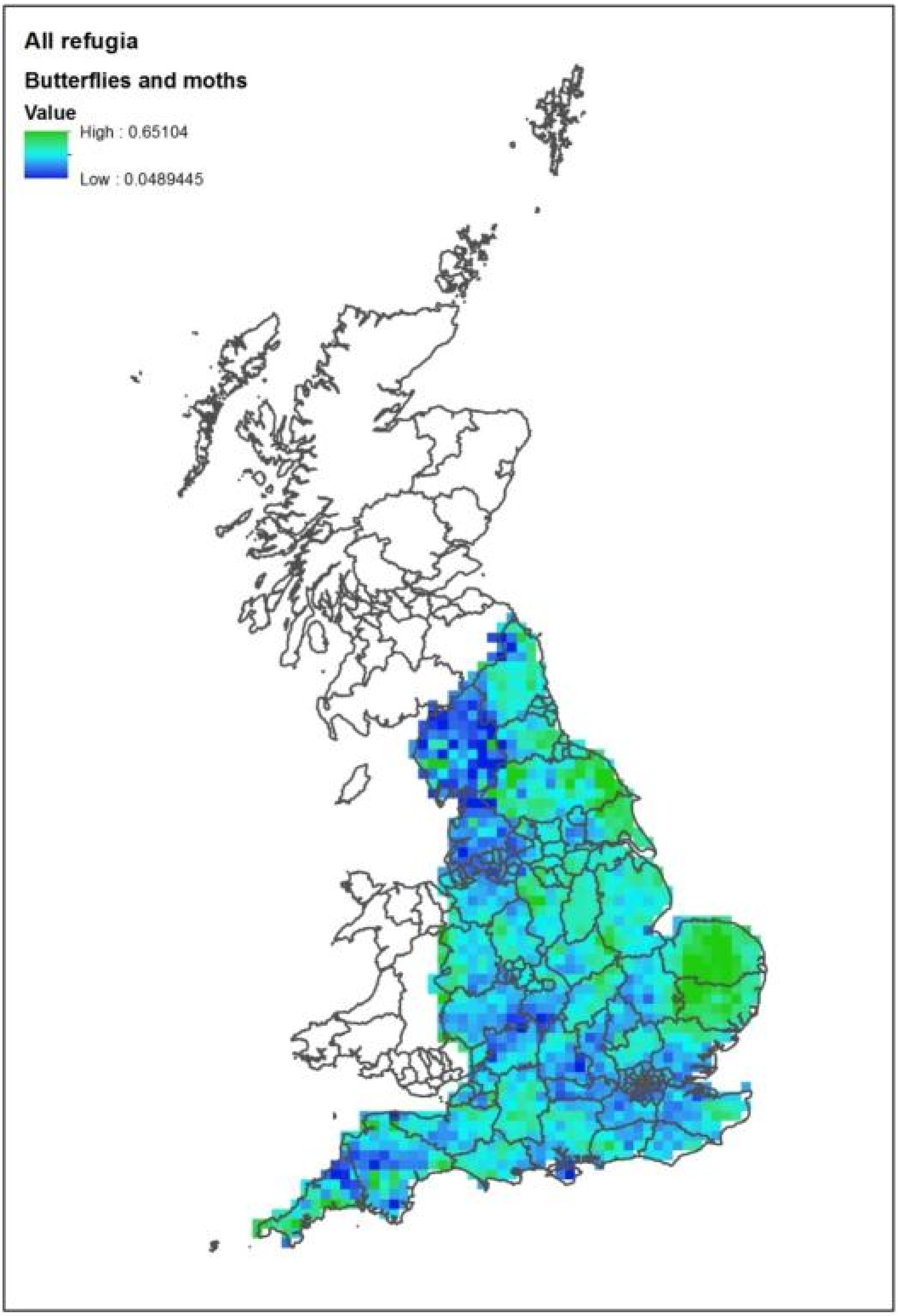
**Appendix 2 Figure 4a** Map showing refugial areas for higher plants (tracheophytes) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



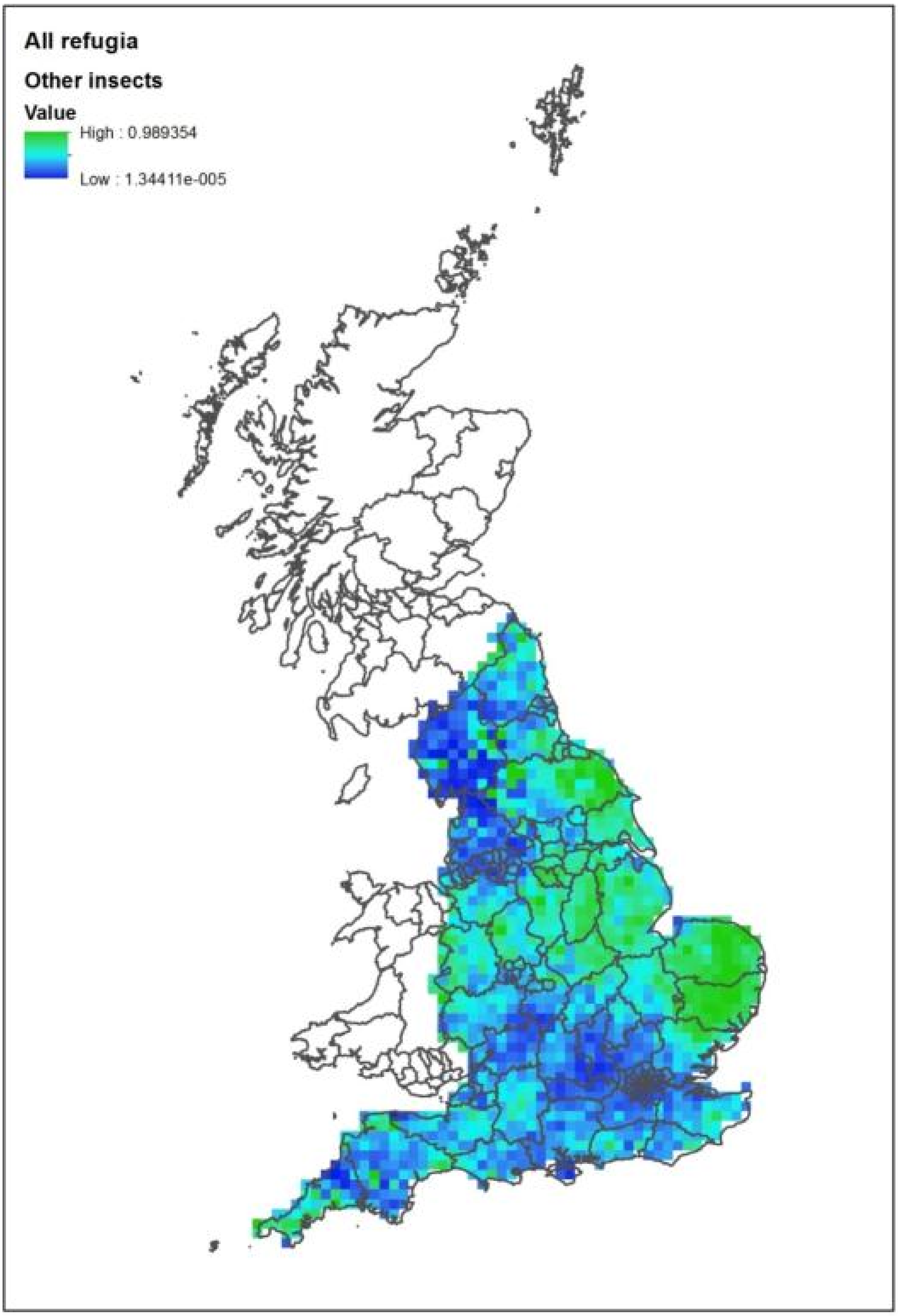
**Appendix 2 Figure 4b** Map showing refugial areas for lower plants (bryophytes) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



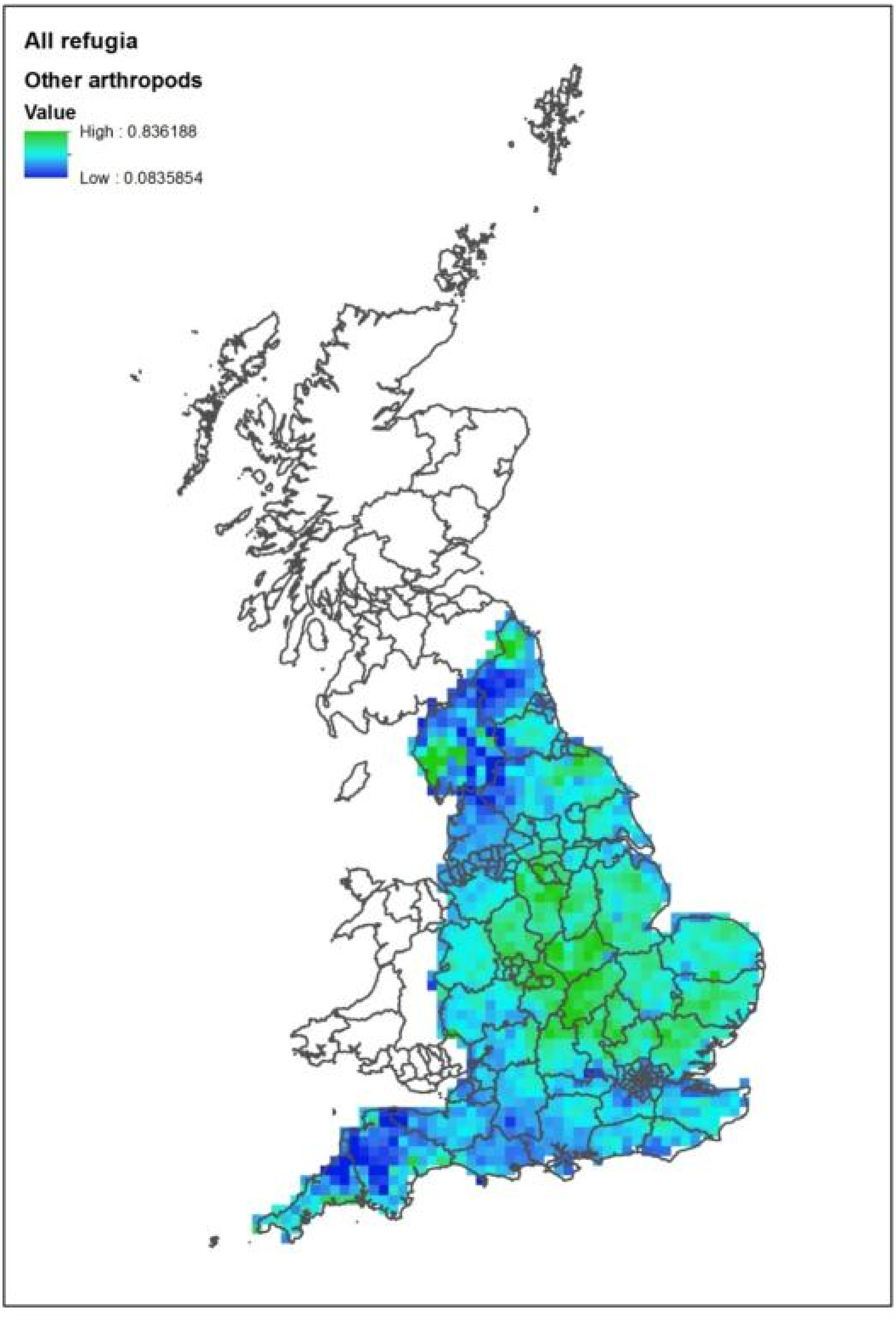
**Appendix 2 Figure 4c** Map showing refugial areas for beetles (Coleoptera) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



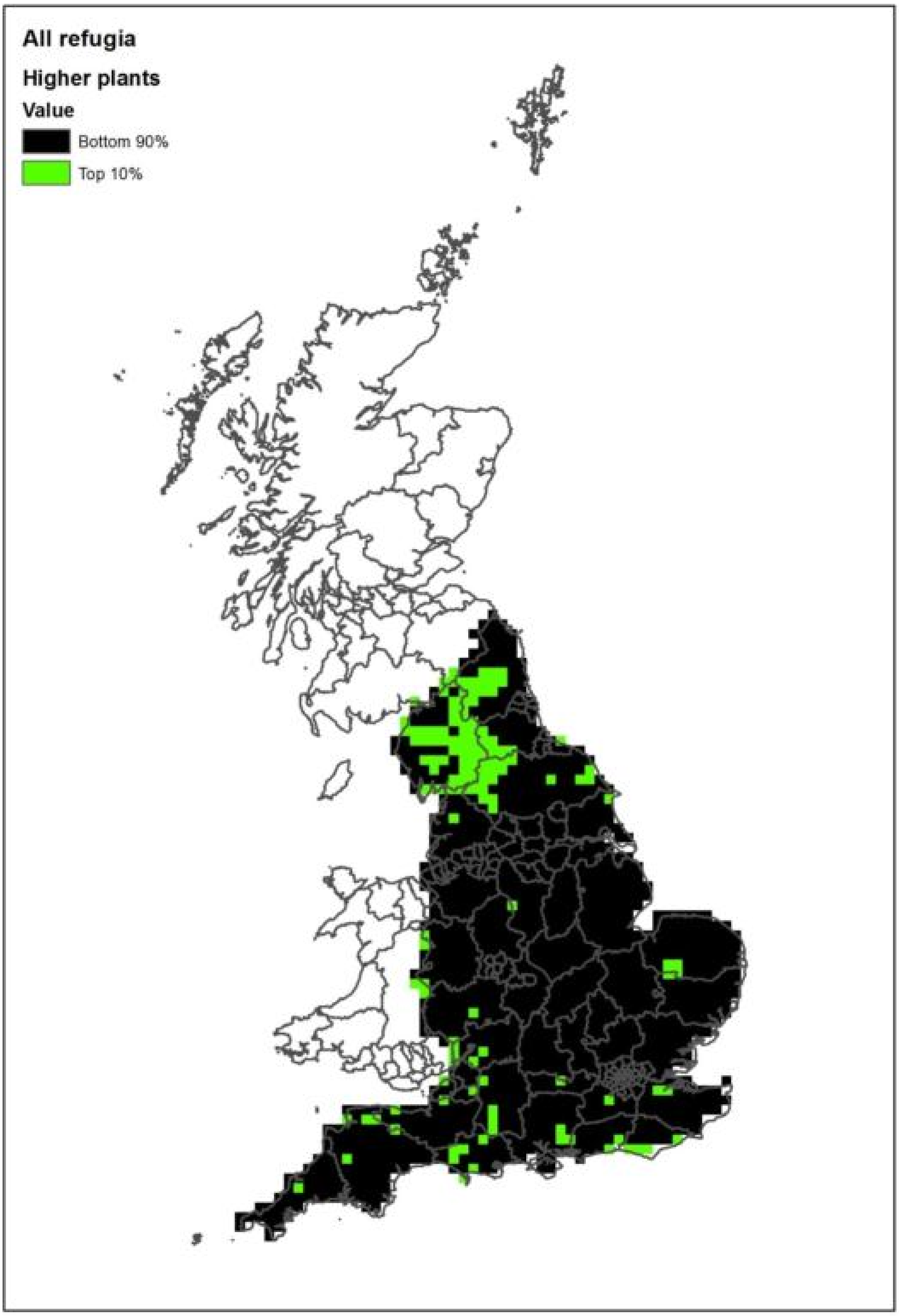
**Appendix 2 Figure 4d** Map showing refugial areas for butterflies and moths (Lepidoptera) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



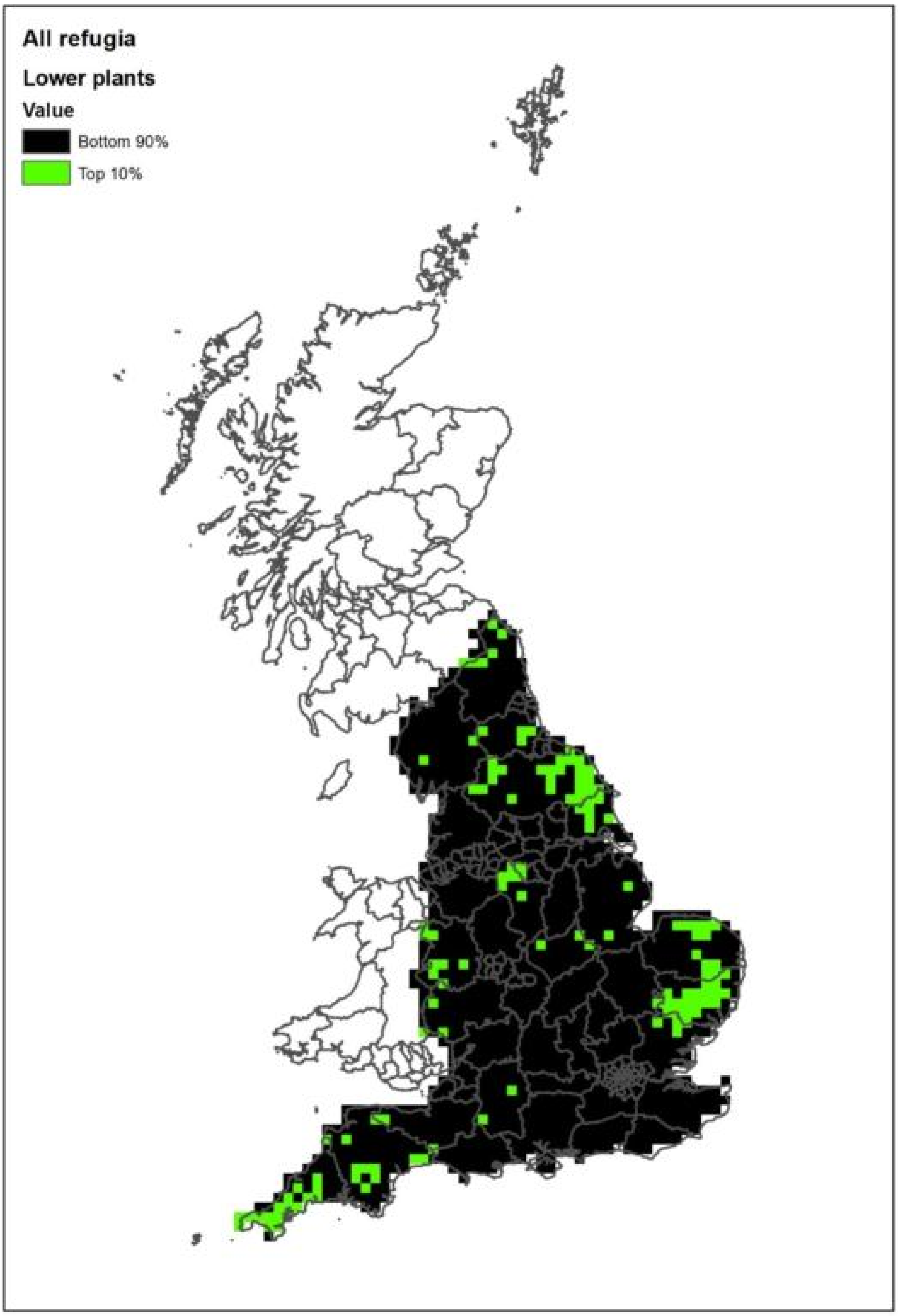
**Appendix 2 Figure 4e** Map showing refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



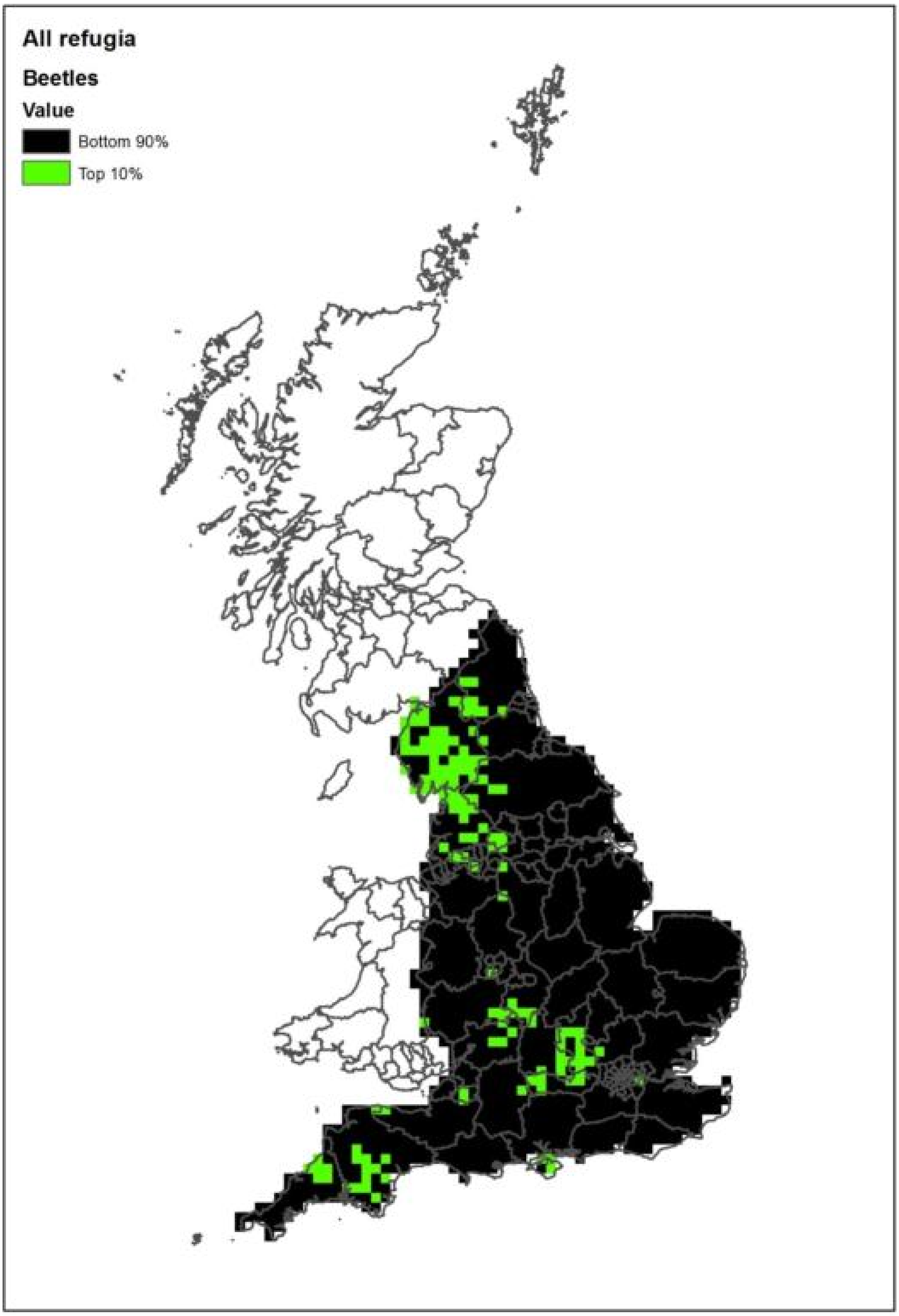
**Appendix 2 Figure 4f** Map showing refugial areas for other arthropods (centipedes, millipedes and spiders) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. The values correspond to the mean (across species) modelled probability of persistence over the last c. 30 years. Thus higher values indicate higher refugium potential.



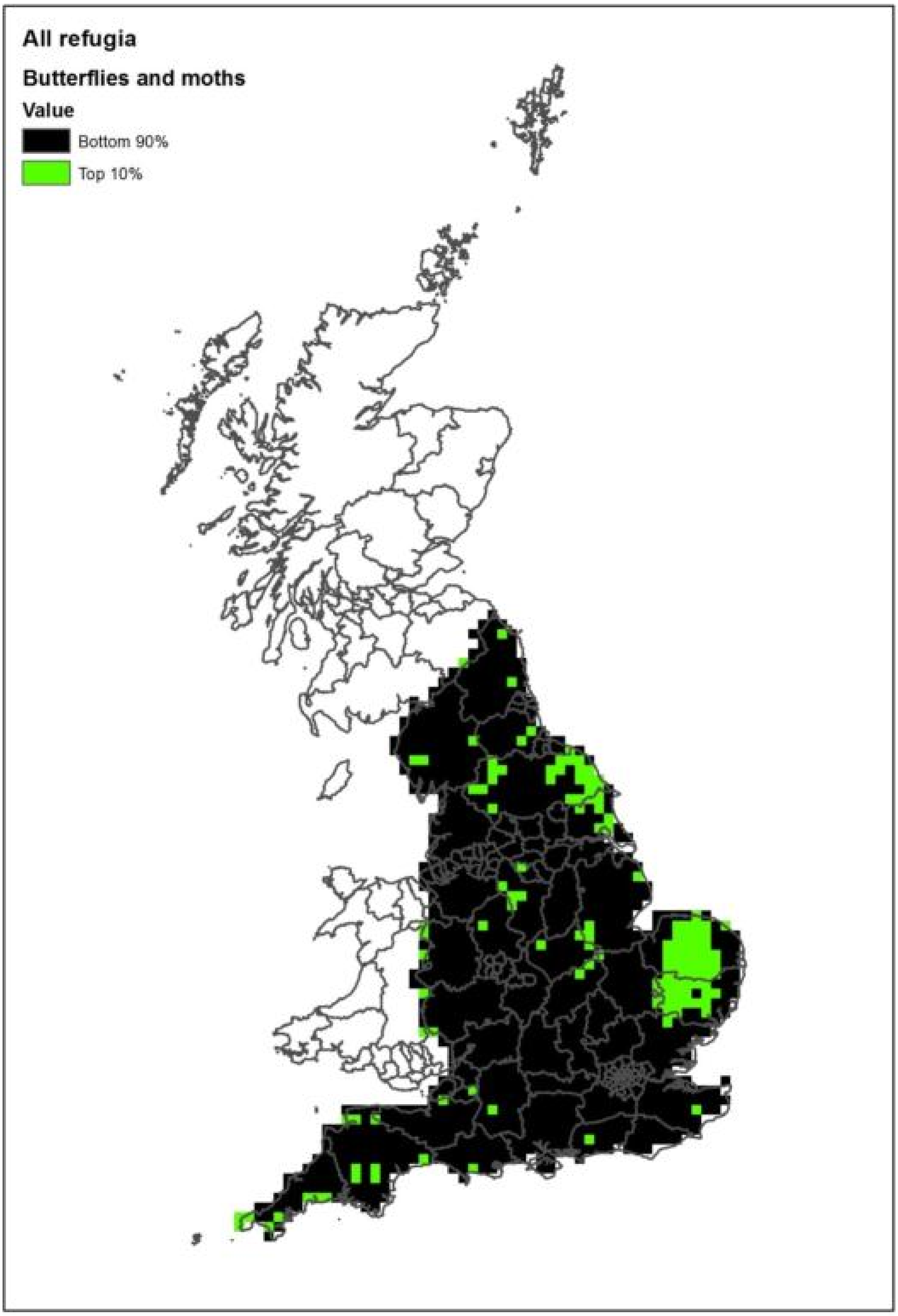
**Appendix 2 Figure 5a** Map showing the location of the top 10% of refugial areas for higher plants (tracheophytes) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



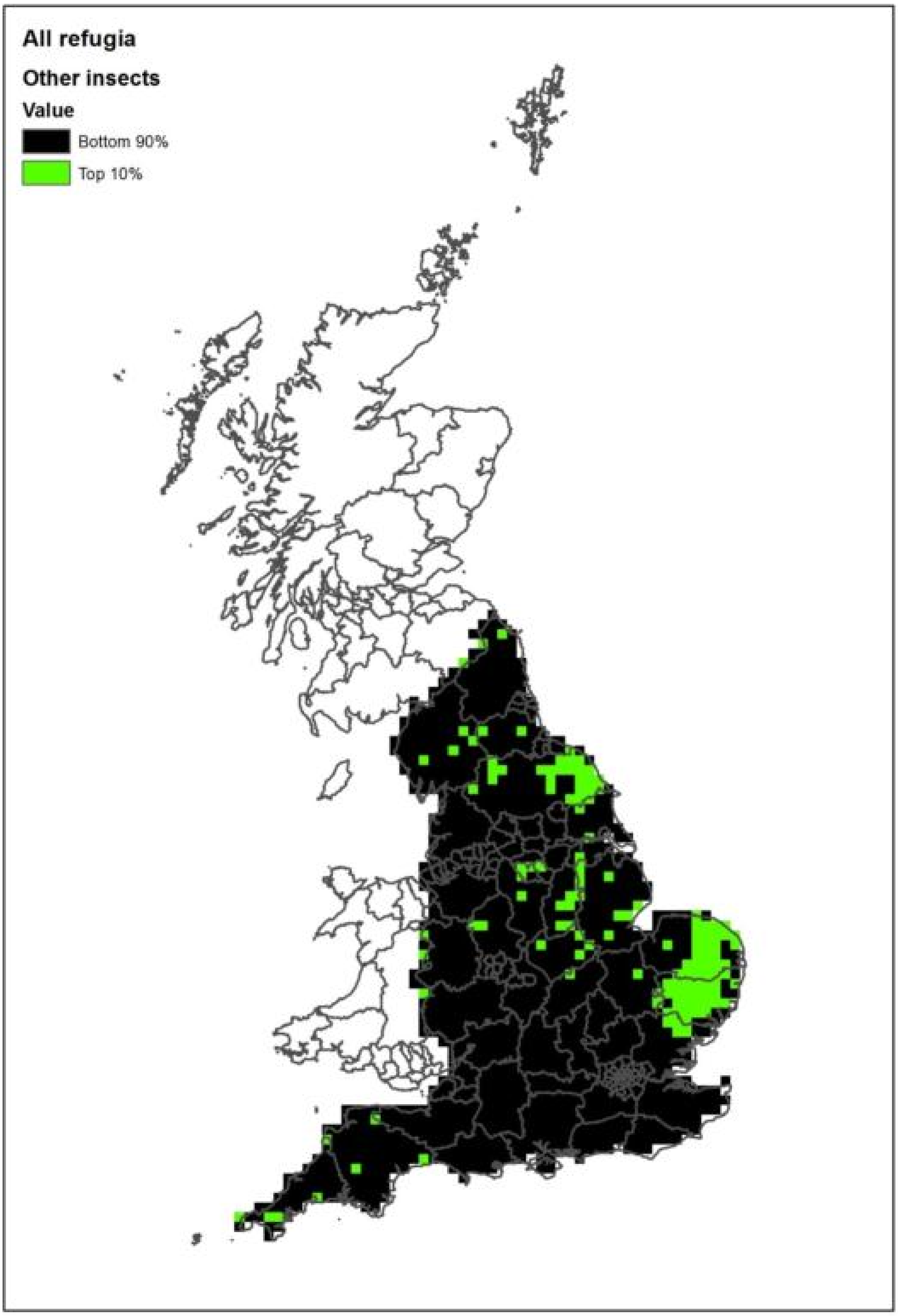
**Appendix 2 Figure 5b** Map showing the location of the top 10% of refugial areas for lower plants (bryophytes) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



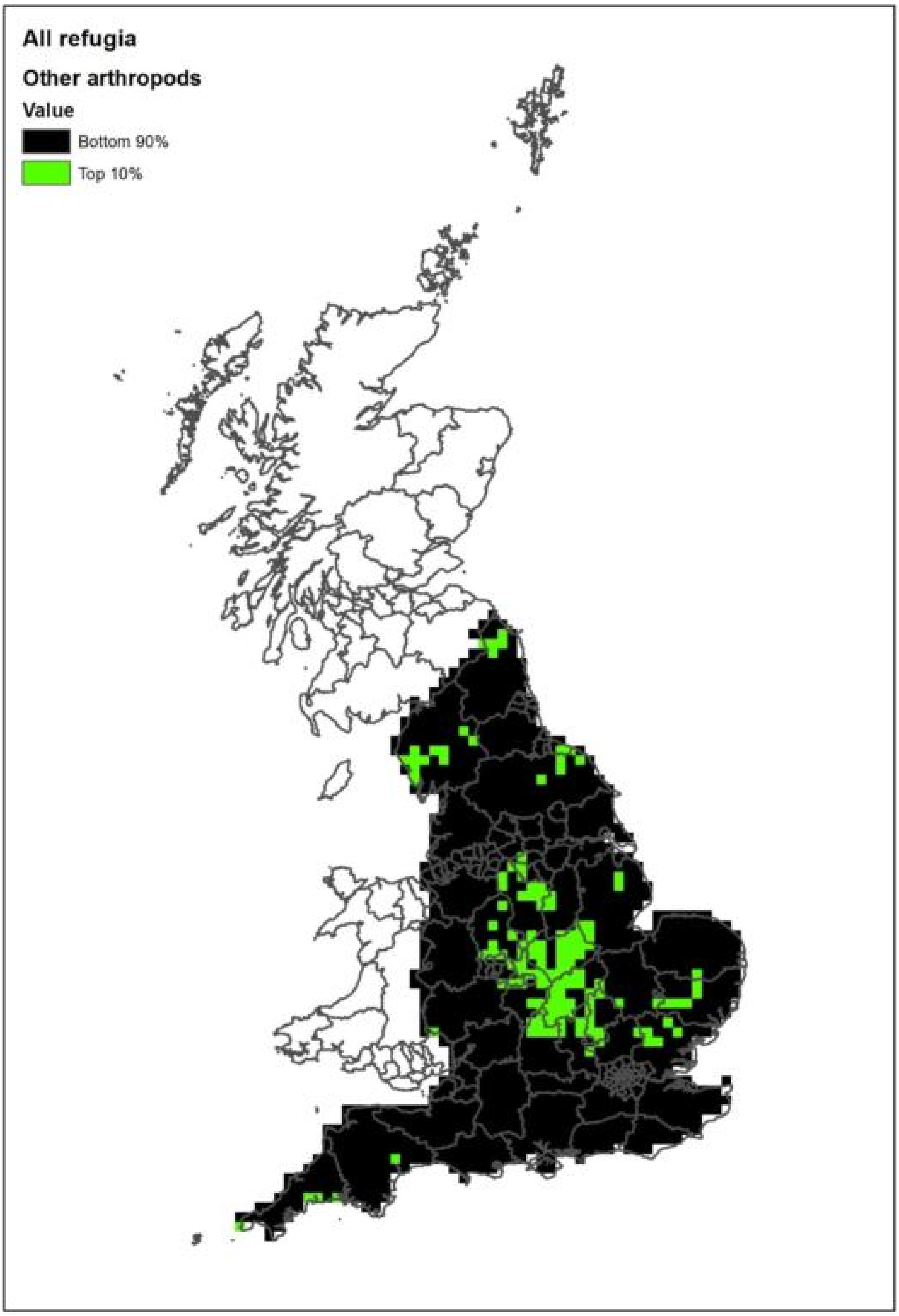
**Appendix 2 Figure 5c** Map showing the location of the top 10% of refugial areas for beetles (Coleoptera) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



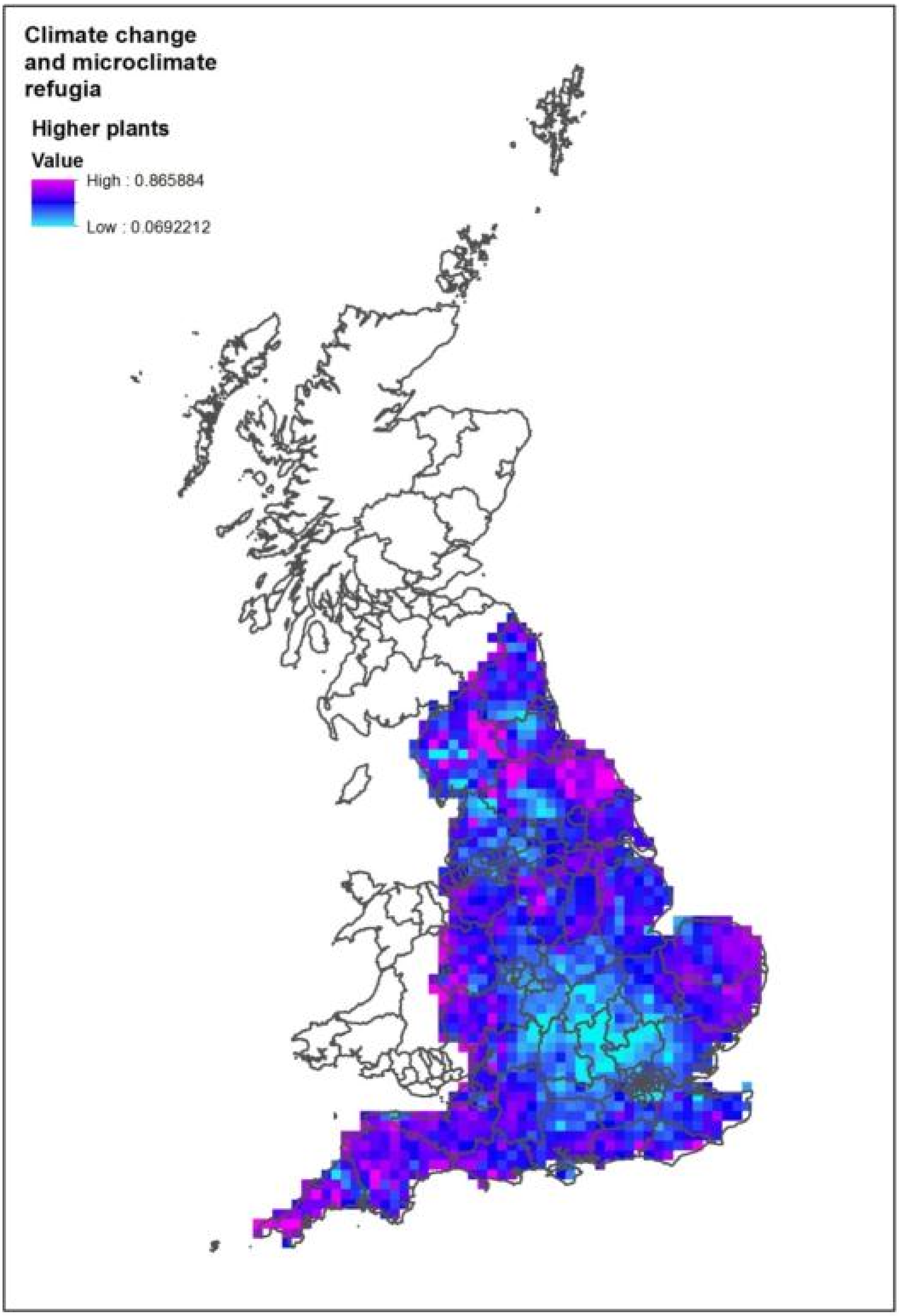
**Appendix 2 Figure 5d** Map showing the location of the top 10% of refugial areas for butterflies and moths (Lepidoptera) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



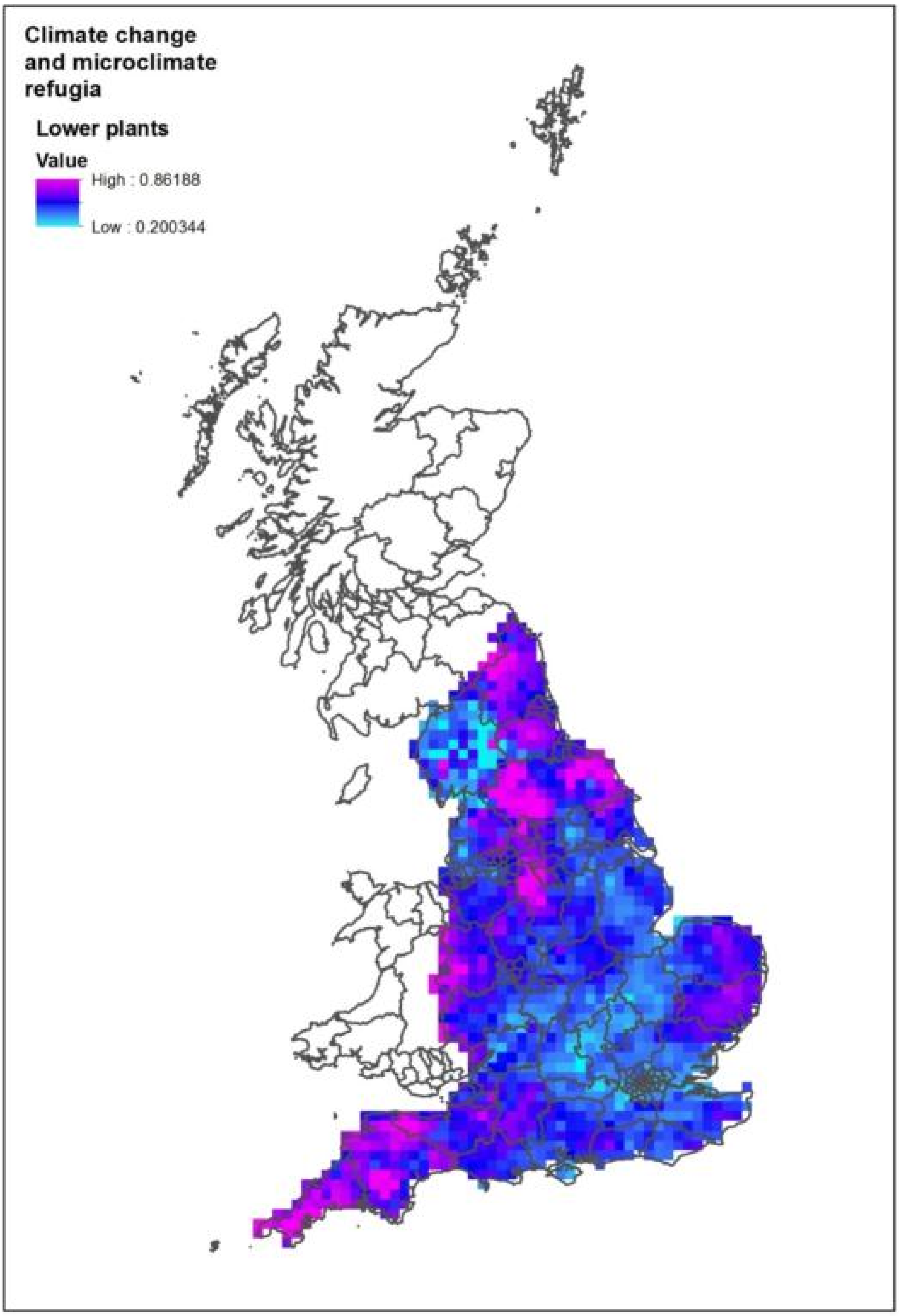
**Appendix 2 Figure 5e** Map showing the location of the top 10% of refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



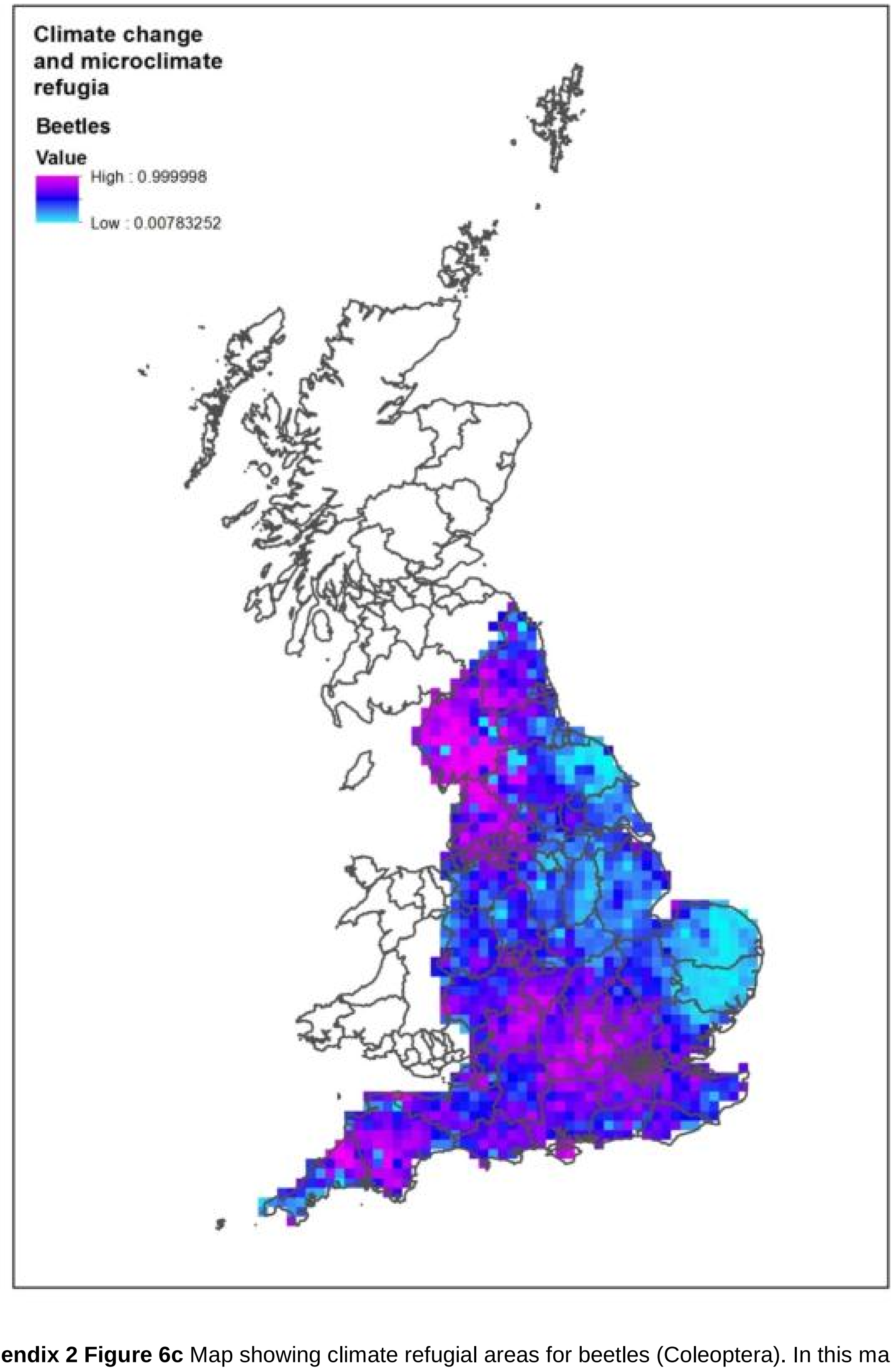
**Appendix 2 Figure 5f** Map showing the location of the top 10% of refugial areas for other arthropods (centipedes, millipedes and spiders) calculated using all relevant variables, not just those related to climate change. In this map, in addition to climatic determinants, locations with appropriate geology or subject to low agricultural intensity are considered to be good refugia. Green colouring represents squares in the top 10%, while black represents those in the bottom 90%.



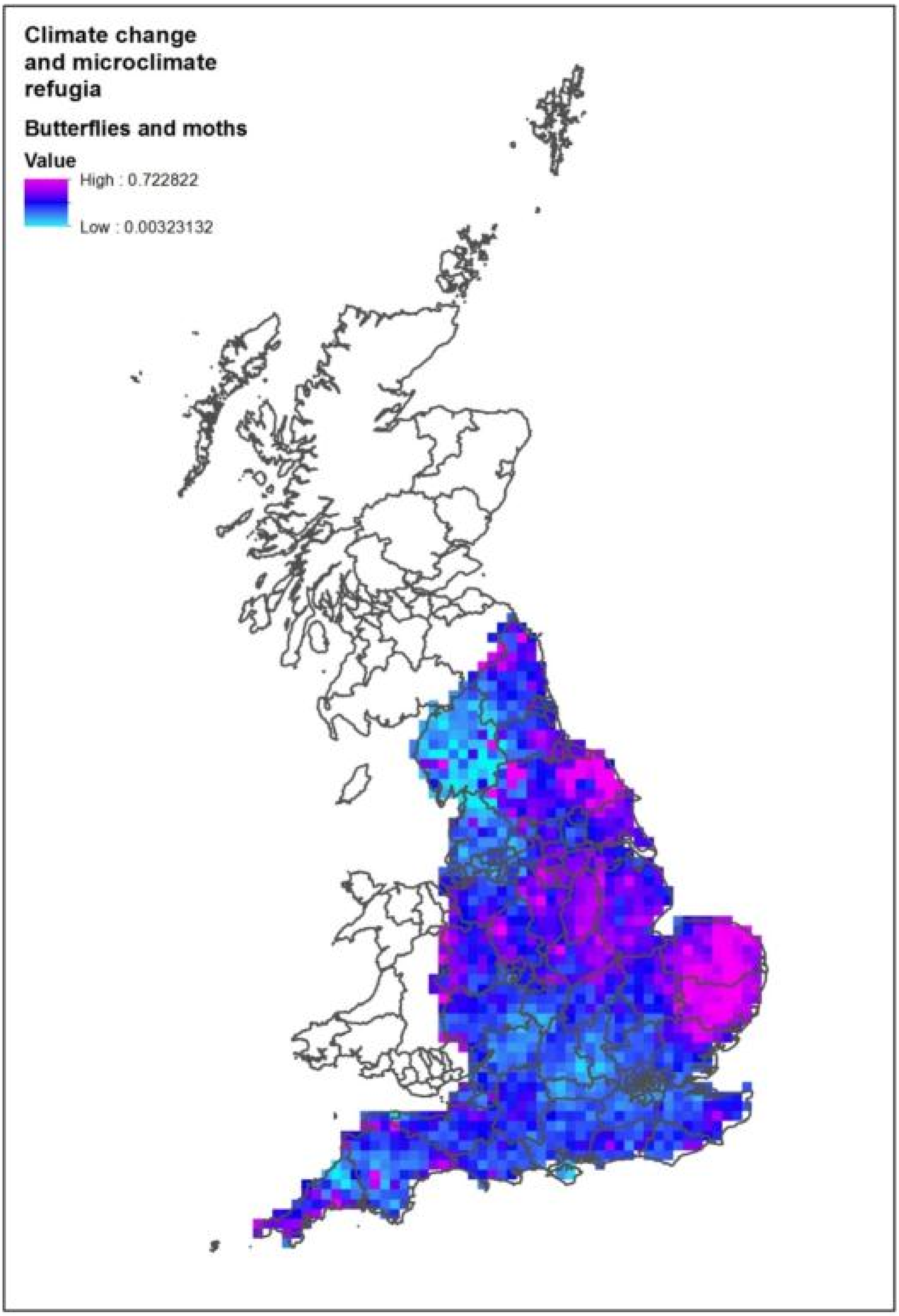
**Appendix 2 Figure 6a** Map showing climate refugial areas for higher plants (tracheophytes). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



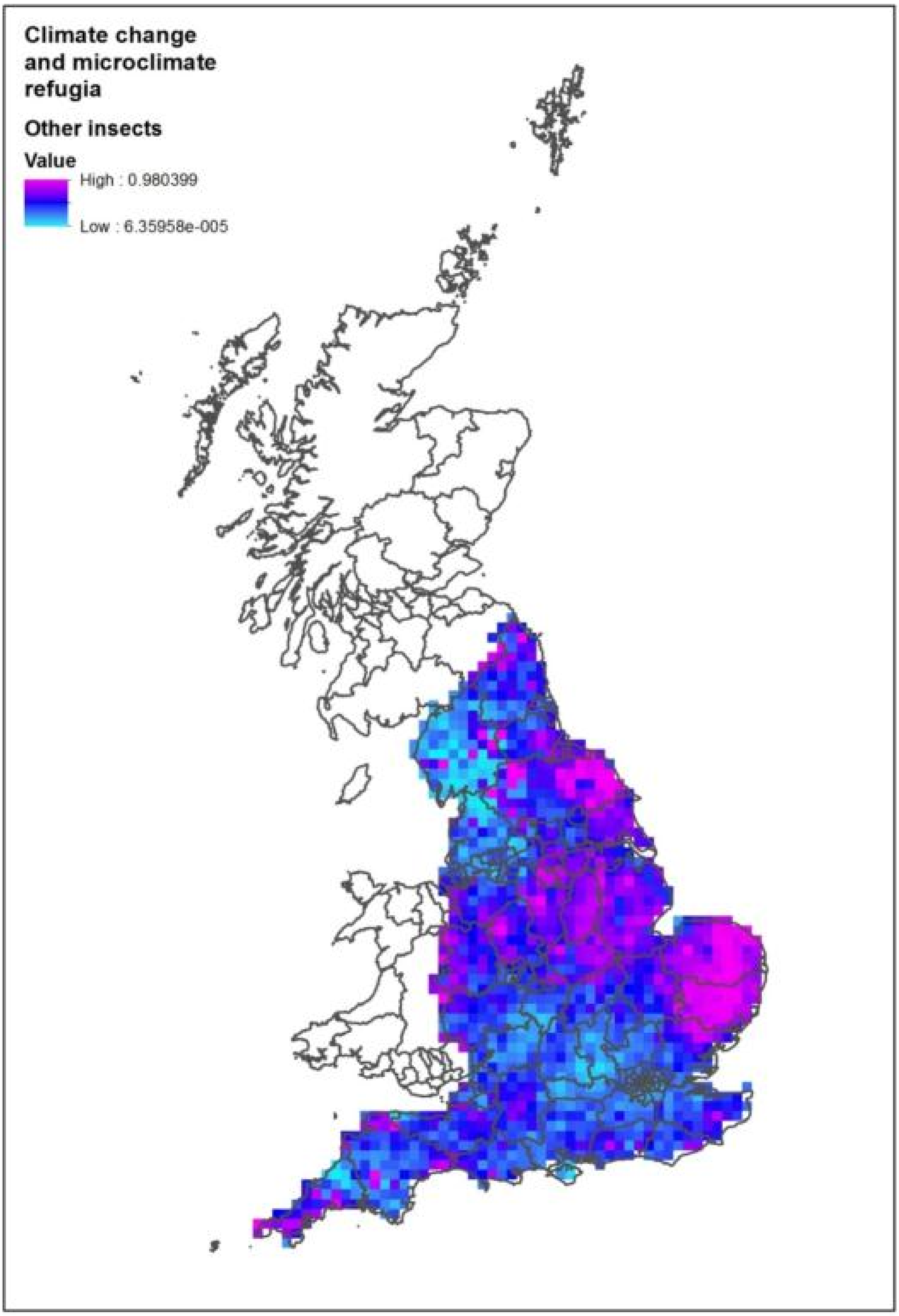
**Appendix 2 Figure 6b** Map showing climate refugial areas for lower plants (bryophytes). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



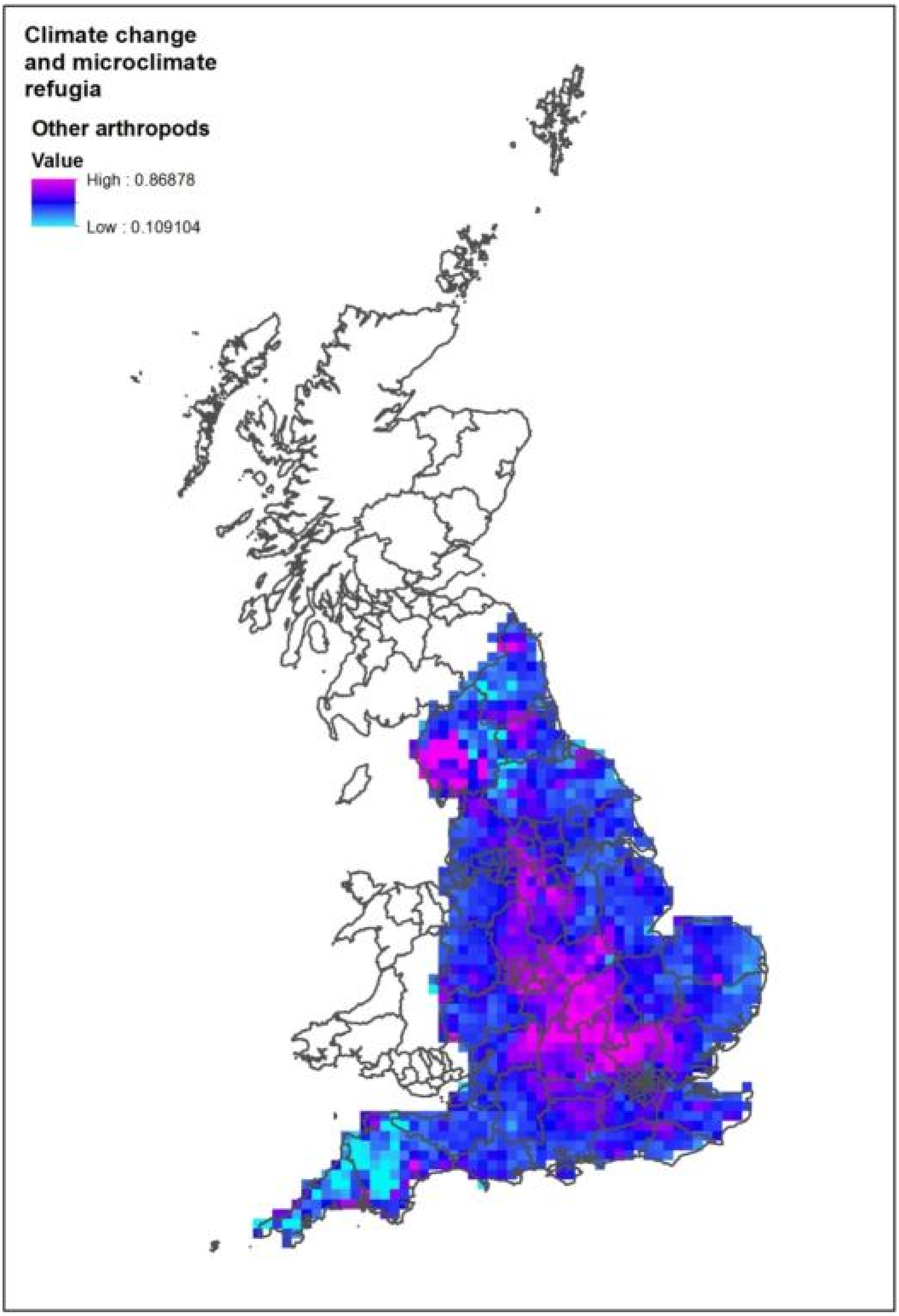
**Appendix 2 Figure 6c** Map showing climate refugial areas for beetles (Coleoptera). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



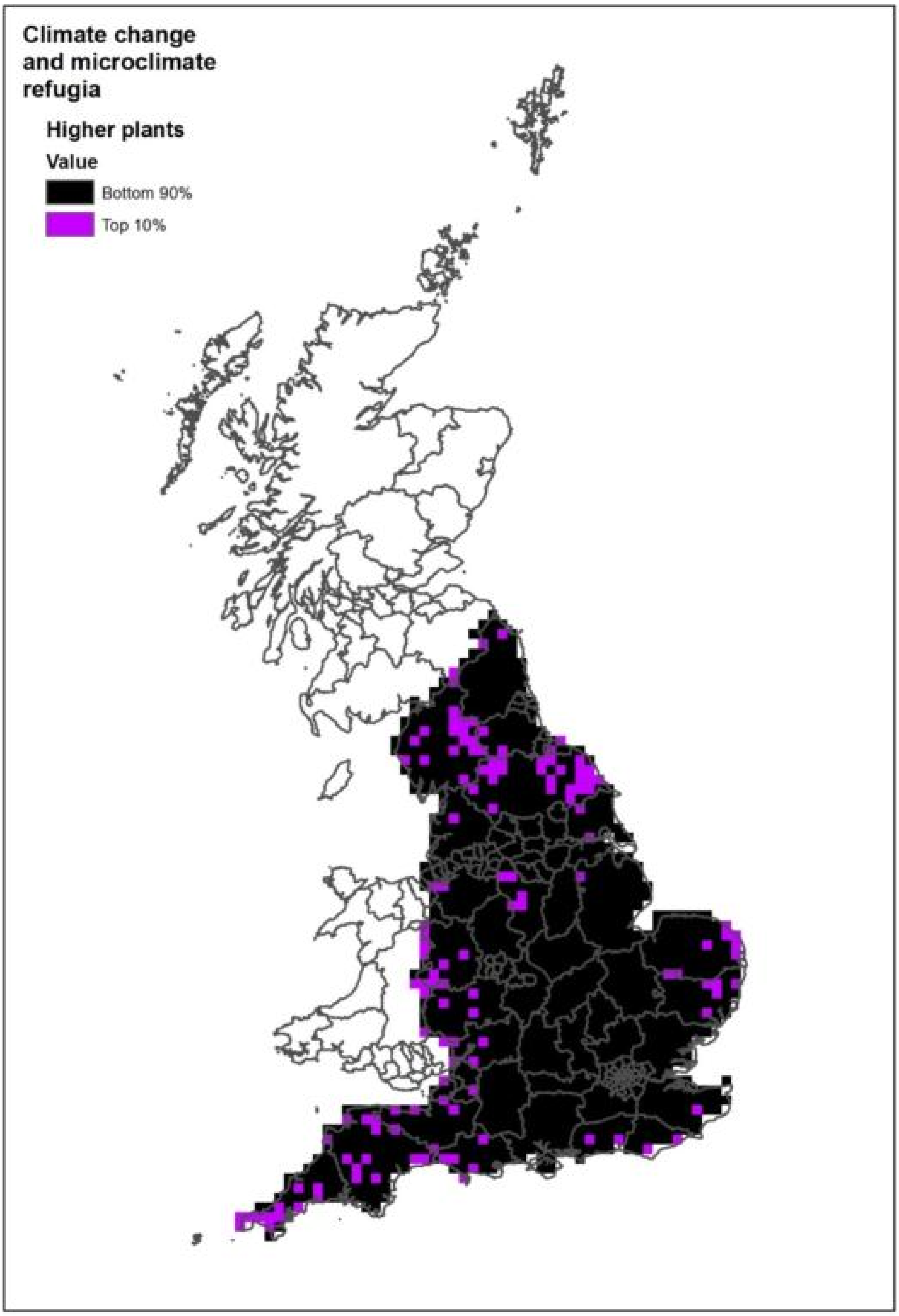
**Appendix 2 Figure 6d** Map showing climate refugial areas for butterflies and moths (Lepidoptera). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



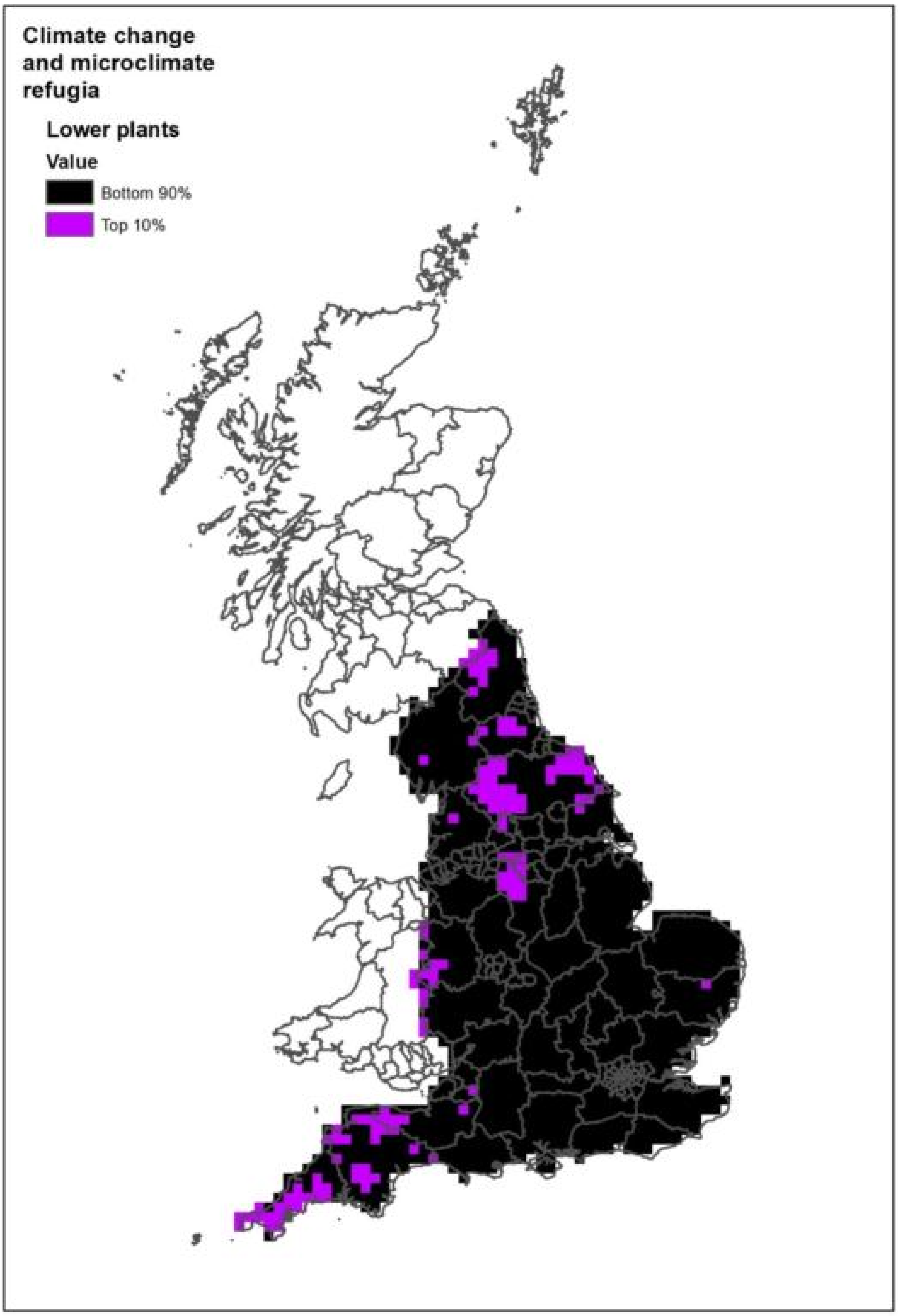
**Appendix 2 Figure 6e** Map showing climate refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



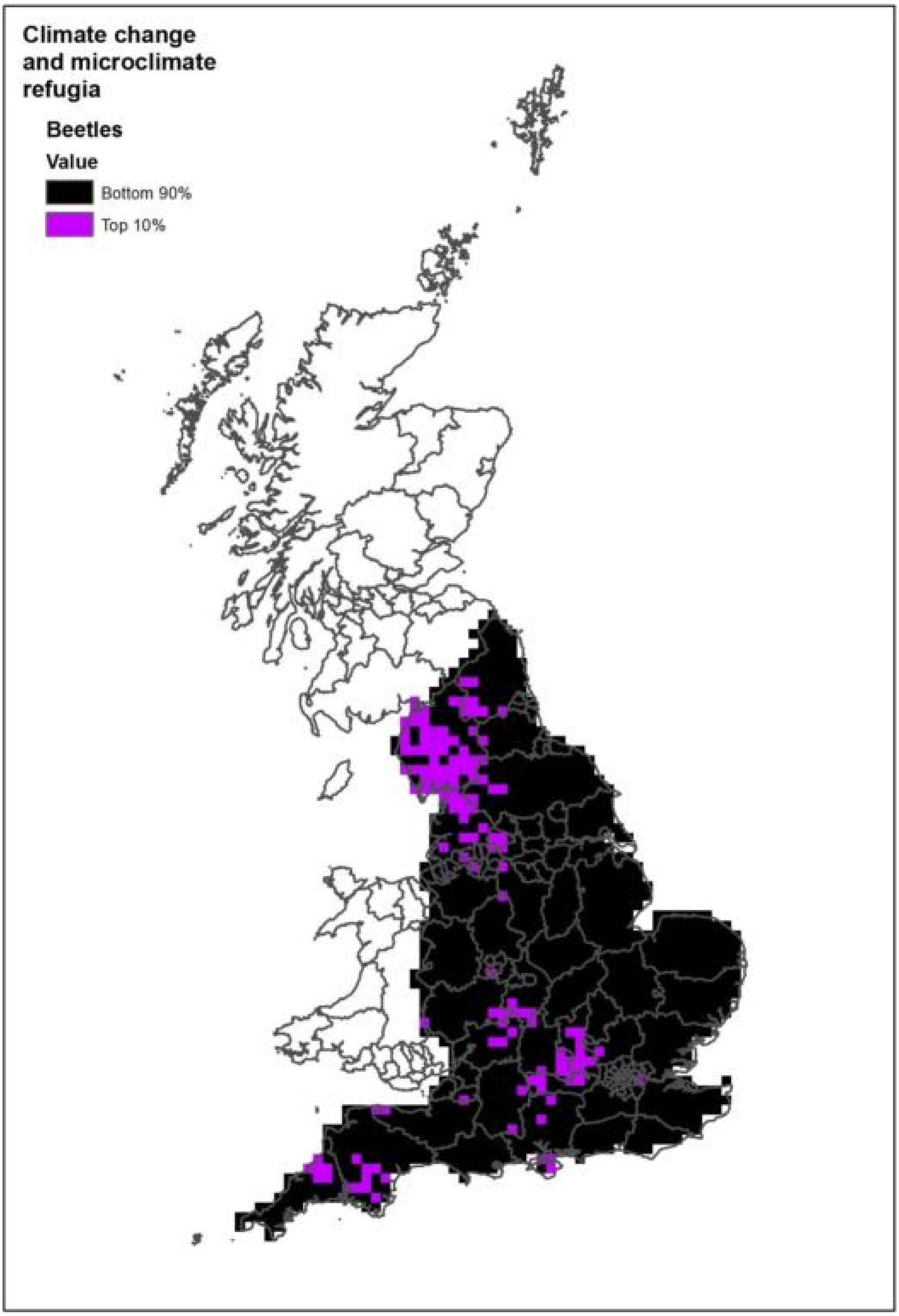
**Appendix 2 Figure 6f** Map showing climate refugial areas for other arthropods (centipedes, millipedes and spiders). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



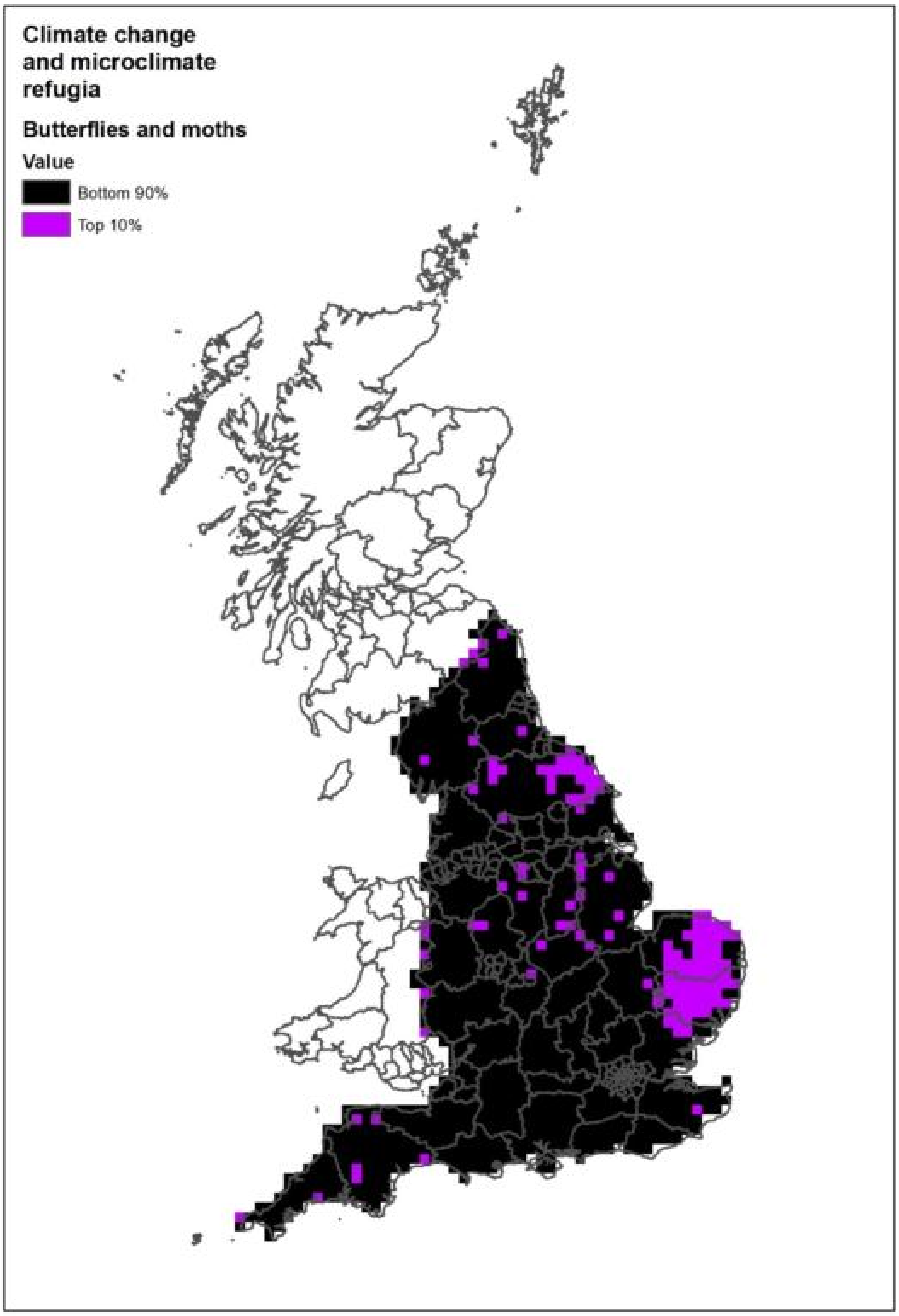
**Appendix 2 Figure 7a** Map showing the location of the top 10% of climate refugial areas for higher plants (tracheophytes). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



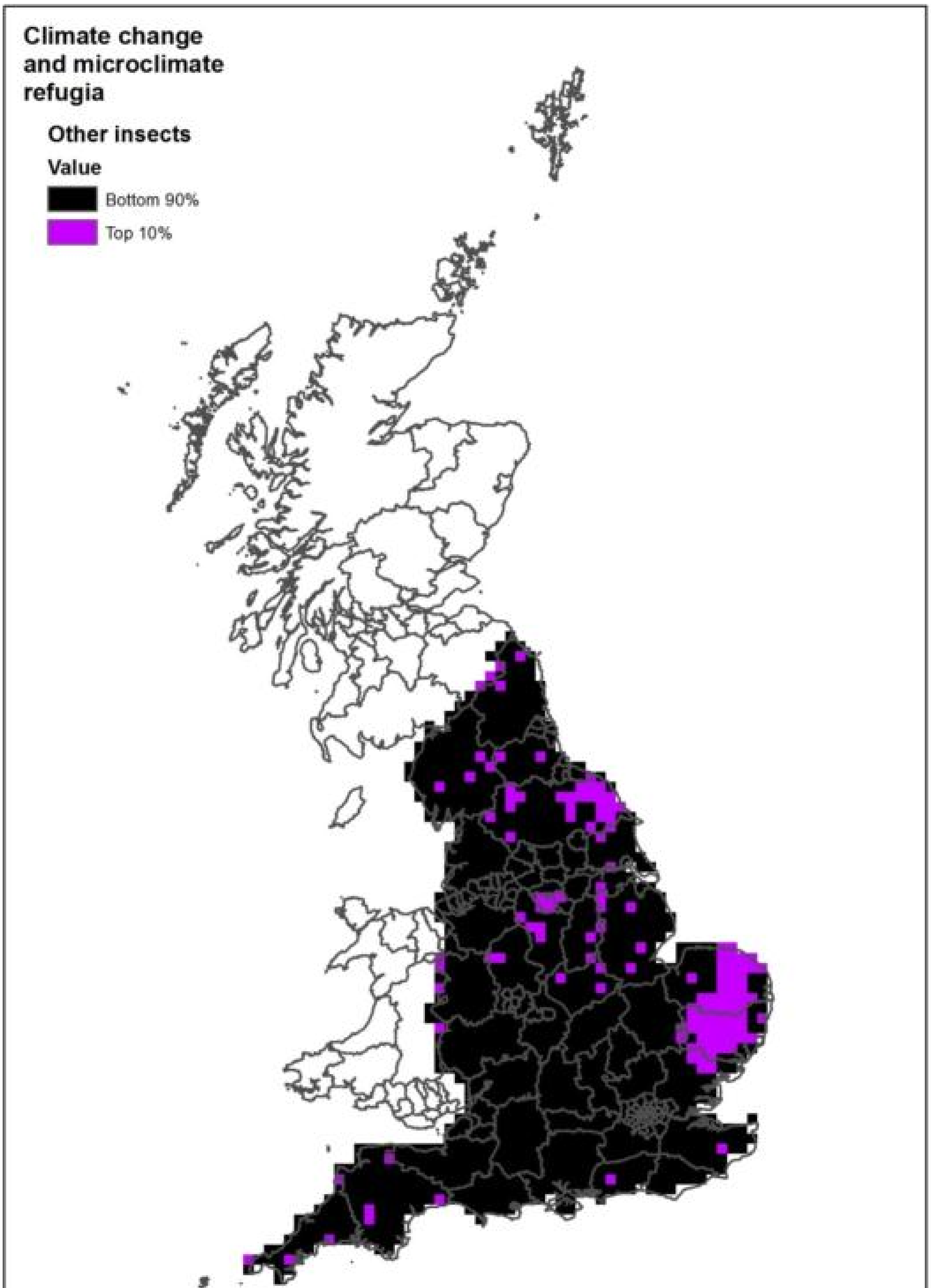
**Appendix 2 Figure 7b** Map showing the location of the top 10% of climate refugial areas for lower plants (bryophytes). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



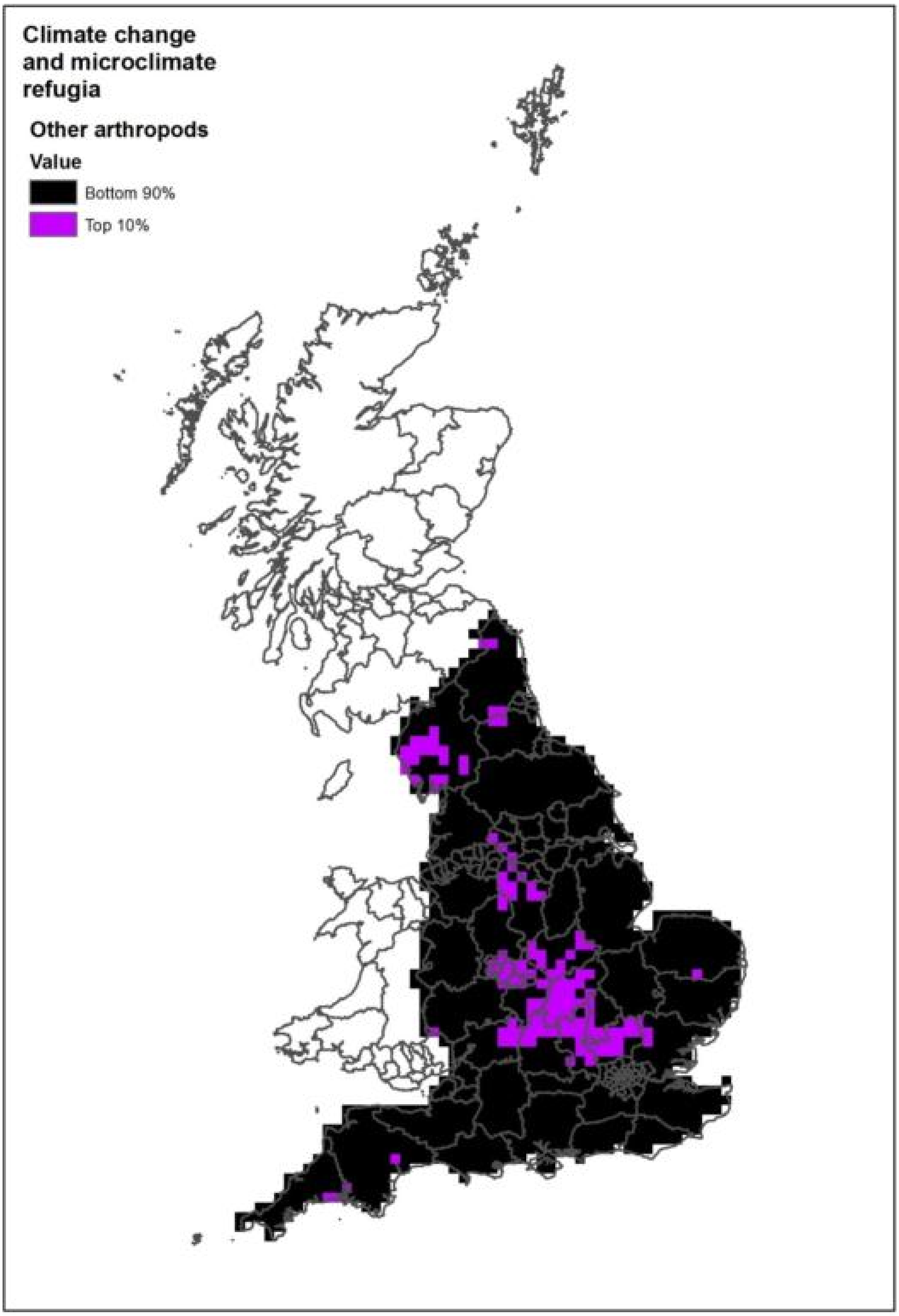
**Appendix 2 Figure 7c** Map showing the location of the top 10% of climate refugial areas for beetles (Coleoptera). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



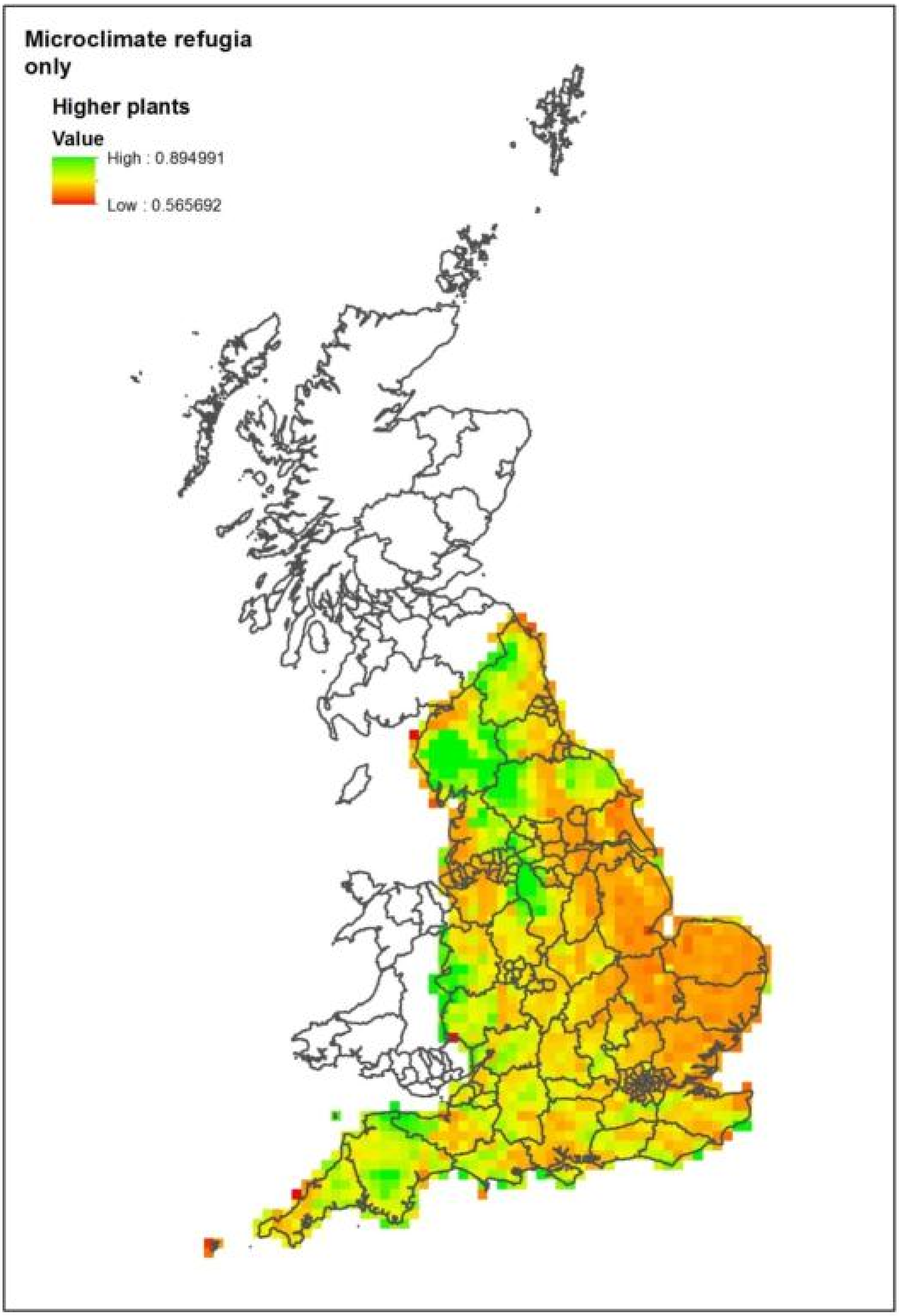
**Appendix 2 Figure 7d** Map showing the location of the top 10% of climate refugial areas for butterflies and moths (Lepidoptera). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



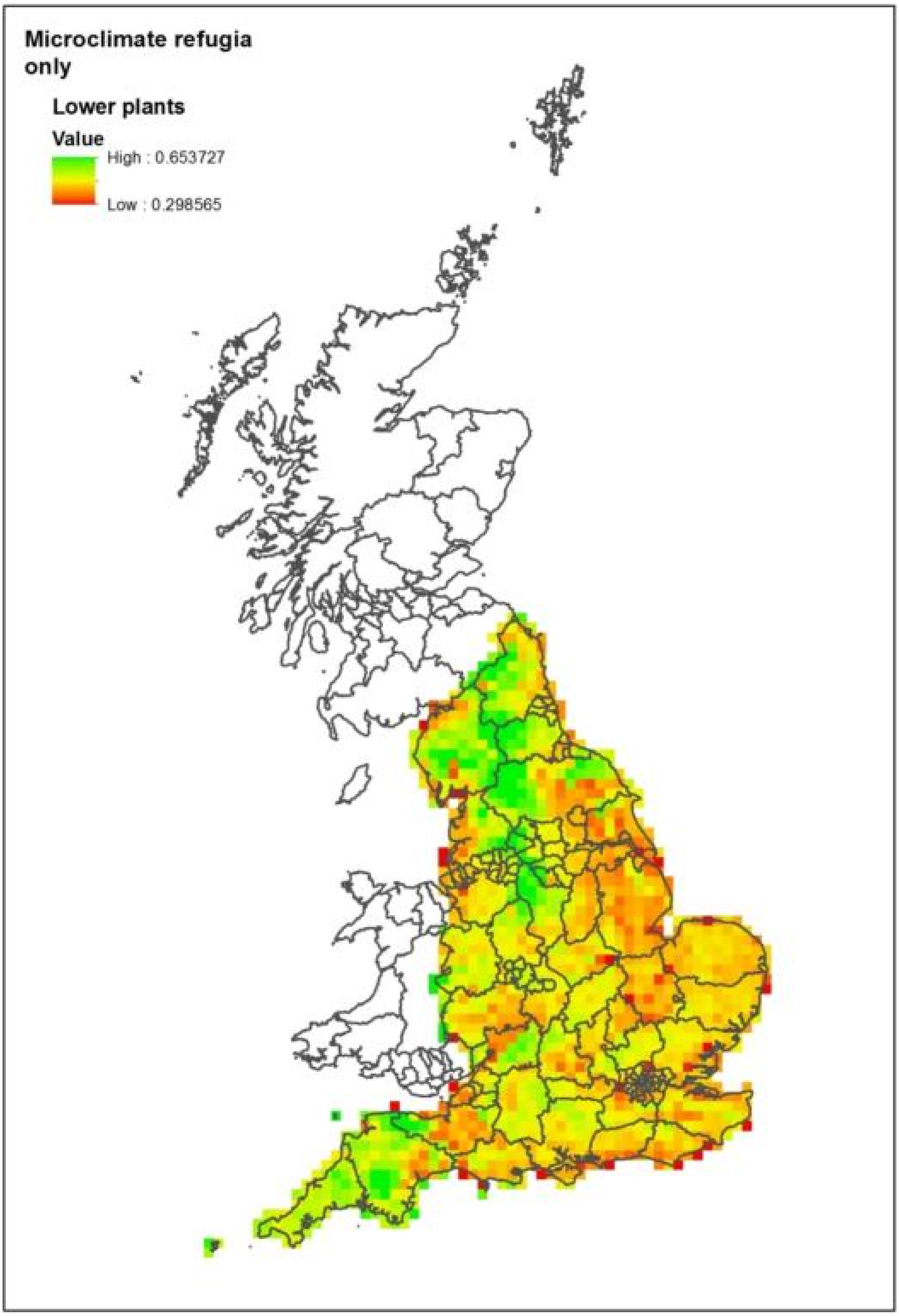
**Appendix 2 Figure 7e** Map showing the location of the top 10% of climate refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



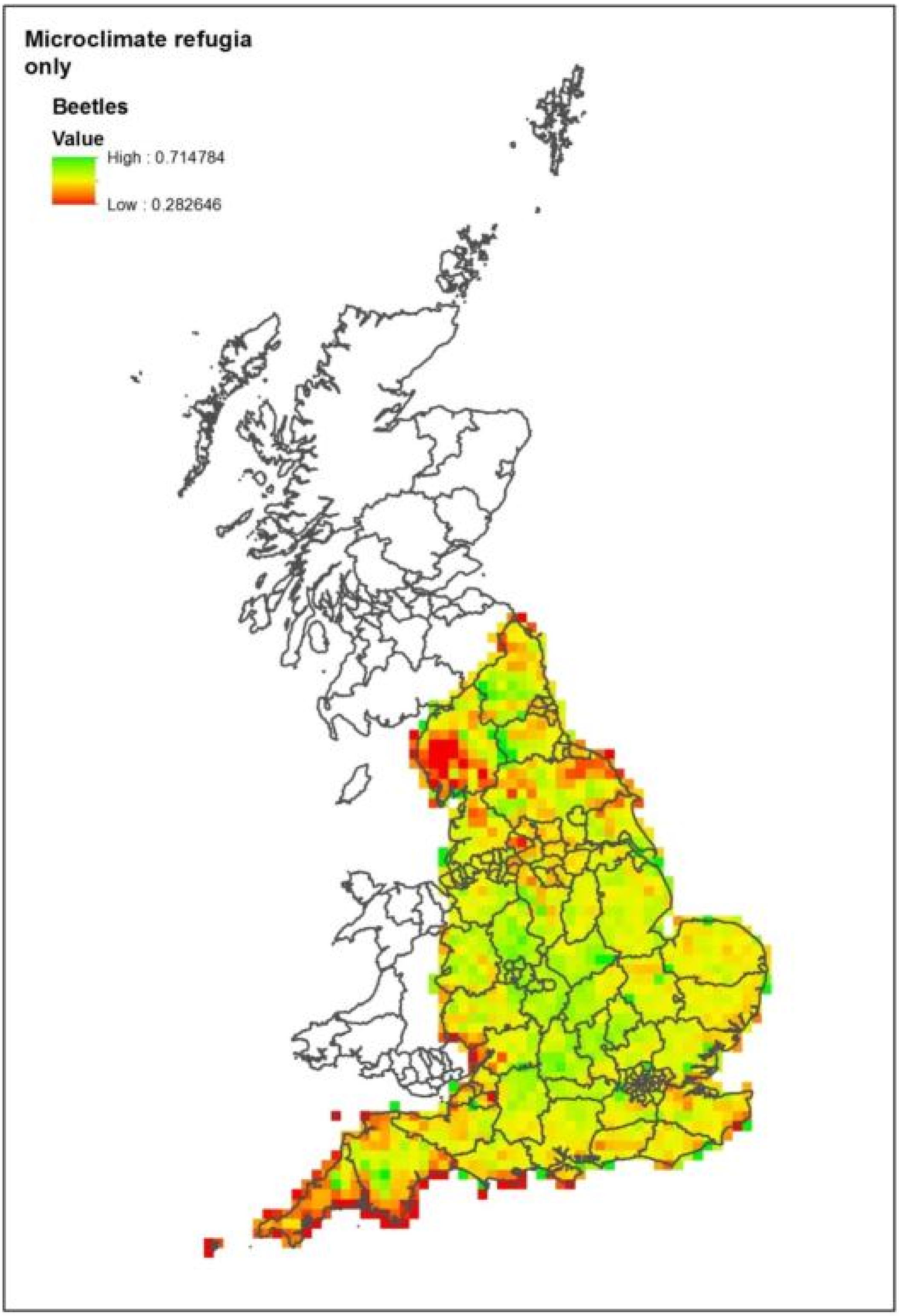
**Appendix 2 Figure 7f** Map showing the location of the top 10% of climate refugial areas for other arthropods (centipedes, millipedes and spiders). In this map, locations with high microclimate heterogeneity as well as those that have experienced less climate change are modelled as being good refugia, but the effects of e.g. agricultural intensity are ignored. Purple colouring represents squares in the top 10%, while black represents those in the bottom 90%.



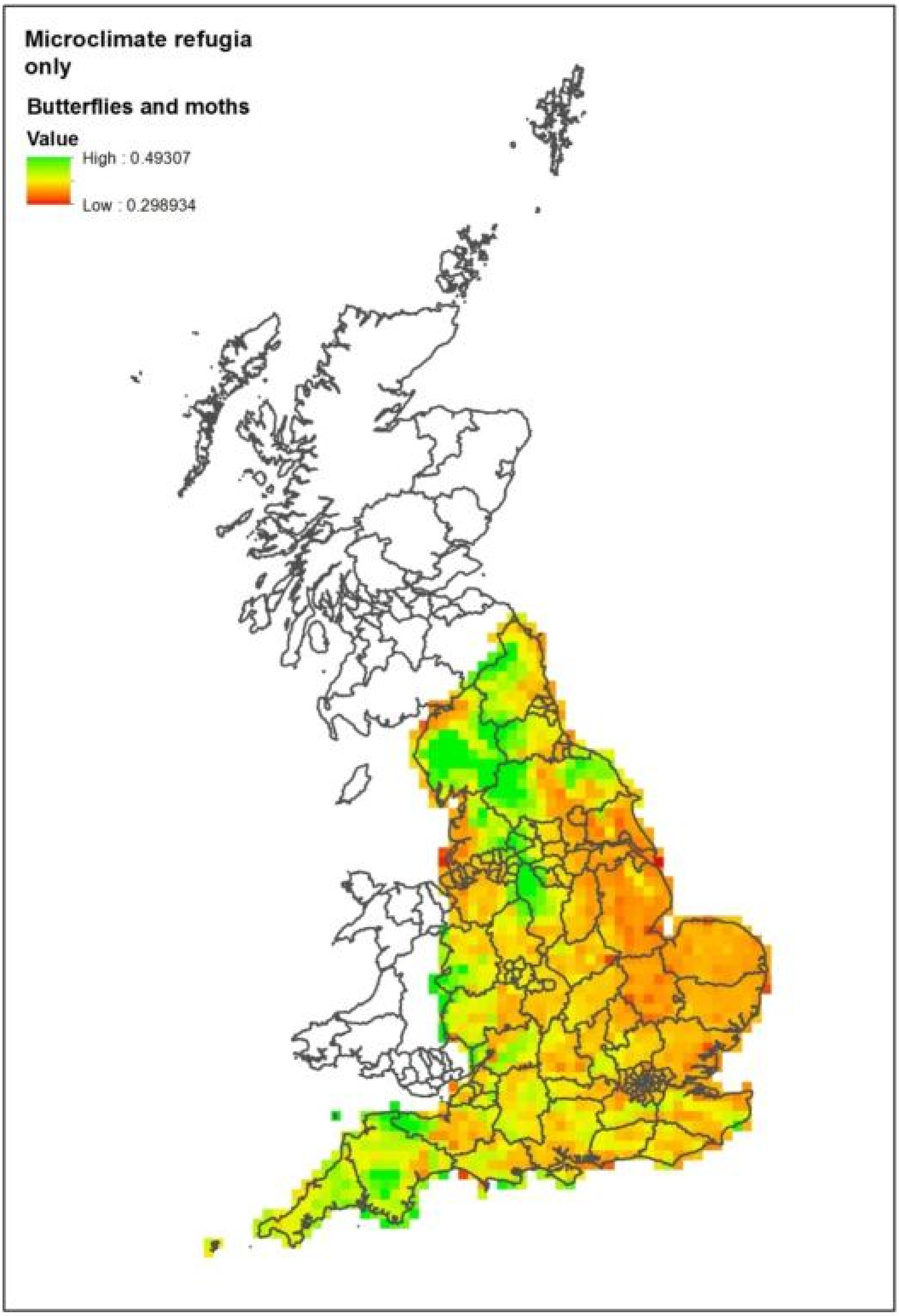
**Appendix 2 Figure 8a** Map showing microclimate refugial areas for higher plants (tracheophytes). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



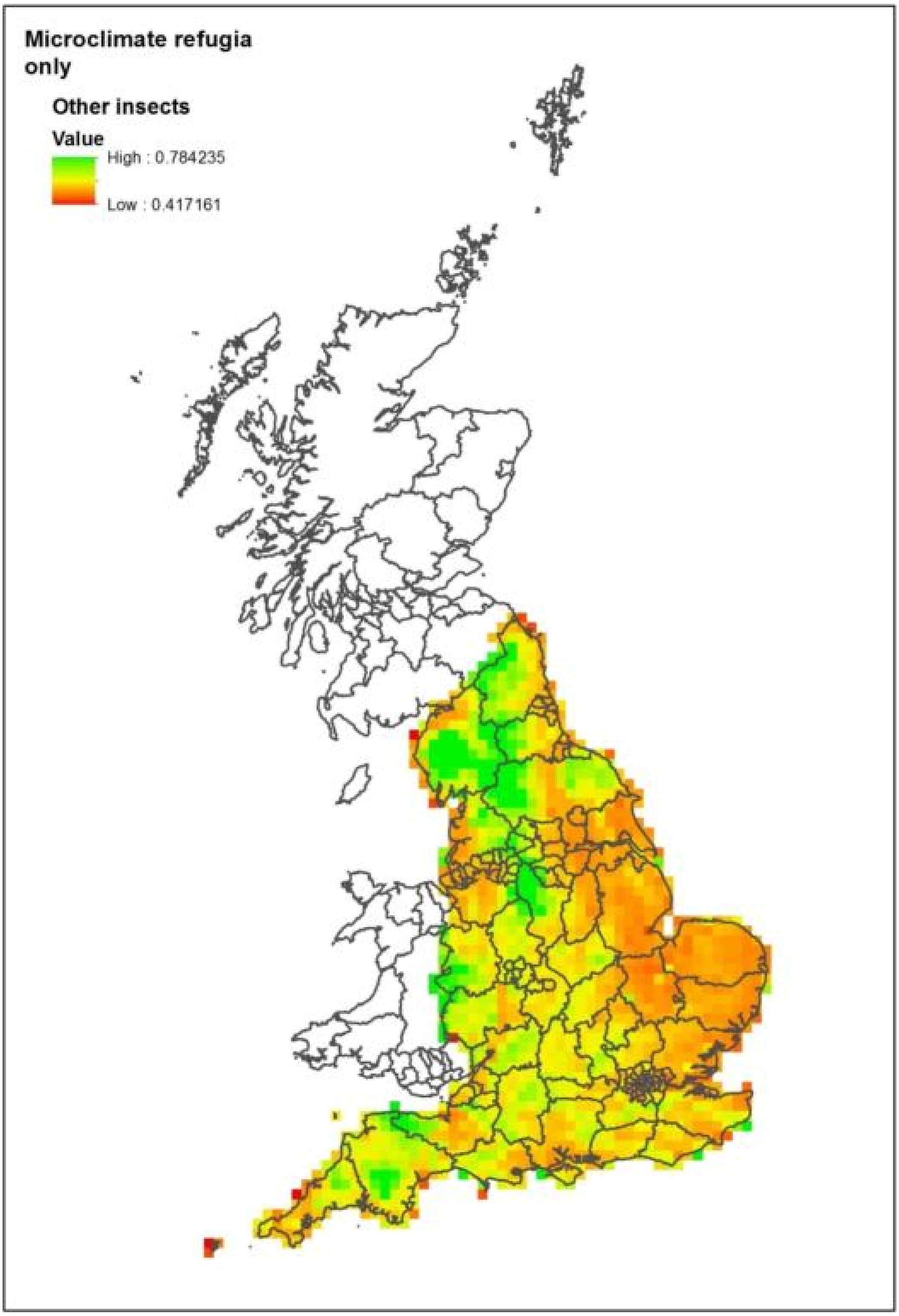
**Appendix 2 Figure 8b** Map showing microclimate refugial areas for lower plants (bryophytes). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



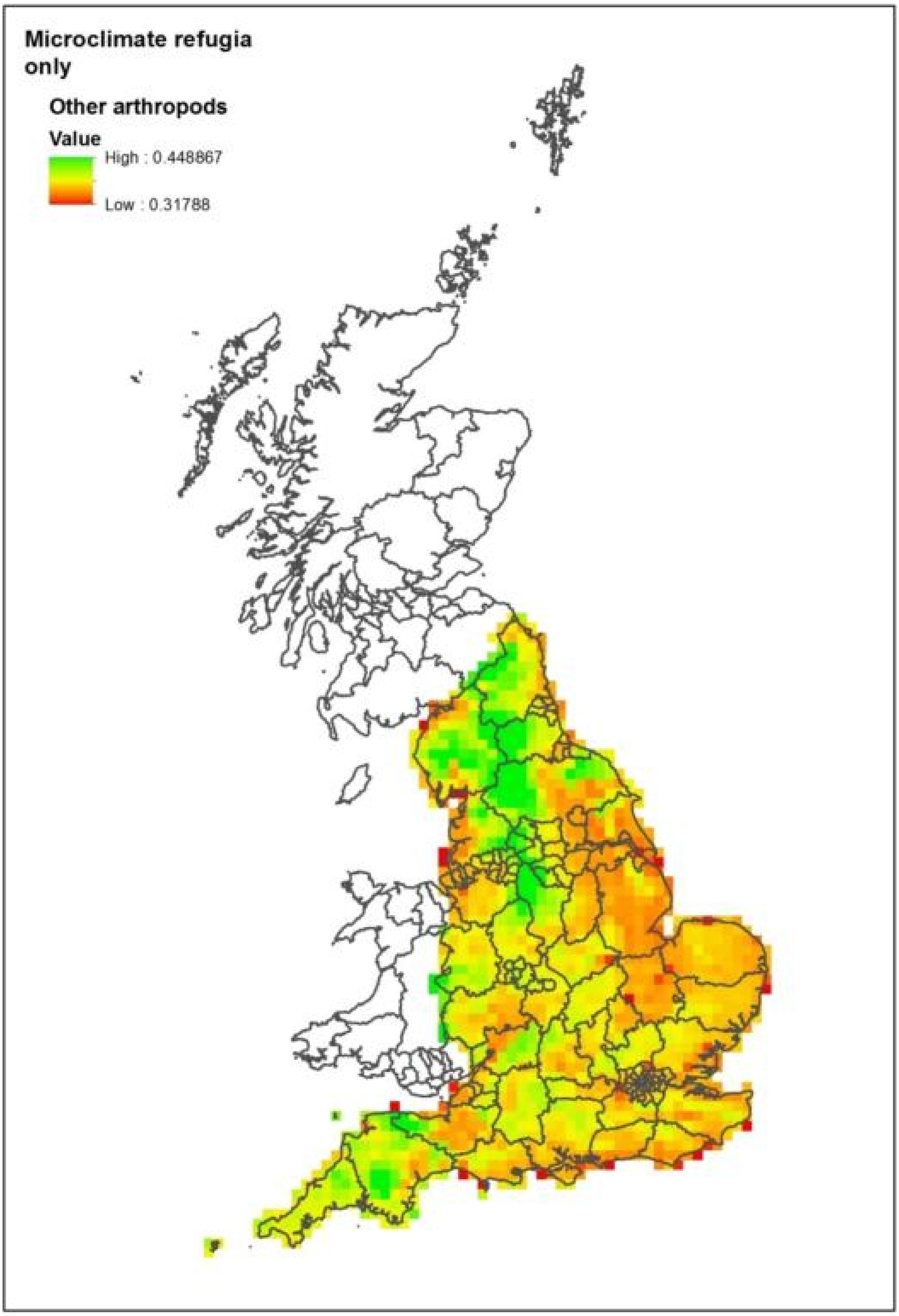
**Appendix 2 Figure 8c** Map showing microclimate refugial areas for beetles (Coleoptera). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



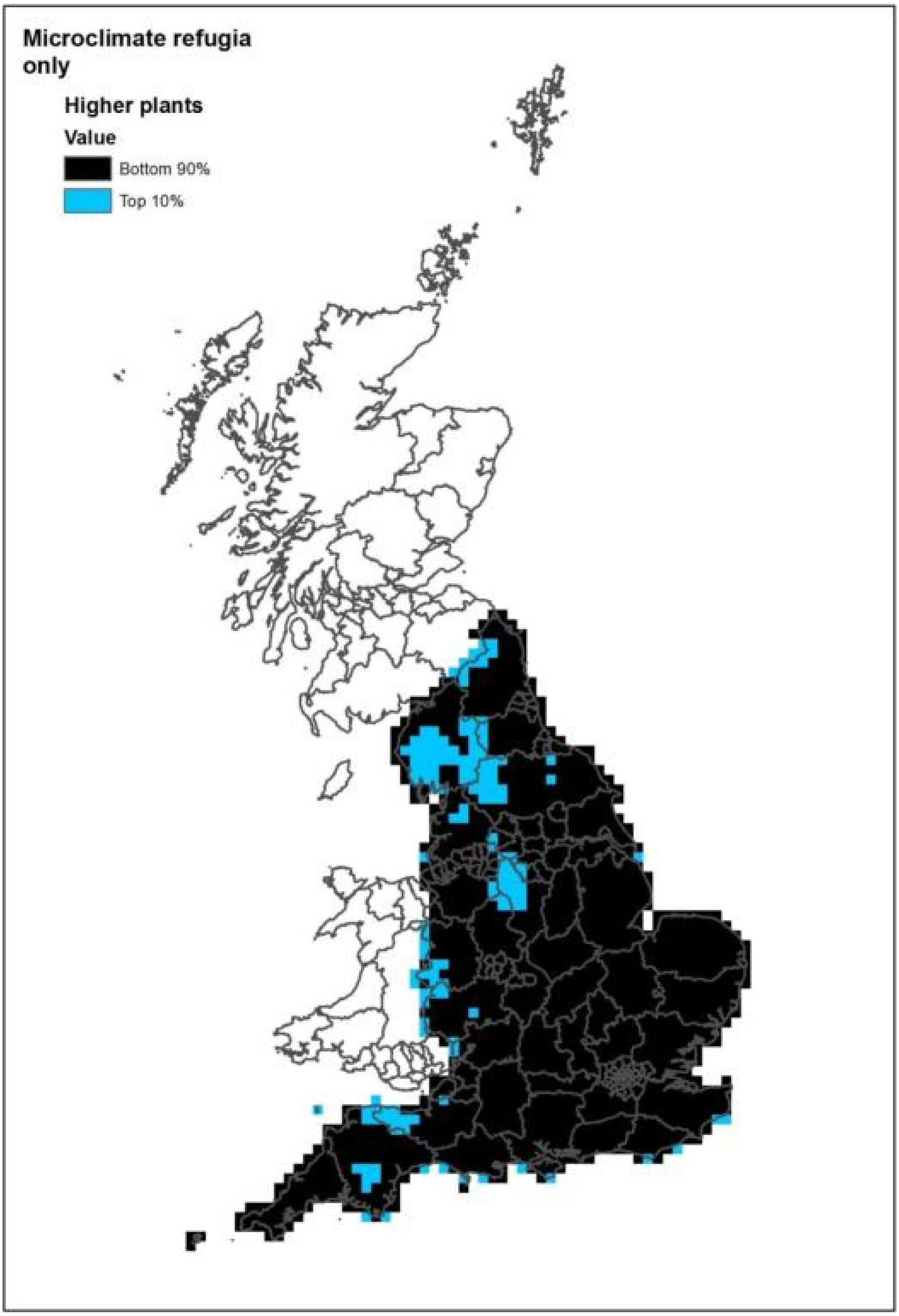
**Appendix 2 Figure 8d** Map showing microclimate refugial areas for butterflies and moths (Lepidoptera). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



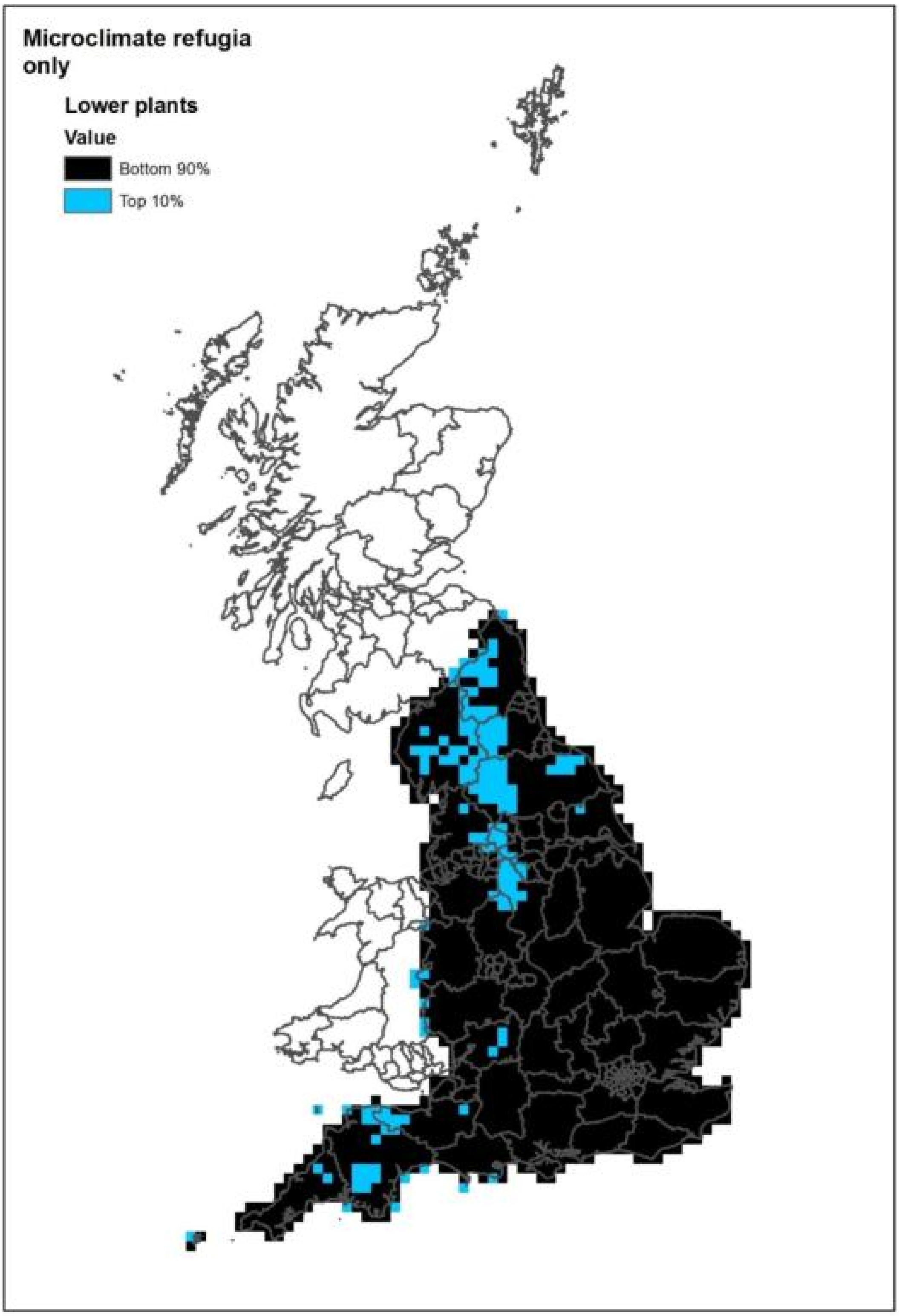
**Appendix 2 Figure 8e** Map showing microclimate refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



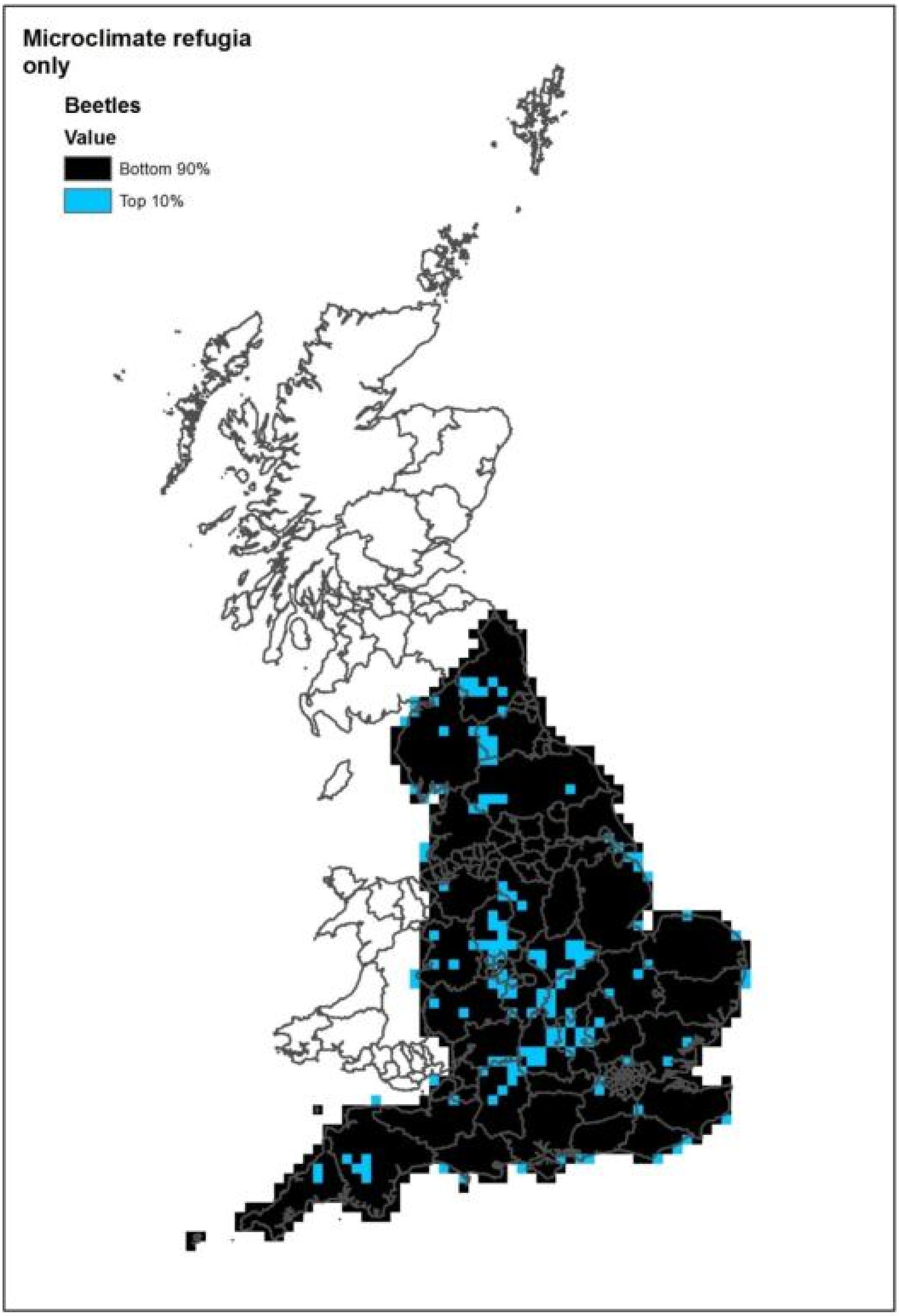
**Appendix 2 Figure 8f** Map showing microclimate refugial areas for other arthropods (centipedes, millipedes and spiders). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. The values correspond to the mean (across species) modelled probability of persistence over the last 40 years. Thus higher values indicate higher refugium potential.



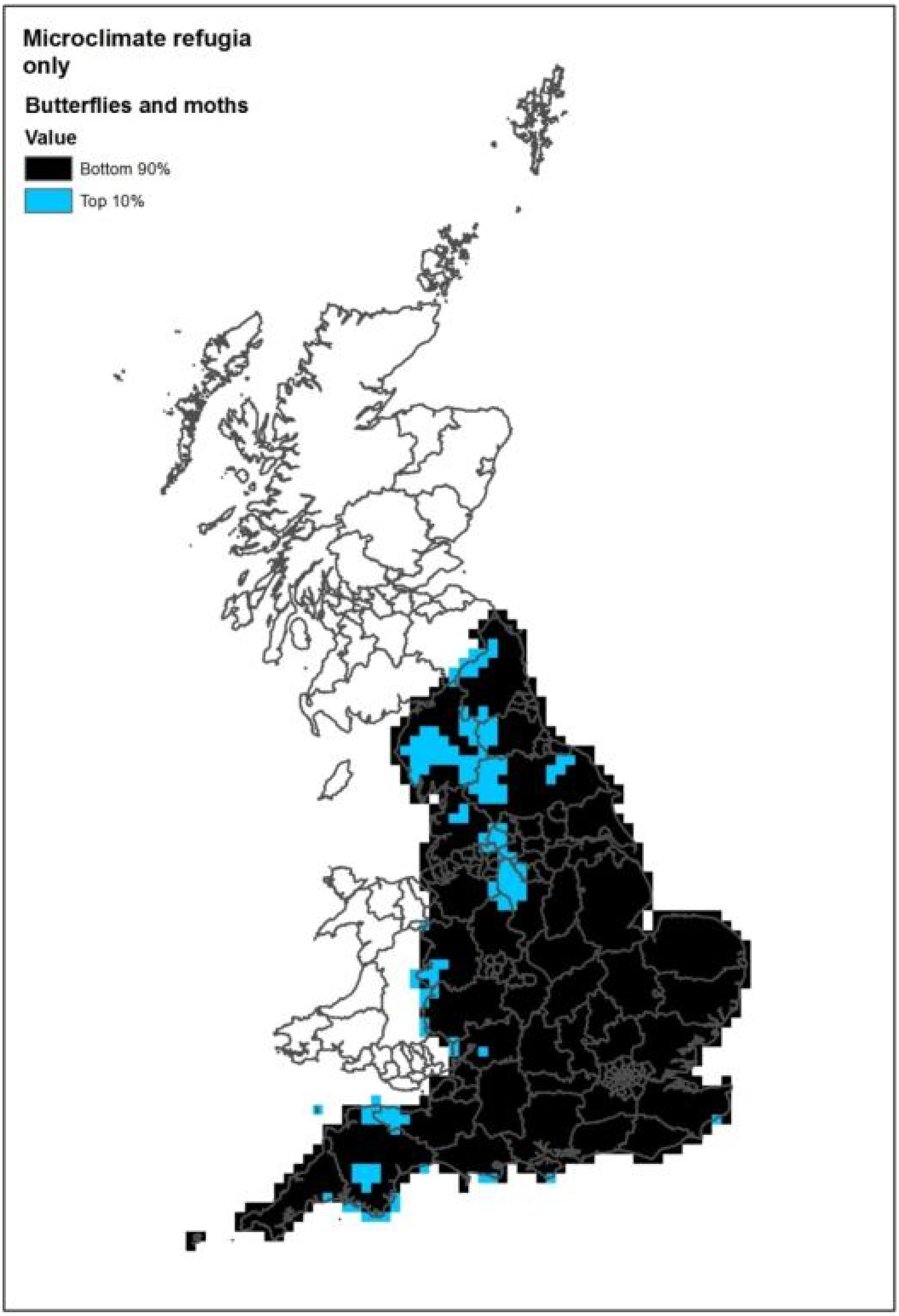
**Appendix 2 Figure 9a** Map showing the location of the top 10% of microclimate refugial areas for higher plants (tracheophytes). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



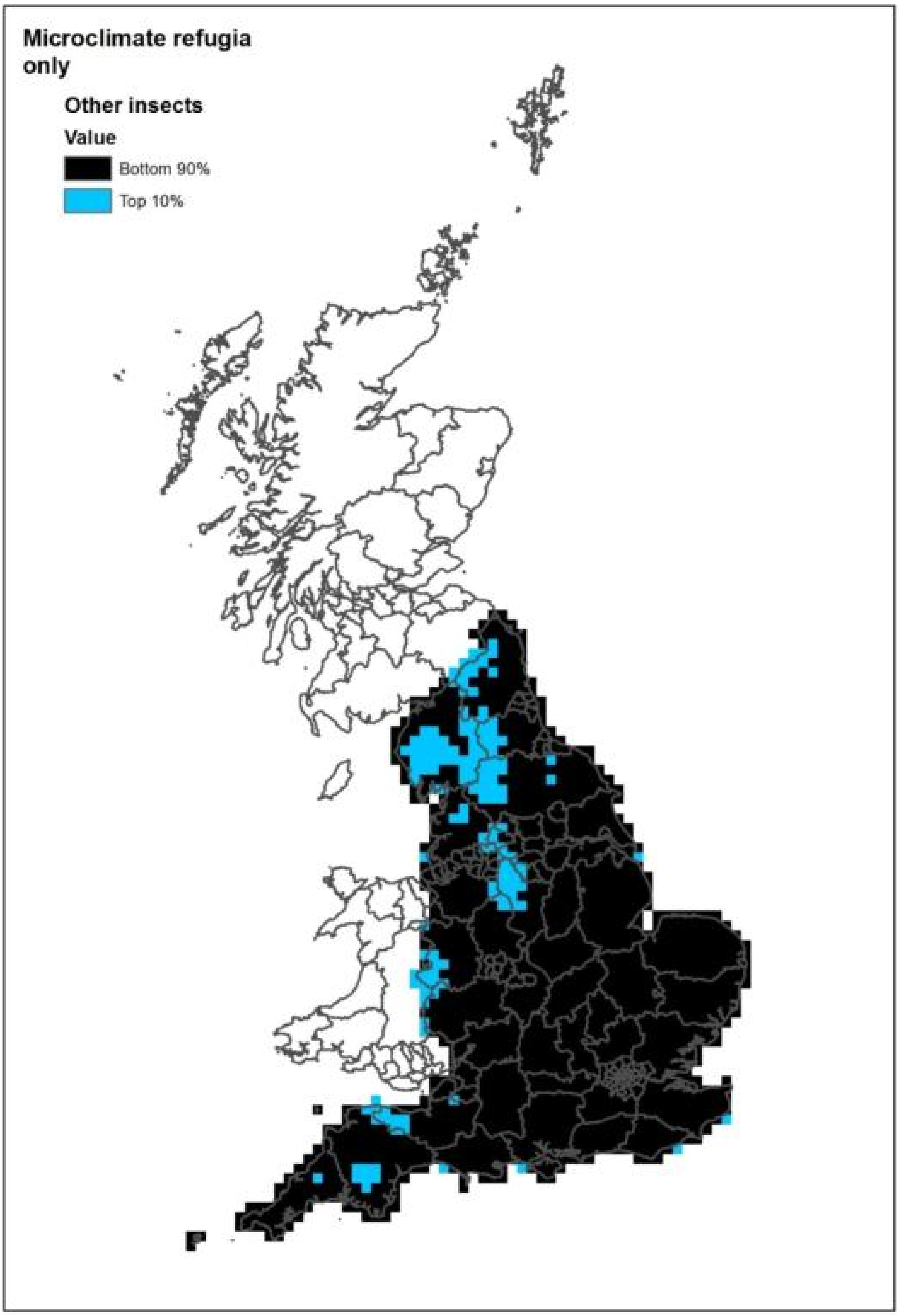
**Appendix 2 Figure 9b** Map showing the location of the top 10% of microclimate refugial areas for lower plants (bryophytes). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



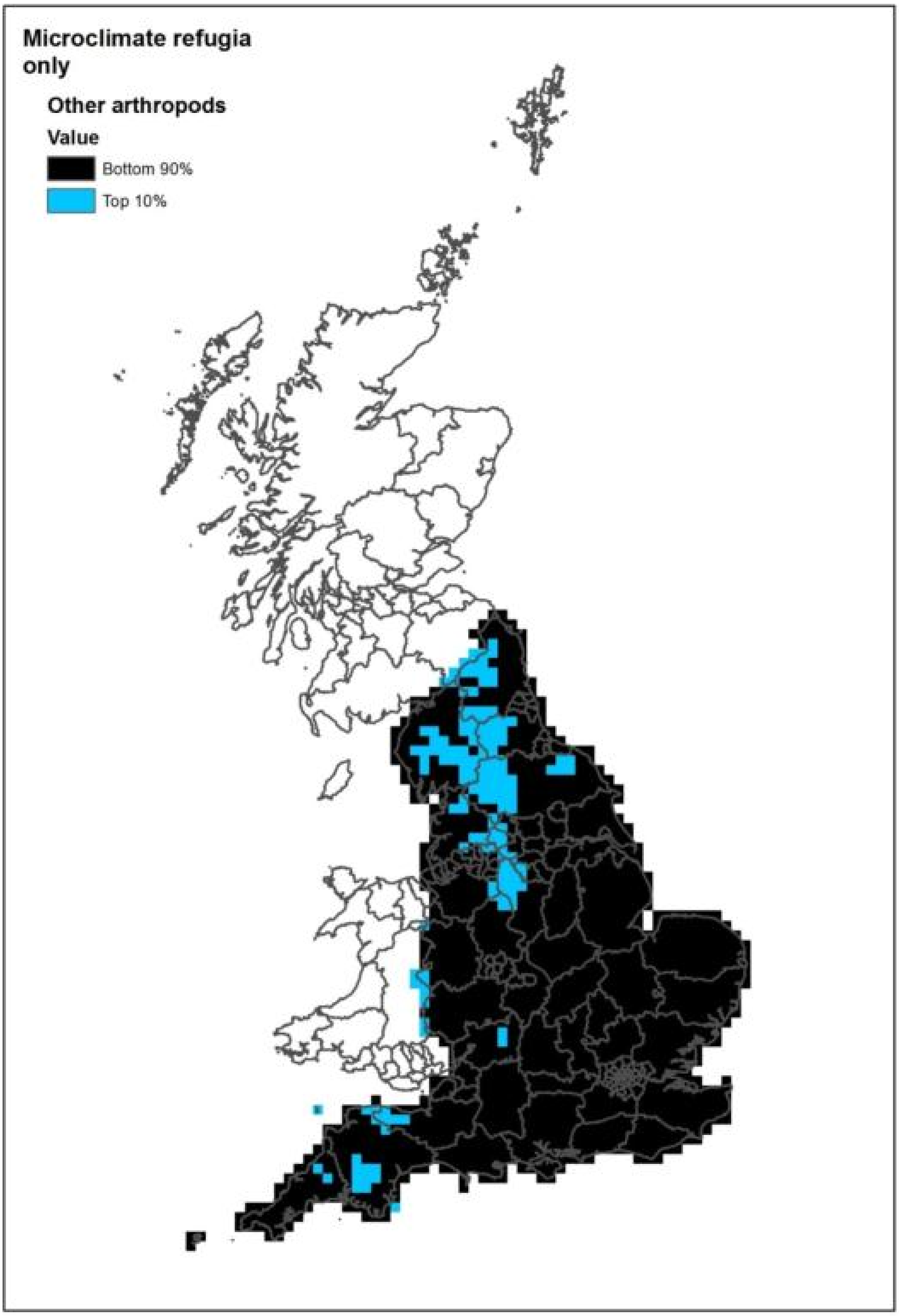
**Appendix 2 Figure 9c** Map showing the location of the top 10% of microclimate refugial areas for beetles (Coleoptera). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



**Appendix 2 Figure 9d** Map showing the location of the top 10% of microclimate refugial areas for butterflies and moths (Lepidoptera). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



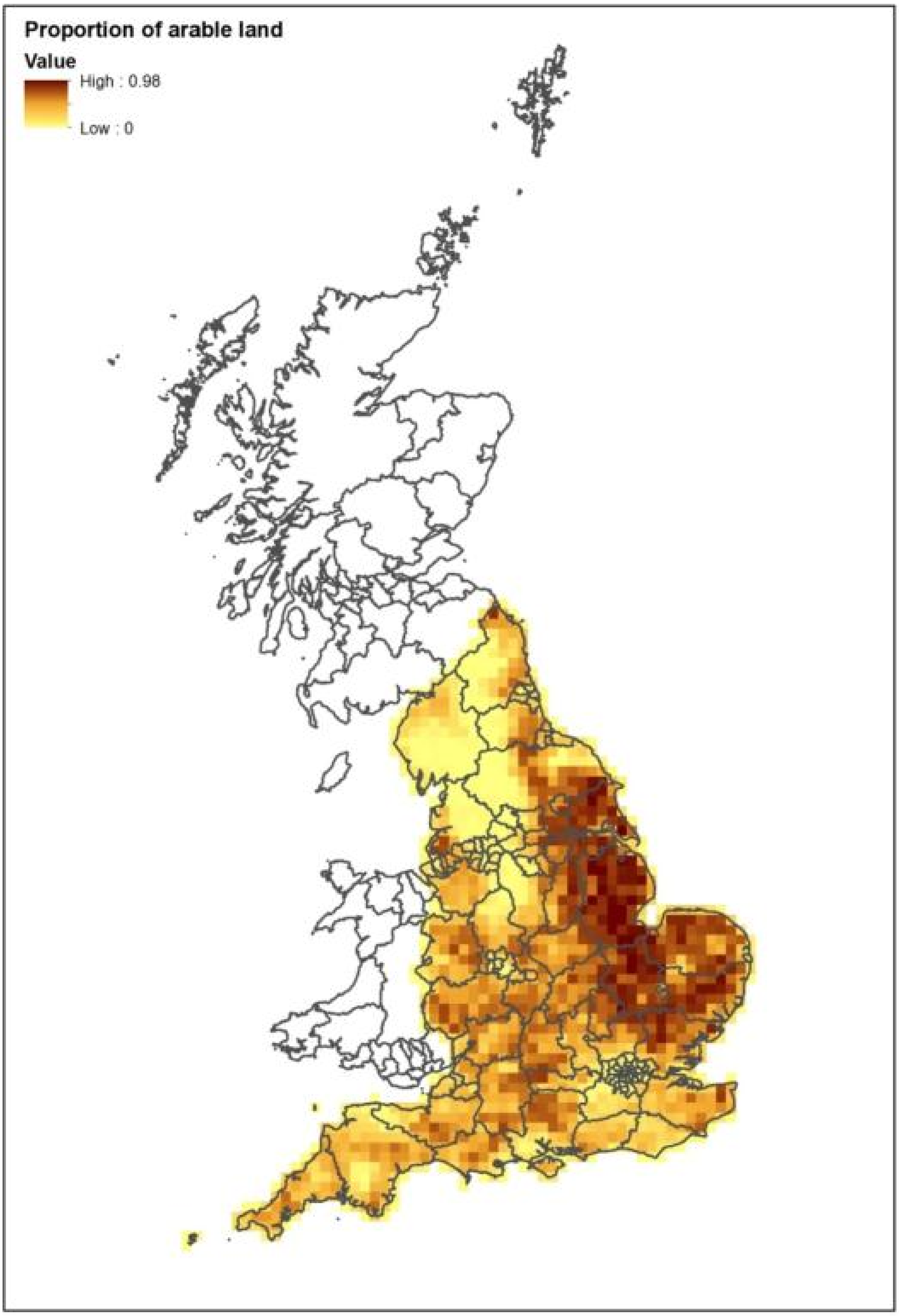
**Appendix 2 Figure 9e** Map showing the location of the top 10% of microclimate refugial areas for other insects (ants, bees, wasps, craneflies, hoverflies, dragonflies, damselflies, grasshoppers and crickets). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.



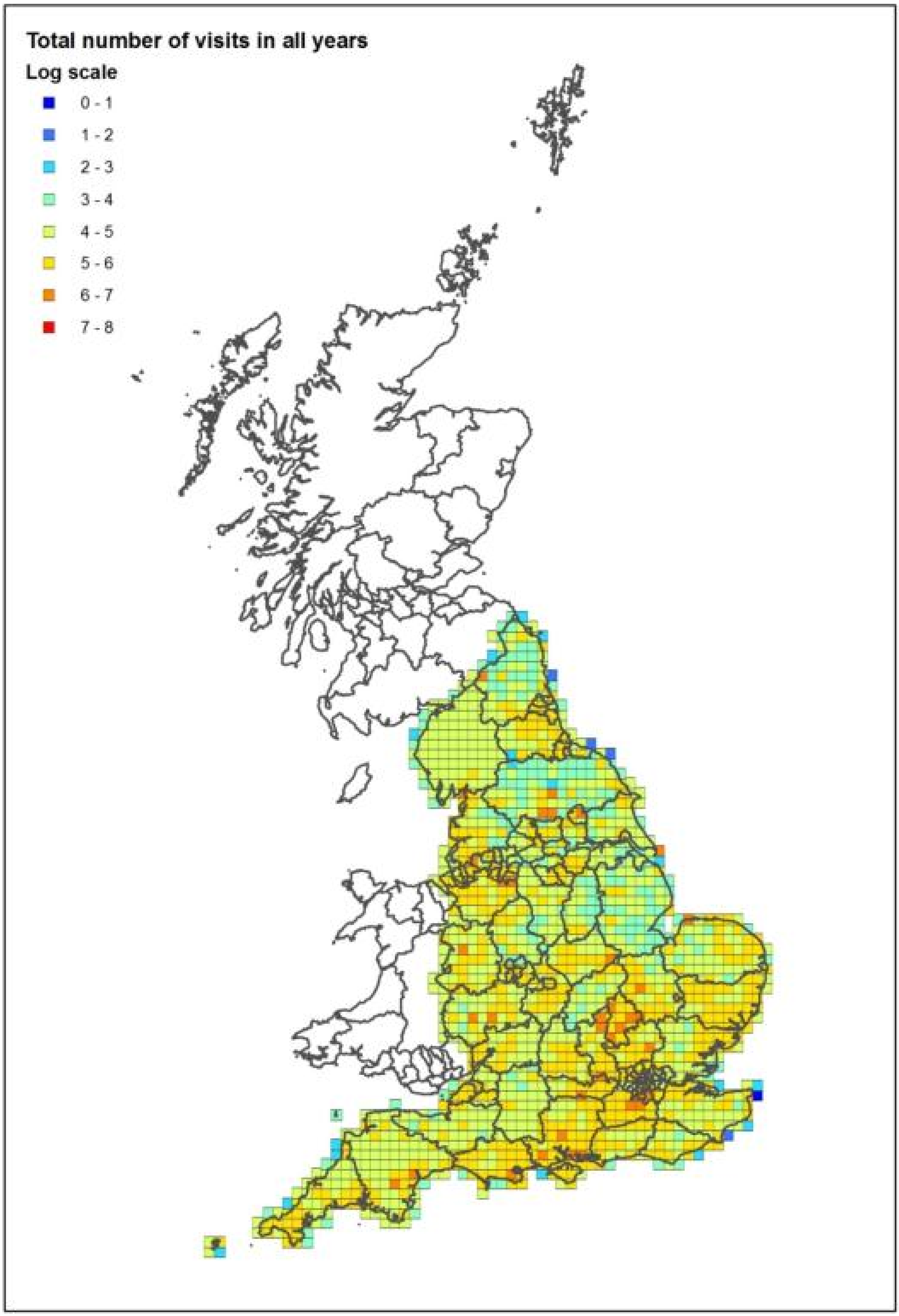
**Appendix 2 Figure 9f** Map showing the location of the top 10% of microclimate refugial areas for other arthropods (centipedes, millipedes and spiders). In this map, locations with high microclimate heterogeneity are modelled as being good refugia, but the effects of other factors, e.g. agricultural intensity, and the extent to which climate change has occurred are ignored. Blue colouring represents squares in the top 10%, while black represents those in the bottom 90%.

# Appendix 3: Maps of national scale explanatory variables

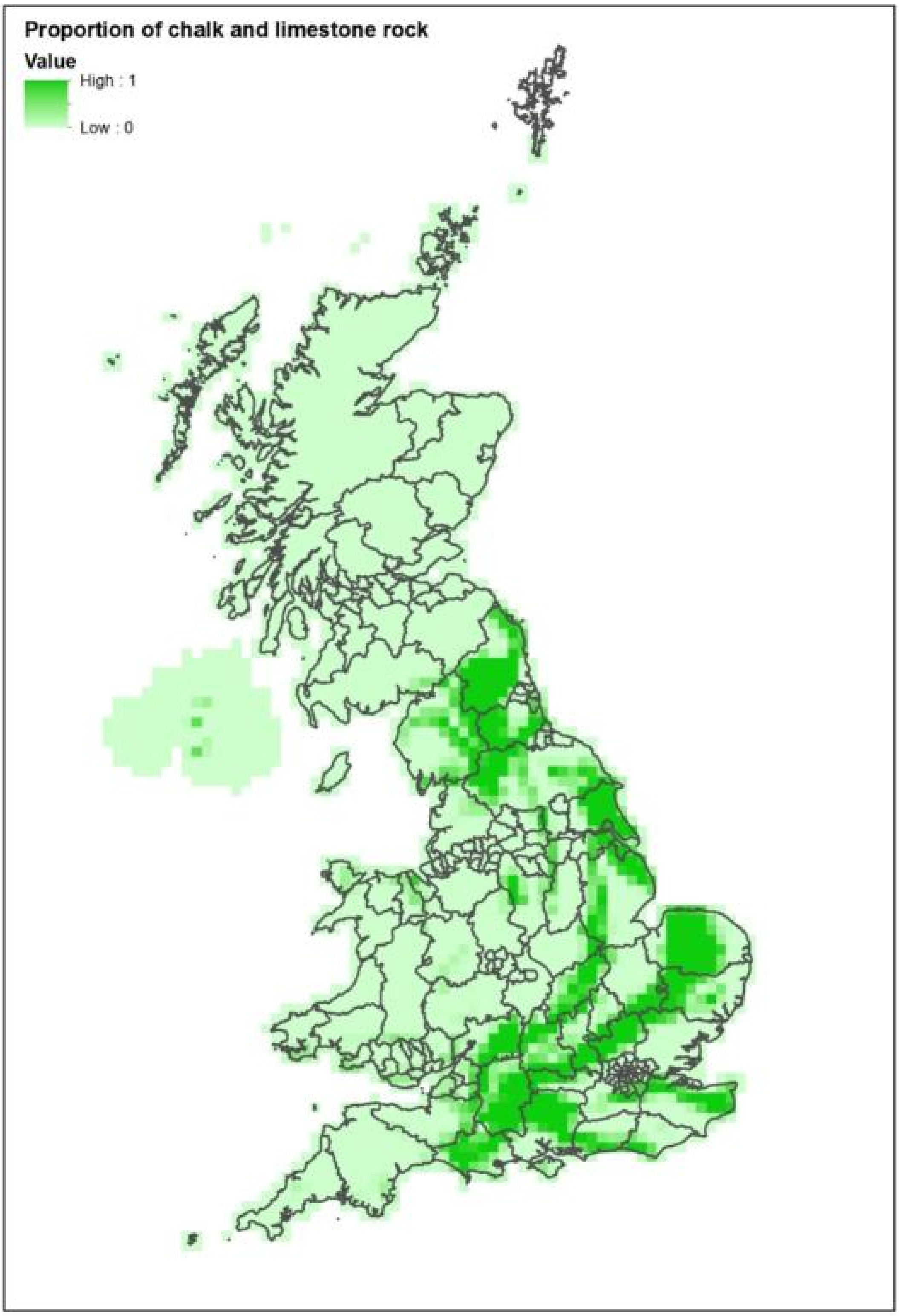
Maps of variables selected for statistical modelling.



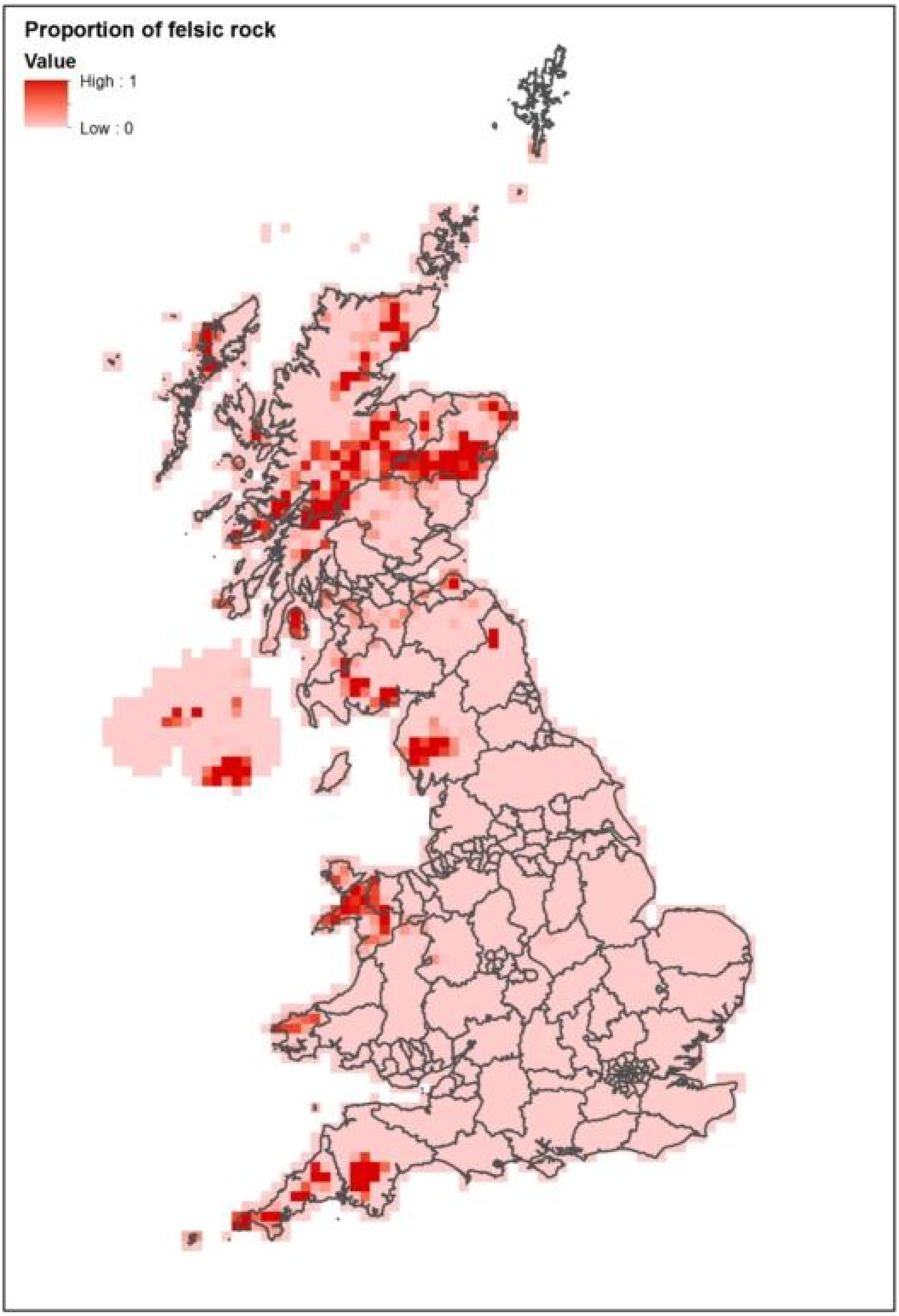
**Appendix 3 Figure 1** Map showing the proportion of arable land in each 10k square (hectad). These data are derived from the CEH LCM2007 land cover data, resampled at 1k resolution. This variable was used as a proxy for agricultural intensification- a potential confounding variable.



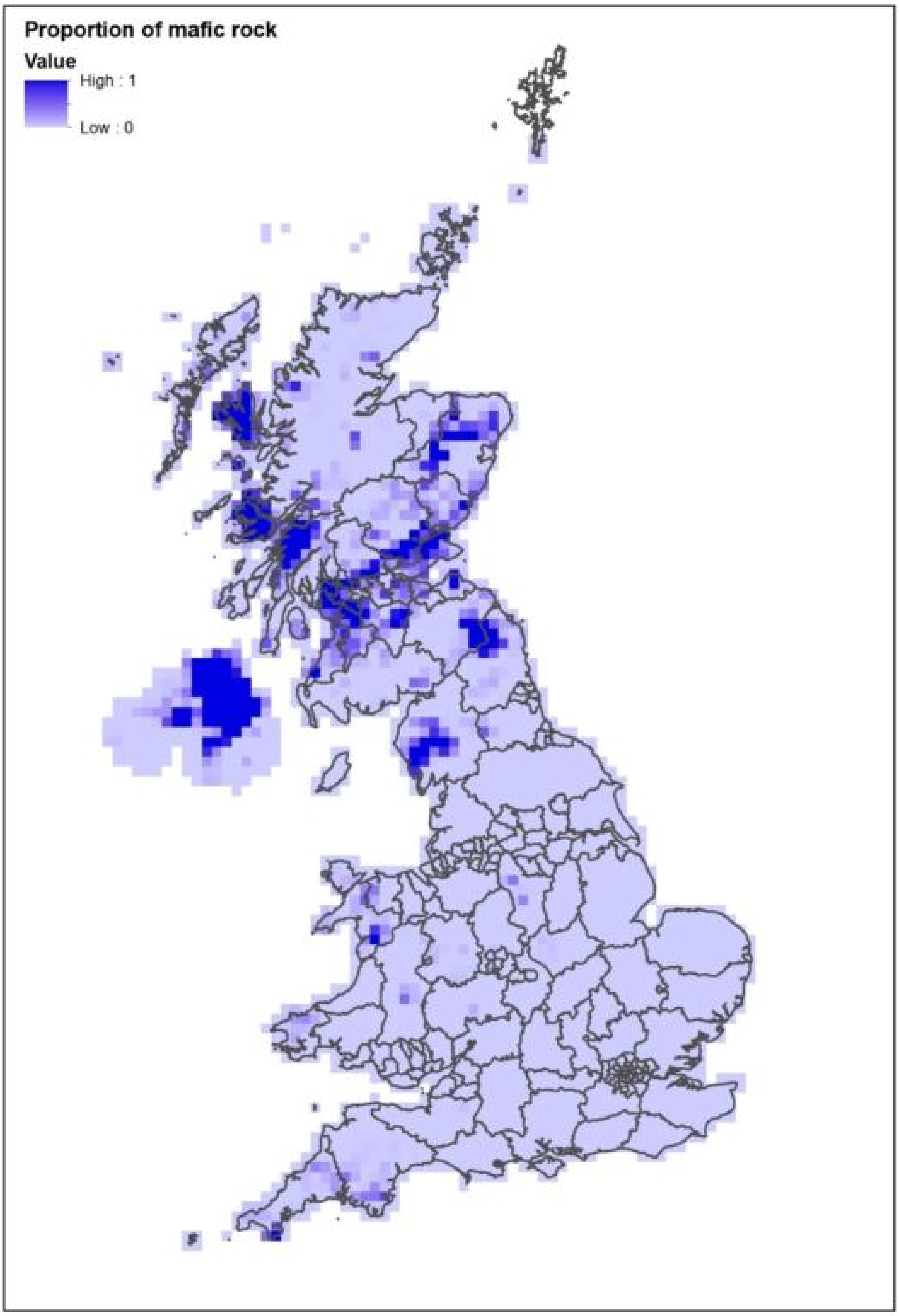
**Appendix 3 Figure 2** Map showing the logarithm of the total number of visits to each 10k square (hectad) in all years (1970-2009). This variable represented recorder effort in the model, a potential confounding variable.



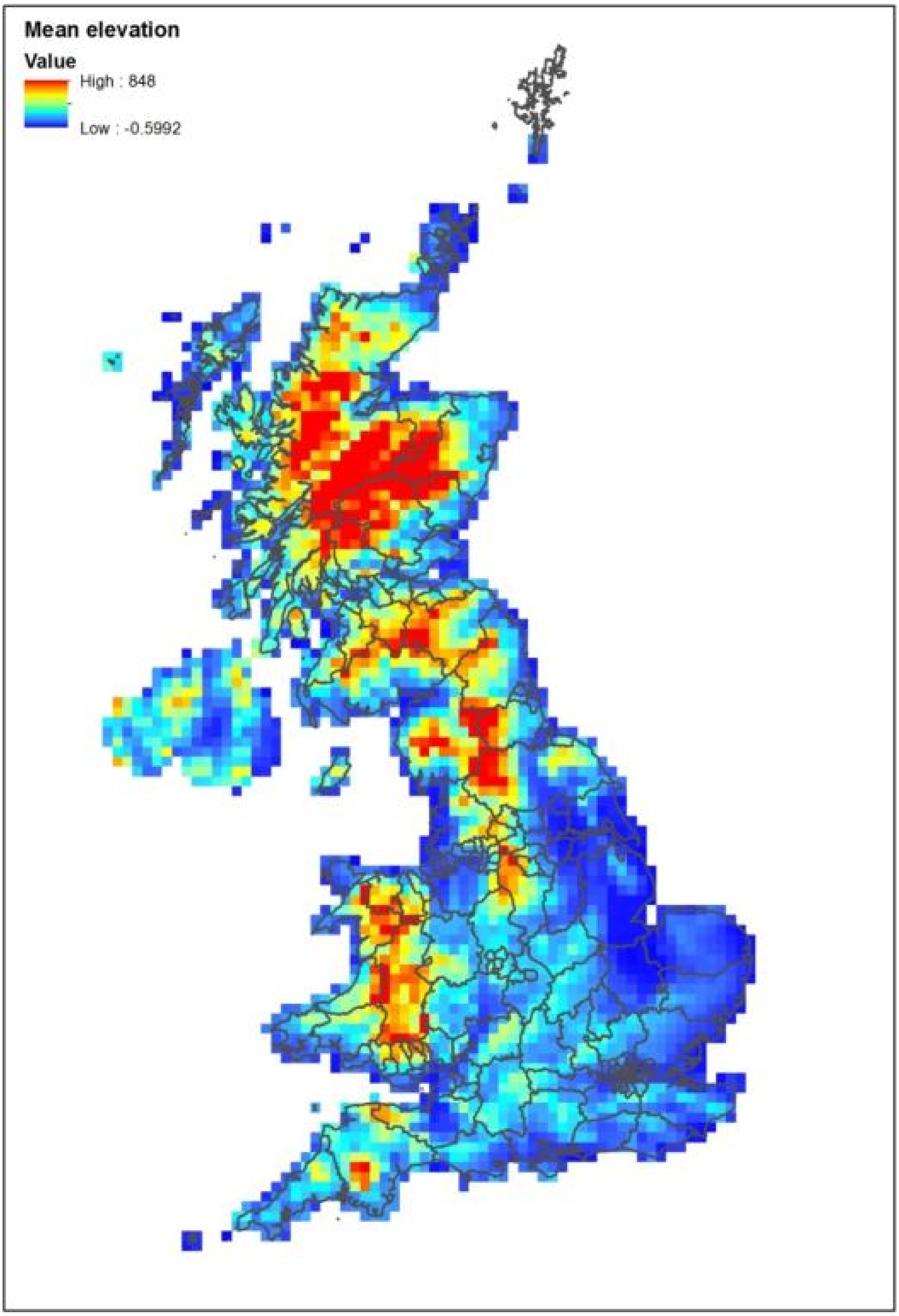
**Appendix 3 Figure 3** Map showing the proportion of chalk and limestone rock in each 10k square (hectad). These data are derived from the BGS 1:625,000 map of bedrock geology (1979, 3rd edition), resampled at 100m resolution. This variable represented chalk and limestone geology in the model, a potential confounding variable.



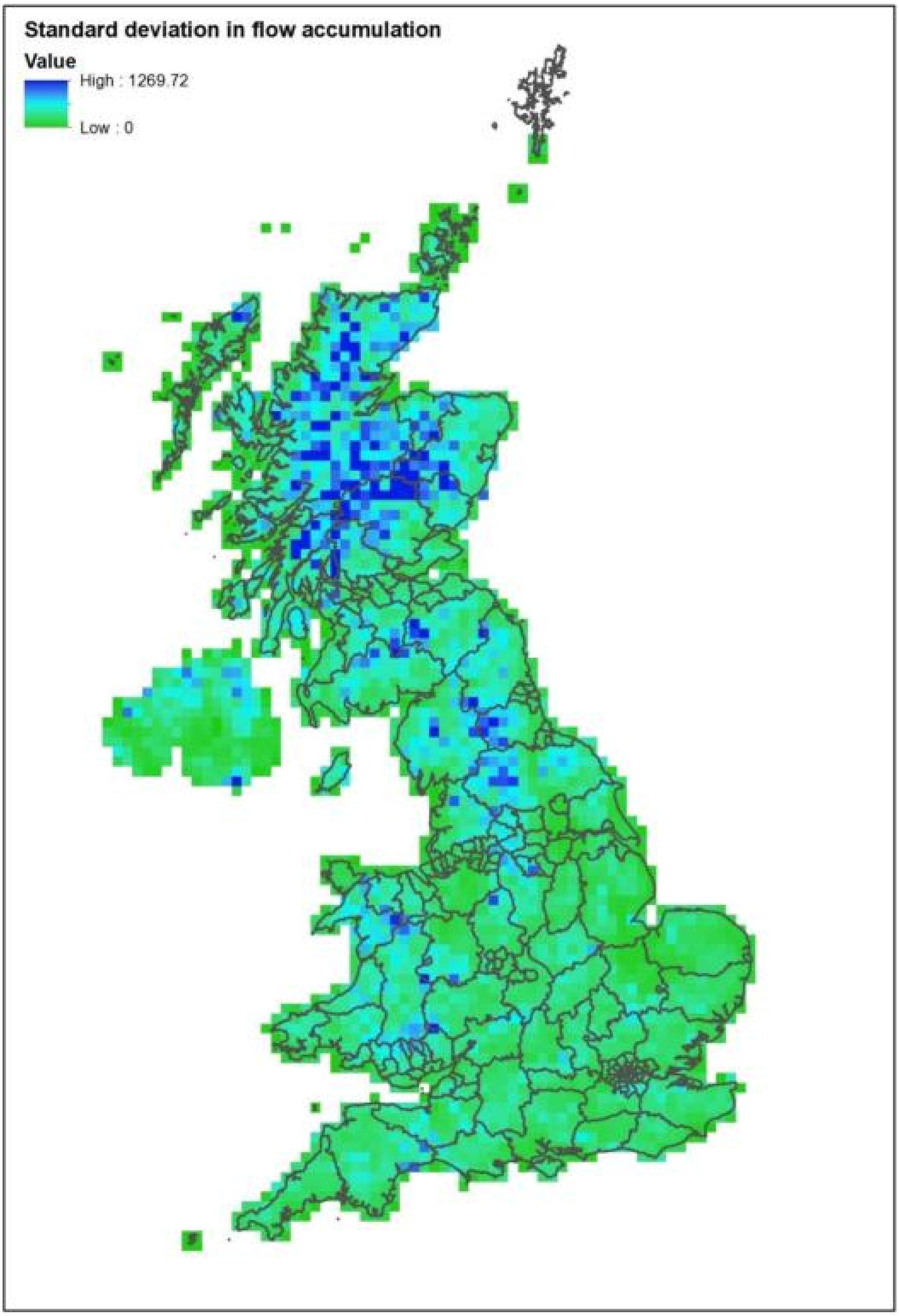
**Appendix 3 Figure 4** Map showing the proportion of felsic rock in each 10k square (hectad). These data are derived from the BGS 1:625,000 map of bedrock geology (1979, 3rd edition), resampled at 100m resolution. This variable represented felsic geology in the model, a potential confounding variable.



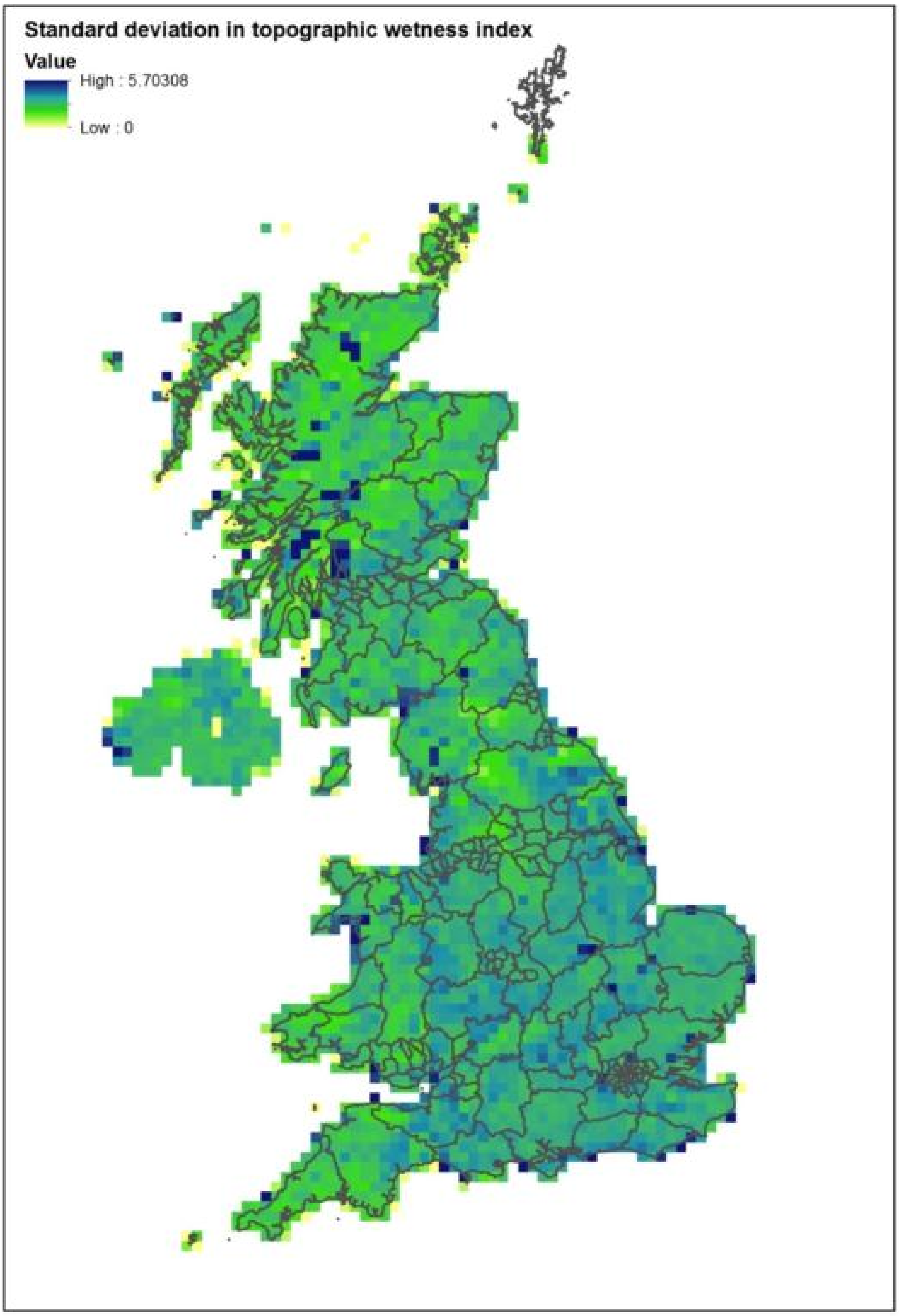
**Appendix 3 Figure 5** Map showing the proportion of mafic rock in each 10k square (hectad). These data are derived from the BGS 1:625,000 map of bedrock geology (1979, 3rd edition), resampled at 100m resolution. This variable represented mafic geology in the model, a potential confounding variable.



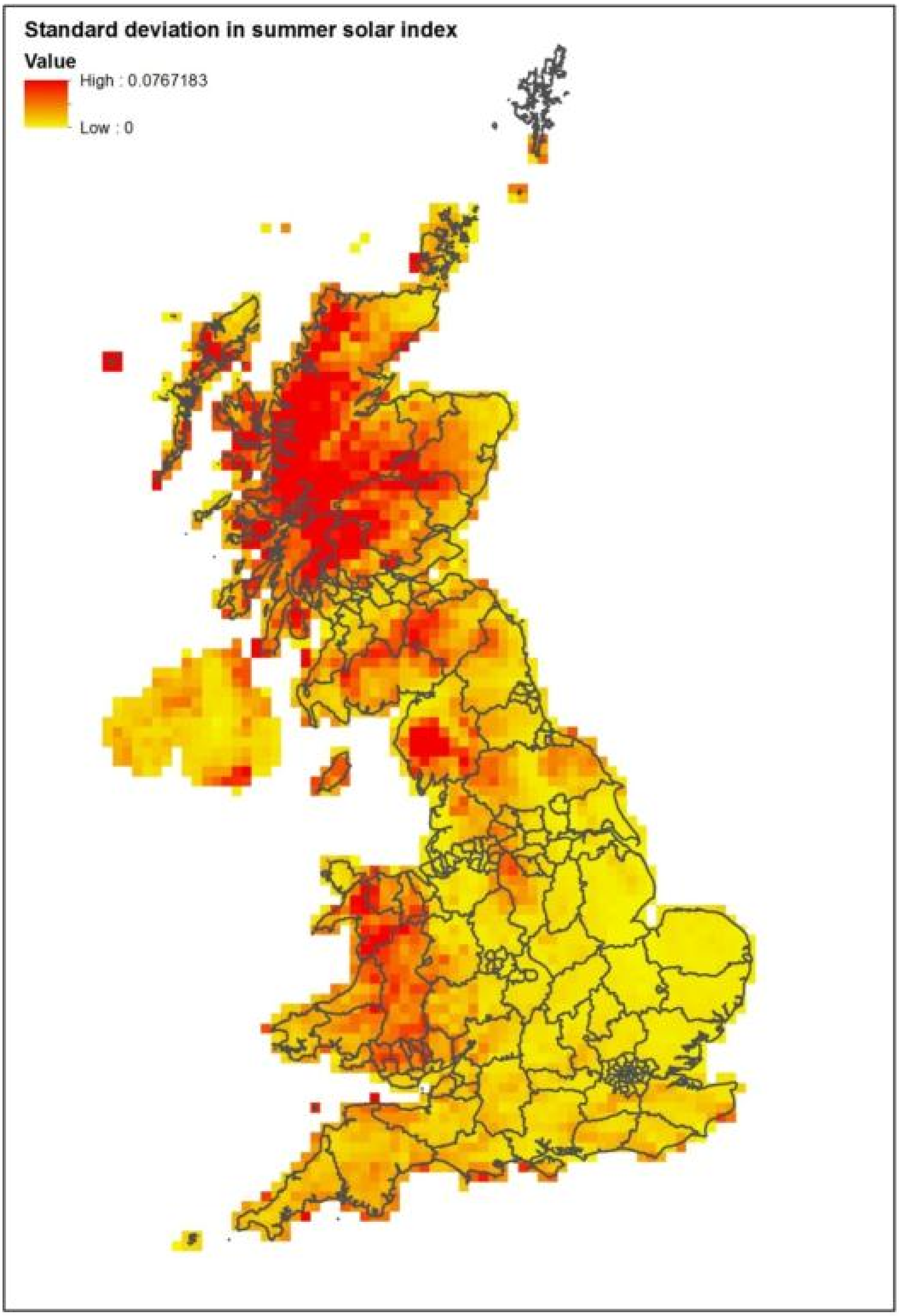
**Appendix 3 Figure 6** Map showing the mean elevation of each 10k square (hectad) as a potential predictor.



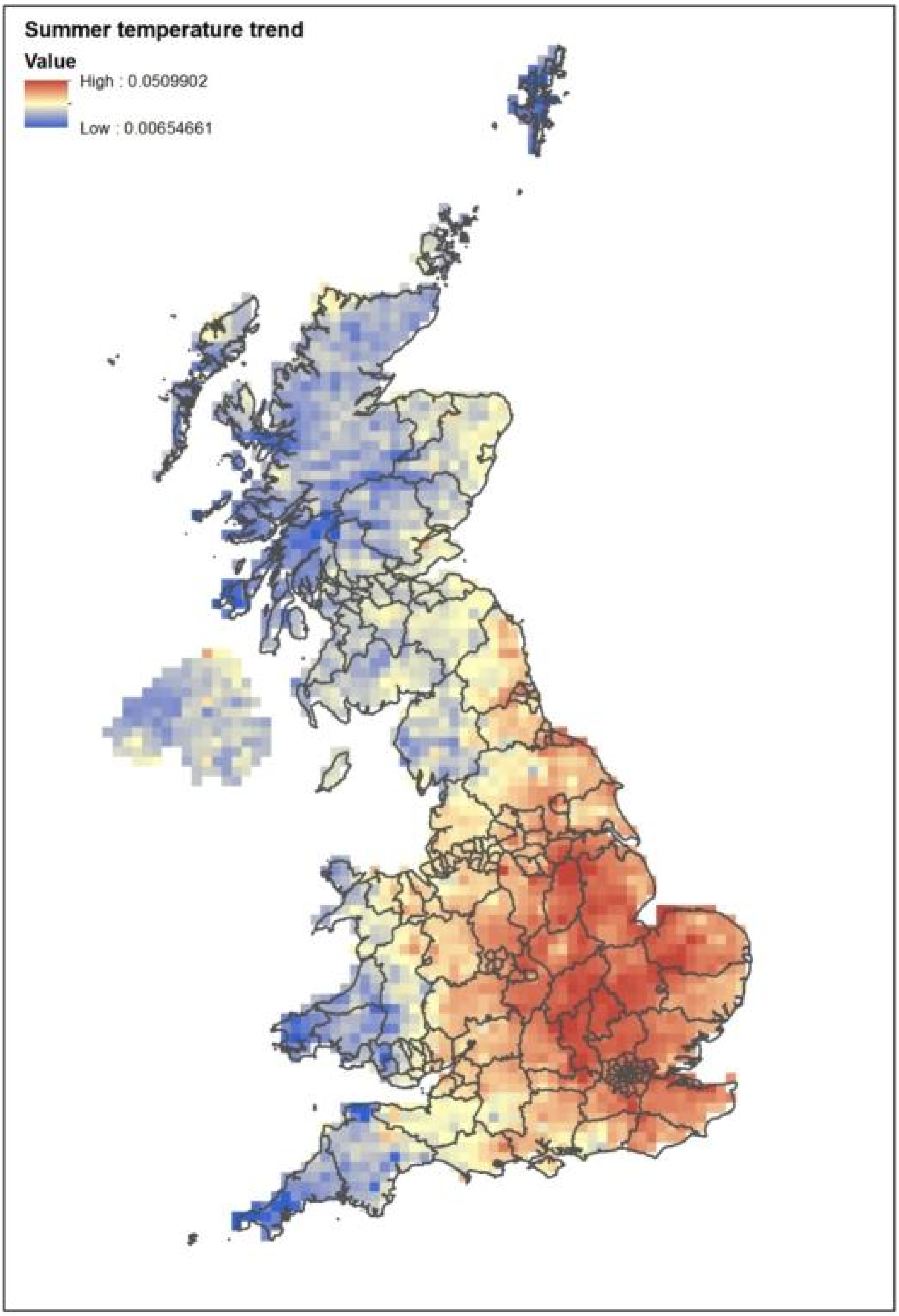
**Appendix 3 Figure 7** Map showing the standard deviation in flow accumulation for each 10 square (hectad). This variable represented water drainage and the potential for cold air drainage effects as a potential predictor. For calculation method see Methods chapter.



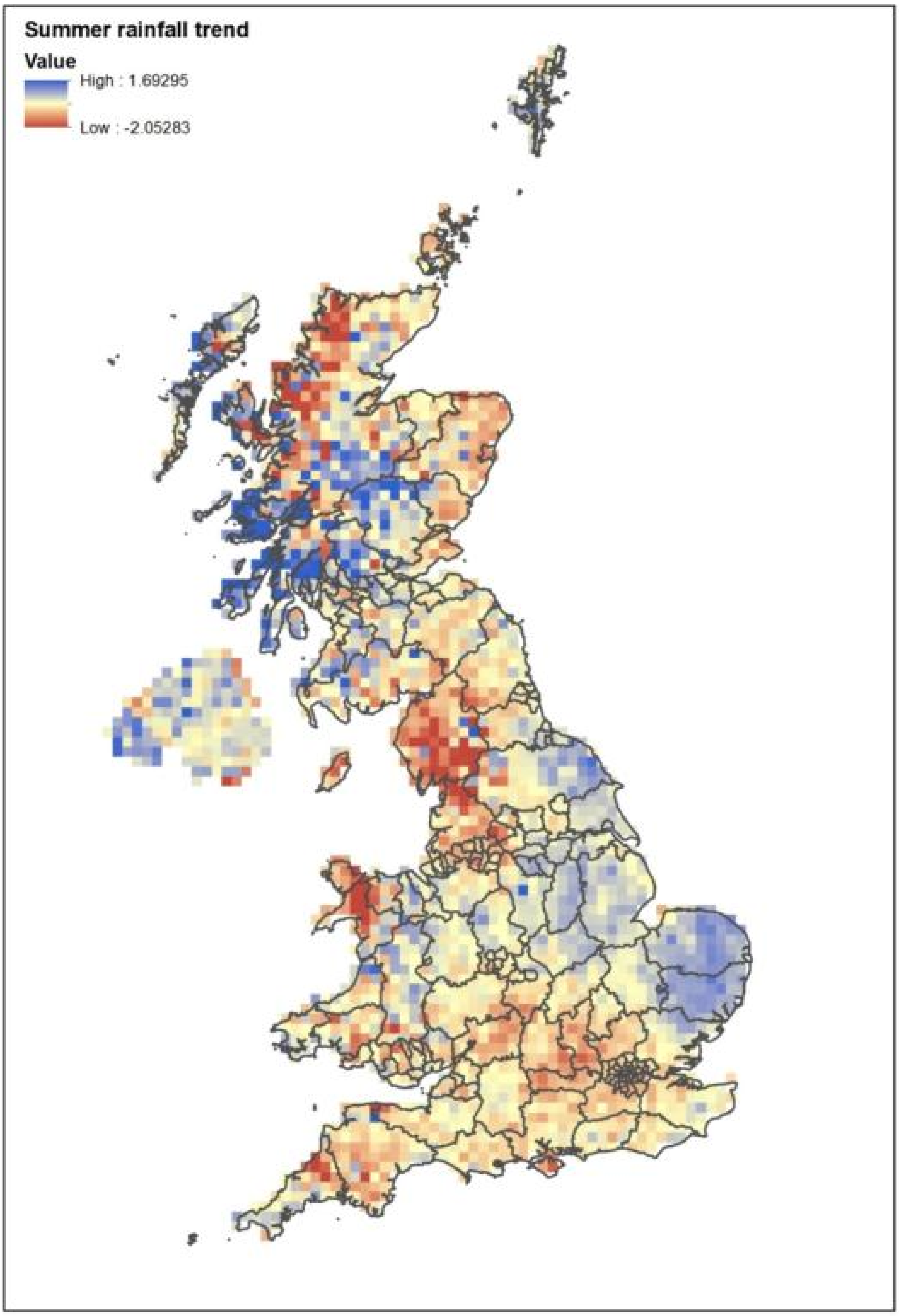
**Appendix 3 Figure 8** Map showing the standard deviation in topographic wetness index for each 10k square (hectad). This variable represented moisture availability as a potential predictor. For calculation method see Methods chapter.



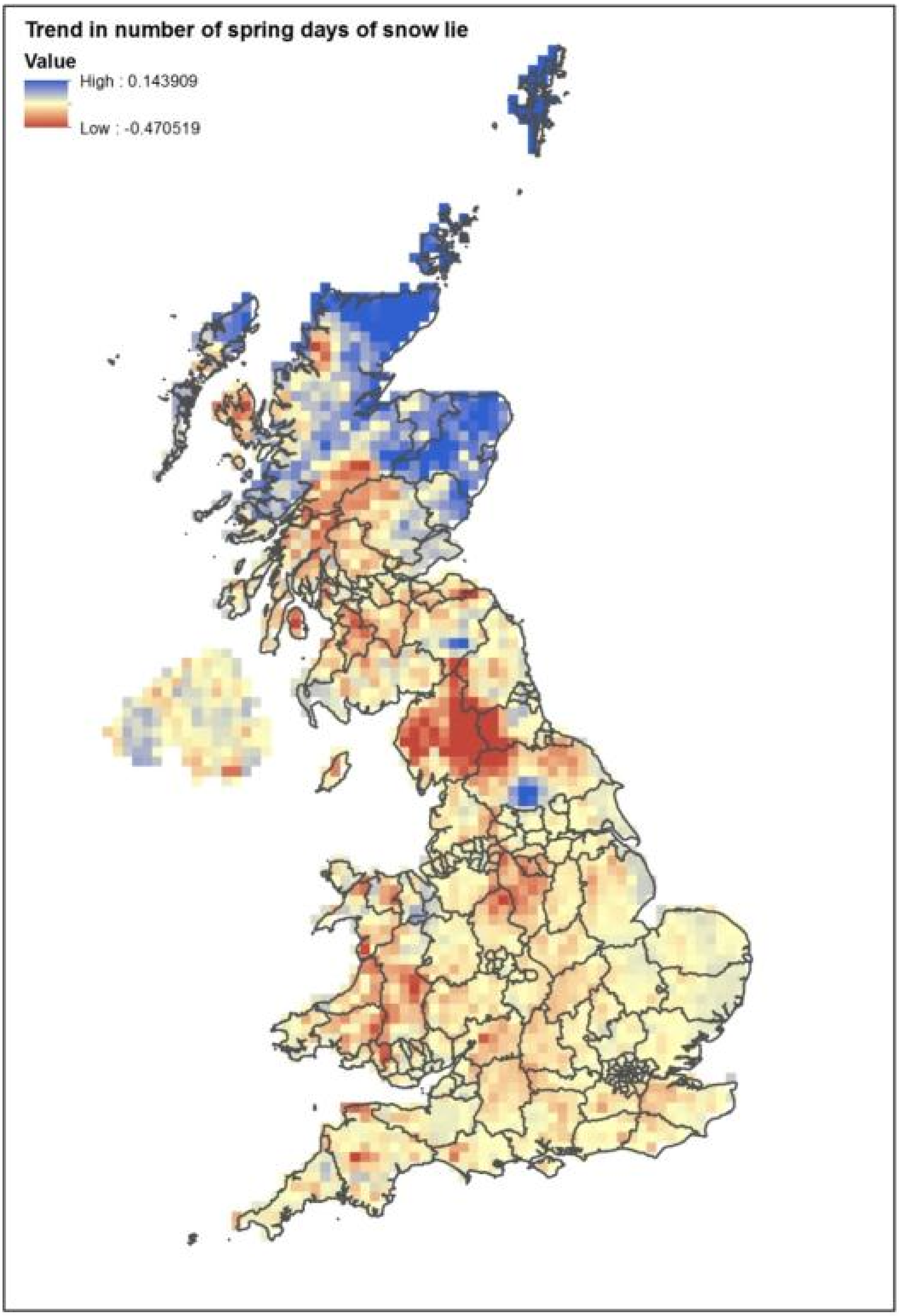
**Appendix 3 Figure 9** Map showing the standard deviation in summer solar index values. This variable represented heterogeneity in summer insolation regime as a potential predictor. For calculation method see Methods chapter.



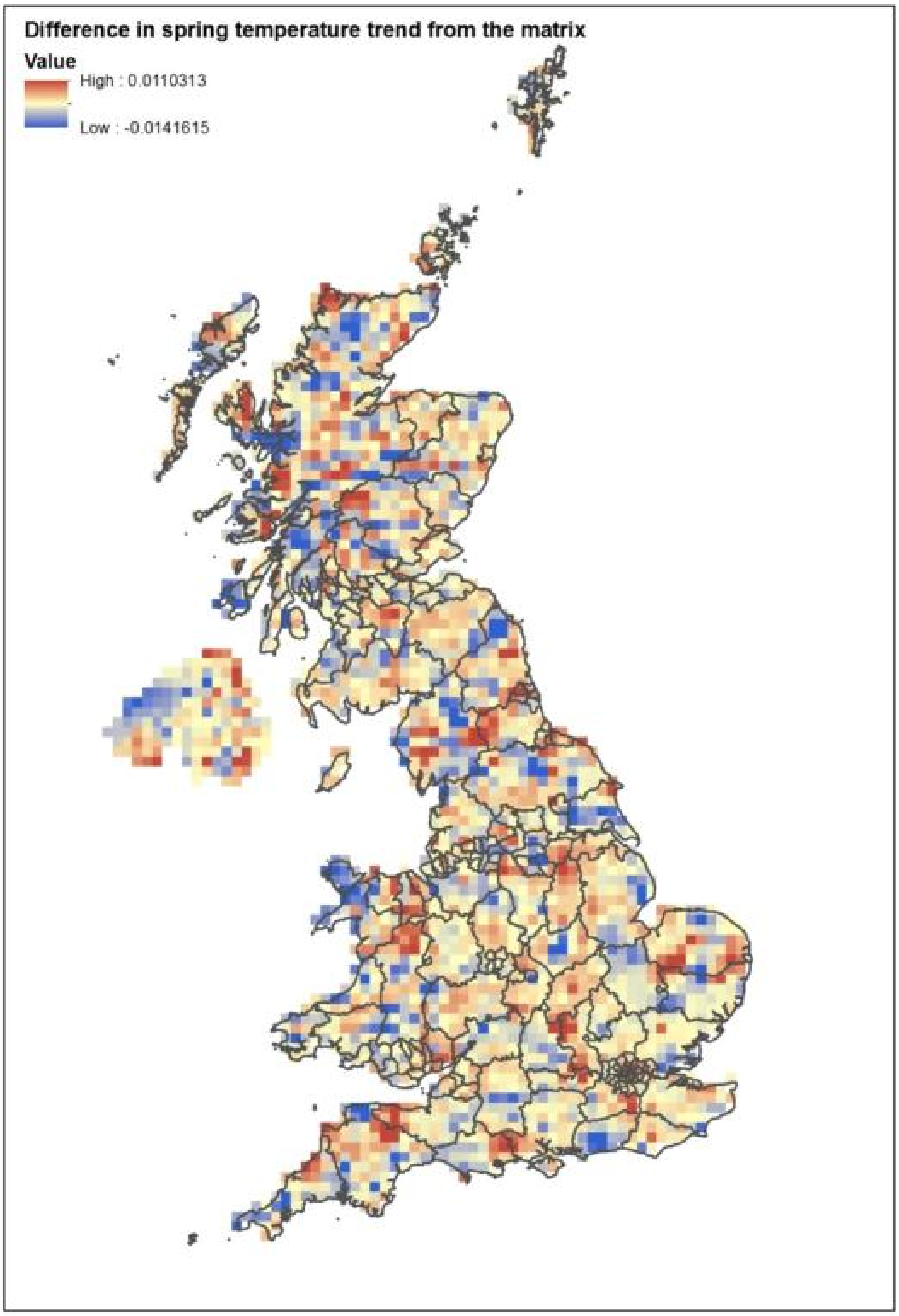
**Appendix 3 Figure 10** Map showing the 1961-2006 trend in summer temperature for each 10k square (hectad), a potential predictor. Trends are derived from the UKCP09 climate data (warming trend in degrees Celsius per year).



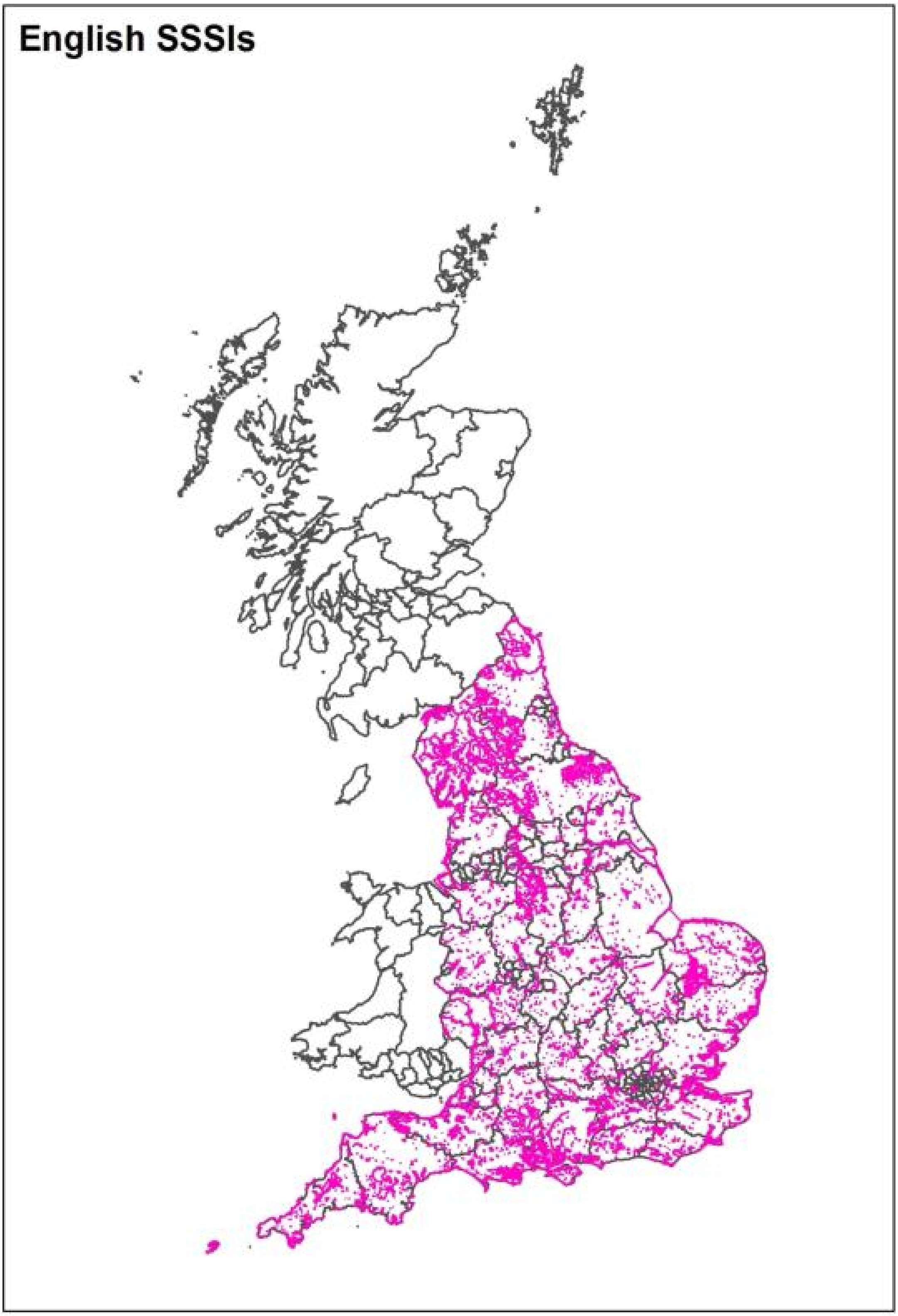
**Appendix 3 Figure 11** Map showing the 1961-2006 trend in summer rainfall for each 10k square (hectad), a potential predictor. Trends are derived from the UKCP09 climate data (rainfall trend in mm per year).



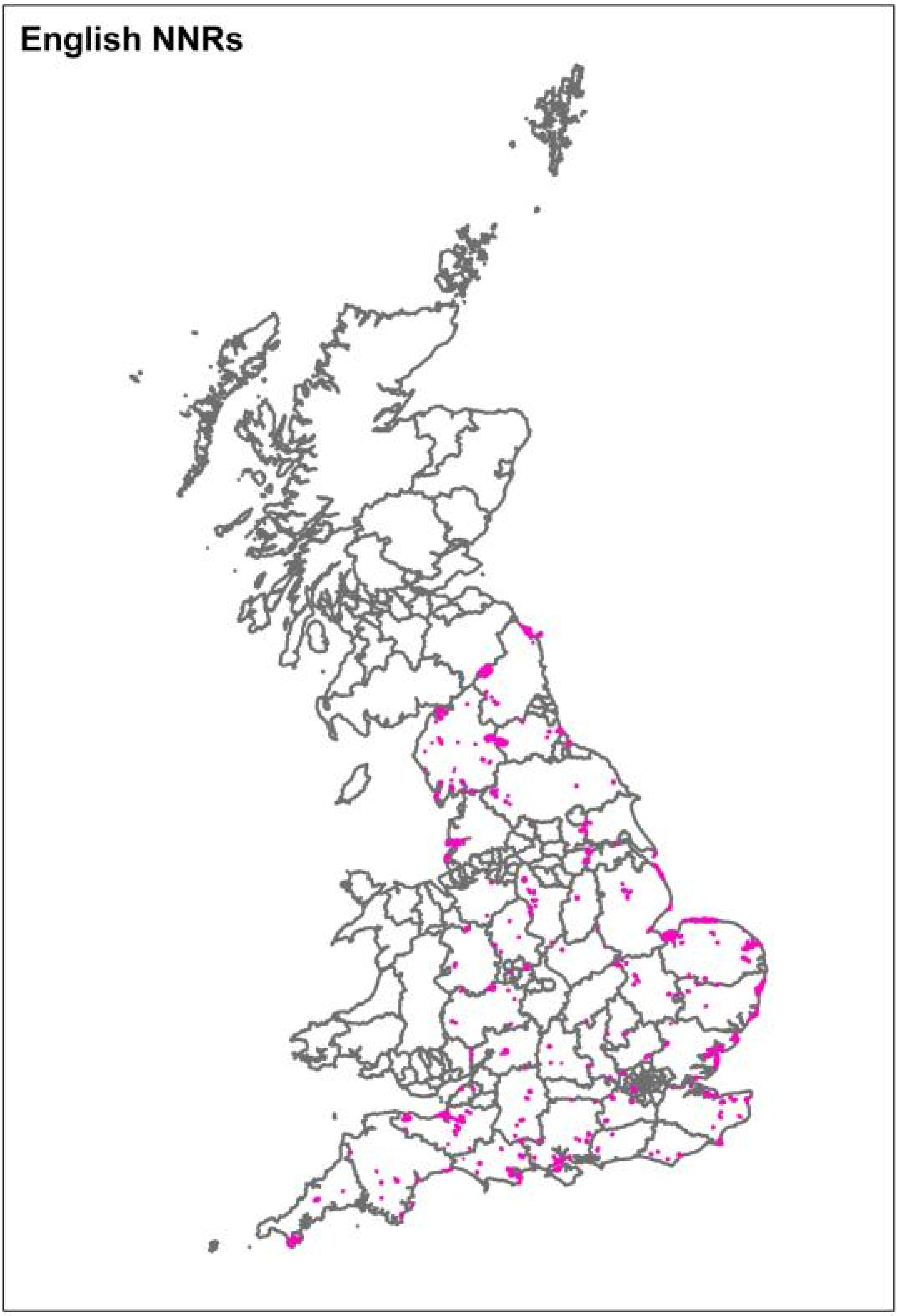
**Appendix 3 Figure 12** Map showing the 1971-2006 trend in the number of spring days of snow lie for each 10k square (hectad), a potential predictor. Trends are derived from the UKCP09 climate data (trend in number of snow days per year).



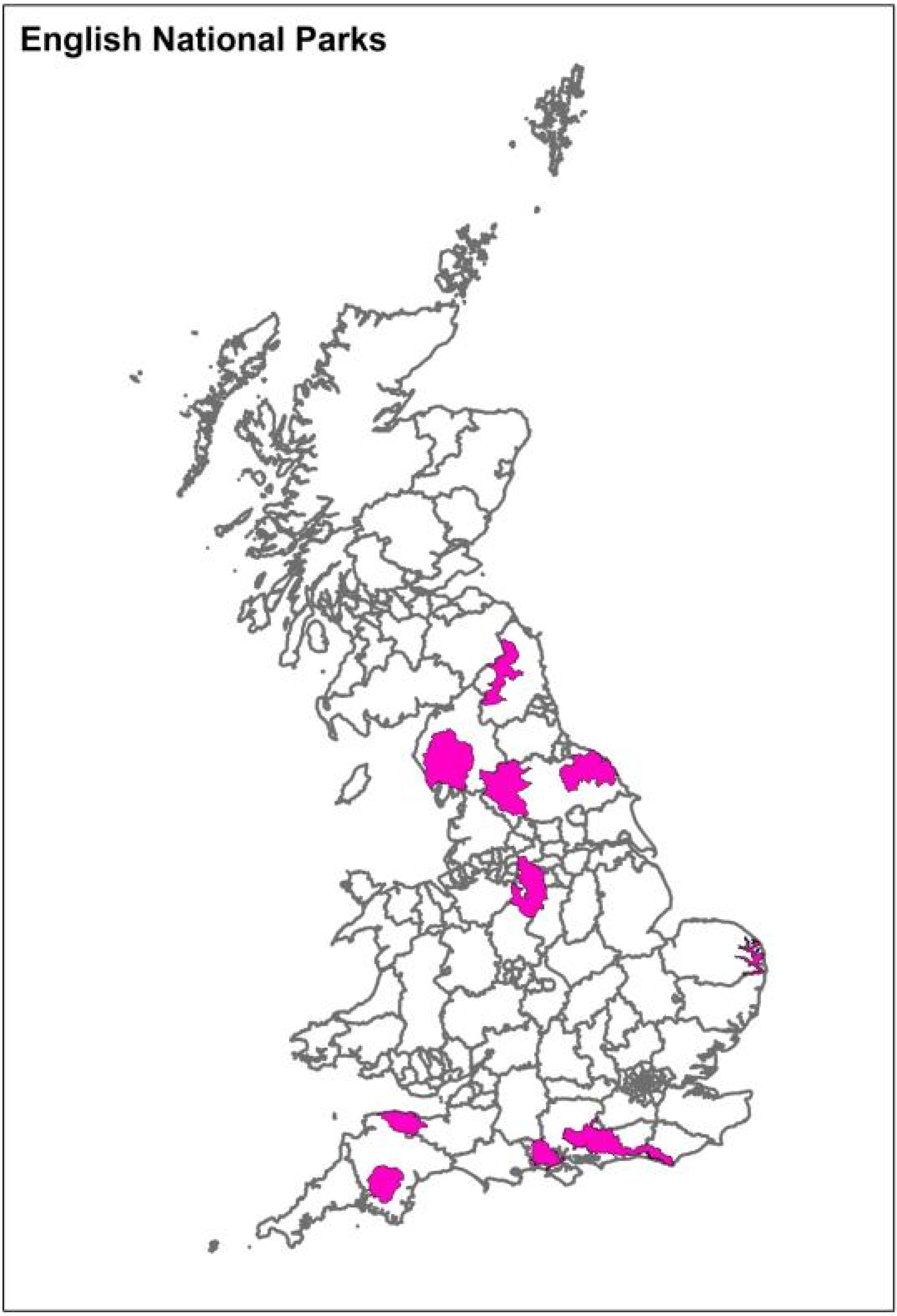
**Appendix 3 Figure 13** Map showing the difference between the spring temperature trend in each 10k square (hectad), and the average of the surrounding 100k window. Positive values indicate a trend warmer than the nearby average, while negative values indicate a trend cooler than the nearby average. This variable was a potential predictor. Trends are derived from the UKCP09 climate data.



**Appendix 3 Figure 14** Map showing the English SSSI (Site of Special Scientific Interest) network.



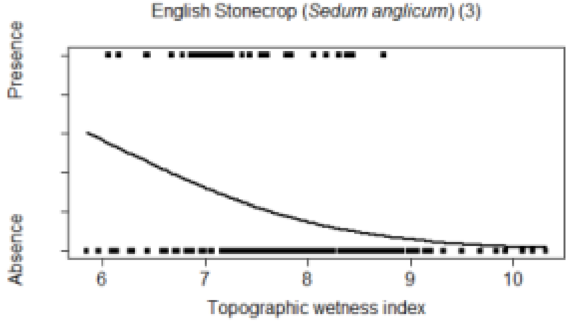
**Appendix 3 Figure 15** Map showing the English NNR (National Nature Reserve) network.

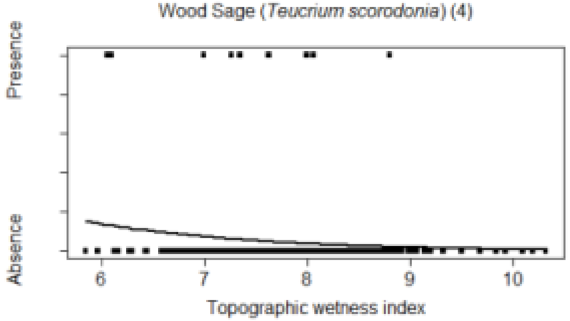


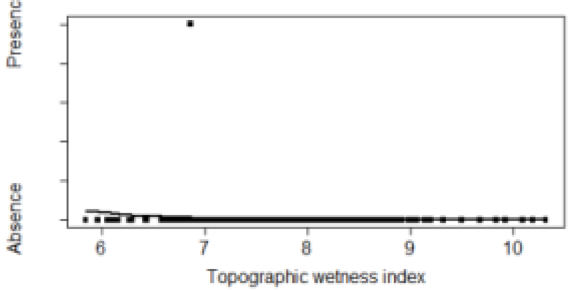
**Appendix 3 Figure 16** Map showing English National Parks.

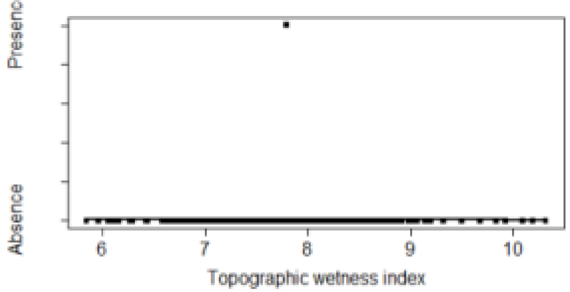
# Appendix 4: Relationships of plants to topographic wetness

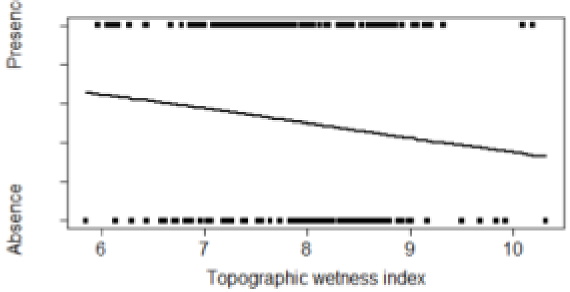
Logistic plots showing the presence and absence of all plant species recorded in field survey as a function of topographic wetness. Curves of best fit are also shown.

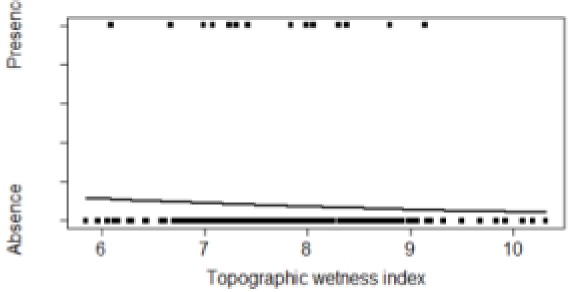

English Stonecrop (*Sedum anglicum*) (3)

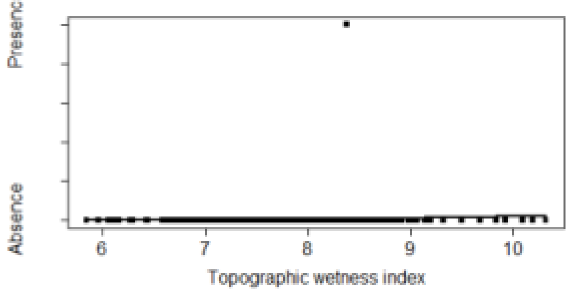

Wood Sage (*Teucrium scorodonia*) (4)

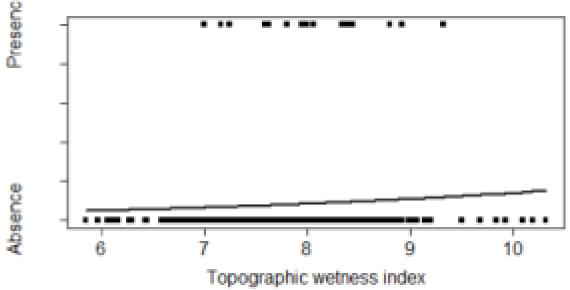

Bird's-foot Trefoil (*Lotus corniculatus*) (4)

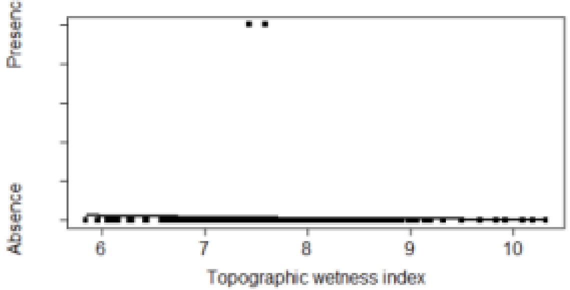

Woolly Thistle (*Cirsium eriophorum*) (4)

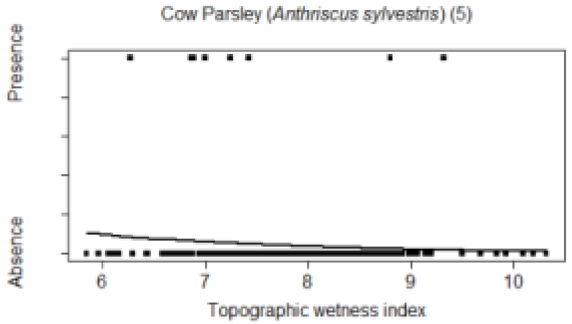

Bracken (*Pteridium aquilinum*) (5)

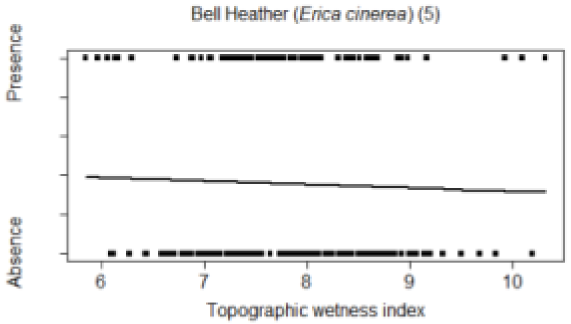

Bluebell (*Hyacinthoides non-scripta*) (5)

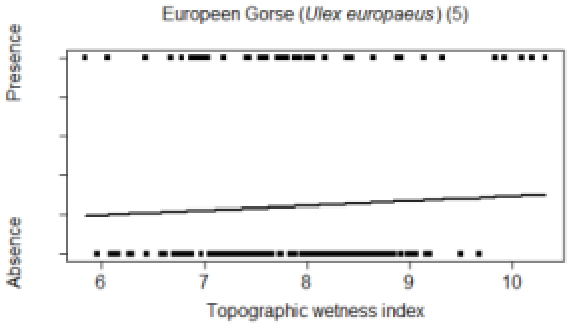

Common Cow-wheat (*Melampyrum pratense*) (5)

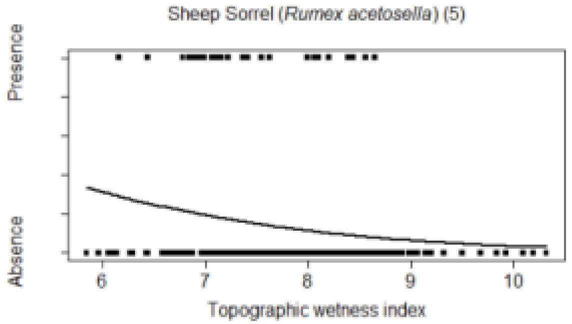

Hawthorn (*Crataegus monogyna*) (5)

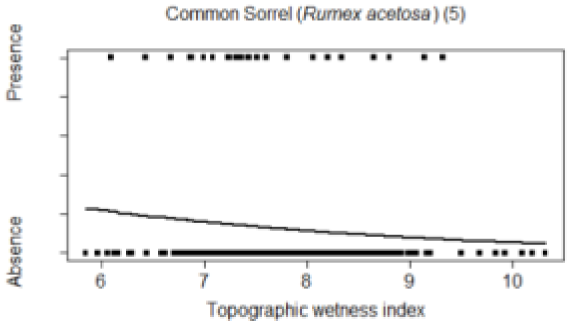

Blackthorn (*Prunus spinosa*) (5)

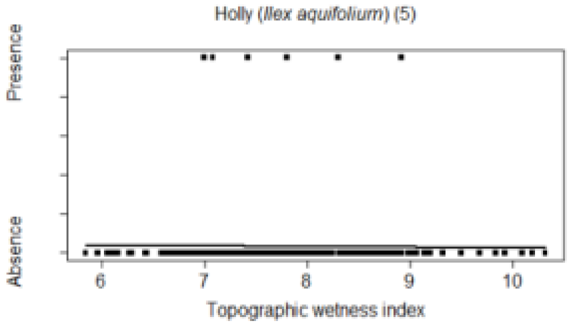

Cow Parsley (*Anthriscus sylvestris*) (5)

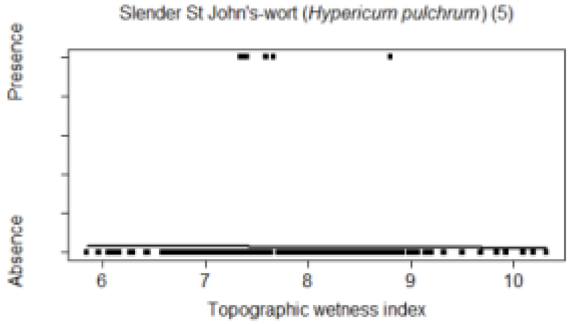

Bell Heather (*Erica cinerea*) (5)

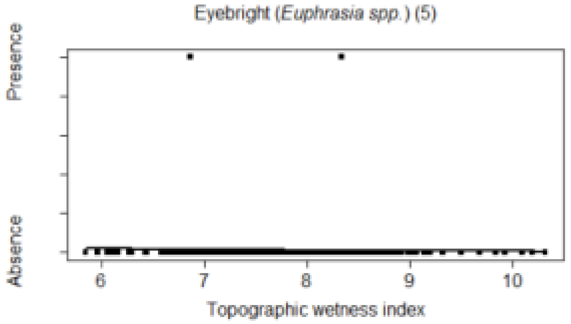

Europeen Gorse (*Ulex europaeus*) (5)

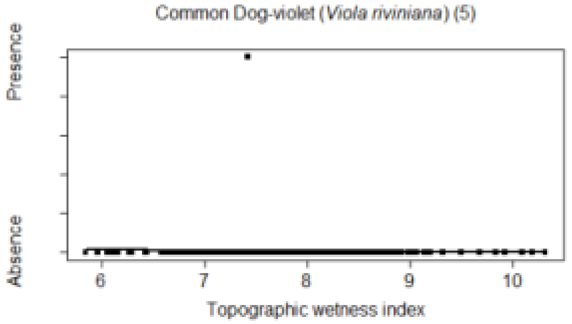

Sheep Sorrel (*Rumex acetosella*) (5)

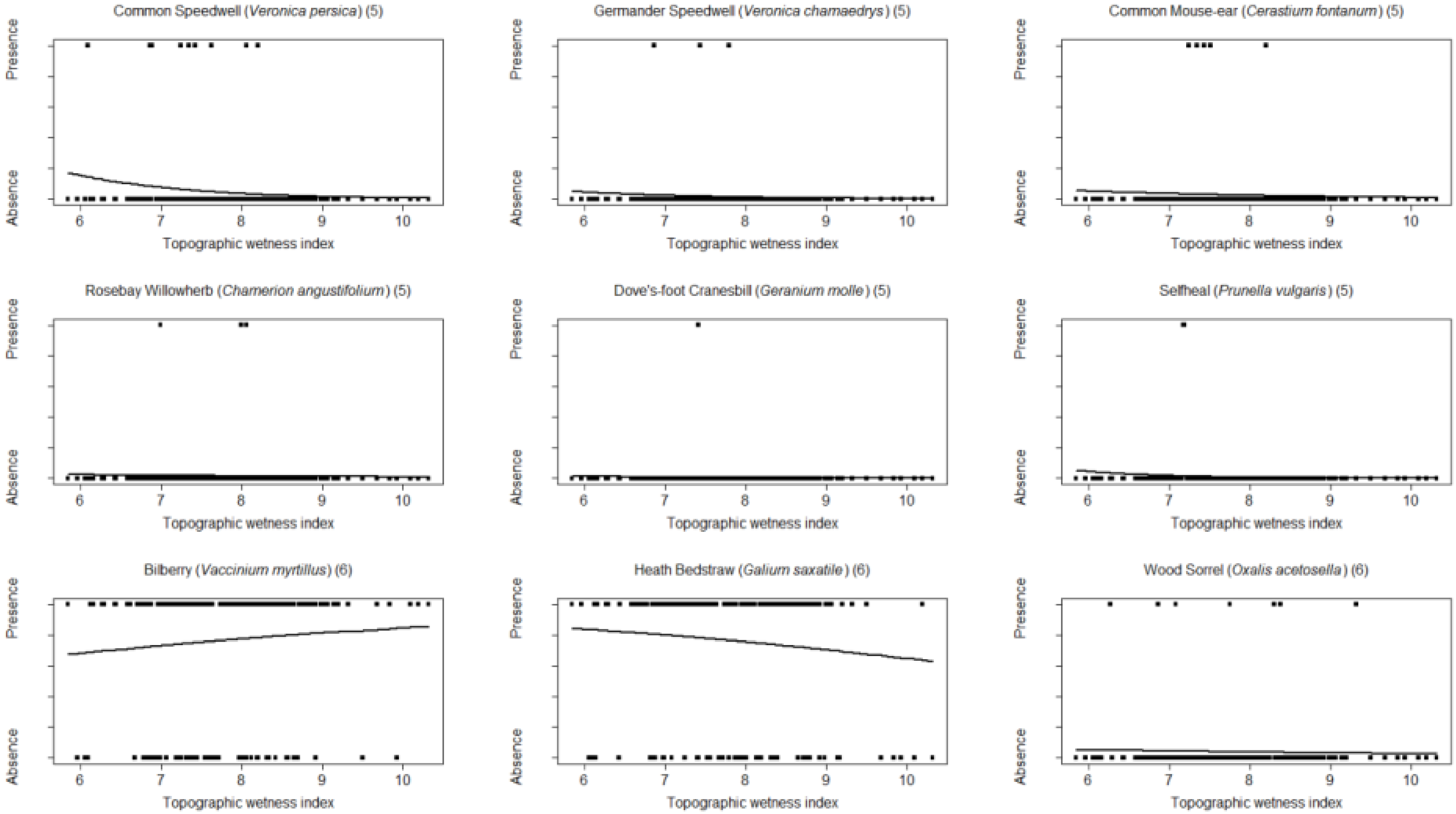

Common Sorrel (*Rumex acetosa*) (5)


Holly (*Ilex aquifolium*) (5)


Slender St John's-wort (*Hypericum pulchrum*) (5)


Eyebright (*Euphrasia spp.*) (5)


Common Dog-violet (*Viola riviniana*) (5)



Common Speedwell (*Veronica persica*) (5)

Germander Speedwell (*Veronica chamaedrys*) (5)

Common Mouse-ear (*Cerastium fontanum*) (5)

Rosebay Willowherb (*Chamerion angustifolium*) (5)

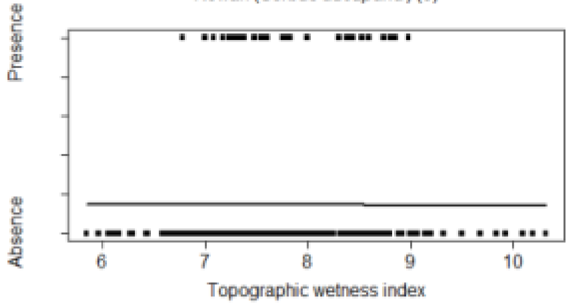
Dove's-foot Cranesbill (*Geranium molle*) (5)

Selfheal (*Prunella vulgaris*) (5)

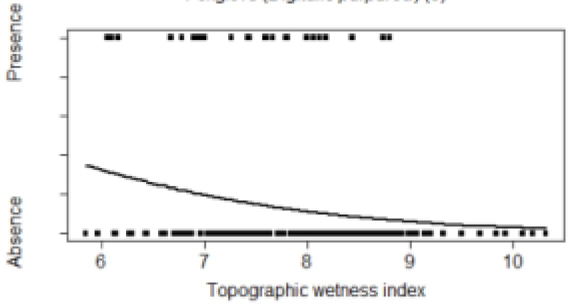
Bilberry (*Vaccinium myrtillus*) (6)

Heath Bedstraw (*Galium saxatile*) (6)

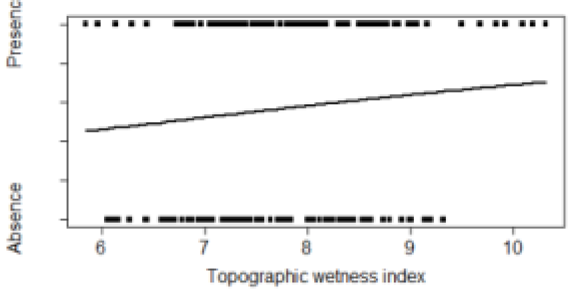
Wood Sorrel (*Oxalis acetosella*) (6)



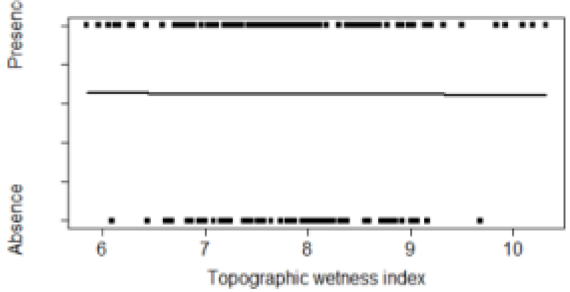
Rowan (*Sorbus aucuparia*) (6)



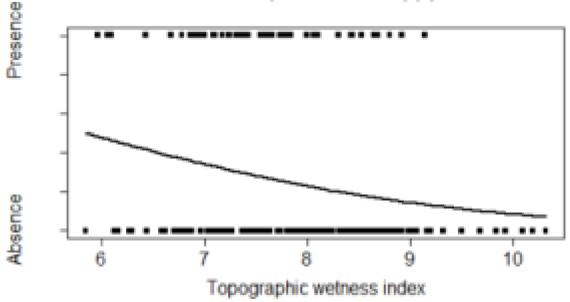
Foxglove (*Digitalis purpurea*) (6)



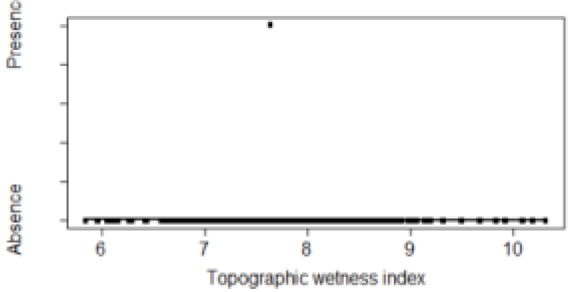
Common Heather (*Calluna vulgaris*) (6)



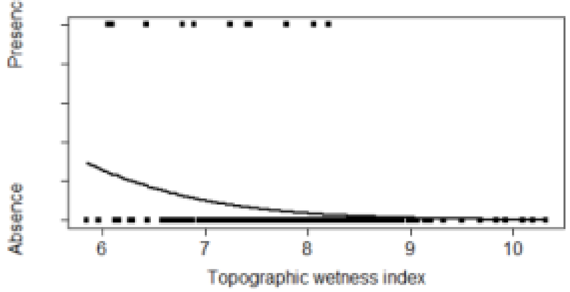
Western Gorse (*Ulex gallii*) (6)



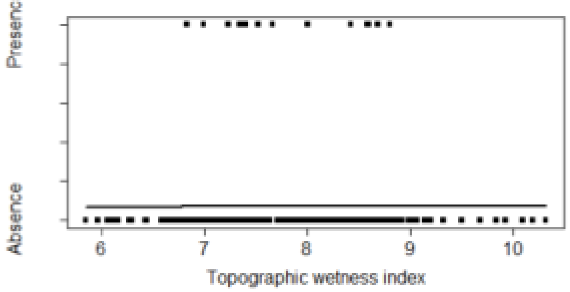
Bramble (*Rubus fruticosa*) (6)



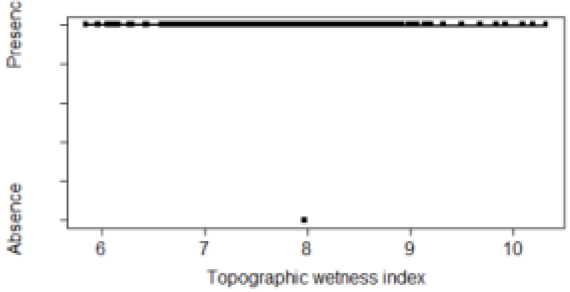
Dodder (*Cuscuta epithymum*) (6)



Lesser Stitchwort (*Stellaria graminea*) (6)



Heath Spotted-orchid (*Dactylorhiza maculata*) (7)



Tormentil (*Potentilla erecta*) (7)