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6. The effects of climate change on the distribution of species in the UK

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Summary

1. There is **high** agreement and a **high** amount of evidence that climate is a key factor limiting the geographical distributions of terrestrial species.

2. There is **high** agreement and a **high** amount of evidence that the overwhelming response of species to climate change is not to adapt to new climatic conditions *in situ* but to shift their distributions to keep track of their climatic niche.

3. There is **high** agreement and a **high** amount of evidence that southerly-distributed UK animal species have already shown a northwards shift in the location of their northern range boundary. Uphill shifts have also been observed in species' high altitude range boundaries but the pattern is less consistent than for latitudinal shifts.

4. There is **medium** agreement and a **low** amount of evidence of retractions at the southern or low-altitude range margins of northern or montane animal species. This may be due in part to methodological issues: extinction is harder to prove than colonisation and is harder to detect than colonisation when using coarse spatial resolution data. It is also difficult to attribute extinctions to climate change. Studies using fine spatial resolution data in butterflies have, however, linked local extinctions at southern range margins to climatic changes.

5. There is **low** agreement and a **medium** amount of evidence that plants species have shifted their distributions in response to climate change. Some species have been reported to show a response while others have not but further studies are required to assess the proportion of species showing a distributional change. The ecology of plants could mean that they are slower to respond to climate change than many animal species.

6. There is no evidence so far of extinctions of species from the UK due to changes in climatic conditions. There is **high** agreement and a **medium** amount of evidence that several species have recently colonised the UK in response to climate warming, but for some species it is difficult to say whether colonisation has been in response to climate change or other drivers of change.

7. There is **high** agreement and a **high** amount of evidence that species are shifting their distributions at different rates. Some are not moving or are retreating where they would be expected to expand (on the basis of climate alone), some are lagging behind climate warming and some are keeping pace.

8. There is **high** agreement and a **low** amount of evidence that variation in rates of range shift has led to changes in community composition, with communities seeing an increase in abundance of southern generalist species.

9. Individual species' physiological tolerances, species' traits, habitat availability, biotic interactions and other drivers of change may all contribute to variation in rates of range shift between species, but there is currently a **low** amount of evidence and **low** agreement as to which, if any, of these factors is most important in driving this variation.

10. Climate Envelope Modelling has been used to predict potential future changes in species' distributions using the correlation between species' distributions and current climatic conditions and future climate projections but many problems have been identified with these methods meaning that at best they currently provide general patterns of expected change rather than strict prognoses for individual species.

11. For UK species, there is **high** agreement and a **high** amount of evidence that southerly-distributed species will gain suitable climate space (but many species are unlikely to be able to colonise this space) and northerly-distributed species will lose suitable climate space, with some potentially losing all of their suitable climate space in the UK.

12. There is **high** agreement and a **high** amount of evidence that because there are far more southerly- than northerly- distributed species in the UK there will be more “winners” than “losers”, but these winners are likely to be declining in other parts of their ranges.

1. RANGE MARGINS AND CLIMATE

1.1 Evidence for climate as a limiting factor for species’ distributions

Understanding constraints on species’ distributions has long been a primary goal of ecological research (Andrewarth & Birth 1954, MacArthur 1972). A hierarchy of interacting factors acting at different spatial and temporal scales determine the locations in which a species occurs (Brown *et al.* 1996, Pearson & Dawson 2003). At a local scale, biotic interactions are considered principally important in determining the distribution of species, whereas at a regional scale soils and habitat are thought to be dominant factors (Pearson & Dawson 2003). At continental and sub-continental scales, climate has long been recognised as playing a dominant role (Grinnell 1917, MacArthur 1972), combining with historical factors (evolutionary history) and dispersal barriers to determine species’ range limits. Evidence for climate being an important factor in limiting species’ distributions comes from a number of different sources, as outlined below.

1.1.1 Correlation between species’ distributions and climatic conditions

Much of the evidence for the importance of climate as a limiting factor comes from the correlation between species’ range limits and geographic variation in climatic conditions. For example, the northern range margins of many butterfly species in the UK coincide with summer temperature isotherms (Dennis 1993), and the northern range margins of some plant species in Europe coincide with minimum winter temperature isotherms (Iverson 1944). Such studies are, however, often criticised because correlations between different climatic variables and other factors mean that the mechanisms limiting species’ distributions are unclear (Gaston 2003, Beale *et al.* 2008).

1.1.2 Mechanistic studies

Across a range of species, experimental studies have provided further insight into how climatic tolerances or requirements limit their distributions (Hodkinson *et al.* 1999). For example, at the northern range boundary of small-leaved lime (*Tillia cordata*) in northern England, it has been shown that temperatures are too cool for full growth of pollen tubes and hence the tree produces sterile seeds and cannot reproduce (Pigott & Huntley 1981). Bryant *et al.* (1997) demonstrated that thermal requirements for life cycle completion are likely to contribute to setting the northern range limits of the comma (*Polygonia c-album*) and peacock (*Inachis io*) butterflies in the UK, and thermal availability for development also appears to be a limiting factor for the pine processionary moth (*Thaumetopoea pityocampa*) in Europe (Battisti *et al.* 2005). For the silver-spotted skipper butterfly (*Hesperia comma*), which reaches its northern range margin in southern England, temperature requirements for egg-laying have been identified as a key limiting factor (Davies *et al.* 2006). The greater horseshoe bat (*Rhinolophus ferrumequinum*) is restricted to the south-west of the UK because of its relatively mild spring temperatures, as cool springs lead to later birth dates which reduces the likelihood that individuals will survive hibernation (Ransome 1994). At their warm range margins, heat and/or drought tolerance can play a role in setting range limits (Engelbrecht *et al.* 2007, Calosi *et al.* 2010). Climate may also limit species’ distributions indirectly through its effects on biotic interactions, as demonstrated by the impact of invasive species on native species along climatic gradients (Thomas 2010). For example, climate will affect the abundance and diversity of natural enemies, competitors and species that constitute resources, as well as a species' ability to compete for resources or resist natural enemies.

1.1.3 Evidence from range shifts

Much of the evidence for a role of climate in limiting species' distributions comes from the observation that species shift their distributions in response to climate change. If a species' distribution is limited by climate, it can respond in one of three ways to changes in climatic conditions over time: 1) evolve tolerances to new climatic conditions *in situ*, 2) shift its distribution through space to remain within its original climatic niche, or 3) change in abundance, including the potential to go extinct. Evidence from the Quaternary fossil record has been used to assess past responses of species to climatic changes. The Quaternary period spans approximately the last two million years, the most recent 800,000 years of which have been characterised by fluctuations with a periodicity of approximately 100,000 years between interglacial conditions, where the climate was broadly similar to that of the present day, and glacial conditions, when global mean temperatures were around 5-7 °C cooler than the recent past (Huntley 2007). Fossil pollen and spores of higher plants preserved in peats and lake sediments have been used to map the changing distribution and abundance patterns of individual plant taxa over this time. Although less abundant, fossils from other taxa, such as Coleoptera, have allowed similar studies for these groups. The most reliable evidence comes from the period since the last glacial maximum around 21,000 years ago as this is within the range of radiocarbon dating (Huntley 2007). This evidence shows a consistent response of species belonging to many different taxonomic groups of terrestrial organisms shifting their distributions through space to track suitable climatic conditions (Graham & Grimm 1990, Huntley 1991).

Observations of species from the past two centuries also reveal fluctuations in species' range margins consistent with changes in climatic conditions. For example, many butterflies in Britain were widespread in the nineteenth century but contracted their distributions at the end of the nineteenth century when conditions were relatively cool, before expanding again as the climate began to warm in the 1940s (Hill *et al.* 2001). Finally, over the past 4 decades species have moved their distributions to higher latitudes and altitudes, consistent with range shifts in response to climate warming. This evidence demonstrates that 1) climate is an important factor limiting species' distributions and 2) that the overriding response is not for species to adapt to new conditions *in situ* but to shift their distributions to keep pace with their climatic niche, although local adaptations may also take place (Bradshaw & Holzapfel 2006). Thomas (2010) used evidence from recent range shifts to ask what proportion of species have shifted their distributions in the direction expected from climate change and hence for what proportion climate is likely to be a range limiting factor. Thomas concludes that over half, and perhaps around two-thirds of observed animal range margins have already shown a response to recent climate warming and that climate is likely to play a role (although it may not be the sole determinant) of the range margins of the majority of terrestrial organisms.

2. OBSERVED RANGE SHIFTS

2.1 Evidence and rates of range shift

2.1.1 Measuring range shifts

The two most common data sources used to test for range shifts are (1) distribution atlases of particular taxa compiled using data collected by volunteers at least two different time periods; and (2) repeats of historical surveys of particular species groups in particular regions. The advantage of the former is that the geographic scope is usually greater, as is the suite of species covered. However, there are problems associated with changes in recorder effort between time periods (Kujala *et al.* 2013). The advantage of the second method is that, provided sufficient detail is available about how the historical survey was undertaken, these same methods can be replicated for the second time period.

Using these data, different methodologies have been used to detect changes in species' distributions in response to climate change. Some studies have simply examined changes in species' area of occupancy and whether signals of climate change can be seen in geographic variation in these trends or variation between species with different traits (Fox *et al.* 2014). Many studies have documented changes in the location of species' range margins, for example using the average latitude of the 10 most northerly occupied grid squares, arguing that these are the locations where responses are likely to be seen first (e.g. Hickling *et al.* 2006). Other authors have preferred to use more of the available data and studied changes in the latitude or altitude of maximum probability of occurrence (Lenoir *et al.* 2008, Crimmins *et al.* 2011, Stafford *et al.* 2013), so while the location of a species' range boundaries may not have changed its “centre of gravity” may have shifted. Some have examined changes in the distribution of juvenile and adults of the same, primarily long-lived species, arguing that if a species' range is shifting in a particular direction there will be greater recruitment of juveniles at that boundary (Zhu *et al.* 2012, Rabasa *et al.* 2013). Finally, changes in community composition at particular locations over time have also been used to demonstrate shifts in the distribution of species, examining whether cool-adapted species have declined and heat-adapted species have increased (e.g. Pauli *et al.* 2007, Holzinger *et al.* 2008).

2.1.2 Global observations

There is high confidence that many plant and animal species in many regions have moved their ranges in response to observed climate change over recent decades (Settele *et al.* 2014). The overwhelming majority of studies of regional climate effects on terrestrial species reveal consistent responses to warming, i.e. range shifts of flora and fauna to higher latitudes and altitudes. Multispecies studies from a variety of taxonomic groups and regions have been used to demonstrate non-random distributional shifts; i.e. that the majority of species have shifted their distributions in the direction expected from climate warming. Evidence comes from shifts to higher latitudes in birds (Thomas & Lennon 1999, Brommer 2004, 2012, Hitch & Leberg 2007, Auer & King 2014), invertebrates (Parmesan *et al.* 1999, Hickling *et al.* 2005, 2006, Pöyry *et al.* 2009, Betzholtz *et al.* 2013, Grewe *et al.* 2013) and fish (Hickling *et al.* 2006, Grenouillet & Comte 2014); and to higher altitudes in plants (Grabherr *et al.* 1994, Lenoir *et al.* 2008, Harsch *et al.* 2009, Matteodo *et al.* 2013), mammals (Moritz *et al.* 2008), invertebrates (Chen *et al.* 2011b, Menendez *et al.* 2014), birds (Pounds *et al.* 1999, Reif & Flousek 2012) and amphibians (Raxworthy *et al.* 2008). However, it should be noted that these observations come from a limited number of species groups and regions and so there is only medium confidence in the evidence for range shifts in response to climate change when looking across all species groups and regions (Settele *et al.* 2014).

The average rate of latitudinal range shift across all species that have been studied is 16.9 km per decade and for altitudinal shifts is 11.0 m per decade (Chen *et al.* 2011a). Species are shifting their distributions most rapidly in regions where climatic warming has been greatest (Chen *et al.* 2011a, Menendez *et al.* 2014), further supporting the argument that recent range shifts have been a response to climatic warming. Contemporary latitudinal rates of range shift are comparable with those in response to the rapid climatic changes that took place following the transition from cold glacial conditions to warmer Holocene climates, estimated at 2-20 km per decade (Huntley 2007). A caveat here is that these Quaternary estimates are largely based on evidence from trees, for which the best data are available. Identification of refugial populations has led to the suggestion that actual historic rates of range shift may actually have been slower than previously thought (McLachlan *et al.* 2005, Pearson 2006), but evidence from extensively glaciated areas suggest that rates fall within the range given above.

2.1.3 Evidence from the UK: cool range margin shifts in animals

In the UK we have some of the most detailed information available regarding the distribution of species, which comes largely from volunteer-collected observation records dating back many decades. This has enabled the study of range shifts across a broad range of taxonomic groups. Findings from the UK are consistent with those from other regions. For southerly distributed animals in the UK belonging to 16 taxonomic groups (both terrestrial and freshwater), Hickling *et al.* (2006) demonstrated a consistent northward and, to a less consistent extent, upward shift in the location of their cool range margins over 20-25 years, with the only exception being the reptiles and amphibians (probably due to changes in land use and management; see section 2.2.5) (Figure 1). Of the 329 species studied, 275 had shifted their upper latitudinal range margin northwards, 52 southwards and 2 had remained static. In the same analysis 227 species showed an upward shift in their upper altitudinal range margin and 102 species showed a downward shift. Across all species, the average shift in the northern range margin was 31-60 km at a rate of 13.7-24.8 km per decade and in the high altitude range margins was 25 m uphill at a rate of 2.8-10.1 m per decade (depending on the level of subsampling of the data to control for changes in recorder effort) (Hickling *et al.* 2006).

More recent studies have shown that species from other animal taxa in the UK, not included in this analysis, are also shifting their distributions northwards. Fox *et al.* (2011), for example, reported that between 1960-82 and 1983-2009, 12 moth species with a southern distribution in the UK shifted their northern range margins on average 194.8 km (mean shift of 7.8 km per yr). This is extremely rapid compared with other species groups studied, but these species were selected for study because of anecdotal reports that they had shifted their distributions. Overall, there has been no general trend in the area of occupancy of southerly-distributed moths in the UK between 1970 and 2010; some have increased and some have decreased their distributions (Fox *et al.* 2014). Widespread moth species have, however, increased their distributions more in the north of the UK than the south which may be due to improving climatic conditions in these regions (Fox *et al.* 2014).

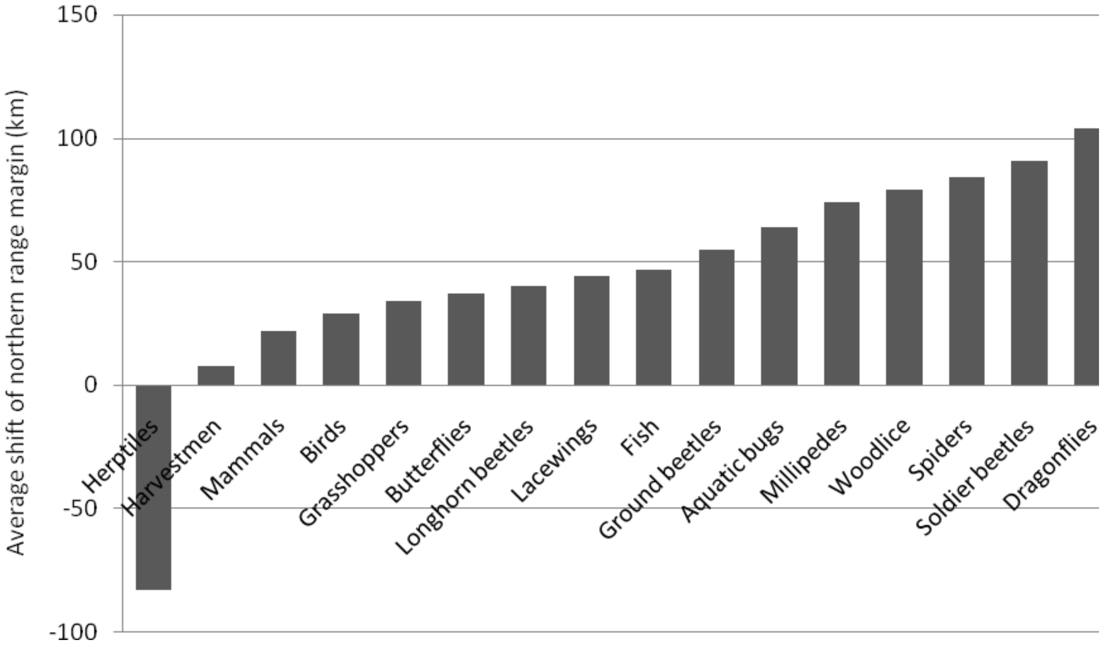


Figure 1. *Average latitudinal shift in the northern range margins of species belonging to 16 taxonomic groups in the UK during recent climate warming. Values calculated as the difference in range margin location between two recording periods (see Table 1 for details of time periods for each taxonomic group). Only species occupying more than twenty 10 km grid squares across the two time periods are included. See Table 1 for number of species included for each taxonomic group and for further details on data and methods see Hickling et al. (2006).*

More work is required on other animal groups to document the percentage of species moving their distributions and the rate at which they are doing so. Furthermore, Hickling *et al.* (2006) only used data up to 2000 and updates are required to examine changes over the past 10 years. The number of species responding might be expected to increase over time as the physiological thresholds of more species are passed and rates of shift may vary over time as rates of warming alter as well as in response to ecological and evolutionary processes at species' range margins (Thomas *et al*. 2001, Mustin *et al.* 2009, La Sorte & Jetz 2012). For butterflies in the UK, Mair *et al.* (2012) showed that rates of range shift were generally faster from 1995-99 to 2005-09 compared with rates from 1970-82 to 1995-99, despite no significant climatic warming during the later period, with species perhaps showing a delayed response to keep pace with climate warming. Mair *et al.* (2012) also showed that individual species' rates of range shift are temporally variable (i.e. their rate of expansion in the first period did not predict that in the second) and the reasons for this require further investigation. Finally, recent studies have suggested that measuring range shifts using changes in the position of range margins may be heavily biased by changes in recording effort over time and so the effect of this requires further examination (Kujala *et al.* 2013).

2.1.4 Evidence from the UK: warm range margin shifts in animals

In line with global observations (Parmesan *et al.* 1999, Brommer 2004, 2012, Doak & Morris 2010, Chen *et al.* 2011b, Grewe *et al.*2013, Settele *et al.* 2014), there is weaker evidence that species in the UK are retracting their distributions at their warm range margins than evidence that species are expanding their distributions at their cool range margins (Parmesan & Yohe 2003). Studies examining shifts of warm, southern range margins of northerly-distributed animal species in the UK have either failed to demonstrate a consistent trend of retractions northwards in birds (Thomas &

Lennon 1999) and butterflies (Hill *et al.* 2002) or have demonstrated shifts but at a slower rate than that of expansions at the cool, northern range margins of southerly-distributed species (dragonflies and damselflies, Hickling *et al.* 2005).

Several hypotheses have been proposed to explain asymmetric rates of boundary shifts. It has been suggested that species may be less constrained by climate at their warm range margins than other factors such as habitat and biotic interactions (Darwin 1859, Connell 1961, Brown *et al.* 1996). It has been shown that maximum temperature tolerances, unlike minimum temperature tolerances, are conserved across taxa (Kellermann *et al.* 2012, Araujo *et al.* 2013), and so it has been suggested that species, particularly at high latitudes and altitudes where climates are cooler, have "thermal safety margins" i.e. a large gap between maximum temperatures experienced and tolerated (Deutsch *et al.* 2008, Khaliq *et al.* 2014). If this were the case, more climate change would be required to induce changes at trailing range margins than leading range margins (Sunday *et al*. 2012). However, there is little convincing evidence in the literature that this is the case (Thomas 2010, Cahill *et al.* 2014) and a recent analysis using more realistic measures of the thermal conditions experienced by individuals, in particular considering thermal extremes, showed that most species are at or exceeding their heat tolerance limits at their warm range margin (Sunday *et al.* 2014). Species may thus be able to exploit fine-scale topographic heterogeneity or adapt behaviourally at trailing-edge range margins and hence persist in locations with favourable microclimates for longer than would otherwise be expected before regional extinction occurs (Parmesan *et al.* 1999, Hampe & Petit 2005, Gillingham *et al.* 2012, Varner & Dearing 2014, Sunday *et al.* 2014). Alternatively, species, in particular long-lived species, such as trees, may persist in regions even though climatic conditions are unsuitable (Rabasa *et al.* 2013) resulting in an extinction debt (Dullinger *et al.* 2012). Species may alternatively be limited by different abiotic factors at their cool and warm range margins and thus climatic changes may not act equally at different boundaries (Engelbrecht *et al.* 2007, Svenning & Condit 2008).

Limited evidence of retractions at warm range boundaries may also be due in part to detection problems. It may be the case that extinctions are slow to detect using fairly coarse-scale data (usually 10 × 10 km grid squares, Thomas & Lennon 1999, Hill *et al.* 2002, Hickling *et al.* 2006) because every population in a grid square must go extinct before extinction is recorded, whereas only one species record is required to record a colonisation event (Thomas *et al.* 2006). Evidence for climate-related retractions at species' warm range margins has been detected through the use of fine spatial resolution data. Populations extinctions have been attributed to changes in climatic conditions after 1970 at the warm range margins of 3 out of 4 northerly distributed butterfly species in the UK: the northern brown argus (*Aricia artaxerxes*) has retreated northwards by 73 km, the Scotch argus (*Erebia aethiops*) has retreated northwards by 80 km and the mountain ringlet (*Erebia epiphron*) uphill by 149 m (Franco *et al.* 2006, Thomas *et al.* 2006, Gillingham *et al.* in press). These rates of retraction are comparable with those expected from temperature changes, 88 km north and 98 m uphill and surpass rates of expansion at cool range margins (Thomas *et al*. 2006). The use of fine-scale data has also proved successful in detecting warm range margins extinctions in butterflies in North America (Parmesan 1996) and in butterflies and dung beetles in the mountains of Spain (Wilson *et al.* 2005, Menendez *et al.* 2014) and so such studies for other taxa in the UK are likely to provide valuable information as to whether species are showing climate-related retractions. Problems remain, however, with proving extinctions and with attributing extinctions to climate change (Menendez *et al.* 2014).

Other studies have used different methods to examine responses of northerly-distributed species in the UK to climate change. Some studies suggest these species are responding negatively to climate change, as would be expected; for example, population declines at the warm range margin of the Arctic charr (*Salvelinus alpinus*) have been demonstrated (Winfield *et al.* 2010). Stafford *et al.* (2013) detected southern range margin retraction of colonies of northerly distributed sea bird species in the UK between the time periods 1984-1989 and 1998-2002 by examining changes in the centre of gravity of species' distributions. Fox *et al.* (2014) showed that the majority (94 %) of northerly-distributed macro-moth species in the UK declined in their area of occupancy from 1970 to 2010. More work is required to assess the percentage of species undergoing retractions at their warm range margins, the rates of retreat and to determine whether retractions are a response to climate change.

2.1.5 Range shifts in the UK: plants

Globally there is evidence that plants are shifting their distributions to higher altitudes (Settele *et al.* 2014). Studies in other parts of Europe, for example, have shown shifts along altitudinal gradients in plants (Grabherr *et al.* 1994, Klanderud & Birks 2003, Peñuelas & Boada 2003, Walther *et al.* 2005, Pauli *et al.* 2007) although others have failed to detect such shifts (Bassler *et al.* 2013). Britton *et al.* (2009) and Ross *et al*. (2012) have detected changes in the species composition of Scottish mountain plant communities, with an increase in southern generalist species and a decline in northern specialist species, as would be expected from climate change. However, other drivers of change, including increased nitrogen deposition and changing grazing pressure are also likely to have played a role in this change. The Scottish mountains are included in the Global Observation Research Initiative in Alpine Environments (GLORIA) project which has a network of monitoring sites with the aim of detecting vegetation changes in alpine ecosystems (Pauli et al. 2004).

Globally, latitudinal shifts in plant species have received much less attention (Zhu *et al*. 2012) but there is a suggestion that latitudinal shifts are lagging far behind climate trends compared with altitudinal shifts and shifts in other taxa (Settele *et al.* 2014). Similarly, in the UK, there is less consistent evidence for latitudinal range shifts in plants than there is for animals but several studies have suggested that plant species are showing a response. Resurveys of 2 × 2 km grid squares across the UK by the Botanical Society for the British Isles (BSBI) between 1987 and 2004 identified the northwards spread of some southerly-distributed plant species, such as the bee orchid (*Ophrys apifera*) (Braithwaite *et al.* 2006). Amano & Freckleton (2014) also found that between the time periods 1930-1960 and 1987-1999, 225 out of 284 plant species in the UK had showed a northward shift in their mean latitude and there was evidence of shifts at both northern and southern range boundaries. Similarly, Powney *et al.* (2014) found warmth-loving species have increased their area of occupancy in the north of the UK, suggesting species may be tracking their climate envelopes northwards. Sites in the UK were included in an analysis of forests across Europe and North America which found an increase in warmth-loving understorey plants over recent decades, with magnitude of thermophilisation being greater in regions which has experienced more warming (De Frenne *et al.* 2013). Groom (2013) also examined the change in the centre of gravity of the distribution of all but the rarest UK plant species between the time period 1978-1994 and 1995-2011. Of the species with increasing distribution size, there was a bias towards a northward shift in their centre of gravity which was greater in northern England and Scotland. For species with declining distributions, there was no overall trend for shifts in a particular direction, but taking regions separately there were trends for shifts northwards in northern England, although the trend was southwards in Scotland. Other studies, however, have failed to find such patterns. The Countryside Survey in 2007 reported that distributional changes in the direction expected from climate change had not been detected in repeated surveys of fixed plots since 1978 (Carey *et al.* 2008) and the BSBI resurveys found no evidence of decline at the southern range boundaries of northerly-distributed species (Braithwaite *et al.* 2006). The extent to which other environmental changes, such as habitat conversion and nitrogen deposition, may be driving these patterns is unclear (Powney *et al.* 2014). Groom (2013), for example, found that there was no trend for a greater shift northwards in thermophilic species, as would be expected from a response to climate.

Doxford & Freckleton (2012) have shown for plant species in the UK, that colonisation and extinction processes occur at a local scales and long-distance dispersal events appear to be rare, suggesting that rates of range expansion might be expected to be slow. Long-lived species, such as trees, may also be able to persist in a region for a considerable time at their warm range margins even though climatic conditions have become unsuitable for reproduction or establishment of seedlings, leading to a very long lag time for local extinctions (Rabasa *et al.* 2013). Clearly more work is required to assess the extent to which plants are shifting their distributions in the UK, and for what reasons.

Further discussion of this topic can be found in the accompanying paper by Carey (2015).

2.1.6 Colonisations and extinctions in the UK

In addition to shifts in the location of range margins, it might also be expected that northerly-distributed species could go extinct from the UK if they run out of suitable climate space, and that species will colonise the UK from continental Europe as the climate becomes suitable for them, provided they have the capacity to reach the UK and there is suitable habitat available for them to establish. Thus far there have been no documented extinctions of species from the UK that can be attributed to climate warming. There are, however, reports of species colonisations linked to climate warming, including the Nathusius' pipistrelle bat (*Pipistrellus nathusii*) (Lundy *et al.* 2010) and the southern emerald (*Lestes barbarus*) and small red-eyed (*Erythromma viridulum*) damselflies (Watts *et al.* 2010). Several species of bird have also colonised the UK in recent decades (Hiley *et al.* 2013), such as the little egret (*Egretta garzetta*), but it is often difficult to disentangle whether colonisations are a result of changes in the climate or in other factors such as land management practices. Thus far, studies have been on a species-by-species basis and work is required to quantify arrival rates and the percentage of these that are associated with climate warming.

2.2. Variation in rates of range shift

Substantial variation in rates of range shift between species is consistently observed in multispecies analyses worldwide (e.g. Holzinger *et al.* 2008, Moritz *et al.* 2008, La Sorte & Jetz 2012, Rabasa *et al.* 2013, Menendez *et al.* 2014). This is consistent with evidence from Quaternary range shifts which shows that species responded individualistically to climate change (Huntley 1991). While some variation is seen between taxonomic groups (Devictor *et al.* 2012, Bassler *et al.* 2013), much wider variation is found between species within taxonomic groups (Chen *et al.* 2011a) (Figure 2). Within the UK butterflies, for example, some species' distributions have remained static and some, such as the grizzled skipper (*Pyrgus malvae*) and brown hairstreak (*Thecla betulae*), have even moved in the opposite direction to that expected from climate change, probably in response to other environmental changes. By contrast, other species, such as the comma butterfly (*Polygonia c-album*), have shifted their distributions polewards at rates of over 10 km per year.

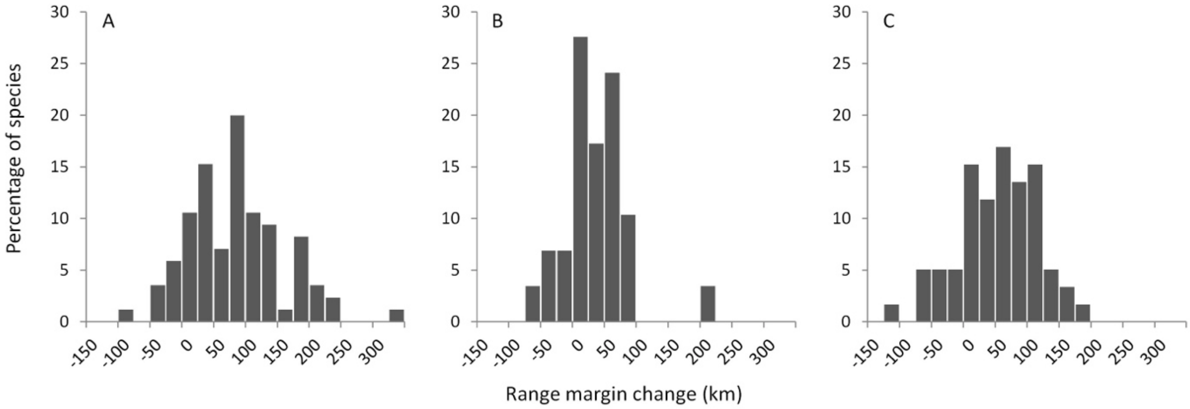


Figure 2. *Shifts of the northern range margins of southerly-distributed animal species in Britain belonging to three taxonomic groups (A) spiders, (B) butterflies and (C) ground beetles. Positive values indicate a northward shift and negative values a southward shift. See Table 1 for details of numbers of species and dates between which range margin shifts were calculated.*

Much of the concern for the survival of species as the climate changes arises from the possibility that species will not be able to shift their distributions to keep pace with climate warming, leading to reductions in range extent or potentially extinction if there is no overlap between current and future suitable climatic space (Thomas *et al.* 2004, Thuiller *et al.* 2005b, Schippers *et al.* 2011). The distributions of many taxa appear not to have fully occupied available climate space during the present interglacial, suggesting some species are unable to shift their distributions to keep pace with changing climatic conditions (Araújo & Pearson 2005, Svenning & Skov 2007, Normand *et al.* 2011). This may be more of a problem for species responding to contemporary climate change given the rapid rate of climate warming that is predicted, particularly under medium and high emissions scenarios (Loarie *et al.* 2009, Settele *et al.* 2014) and the human-dominated landscapes they must traverse. By comparing observed range shifts with those predicted from rates of climate change, it has been reported that species and communities worldwide are “lagging” behind climate warming (Popy *et al.* 2010, Bedford *et al.* 2012), including butterflies and birds in the UK (Warren *et al.* 2001, Menéndez *et al.* 2006, Devictor *et al.* 2012). Translocation experiments have also shown that species are able to persist beyond their current cool range margins, suggesting lags, as has been found for the marbled white (*Melanargia galathea*) and small skipper (*Thymelicus sylvestris*) butterflies in northern England (Willis *et al.* 2009a). However, in their recent meta-analysis Chen *et al.* (2011a) calculated that globally latitudinal shifts are not consistently lagging behind the climate, with 9 out of 20 species groups on average keeping pace with or surpassing climate warming. By contrast, for altitudinal shifts, 28 out of 30 taxonomic groups are showing lags (Chen *et al.* 2011a). Species groups in the UK are consistent with this observation, with 7/16 shifting fasting enough to keep pace with latitudinal shifts in temperature (Table 1) but none of the 16 groups studied shifting uphill fast enough to keep pace (Table 2). This is surprising given that dispersal distances required to keep pace with altitudinal shifts in suitable climate space are much shorter those required for latitudinal shifts and species would be expected to be more vulnerable in extensive flat landscapes than mountainous regions (Settele *et al.* 2014). However, coarse-resolution studies of altitudinal shifts may under-represent the changes that are actually taking place. The data underlying table 2 is at 10 km resolution, and squares of this size will often encompass the expected elevational range shifts of <=100 m. Furthermore, in upland areas, variation in temperature with aspect can be larger than change with altitude (Suggitt *et al.* 2011), and so species may adapt by shifting their distribution around rather than uphill.

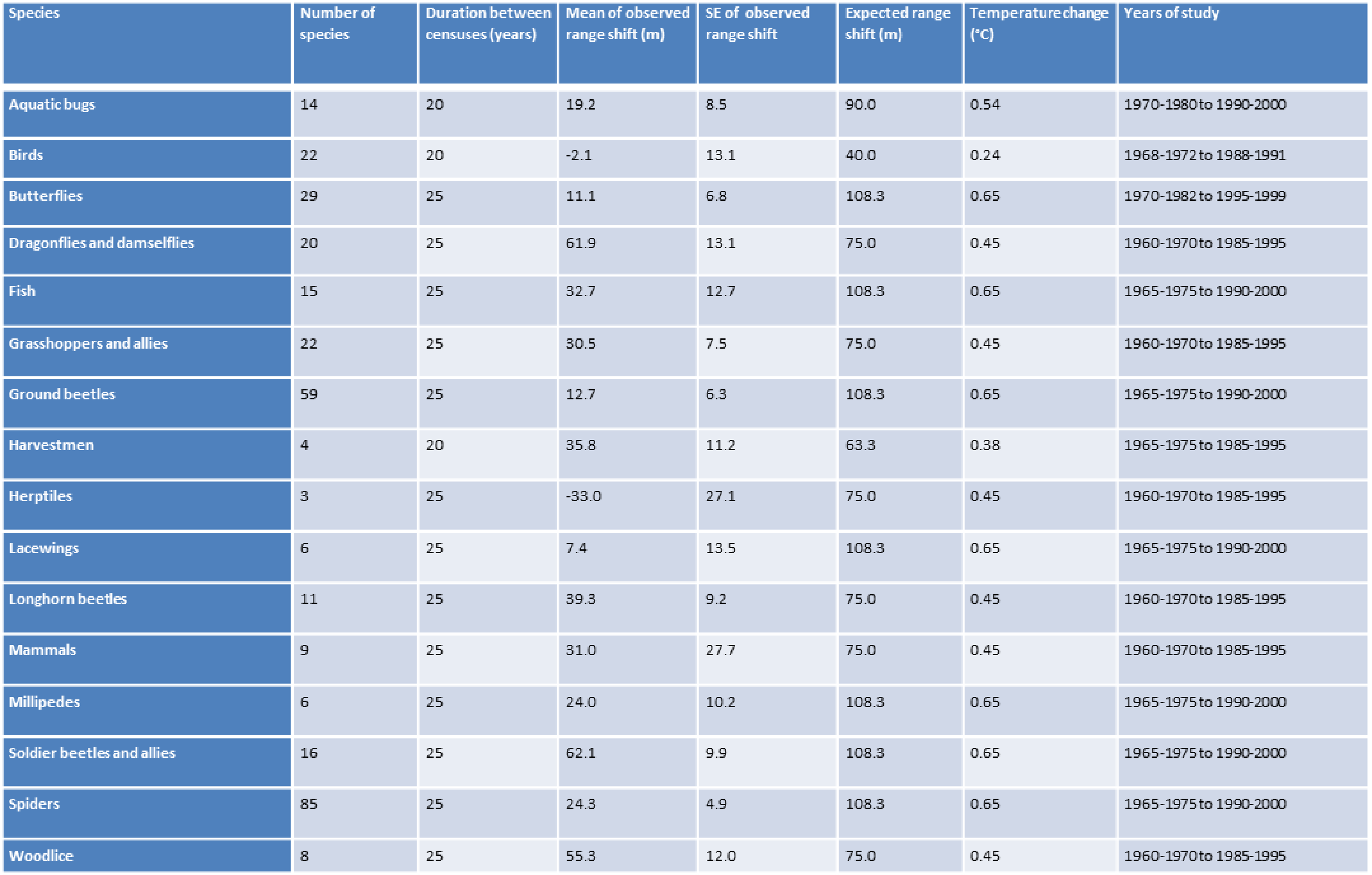
Understanding variation in rates of range shift is important to help identify species at risk of range contraction or even extinction and hence requiring conservation action (Thomas *et al.* 2004, Thuiller *et al.* 2005, Arribas *et al.* 2012, Foden *et al.* 2013). Individualistic responses also have important consequences for future community structure, with the creation of nonanalog communities (extant species present in historically unknown combinations) (Kullman 2006, Hobbs *et al.* 2009, Keith *et al*. 2009), as observed in the fossil record in response to historical climate changes (Jackson & Overpeck 2000, Stewart 2009), and may also have consequences for ecosystem functioning (Montoya & Rafaelli 2010, Walther 2010). There is increasing understanding of the mechanisms that can generate variation in rates of range shift (Settele *et al.* 2014). However, it remains unclear which, if any, of these factors are of primary importance in determining rates of range expansion. Further work is essential to identify important factors so that at risk species can be identified and conservation efforts focussed on these species (Williams *et al.* 2008, Heller & Zavaleta 2009). Potential factors affecting rates of range shift are discussed below.

2.2.1 Exposure

A species' response will first depend on its exposure to climatic changes. Changes in climatic conditions have varied between regions (Dobrowski *et al.* 2013) and are projected to continue to do so (IPCC 2013). This has led to spatial variation in the magnitude of species' distributional responses (Chen *et al.* 2011a, Menendez *et al.* 2014). In the UK, temperature increases have so far been greater in the south of the UK than the north and rainfall is projected to increase in the north-west but potentially decrease in the south, with seasonal differences also possible, in particular proportionally less rain falling in summer and more in winter (Met Office 2011). This could be particularly important if it led to increased water shortage in summer in the relatively dry south and east of England. Hence species with different distributions in the UK will be exposed to different magnitudes and patterns of climatic change and hence are likely to respond differently.

Species	Number of species	Duration between censuses (years)	Mean of observed range shift (km)	SE of observed range shift	Expected range shift (km)	Temperature change (°C)	Years of study
Aquatic bugs	14	20	64.2	19.7	60.0	0.54	1970-1980 to 1990-2000
Birds	22	20	28.6	20.0	26.7	0.24	1968-1972 to 1988-1991
Butterflies	29	25	36.7	9.7	72.2	0.65	1970-1982 to 1995-1999
Dragonflies and damselflies	20	25	104.2	17.0	50.0	0.45	1960-1970 to 1985-1995
Fish	15	25	47.2	15.4	72.2	0.65	1965-1975 to 1990-2000
Grasshoppers and allies	22	25	33.6	8.0	50.0	0.45	1960-1970 to 1985-1995
Ground beetles	59	25	55.1	8.4	72.2	0.65	1965-1975 to 1990-2000
Harvestmen	4	20	7.9	29.8	42.2	0.38	1965-1975 to 1985-1995
Herptiles	3	25	-83.0	29.8	50.0	0.45	1960-1970 to 1985-1995
Lacewings	6	25	44.3	27.9	72.2	0.65	1965-1975 to 1990-2000
Longhorn beetles	11	25	40.0	10.4	50.0	0.45	1960-1970 to 1985-1995
Mammals	9	25	22.4	38.4	50.0	0.45	1960-1970 to 1985-1995
Millipedes	6	25	73.7	17.0	72.2	0.65	1965-1975 to 1990-2000
Soldier beetles and allies	16	25	91.1	13.3	72.2	0.65	1965-1975 to 1990-2000
Spiders	85	25	83.9	7.9	72.2	0.65	1965-1975 to 1990-2000
Woodlice	8	25	78.8	18.4	50.0	0.45	1960-1970 to 1985-1995

Table 1. *Observed and expected latitudinal range shifts of various taxonomic groups in the UK. Observed shifts are changes in the location of northern range margins calculated by Hickling et al. 2006. Positive values are northwards shifts and negative values are southwards shifts. Expected range shifts calculated by Chen et al. 2011a. Taxa in bold have kept pace with climate warming.*



Species	Number of species	Duration between censuses (years)	Mean of observed range shift (m)	SE of observed range shift	Expected range shift (m)	Temperature change (°C)	Years of study
Aquatic bugs	14	20	19.2	8.5	90.0	0.54	1970-1980 to 1990-2000
Birds	22	20	-2.1	13.1	40.0	0.24	1968-1972 to 1988-1991
Butterflies	29	25	11.1	6.8	108.3	0.65	1970-1982 to 1995-1999
Dragonflies and damselflies	20	25	61.9	13.1	75.0	0.45	1960-1970 to 1985-1995
Fish	15	25	32.7	12.7	108.3	0.65	1965-1975 to 1990-2000
Grasshoppers and allies	22	25	30.5	7.5	75.0	0.45	1960-1970 to 1985-1995
Ground beetles	59	25	12.7	6.3	108.3	0.65	1965-1975 to 1990-2000
Harvestmen	4	20	35.8	11.2	63.3	0.38	1965-1975 to 1985-1995
Herptiles	3	25	-33.0	27.1	75.0	0.45	1960-1970 to 1985-1995
Lacewings	6	25	7.4	13.5	108.3	0.65	1965-1975 to 1990-2000
Longhorn beetles	11	25	39.3	9.2	75.0	0.45	1960-1970 to 1985-1995
Mammals	9	25	31.0	27.7	75.0	0.45	1960-1970 to 1985-1995
Millipedes	6	25	24.0	10.2	108.3	0.65	1965-1975 to 1990-2000
Soldier beetles and allies	16	25	62.1	9.9	108.3	0.65	1965-1975 to 1990-2000
Spiders	85	25	24.3	4.9	108.3	0.65	1965-1975 to 1990-2000
Woodlice	8	25	55.3	12.0	75.0	0.45	1960-1970 to 1985-1995

Table 2. *Observed and expected altitudinal range shifts of various taxonomic groups in the UK. Observed shifts are changed in the location of upper range margins calculated by Hickling et al. 2006. Positive values are uphill shifts and negative values are downhill shifts. Expected range shifts calculated by Chen et al. 2011a. None have kept pace with climate warming.*

2.2.2 Species' physiological responses and tolerances to climate

Changes in distribution are ultimately driven by the effect of new environmental conditions on the physiology of individuals, which translate into changes in population growth rates and thus the locations in which populations of a species can persist (Helmuth *et al.* 2005, Helmuth 2009). Firstly, responses will depend on whether a species' distribution is at equilibrium with its climatic tolerances. While climate is clearly an important limiting for many species, other factors are more important in controlling the distributions of others. Narrow range endemics, for example, may be restricted to geological outcrops or single lakes and only occupy a narrow range of their potential climatic niche (Thomas 2010). Land use and human intervention has also reduced the distributions of many species. Some "upland" species of birds (e.g. hen harrier *Circus cyaneus*) and mammals (e.g. pine marten *Martes martes*) are likely to have become restricted to these regions because of past persecution and not because climate is most suitable for them there (Anderson *et al.* 2009b). In these cases, climatic changes may not induce an immediate change in distribution if the remaining distribution of the species is not at the edge of its climate space. More broadly, there is debate as to how close species are to their physiological thermal-tolerance limits, in particular at their warm range margins (Khaliq *et al*. 2014, Sunday *et al.* 2014) and hence how rapidly responses would be expected (see section 2.1.4 for discussion).

Secondly, for species that are at equilibrium with their climatic niche, species vary in their degree of thermal specialisation. A given change in temperature will translate into a greater change in performance in a thermal specialist than a thermal generalist (Deutsch *et al.* 2008, Huey *et al.* 2012). Species with a narrower thermal niche are likely to be at greater risk of reduced range size or extinction because the same change in climate would lead to a much greater loss of suitable climate space within their current distribution than for climate generalists (Huntley *et al.* 2008).

Furthermore, species are limited in their distributions by different aspects of the climate (Williams *et al.* 2012). For example, some species appear to have expanded their distributions at their warm range margins in response to winter warming in the UK, such as the Dartford warbler (*Sylvia undata*) (Wotton *et al.* 2009, Bradbury *et al.* 2011), whereas others appear to have responded to changes in summer temperatures, such as the silver-spotted skipper butterfly (*Hesperia comma*) (Davies *et al.* 2006). Warming rates vary between seasons, for example, summer warming has been greater than winter warming in the UK (Met Office 2011). This fact combined with different climatic triggers for different stages of species' life cycles will lead to unpredictable timing and extent of responses.. In addition, temperature is not the only aspect of the climate that is changing; species will be differentially sensitive to changes in rainfall, creating variation in patterns of range shift and even shifts in the opposite direction to that expected from changes in temperature alone (Berry *et al.* 2003, Tingley *et al.* 2009, 2012, Crimmins *et al.* 2011, McCain & Colwell 2011, Pauli *et al.* 2012, VanDerWal *et al.* 2013). Many butterfly species in the UK for example, are sensitive, directly or indirectly, to drought and decreases in precipitation may negate any benefits of warming temperatures (Oliver *et al.* 2013). In many cases a combination of factors is likely to be important and interactions between climate variables can substantially alter patterns of range shift (Crozier & Dwyer 2006). For example, the garden tiger moth (*Arctia caja*) in the UK has decreased its distribution in the UK in response to warmer and wetter winters and springs (Conrad *et al.* 2002). Finally, the importance of climatic variability and extremes for controlling species' distributions is being increasingly recognised and changes in these may be more important for some species than others (Beever *et al.* 2010, Buckley & Kingsolver 2012, Ashcroft *et al.* 2014, Vasseur *et al.* 2014).

Species may show genetic adaptation to local climatic conditions, as has been shown, for example, in studies of *Drosophila* spp (Hoffmann *et al.* 2003). As such, populations at species' cool range margins, which would be expected to benefit from climate warming, may not if they are adapted to relatively cool local climatic conditions (Hellmann *et al.* 2012). There may also be other physiological constraints on species' abilities to shift their distributions, such as adaptation to photoperiod which depends only on latitude (Lehmann *et al.* 2014).

Understanding the factors controlling species' distributions and species' physiological responses to various aspects of the climate may be crucial to predict species' responses to climate change. However, these factors have been elucidated for very few species.

2.2.3 Capacity for adaptation within current distributions

The magnitude of responses to climate change will also be modified by species' ability to adapt to new conditionals in situ. Species with greater abilities to acclimate and with greater capacity for behavioural thermoregulation may be able to persist in an area longer before conditions become such that a change in distribution is induced (Kearney & Porter 2009, Somero 2010, Huey *et al.* 2012, Khaliq *et al.* 2014). For example, mammals in USA with flexibility in the time at which they are active have been shown to be less likely to have contracted their distributions (McCain & King 2014). Plants in UK that show plasticity in their phenology have been less likely to shift their distributions, suggesting that they have adjusted to current climatic changes by altering the timing of events rather than shifting their distributions (Amano & Freckleton 2014).

Globally, there is increasing interest in the role that microclimate can play in buffering species against changing climates and the consequences this will have for range shifts (Hannah *et al.* 2014). Vegetation structure, topographic variation and microhabitats can all alter the climatic conditions that individuals experience. Forests and sheltered microhabitats, for example can buffer individuals against extremes of temperature and drought (Scheffers *et al.* 2014) and relatively slow changes in the community composition of forest ground flora in sites across Europe, including the UK, have been attributed to the forest canopy cover buffering the impacts of climate warming (De Frenne *et al.* 2013). Across 4 landscapes in the UK, butterflies and moths were less likely to go locally extinct in areas with cooler microclimates (Suggitt *et al.* 2014). Exploitation of particularly cool or humid microclimates has the potential to allow populations to persist for longer than average climatic conditions would suggest at their warm range margins. This has led to interest in the identification of sites with conditions that would allow them to act as refugia (Keppel *et al.* 2012), where populations of species are able to persist despite climatic conditions generally being unsuitable. Work has begun in the UK to identify where these sites might be (Suggitt *et al.* 2013). Within- and between-patch heterogeneity is important to offer species a range of microclimates which they can exploit as required in response to prevailing climatic conditions. This can be achieved, for example, through slope creation and variation in vegetation height (Suggitt *et al.* 2014).

More generally, the use of fine-scale and physiologically relevant data rather than broad scale climatic averages may help to explain apparent variation in species' responses. Fine-scale microclimate and distribution data have been used to show that species that don't appear to be responding to climate change at a regional scale are responding as expected at a local scale by exploiting microclimatic variation in the landscape, as has been shown for the silver-studded blue butterfly in the UK (Hodgson *et al.* in press).

2.2.4 Capacity to shift distributions

Responses will be further modified by the ability of species to shift their distributions. For species to expand their distributions at their leading range margins, they require suitable habitat within dispersal distance of their current range margin, and to be able to establish viable populations in these areas (Hampe 2011). Thus, aspects of species' current distributions and life history traits are predicted to determine the rate at which they can expand at their cool range margins.

a) Life history traits

One important determinant of a species' rate of expansion is expected to be its dispersal ability and this is supported by modelling studies (e.g. Benito *et al.* 2014). Some trait analyses have supported this; for example, butterfly species with poorer dispersal abilities have demonstrated slower rates of expansion in Finland (Pöyry *et al.* 2009) and the UK (Warren *et al.* 2001) and similar patterns have been shown in Odonata across Europe (Grewe *et al.* 2013). However, such studies often find the relationship between dispersal ability and rate of range shift to be weak and other studies have failed to find evidence to support this relationship (Tingley *et al.* 2012, Bradshaw *et al.* 2014). Studies of range shifts in plants have also struggled to find relationships between dispersal mode and rates of shift (Matteodo *et al.* 2013). Dispersal ability is extremely difficult to measure, particularly because of the importance of rare long-distance dispersal events (Clarke 1998). Hence the proxies of dispersal ability used in these studies may not be appropriate to explain the effect of dispersal ability on rates of range expansion.

Life history characteristics related to high net reproductive rates, such as early reproduction, frequent reproduction and high fecundity are also expected to increase rates of range shift. Again, modelling studies have suggested the importance of these traits (Willis *et al.* 2009b), and multispecies-analyses comparing traits and rates of range expansion have supported this for fishes (Perry *et al.* 2005, Grenouillet & Comte 2014), plants (Lenoir *et al.* 2008, Amano & Freckleton 2014), mammals (Moritz *et al.* 2008) and insects (Betzholtz *et al.* 2013). Although most of these examples come from other regions, the principles would be expected to hold for UK species: higher reproductive rates increase propagule pressure and hence the probability and number of individuals reaching new areas, facilitating population establishment and reducing the risk of Allee effects preventing population establishment. Furthermore, once a new area is colonised, high population growth rates can rapidly overcome small population sizes where extinction risk from environmental and demographic stochasticity is great. Again, signals of these traits tend to be weak in multi-species analyses and some studies have found evidence to the contrary (Auer & King 2014). For example, Tingley *et al.* (2012) found that birds in the USA with small clutch sizes had shifted their distributions the most. They argue that birds with greater longevity (which is inversely related to clutch size) can use learning about breeding success from previous years into selection of breeding sites. McCain & King (2014) found mammals with a small body size (correlated with high reproductive rates) were less likely to have altered their distribution size, arguing that they are more capable than larger species of exploiting microclimatic variation with their current distribution.

Finally, it is expected that specialist species are less likely to track climatic conditions than generalist species because suitable habitat will be more fragmented and so less available within dispersal distance and fewer dispersers will be available to colonise new habitats (Travis 2003, Broenniman *et al.* 2006, McInerny *et al.* 2007). Of the southerly-distributed butterfly species in the UK, all of which would be expected to expand their distributions northwards in response to climate warming, 26/28 specialist species have actually contracted their distributions – most probably associated with habitat changes – whereas half of the generalist species have expanded their distributions (Warren *et al.* 2001). It also appears that plant species that have expanded their distributions in the UK recently have been widespread generalist species (Preston *et al.* 2002, Britton *et al.* 2009, Powney *et al.* 2014). Similar patterns have been shown in butterflies (Pöyry *et al.* 2009, Mattila *et al.* 2011, Betzholtz *et al.* 2013), birds (Jiguet *et al.* 2007) and plants (le Roux & McGeoch 2008) in other regions. This has led to communities becoming increasingly dominated by warmth-loving generalist species, as observed in butterflies (González-Megías *et al.* 2008) and plants (Britton *et al.* 2009) in the UK. As with other traits, however, there are also studies that demonstrate opposite patterns (Lurgi *et al.* 2012); for example, Auer & King (2014) found diet specialist birds in North America were more likely to have shifted their distributions than diet generalists.

Thus far results from trait analyses have been inconsistent and generally shown weak predictive power (Holzinger *et al.* 2008, Moritz *et al.* 2008, Pöyry *et al.* 2009, Auer & King 2014). When looking across several studies, Angert *et al.* (2011) found some traits relating to dispersal ability, reproductive rate and ecological generalisation were positively but only weakly associated with rates of range shift. This could be due to a variety of reasons. Existing estimates or proxies of life history traits may be inappropriate or inaccurate. There may be interactive effects which complicate patterms; for example, body size may be positively correlated with dispersal ability but negatively correlated with reproductive rate (Lurgi *et al.* 2012). The importance of different traits may vary between elevational gradients and latitudinal gradients (Auer & King 2014) and between taxonomic groups due to their differing physiologies. Weak and inconsistent signals of traits may, however, suggest that other factors, such as individualistic physiological responses to climate, are more important in determining rates of range shift, and predicts limited utility of assigning conservation priorities through trait analysis.

b) Habitat arrangement and quality

The quality and arrangement of habitat in the landscape will also affect the rate of range shift at species' leading-edge range margins as, to expand, species require suitable habitat they can establish in within dispersal distance. Globally, there is high confidence that high levels of climate change will reduce the viability of spatially-restricted species which are limited in their ability to shift their distributions (Settele *et al.* 2014) as deteriorating climatic conditions at their warm range margin will lead to range contractions and possibly extinction (Ohlemüller *et al.* 2008, Dirnböck *et al.* 2011). This includes mountain top or continent edge species for which dispersal barriers to newly suitable climatic conditions will be too great to overcome (Broenniman *et al.* 2006, Forero-Medina *et al.* 2011). Species at high altitudes have failed to shift their distributions because they have nowhere to move to (Moritz *et al.* 2008, Auer & King 2014, McCain & King 2014), for example, 16 mountain butterfly species in the Sierra de Guadarrama mountain range in central Spain have experienced an average of a 22 % reduction in distribution area over 30 years as their low altitude range margins have retracted but their high latitude range margins have been unable to expand (Wilson et al. 2005). Similarly, single-lake endemics or species confined to geological outcrops are at risk because they are surrounded by environments fundamentally unsuitable for them (Thomas 2011). Losses of range extent may also be expected to occur in mountain-top species in the UK, but similar studies have not yet taken place.

Anthropogenic habitat fragmentation will hinder species' abilities to track their climatic niches (Travis 2003, Opdam & Wascher 2004, Vos *et al.* 2008, Schippers *et al.* 2011). This is likely to be particularly problematic for specialist species as suitable habitat will be more fragmented, but could also affect relatively generalist species (Warren *et al.* 2001). For example, for the speckled wood butterfly (*Pararge aegeria*), the availability of woodland, its primary habitat, has been an important determinant of its rate of northward range expansion (Hill *et al.*1999) and it has colonised new areas more rapidly in regions with greater cover of woodland (Hill *et al.* 2001), even though it can also be found around hedgerows and other common habitats.

An understanding of how the arrangement of habitats within the landscape can facilitate range shifts could help when developing adaptation strategies for species. Thus far most information comes from modelling studies. Saura *et al.* (2013), for example, showed that habitat stepping stones are crucially important for species with certain characteristics but that these stepping stones must be of sufficient size and/or quality to be of conservation value. Hodgson *et al.* (2012) showed the importance of corridors and chains of stepping stones for species moving through the landscape. A small number of empirical studies have also demonstrated the importance of the spatial arrangement of habitats for rates of range expansion. For example, range expansion of the silver-spotted skipper butterfly (*Hesperia comma*) in southern Britain is severely limited by fragmentation of suitable habitat where its obligate larval host plant, sheep's fescue (*Festuca ovina*), grows (Wilson *et al.* 2009) and patch connectivity has been shown to be important for both colonisation of new patches and subsequent survival in these patches (Lawson *et al.* 2012). Not only will new patches be more likely to be colonised if they are closer to existing population, but when patches are first colonised, populations will be small and hence extinction prone and so continued immigration from nearby patches will help to support these populations.

There is also evidence for the importance of habitat patch quality for range expansion. Larger, better quality habitat patches will support larger populations and hence produce more dispersers to colonise new patches at expanding range margins (Hodgson *et al.* 2009). For newly colonised patches, populations are more likely to be able to reach a sustainable size in larger habitat patches and to be able to do so more rapidly in higher quality habitat patches (Lawson *et al.* 2012). Mair *et al.* (2014) showed that for butterflies in the UK, stable abundance is a pre-requisite for range expansion and so concluded that conservation management to stabilise and increase population sizes within the core of species' distribution is required.

Species may also benefit from the availability of within- and between-patch microclimatic variation at their expanding range boundary. Firstly, in locations with greater landscape heterogeneity, range edge populations have been shown to be more resilient which may help to promote the persistence of populations at leading range boundaries and hence aid expansion in response to climate warming (Oliver *et al.* 2014). Secondly, the availability of sites with particularly warm or sheltered microclimates within dispersal distance may facilitate range expansion by providing footholds for new populations to establish in and persist in climatically poor year (Bennie *et al.* 2013, Greenwood *et al.* 2014). Larger habitat patches are likely to encompass greater microclimatic variation, again emphasising the importance of patch size (Lawson *et al.* 2014a).

The need for high-quality habitats that are unusual in the UK landscape underpins the observation that many species have disproportionately colonised protected areas (Sites of Special Scientific Interest) as they have expanded their ranges (Thomas *et al.* 2012, Lawson *et al.* 2014b, Gillingham *et al.* 2015) and have disproportionately persisted in protected areas warm range margins (Gillingham *et al.* 2015). This is discussed further in the Technical Report *Implications of Climate Change for SSSIs and Other Protected Areas.*

c) Ecological and evolutionary processes at range margins

Rates of expansion may be further modified by ecological and evolutionary processes at species' cool range margins. Dispersal behaviour alters with climatic conditions (Sparks *et al.* 2005, Massot *et al.* 2008, Cormont *et al.* 2011) and evolution of increased dispersal propensity (Bridle *et al.* 2014) and ability has been observed at expanding range margins (Thomas *et al.* 2001, Phillips *et al.* 2010a), including in the speckled wood butterfly (*Pararge aegeria*) (Hughes *et al*. 2003) and the long-winged conehead (*Conocephalus discolor*) and Roesel's bush cricket (*Metrioptera roeselii*) (Simmons & Thomas 2004) in the UK. Habitat availability may also change through time. Many species are restricted in their habitat use at their cool range margins (Thomas 1993, Thomas *et al.* 1999) and so will expand their habitat associations as the climate warms (Thomas *et al.* 2001, Davies *et al.* 2006), leading to increased habitat availability and population sizes, decreased habitat fragmentation and hence increasing colonisation rates, as has been observed in the silver-spotted skipper butterfly (*Hesperia comma*) in the UK (Wilson *et al.* 2010). The reverse processes of increasing specialisation, resulting in reduced habitat area and potentially increased fragmentation of suitable breeding locations, might be expected for northern and upland species, but evidence is lacking. Adaptation to become specialised on widespread resources can also aid range expansion; for example the brown argus butterfly has strengthened its preference for a widespread host plant and has expanded extremely rapidly at its northern range margin in the UK (Bridle *et al.* 2014).

d) Biotic interactions

There are several ways in which biotic interactions could generate some of the observed interspecific variation in rates of range shift, which have been discussed in several recent reviews (Tylianakis *et al.* 2008, Lavergne *et al.* 2010, van der Putten *et al.* 2010, Gilman *et* *al.* 2010, Hellmann *et al.* 2012). For example, species' distributions may not be limited directly by climate but instead by the effect of climate on interacting species. In some cases, species' distributions are limited by those of resource species (e.g. a specialist parasite or herbivore with its host or a pollinator-dependent plant with its pollinator), which is itself limited by climate. Thus a species' rate of expansion may be limited by the range shift of a resource species. For example, the northern range margin of the brimstone butterfly (*Gonepteryx rhamni*) in Britain is thought to be limited by the distribution of its host plants, common buckthorn (*Rhamnus catharticus*) and alder buckthorn (*Frangula alnus*), rather than directly by climatic factors (Gutiérrez & Thomas 2000). However, this situation may be unusual; analyses of the range margins of butterflies and moths and their hosts revealed that most host-specialist Lepidoptera have geographic range sizes in Britain that are considerably smaller than the range sizes of their hosts (Quinn *et al.* 1997, 1998). In contrast, invertebrate herbivores are typically more dispersive than their host plants (Kinlan & Gaines 2003) and more responsive to temperature changes (Berg *et al.* 2010) and so might eventually be limited in their ability to shift their distribution by their hosts. The black-veined white butterfly (*Aporia crataegi*) in the Sierra de Guadarrama mountains in central Spain, for example, has failed to shift its high altitude range margin uphill due to absence of its host plant at higher elevations (Merrill *et al.* 2008). Differences in dispersal ability as well as different physiological responses to climate could generate significant spatial mismatch between interacting species (i.e. reduction in range overlap) resulting in loss of range extent of species (Preston *et al.* 2008, Kissling *et al.* 2010, Schweiger *et al.* 2012), although there could also be cases of increasing coincidence.

Competitive interactions may also alter patterns of range shifts. A number of classic ecological studies show that species can be prevented from filling their entire climatic niche by the presence of competitors. Also, the outcome of competitive interactions may alter with climatic conditions (Davis *et al.* 1998) and thus play a role in determining species' future distributions (Meier *et al.* 2011). Furthermore, a requirement of range shift is that a species can establish once it has reached a newly climatically suitable area. The presence of competitors may hinder a species' ability to colonise new communities (Ibáñez *et al.* 2009, Urban *et al.* 2012b). This could include individuals of species that are also shifting their ranges but arrive and establish first. Conversly, the loss of competitors at species' trailing edge boundaries may allow other species to spread in the opposite direction to that expected from a response to climate change (Lenoir *et al.* 2010). The presence of herbivores may also inhibit establishment of plant species beyond their current range margins (Munier *et al.* 2010).

The view in the literature is generally that changes in biotic interactions will reduce species' abilities to respond to climate change. However, in some cases changes in species interactions may facilitate range shifts. Rates of range expansion may be increased if species are not subject to herbivory (Lakeman-Fraser & Ewers 2013) or attack from natural enemies (Moorcroft *et al.* 2006) at their expanding front as escape from this pressure will increase population growth rates and sizes and hence rates of expansion. Specialist enemies or herbivores may not be present in newly colonised areas and generalists may not search in appropriate locations to find the invading species. Escape from natural enemies has been observed in invasive species (Phillips *et al.* 2010b) but the few studies in species responding to climate change have found mixed results, with studies of plant species failing to demonstrate reduced pressure (Skou *et al.* 2011). Menéndez *et al.* (2008) did, however, find lower levels of parasitism of larvae of the brown argus butterfly (*Aricia agestis*) in newly colonised areas compared to areas with long established populations, although they did not relate the effects of reduced rates of parasitism to expansion rates. Warmer summers have also enabled the brown argus butterfly (*Aricia agestis*) to utilise additional host plant species at its expanding range margin in the UK. The newly available Geranium host species are extremely widespread and this has led to very rapid range expansion in this butterfly (Pateman *et al.* 2012).

These are just some of the diverse ways in which biotic interactions could alter species' range shifts in response to climate warming. Very few observations still exist, however, and more work should be done to establish the effects of biotic interactions on range shifts. However, the evidence that does exist indicates that the effects of changes to the relationships among species on range shifts are diverse and difficult to predict a priori, so conservation and management should be adaptable and robust to uncertainty where possible.

2.2.5 Other drivers of change

Climate change is not the only force acting on species' distributions, and other pressures may affect patterns of range shift (La Sorte & Thompson 2007). Other human pressures could drive range shifts in species independently or in combination with changes in the climate. For example, urbanisation may facilitate the spread of species associated with disturbed habitats (La Sorte & Thompson 2007). Reduction in grazing pressure at high altitude in some regions could explain the upward shift of the treeline rather than climate change, as has been found in the case of Scots pine (*Pinus sylvestris*) in Scotland (French *et al.* 1997). Nitrogen deposition may be associated with the spread of plant species that favour these conditions (Britton *et al.* 2009, Powney *et al.* 2014) with possible consequences for herbivores feeding on these plants: there has been an increase in the distributions of Lepidoptera with larvae that feed on N-loving plants in Sweden (Betzholtz *et al.* 2013) and the UK (Fox *et al.* 2014). Reduced human persecution and use of pesticides and changes in land management may have led to recolonisation regardless of changes in climatic conditions, as may be the case for birds such as the common crane (*Grus grus*) that have recently recolonised the UK. Direct conservation management and re-establishment programmes have also been responsible for some range increases. The accidental movement of organisms may have facilitated range expansion through artificial long distance dispersal events into new climatically suitable regions (Robinet *et al.* 2012) and the planting of ornamental plants may facilitate range expansions, as has been observed with the planting of one of the brimstone butterfly's (*G. rhamni*) hosts alder buckthorn (*Frangula alnus*) in North Wales which has permitted the range expansion of the butterfly (Gutiérrez & Thomas 2000).

Human factors may also explain the lack of or weak range shifts observed in some species (Archaux 2004, Popy *et al.* 2010, Rowe *et al.* 2010, Settele *et al.* 2014) or even shifts in the opposite direction to that expected from climate change (Stafford *et al.* 2013). As mentioned above, anthropogenic habitat degradation and destruction can inhibit rates of range expansion and even lead to range retractions (Forister *et al.* 2010), as has been observed in amphibians and reptiles in the UK (Hickling *et al*. 2006). Grazing might also inhibit colonisation by plants of areas beyond their current leading-edge range margins (Speed *et* *al.* 2012). The interacting effects of climate and land use change are discussed in the Technical Report *Interactions Between Climate Change and Land Use Change Impacts: Addressing Attribution Problems.*

3. PREDICTING FUTURE DISTRIBUTIONS

3.1 Climate envelope modelling

Climate envelope models (CEMs) (alternatively termed species distribution models or ecological niche models) have been the main approach used to project species' future distributions under different climate change scenarios (e.g. Midgley *et al.* 2002, Berry *et al.* 2003, Guisan & Thuiller 2005, Huntley *et al.* 2008). This approach uses phenomenological models to infer a relationship between a species' current distribution and the climatic conditions where it occurs, either statistically or using machine learning methods such as Artificial Neural Networks or genetic algorithms. This relationship is then used to project the future distribution of species based on climate projections from general circulation models (GCMs).

One of the main uses of modelling species' future projections has been to identify species most vulnerable to climate change in order to focus conservation resources and develop conservation plans (Williams *et al.* 2008, Rowland *et al.* 2011). Species for which future suitable climate space is reduced or for which there is little or no overlap between current and future suitable climate space are identified as likely to be at particular risk (Midgley *et al.* 2003, Thomas *et al.* 2004, Thuiller *et al.* 2005, Ohlemüller *et al.* 2008), especially those species which have slower rates of range shift (Settele *et al.* 2014). CEMs have also been used to identify species with the potential to benefit from climate change and hence have helped to revaluate the conservation status of species (Thomas *et al.* 2011). Outputs of CEMs have also been used to inform future conservation strategies, for example to select areas which might aid species to shift their distributions and future biodiversity hotspots in need of protection (Phillips *et al.* 2008, Vos *et al.* 2008, Hole *et al.* 2009, Crossman *et al.* 2012, Summers *et al.* 2012).

3.2 Limitations and improvements

The reliability of projections from CEMs has, however, been the subject of considerable debate in the literature (Davis *et al.* 1998, Pearson & Dawson 2003, Hampe 2004, Botkin *et al.* 2007, Beale *et al.* 2008). Some uncertainty is associated with the reliability of future climate projections from GCMs and some relates to methods used for model selection (Araújo & Guisan 2006, Pearson *et al.* 2006), although ensemble models are going some way to address this (Araújo & New 2007). Much of the debate, however, relates to sources of interspecific variation in rates of range shift (as discussed in section 2.2 of this report) and being able to capture these in projections of future range shift. Efforts have been made to improve models in order to generate more realistic projections of species' future distribution (Huntley *et al.* 2010). Fundamentally, CEMs in their basic form project changes in the climatic tolerances of species as inferred from recent climate, so their predictions should be interpreted as a potential distribution, rather than the most likely actual distribution in the future.

Models nearly always assume that species are at equilibrium with their climatic tolerances, which may not be the case (Svenning & Skov 2004). There are also problems associated with models correctly identifying the climatic variables driving species' distributions thus producing erroneous projections of future distributions based on climatic changes. Some models only consider temperature but it is important to consider other climate variables (Dobrowski *et al.* 2013). The development of mechanistic models which use knowledge of species' physiological responses to climate instead of or in addition to correlative approaches has added realism to projected responses to climate change (Kearney & Porter 2009, Buckley *et al.* 2010, La Sorte & Jetz 2010, Diamond *et al.* 2012, Overgaard *et al.* 2014). However, this type of data is not available for the vast majority of species.

Models are also usually based on coarse-scale data (such as 50 × 50 km grid squares) which is not an accurate reflection of the actual climatic conditions being experienced by individual organisms (Faye *et al.* 2014, Kollas *et al.* 2014, Varner *et al.* 2014). Thus models may over predict loss of climatic space by missing fine-scale microclimatic variation which may allow species to persist in an area that appears unsuitable from average climate conditions (Randin *et al.* 2009, Gillingham *et al.* 2012), substantially altering assessments of vulnerability (Slavich *et al.* 2014). Alternatively, the use of coarse-scale data may overestimate the climatic tolerances of a species and hence its ability to persist in an area (Trivedi *et al.* 2008). Measuring and modelling microclimatic variation has historically been challenging (Suggitt *et al.* 2014) but new methods of modelling microclimate using weather station or modelled climate data along with information about topography and habitat structure are being developed (Bennie *et al.* 2008, Kollas *et al.* 2014). Combining information about an organism's physiological responses to climate with microclimatic information can further improve models of range shifts (Bennie *et al.* 2013).

Simulations, rather than statistical models, are the only feasible way to predict distribution changes incorporating dispersal, biotic interactions and other realistic processes (Urban *et al.* 2013). For example, combined niche-based and metapopulation models provide spatially explicit predictions of range shifts (Keith *et al.* 2008, Anderson *et al.* 2009a, Fordham *et al.* 2012). Dispersal is typically very difficult to parameterise, not least because little is known about rare long-distance dispersal events which are likely to have a disproportionate effect on rates of spread (Clark 1998, Higgins *et al.* 2003). Furthermore, behavioural interactions affect dispersal in complex ways and dispersal ability is under evolutionary selection at expanding range margins. Increasingly realistic models of dispersal are, however, being incorporated into model projections (Engler & Guisan 2009, Nathan *et al.* 2011b). Models have also been developed which incorporate biotic interactions such as competition and food resources into predictions of future distributions (Meier *et al.* 2011, Acevedo *et al.* 2012, Schweiger *et al.* 2012), although these mostly consider only interactions between two species and the importance of multi-species interactions has been emphasised (Araújo *et al.* 2011, Urban *et al.* 2012a). Finally, models have been developed which incorporate habitat availability and landscape connectivity and changes in habitat availability over time arising from disturbance and changes in vegetation structure (including how these processes might change in response to climate change) and future human land use (Midgley *et al.* 2010, Meier *et al.* 2012).

Models also assume that the overall consequence of other factors acting on species' distributions (e.g. biotic interactions) will remain the same under future climatic conditions, which again, might not be the case. Models assume populations are genetically homogenous across a species' range and so where intra-specific genetic variability and sub-species across ranges is present, the value of CEMs is severely limited.

Future challenges arise from building models which incorporate these different factors (Urban *et al.* 2013), in particular because many of these processes act at different spatial and temporal scales (Huntley *et al.* 2010, Boulangeat *et al.* 2012). Some studies have, however, included multiple factors in projections of future distributions (Brook *et al.* 2009, Iverson *et al.* 2011, Schweiger *et al.* 2012). Increasing model complexity, however, comes with problems of data availability and computational demands. Critically, it is also not known whether complex models will actually result in increased accuracy of predictions.

Despite these issues, simple CEMs can provide a basic assessment of species likely to be at risk due to loss of suitable climate space or because future suitable climate space is disjunct from a species' current distribution, although the problems with these models outlined above must be borne in mind when interpreting results.

3.3 Global projections

Certainty regarding past species movements in response to changing climate, coupled with projections from a variety of models and studies, provides high confidence that such species movements will be the norm with continued warming (Settele *et al*. 2014). However, it is likely that there will continue to be variation in the rates at which species can shift their distributions and hence their vulnerability to climate change. Modelling studies suggest that lags will continue for the coming century (Iverson *et al.* 2004, Nathan *et al.* 2011a, Schloss *et al.* 2012, Corlett & Westcott 2013). Settele *et al.* (2013) synthesised the projected abilities of several species groups to track future climate change based on a comparison between future climate velocity (the rate of change of climate across a landscape) and species displacement rates (the speed at which species can shift their distributions). They find that climate velocities exceed rates of displacement for several species groups and conclude that there is medium confidence that many species will be unable to move fast enough during the 21st century to track suitable climates under mid- and high-range rates of climate change (Settele *et al.* 2014).

3.4 Projections for the UK

Among the first studies to assess such risks was the Modelling Natural Resource Responses to Climate Change (MONARCH) project, which used CEMs to project the future distributions of all Biodiversity Action Plan (BAP) species for which good European-level distribution data were available under low and high emissions for the 2020s, 2050s and 2080s using the UK Climate Impact Programme's (UKCIP02) climate scenarios (Harrison et al. 2001, Berry *et al*. 2005, 2007, Walmsley *et al*. 2007). As this project focussed particularly on conservation priority species, many had restricted distributions that were clearly defined by factors other than climate. A key assumption of CEMs is that species are at equilibrium with their climatic requirements and so this undermined the value of the CEM approach for many rare species in particular. The 32 species for which outputs were considered relatively robust fell into four categories. 1) *Gain of suitable climate space*: as expected these tended to be those species currently with a southerly distribution in the UK, such as the stone-curlew (*Burhinus* *oedicnemus*), Adonis blue butterfly (*Lysandra bellargus*), greater horseshoe bat (*Rhinolophus ferrumequinum*) and stinking hawk's-beard (*Crepis foetida*). 2) *Loss of suitable climate space*: these were predominantly species with northern distributions, some of which were projected to lose all or almost all of their suitable climate space in the UK by the 2080s under high emissions scenarios, including the common scoter (*Melanitta nigra*), oblong woodsia (*Woodsia ilvensis*), twinflower (*Linnea borealis*), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). Some currently ubiquitous species, such as the song thrush (*Turdus philomelos*), were also projected to lose climate space in the south of the UK under future climate scenarios, possibly resulting from the effects of hotter and drier summers on food availability. 3) *No change in suitable climate space*: some species were not predicted to undergo any range shift because the whole of the UK would remain climatically suitable for them, such as the tree sparrow (*Passer montanus*) and linnet (*Carduelis cannabina*). 4) *Shift in suitable climate space*: others were expected shift their entire distributions as they experience gains in suitable climate space in the north but loses in the south, such as the stag beetle (*Lucanus cervus*), Barbastelle bat (*Barbastella barbastellus*) and cornflower (*Centaurea cyanus*). Species for which projected future climate space does not overlap with current climate space have also been identified, such as the natterjack toad (*Epidalea calamita*) (Berry *et al.* 2002).

A very recent report (Pearce-Higgins *et al.* 2015) has assessed potential changes in the spatial distributions of over 3,000 plants and animals that occur in England. Using a basic framework which compared projected future distributional changes with recently observed changes, 640 (21%) of 3,048 species considered were classified as being at high risk from climate change under a 2 ˚C warming scenario, and 188 (6%) at medium risk. A greater number of species could potentially expand their range in Great Britain, representing a medium or high opportunity for 486 (16%) and 1,164 (38%) species respectively, at this geographic scale. This is because more species reach their northern range margin in England than their southern range margin. This basic assessment excluded consideration of potential confounding and exacerbating factors, such as the availability of suitable habitat, and restricted dispersal ability, that might limit the ability of species to shift their distributions. A more comprehensive framework, which accounted for some of these factors, was applied to 402 species. This analysis showed that a greater proportion of species (35 %) were at high or medium risk from climate change compared to 42 % likely to facing opportunity under a 2 ˚C warming scenario.

Other studies have assessed risks across broad taxonomic groups. For the UK lichen flora, for example, Ellis *et al.* (2007) show that northern-montane and northern boreal groups are particularly under threat. These results are discussed in more detail in the Technical Report *Impacts of Climate Change on Lichens and Bryophytes*. Species from the UK have also been included in studies of risk to species across Europe. For example, across European mountain ranges, lower threats to mountain flora in Scottish mountains have been identified as rainfall is projected to increase in Scotland, compared to other mountain ranges in more southerly parts of Europe where rainfall is projected to decrease (Engler *et al.* 2011). Projected impacts of climate change on plant communities are discussed extensively in the Technical Report *Impacts of Climate Change on Terrestrial Habitats and Vegetation Communities*. By comparing different species groups, potential changes in species' interactions have also been tested for. Polce *et al.* (2014), for example, projected the potential future distribution of orchards and their pollinators in the UK (using the projected climate for 2050 from the SRES A1B Emissions Scenario) and found a spatial mismatch in those areas in the future that will be most suitable for orchards and those that will have a high richness of pollinators.

Recent climate change atlases of birds (Huntley *et al.* 2007) and butterflies (Settele *et al.* 2008) have also modelled species' future projected climate space on a European scale. Taking a broader geographical view is important because from a conservation perspective particular interest should be given to those that species which are endemic or genetically distinct or which currently or are projected to have a significant proportion of their worldwide distribution in the UK. For example, the Scottish crossbill (*Loxia scotica*) is projected to lose all of its suitable climate space (Huntley *et al.* 2008).

As outlined above, however, there are many problems associated with such models and results using CEMs published to date should, in most instances, be interpreted as the general patterns of expected change, rather than strict prognoses for individual species. Heat, and perhaps drought, associated species are expected to prosper in the UK, whilst cold-adapted species will retreat, with major potential changes in the locations of greatest abundance. More species have cool range margins than have warm range margins in the UK. Of species belonging to the 16 taxonomic groups studied by Hickling *et al.* (2006), 329 species have their northern range margin in the UK compared with just 39 that have their southern range margin in the UK. Thus the likelihood is that there will be more “winners” than “losers” in the UK, but these same expanding UK species may be declining elsewhere in their ranges in central or southern Europe. This general conclusion appears robust and is in line with recently observed changes.

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