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**IMPACTS OF CLIMATE CHANGE ON EUROPEAN
INVERTEBRATES, WITH REFERENCE TO THE
VULNERABILITY
OF BERN CONVENTION SPECIES**

FINAL VERSION

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EXECUTIVE SUMMARY

- There is strong evidence that invertebrates have responded to recent climate change.
- Changes to phenology, demographic processes (mortality and fecundity), and habitat associations have been observed within populations of invertebrates. There is some evidence for evolutionary responses to dispersal capacity and diapause induction.
- Invertebrate species distributions have expanded at high latitude or elevation range margins, and have contracted at low latitude or elevation margins. Rates of leading edge range expansion are constrained by habitat availability or dispersal ability. For some species, rear edge range contractions do not appear to show a marked time delay following climate warming.
- Species richness has not increased as much at high latitudes as predicted by the biogeographic associations of species, because of constraints of habitat loss on range expansions. Wide-ranging or generalist species, and species associated with low latitudes or elevations, now represent a higher proportion of species in some invertebrate communities, compared with habitat specialists or species associated with cool high latitudes or elevations.
- The possible roles of biotic interactions on species responses to climate change are poorly resolved, with implications for the effects of emergent disease or invasive alien species.
- Climate change may have important effects on invertebrates which provide ecosystem services such as nutrient cycling or pollination, or “disservices” such as disease vectors and forestry pests.
- Bioclimate models applied to the potential distributions of European butterflies in 2080 suggest that 48-78% of species will suffer >50% reductions in distribution size, if they are unable to shift their distributions to track suitable climates. There are marked differences in projected distribution losses between scenarios based on 2.4°C and 4.1 °C temperature increases.
- Bern Convention invertebrates are characterised by high habitat specificity and narrow distributions. Their sensitivity and lack of adaptive capacity suggests high vulnerability to climate change.
- Planned adaptation may be vital to conserve Bern Convention invertebrates under climate change. The possible roles of landscape-scale conservation, assisted colonization, and management for habitat heterogeneity are considered, as are monitoring, research and policy implications.

1. INTRODUCTION

Evidence for anthropogenic climate change is now overwhelming (IPCC 2007), and recent reviews and meta-analyses also show that a wide variety of ecological systems and taxa have changed in ways consistent with recent warming (Hughes 2000, Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003, Rosenzweig *et al.* 2007). Many examples of ecological responses to climate change have been drawn from research conducted on invertebrates, and the rapidity with which invertebrate species and communities have responded to recent warming implies that continuing climate change will have important effects on invertebrate distributions and diversity.

Climate influences the distribution in space and time both of environmental conditions, and of resources (other organisms for heterotrophic invertebrates) for the growth and survival of species, and therefore is widely considered to be the major determinant both of species distributions (e.g. MacArthur 1972, Gaston 2003) and of global biodiversity patterns (e.g. Currie 1991, Hawkins *et al.* 2003). As small, ectothermic organisms, invertebrates are particularly sensitive to fluctuations in temperature, moisture, and other environmental conditions (e.g. pH, salinity). Furthermore, many invertebrates have short life cycles, high rates of fecundity and mortality, and dispersive forms in some stages of their life cycles. Hence invertebrate population dynamics, distributions and phenology can respond rapidly to changes in climatic conditions. Furthermore, invertebrate communities are diverse compared with other taxonomic groups, so that there is scope for invertebrate richness and composition to show marked changes over time and space in response to environmental change. These changes to invertebrate population dynamics, distributions and diversity result from individualistic species responses to the effects of climate and other drivers of environmental change, but can lead to significant changes to biotic interactions both among invertebrates (e.g., competition, predator/prey, and host/parasitoid dynamics) and of invertebrates with other taxonomic groups (e.g., availability of host resources for invertebrates, or effects of pathogens, parasites and predators on invertebrates). The consequent effects of climate change on the dynamics, distributions and diversity of invertebrates may therefore have pronounced impacts on their conservation status.

This report presents evidence of invertebrate responses to recent climate change, and modelled responses of invertebrates to future change, in order to shed light on the mechanisms by which invertebrates will be affected by continuing change, and to address the potential threats of climate change to invertebrate biodiversity. The report uses examples from a wide range of invertebrate taxa, before focusing on the potential vulnerability of Bern Convention species. The ecological traits of species which influence their sensitivity to climate change are considered for specific case studies, and to provide a framework for how species will be threatened both directly by climate change, and by its interactions with additional threats to biodiversity (e.g., habitat loss and invasive species). General recommendations are then proposed for adapting the conservation of invertebrates to climate change.

2. INVERTEBRATE RESPONSES TO RECENT CLIMATE CHANGE

Biological systems respond to a wide range of environmental drivers, and current declines in the global distributions, population sizes and genetic diversity of species are associated with anthropogenic processes such as habitat loss and fragmentation, pollution, over-exploitation of natural resources and the spread of invasive alien species (Sala *et al.* 2000). However, meta-analyses of studies conducted for a wide variety of taxa and geographical regions have shown convincing evidence that biological systems have changed in ways consistent with, and only satisfactorily explained by climate change (Parmesan & Yohe 2003, Root *et al.* 2003). The two best-documented climate-related biological changes are changes in phenology and shifts in species distributions to higher latitudes and elevations (Hughes 2000, Walther *et al.* 2002). The former of these, distribution change, is of more direct interest from a conservation perspective, given the utility of species range size in monitoring the conservation status and likely extinction risk of species. However, phenological change may have implications for the future responses of species and communities to climate change, if it has the capacity to modify phenological overlap between interacting species. In addition, a number of studies have identified the effects of climate change on a number of related ecological processes which could help to explain the vulnerability of species to climate change, and the scope for their successful conservation, for example demographic processes (growth, mortality and fecundity), habitat associations, and evolutionary responses. Changes to species distributions have influenced

patterns of species richness and composition, which in turn may influence future biotic interactions. The evidence for these ecological responses to climate change by invertebrates is now considered, both as evidence for the pervasive effects of climate change, and as background information on the mechanisms which influence species responses to climate change.

2.1 Phenological change

Many studies have shown species becoming active, migrating or reproducing earlier in the year associated with increased temperatures, which lead to faster growth rates or earlier emergence from winter inactivity (Roy & Sparks 2000, Peñuelas et al. 2002, Stefanescu et al. 2003). Long-term data from insect recording schemes in Europe have provided valuable evidence for advancement in appearance dates of adult insects as temperatures have increased. In Britain, the annual first appearance dates between 1976 and 1998 for 28 out of 33 butterfly species analysed were earlier at higher temperatures, and an increase in temperature of 1°C led to an average advance in first flight date of 4.5 days (Roy & Sparks 2000). First appearance by butterflies has also advanced in Catalonia (Spain) associated with higher temperatures and lower rainfall in winter or spring (Stefanescu et al. 2003). 17 species of British Odonata advanced the first quartile dates of their flight periods by a mean of 1.5 days per decade (3 days per 1°C temperature increase) between 1960 and 2004 (Hassall et al. 2007). In Austria, three butterfly species, the bee *Apis mellifera* and the cockchafer *Melolonthus melolonthus* showed 3 to 5 day advances associated with 1°C warmer February-April temperatures (Scheifinger et al. 2005). The peak emergence dates of 104 microlepidopteran species in the Netherlands advanced on average by 11.6 days between 1975 and 1994, accompanying a 0.9°C increase in annual mean temperature (Ellis et al. 1997, Kuchlein & Ellis 1997).

Increasing temperatures have also allowed a number of species to remain active for longer during the year (Roy & Sparks 2000). For British butterflies, advances in first appearance dates were accompanied by longer annual flight periods in 24 species (overall average +3 days per decade; n = 35 species), with the increase particularly marked in multivoltine species that were able to increase their number of generations in some parts of their range.

Recent reviews of phenological studies show mean advances in the timing of spring events by 2.3-5.1 days per decade for a wide range of taxonomic groups (Parmesan & Yohe 2003, Root et al. 2003). Tree life-cycles have only advanced by an average of three days accompanying recent climate change, compared with five days per decade for invertebrate life cycles (Root *et al.* 2003). Subtle differences between the cues involved in phenology at different trophic levels could lead to temporal mismatches between the emergence of invertebrate larvae and the availability of their food: for example, increases in mean winter temperature without an accompanying decline in the number of frost days have reduced synchrony between egg hatching by the winter moth *Operophtera brumata* and budburst by its host *Quercus robur* (Visser & Hollemann 2001). In this system, the advances in the phenology of phytophagous insects have in turn not been tracked by the passerine birds which predate them (Visser et al. 1998 2006). Nevertheless, recent research suggests that phytophagous insect larvae may show rather rapid adaptation to changed temporal availability of food supplies, and that the reduction in predation because of mistimed bird reproduction might offset any reduction in performance because of phenological mismatch with host plants (Both et al. 2009).

Phenological change can also alter the climatic conditions typically experienced by species at particular stages of their life cycle. Many British butterfly species have advanced their flight periods, but the consequences in terms of climatic conditions experienced by the adult, reproductive stages of the species depends on their life histories: species with spring flight periods may not experience markedly increased temperatures if their adult emergence shifts to typically cooler, earlier dates, but species with late summer emergence may now experience much hotter temperatures during their flight, reproduction and egg-site selection because of both hotter general conditions, and because they emerge at a generally hotter time of year. Thus, between 1985 and 2004, the spring flying butterfly *Anthocharis cardamines* was estimated to have experienced a 0.4°C decrease in flight period temperatures, whereas the summer/autumn species *Hesperia comma* was estimated to experience a 2.8°C increase (Wilson et al. 2007a).

2.2 Demographic responses

As well as showing how increasing temperatures lead to advances in phenology, long-term butterfly monitoring data have shown the relationships between population size and weather conditions (Roy et al. 2001). Annual population sizes of most British butterflies are positively related to warm dry conditions during the spring and summer of flight, and warm wet conditions the preceding year. However, the precise relationship depends on the life history of the species concerned. For example, the population sizes of several bivoltine species are most strongly associated with high temperatures in the current spring or summer, which provide suitable conditions for larval and pupal development. In contrast, hot or dry conditions in the previous year are associated with population declines in species such as ringlet *Aphantopus hyperantus* and speckled wood *Pararge aegeria*, whose larvae feed on plants growing in moist or partly shaded habitats and may be susceptible to increased drought stress. Evidence of similar negative relationships between population size and hot or dry conditions at the lower latitude or elevation limits of species ranges would be valuable in estimating the direct threats to species from climate change at their “warm” range margins. Data from 406 light traps in the UK Rothamsted Insect Survey show that increasingly warm wet winters have increased mortality in the garden tiger moth *Arctia caja*, leading to declines in population density and a shift in the centre of distribution and abundance of the species towards cooler, higher latitudes (Conrad et al. 2001 2002 2003).

Temperature directly influences invertebrate mortality, with reduced survivorship towards both lower and upper thermal tolerances (Ratte 1985). For example, the proportion of individuals developing to adulthood in the butterflies peacock *Inachis io* and comma *Polyommatus c-album* was >60% at temperatures of 15-30°C, but at temperatures of 9°C and 34°C respectively 0% and 20-40% of individuals reached maturity (Bryant et al. 1997). The upper latitude range margins of these species correspond to the 15°C July isotherm perhaps as a consequence of their requirements for sufficiently warm temperatures for summer larval survival and development. In central Spain, the Black-veined white butterfly *Aporia crataegi* occupied elevations of c. 600-1800 m in 1967-73, but by 2006 the lowest elevation populations of the species occurred at c. 900 m, even though larval host plants for the species survived at much lower elevations (Merrill et al. 2008). Regional mean annual temperatures during the same period increased by 1.3 °C (equivalent to a 225 m uphill shift in isotherms) and field translocation experiments with egg batches of the species showed that summer egg and young larval mortality decreased with elevation, implying direct increases in immature stage mortality caused by high temperatures in this species.

For many temperate invertebrates, mortality during the overwintering period may have important effects on population dynamics and the geographical limits to species distributions (Bale et al. 2002). The minimum temperatures that can be experienced by overwintering stages may set the upper latitudinal limits to species ranges, and increases in winter temperatures may increase overwintering survival and lead to range expansions to higher latitudes (Crozier 2003). In contrast, low temperatures may be beneficial for species that spend winter in an inactive diapause, since reduced metabolic rate in cooler microhabitats may lead to increased survival and fecundity (Irwin & Lee 2000 2003). Survival by overwintering adult insects may be affected both by temperature and moisture conditions: for example, the Peacock butterfly *Inachis io* shows greater overwintering survival at 2°C than 10°C, and in drier versus wetter conditions (Pullin & Bale 1989), which may influence the location of the low latitude range margin for this species (Bryant et al. 1997).

Changes to ambient temperature, moisture availability and atmospheric CO₂ can influence insect growth and larval host plant quality. Elevated CO₂ concentrations lead to reduced nitrogen levels and increased C:N ratios in leaves, and hence reduced insect performance (growth rate, weight gain and survival) (Coviella & Trumble 1999, Zvereva & Kozlov 2006). Most experimental studies show a positive effect of temperature on insect herbivore performance, such that there is no significant change in performance when CO₂ and temperature increase together (Zvereva & Kozlov 2006).

Temperature conditions directly influence the fecundity (e.g. gametogenesis, sex determination and spawning) of many aquatic invertebrates (Hogg & Williams 1996, Lawrence & Soame 2004). Therefore the effects of climate change on the population dynamics of coastal invertebrates which constitute the diet for overwintering birds in northern Europe is a matter for concern (Lawrence and

Soame 2004). There is less clear evidence for direct effects of climate conditions on the fecundity of terrestrial invertebrates. In the butterfly *Hesperia comma*, egg-laying rates in Britain increase at warmer temperatures, potentially allowing the species to increase its fecundity in conjunction with recent warming at its northern range margin (Davies et al. 2006).

2.3 Habitat associations

At increasing latitudes and elevations, some butterflies and beetles become progressively more restricted to warm microhabitats characterized by features such as south-facing slopes, short vegetation and bare ground, implying a temperature limitation for species as they approach their 'cool' range margins (Thomas 1993, Menéndez & Gutiérrez 1996, 2004, Thomas et al. 1998, 1999, Merrill et al. 2008, Ashton et al. 2009). For the butterfly *Hesperia comma* at its northern range margin in Britain, increased temperatures during the flight period between 1982 and 2001/2002 were accompanied by a shift in the microhabitats used for egg-laying, with a greater proportion of eggs laid in 2001/2002 in locations with a reduced percentage cover of bare ground (Davies et al. 2006). Climate change therefore has the capacity to modify the vegetation types which represent habitat for particular species, implying that monitoring of the responses of species populations is vital to ensure that habitat is no longer being managed according to outdated prescriptions.

2.4 Evolutionary responses

Most palaeological evidence suggests that invertebrates have shifted their distributions to track suitable climates over the last 2 million years, rather than adapting *in situ* to changing conditions (Coope 2004). Nevertheless, invertebrates often have large population sizes and short generation times, and changes in selection may occur rapidly during periods of rapid climate change (Thomas 2005). There may be selection for phenotypes that favour rapid expansion at range margins where climate conditions improve, such as those associated with dispersal or the exploitation of novel or widespread resources. Contemporary evolutionary responses at expanding range margins include selection for dispersive forms of butterflies (Hill et al. 1999a, c), ground beetles (Niemela & Spence 1991) and bush crickets (Thomas et al. 2001, Simmons & Thomas 2004), and for increased egg-laying on a widespread host plant relative to a more restricted former host by the brown argus butterfly *Aricia agestis* (Thomas et al. 2001). These adaptations increase the rate at which species are able to track shifting suitable climate space, but once populations have been established there may be a return to selection against dispersive forms, possibly associated with reduced fecundity (Hughes et al. 2003, Simmons & Thomas 2004). Hence forms adapted to range expansion may have been favoured for relatively short periods of evolutionary time, and therefore not readily detected by the fossil record.

The potential for adaptation during changing climates is dependent on the reservoir of genetic variation within populations of species. Many species show adaptations to the local climates experienced in different parts of their geographical range, for example in terms of size, growth rate, diapause induction, or the range of plastic responses that can be elicited from individual genotypes (Nylin & Gotthard 1998, Berner et al. 2004). Species often show adaptive local variation in the day-length reduction that is required to induce winter diapause, with longer day-lengths sufficient to induce diapause at locations such as high latitudes or elevations where conditions deteriorate earlier in the year (Roff 1980). The critical photoperiod for winter diapause induction changed significantly for the pitcher plant mosquito *Wyeomyia smithii* between 1972 and 1996, leading to later cessation of larval activity in warmer summers (Bradshaw & Holzapfel 2001).

Despite widespread genotypic and phenotypic variation across the geographical ranges of species, the ability of populations to adapt to new conditions will depend on their location in the current range. Populations at expanding range margins may be able to adapt relatively rapidly because of gene flow from the core of the species range. However, at the rear or trailing edge of species distributions, new prevailing conditions may be unlikely to have been experienced by populations of the species during its evolutionary past, so that there may not be pre-existing genetic variation to allow adaptation (Thomas 2005). Species ranges have undergone successive shifts towards and away from the poles during Quaternary periods of warming and cooling, and the greatest reservoir of genetic diversity may occur in parts of species ranges which have remained occupied during both glacial and interglacial periods (Hewitt 2004, Schmitt & Hewitt 2004). During current, interglacial conditions, this zone of greatest genetic diversity is located near the lower latitude range margin for most species, where

climate-related extinctions could represent a significant loss of future potentially adaptive variation (Hampe & Petit 2005).

2.5 Latitudinal range shifts

There is strong evidence for poleward shifts in the latitudinal ranges of butterflies associated with recent climate warming. Species ranges shifted northwards during the twentieth century for 22 (63%) of 35 non-migratory European butterflies which had data for both northern and southern margins, with evidence of colonizations at northern range limits for 21 species and extinctions at southern limits for 8 (Parmesan et al. 1999). Only two of the 35 species showed southward shifts.

Several studies have documented range expansions by individual butterfly species beyond their former upper latitudinal margins (e.g. Hill et al. 1999b 2001, Warren et al. 2001, Braschler et al. 2007). Butterflies have been valuable model systems because of a wealth of historical data about their distributions, and because they depend on thermal conditions throughout their life cycles. Recent research suggests that the upper latitude margins of many other invertebrate taxa have also shifted northwards in response to recent climate change (e.g. Hickling et al. 2005 2006). However, there is now strong evidence that the range expansions of most species at their upper latitude margins are failing to track the availability of suitable climate conditions (Warren et al. 2001, Menéndez et al. 2006; see 2.7. below).

Until recently, relatively few range contractions had been recorded at warm, lower latitudinal margins. However, range expansions are easier than contractions to detect because colonizations directly lead to species presence in regions or large-scale grid cells, whereas local extinctions lead to the gradual decline of species to isolated populations within a region, which may be unlikely to persist in the long term (Wilson et al. 2004).

2.6 Elevational range shifts

Many species may be suffering declines at their warm margins that go undetected because their regional populations persist but shift to higher elevations. Two studies have shown increases in the average elevations of atlas grid cells occupied by butterfly species (Hill et al. 2002 for Britain; Konvicka et al. 2003 for the Czech Republic). Actual recent changes in species' elevational ranges may be even greater than recorded in studies based on grid cells, since such cells may include wide altitudinal variation, particularly in mountainous regions (Konvicka et al. 2003). However, it is difficult to attribute these uphill range shifts solely to the effects of climate change, because habitat degradation is typically more severe at lower elevations (Nogués-Bravo et al. 2008).

Sampling discrete locations in different time periods has the potential to detect elevational shifts at a finer resolution, and to control for the effects of habitat degradation. Research on the pine processionary moth *Thaumetopoea pityocampa* shows that this forest pest species has expanded its distribution to higher latitudes and, particularly, to higher elevations in conjunction with recent summer and winter warming (Hódar et al. 2003, Battisti et al. 2005 2006, Robinet et al. 2007). The low elevation limits of 16 butterfly species in the Sierra de Guadarrama mountain range (central Spain) rose on average by 212 m from 1967-73 to 2004, accompanying a 1.3°C rise (equivalent to c. 225 m) in regional mean annual temperature (Wilson et al. 2005). The close correlation between temperature increase and changes in low elevation limits, combined with the fact that larval host plants for many study species were widespread in the region, implied that climate rather than direct habitat change was the most important driver in the system. For these species, increases in upper elevation limits did not change significantly, partly because many species already occupied high altitudes in 1967-73. As a result, there were overall reductions in the elevation ranges of the species, and an average decline of 22% in the estimated distribution area for each species over only 30 years.

Changes between 1970 and 2004/05 to the local scale distributions of three of the four butterfly species which are restricted to high latitudes or elevations in Britain also suggest a role for climate change in causing range contractions, either independently or combined with the effects of habitat loss (Franco et al. 2006). The mountain ringlet *Erebia epiphron* has declined from lower elevations even where larval host plants remain, while the scotch argus *Erebia aethiops* and northern brown argus *Aricia artaxerxes* have declined from lower latitudes even where host plants remain. In contrast with the time delay in species range expansions in response to climate change, the rates at which

distributions have contracted in these studies appear to be keeping pace with rates of climate change (Thomas et al. 2006).

2.7 Changes to species richness and composition

As many species have shifted their distributions to higher latitudes and elevations, so the richness and composition of ecological communities has altered. In terrestrial systems, the evidence is strongest for butterflies. In common with many other taxonomic groups, butterfly species richness is correlated with water-energy budgets: at high latitudes energy appears to be the main limiting factor for species distributions, so that species richness increases with temperature; whilst at lower latitudes water availability is more strongly correlated with species richness (Hawkins and Porter 2003, Hawkins et al. 2003, Stefanescu et al. 2004). As temperatures have increased in Britain, a number of butterfly species have expanded their ranges northwards, and species richness has increased (Menéndez et al. 2006). However, the range expansions are largely restricted to wide-ranging and generalist species, since most habitat-specialist species do not have sufficient habitat availability in anthropogenically modified landscapes to be able to colonize habitats beyond their former range margins (Warren et al. 2001). Hence the composition of butterfly communities in Britain is now increasingly dominated by widespread, generalist species, implying a homogenisation of butterfly community composition which may be occurring more widely in other taxonomic groups.

Near the low latitude margins of butterfly species ranges in central Spain, species richness has declined at all but the highest elevations, since many species have disappeared from low elevation sites. A few species have expanded their distributions to the highest mountain elevations, but butterfly species richness declines further to the south in Spain, so there are few species to compensate for those lost at low- to mid-elevations, and many of these do not have sufficiently widely distributed habitats to be able to colonize the mountains (Wilson et al. 2007b). These declines in diversity of terrestrial invertebrates in south-west Europe mirror the changes predicted by bioclimate modelling for reptile and amphibian communities (Araújo et al. 2006).

Evidence from aquatic invertebrates also points to shifts in species composition consistent with climate warming. In the upper Rhone river thermophilic invertebrate taxa have replaced species associated with cold water conditions (Daufresne et al. 2004), whilst European streams which now dry up more often because of increased frequency of drought conditions have experienced concurrent changes to the composition of invertebrate groups (Fenoglio et al. 2007). However, stream macroinvertebrate communities in the Mediterranean region appear to be characterised by highly dispersive species, leading Bonada et al. (2007) to conclude that the loss of species from temperate streams may be compensated with immigration by southern Mediterranean taxa.

Intertidal macroinvertebrate communities have shown increases in species with more southerly distributions, and decreases in species with more northerly distributions (e.g. Sagarin et al. 1999). However, testing the responses of intertidal communities in warmed versus unwarmed water suggests that changes to community composition cannot be predicted merely from the biogeographic associations of species: instead, changes to species composition appear to result largely from cascading effects caused by the loss or gain of species which are highly-connected to others in the community (Schiel et al. 2004).

It is clear from consideration of climate-related shifts in invertebrate community diversity that the patterns of change will depend on the individualistic responses of the constituent species, but that these responses will be affected by other drivers of environmental change (e.g. direct habitat modification) and by changes to biotic interactions.

2.8 Changes to biotic interactions

An influential paper carried out using laboratory microcosms showed how the performance of three *Drosophila* species at different temperatures depended on their competitive interactions and on the effects of natural enemies (Davis et al 1998). However, there are few convincing empirical tests of the influence of biotic interactions on species responses to climate change in the field. The distributions of host or resource species place clear constraints on the capacity for species to shift their distributions in response to climate change. For example, the butterfly *Aporia crataegi* appears to have

been unable to increase its upper elevation limit in central Spain because its host plants do not grow at elevations higher than c. 1800 m above sea level (Merrill et al. 2008).

Natural enemies may also have important effects, which may vary depending on climate conditions, or because of changes to the distributions of interacting species. Larval mortality of glanville fritillary butterfly *Melitaea cinxia* caused by the parasitoid *Cotesia melitaearum* decreases in cool years, because dark-coloured *M. cinxia* larvae are able to bask to increase their developmental rate, whereas white, immobile *C. melitaearum* cocoons develop too slowly to synchronise their adult emergence with the availability of larvae to parasitise (Van Nouhuys & Lei 2004). When insect species have expanded their distributions northwards, they may suffer reduced mortality at least temporarily if there is a time lag before species-specific natural enemies track their range expansions (Gröbler & Lewis 2008, Menéndez et al 2008). One problem for predicting or managing the effects of such changes is that the specific host species and natural enemies of many invertebrates may be poorly documented, if at all.

3. FUTURE IMPACTS AND VULNERABILITY

3.1 Bioclimate models of future species ranges

Geographic-scale correlations of species distributions with particular climate conditions can be used to infer climatic constraints on species ranges, and thus to model 'bioclimate envelopes' for individual species (Pearson & Dawson 2003). Such models have been used to predict the future ranges of a number of insects, particularly butterflies (e.g. Hill et al. 1999b 2002, Araújo & Luoto 2007, Schweiger et al. 2008, Settele et al. 2008). These models use variables which may have *a priori* associations with insect distributions, for example annual cumulative temperatures above a threshold level (affecting rates of growth and development), minimum winter temperatures (affecting overwintering survival) and moisture availability (affecting primary production).

Climate envelope models fit current species distributions well both at upper and lower latitude range margins (Hill et al. 2002), and appear to perform well for a variety of taxa (Huntley et al. 2004). The models are relatively accurate for species whose distributions are contiguous, with the bounds likely to be set by climatic limitations either on the species itself or on some vital interacting species such as a larval host plant. Models perform less well for species that have widespread but scattered distributions, where habitat restrictions and / or local colonization-extinction dynamics may dominate distribution patterns within the climatically-suitable range (Luoto et al. 2005). Factors such as biotic interactions, local topographical variation and local evolutionary adaptation could also lead to discrepancies between observed distributions and those modelled based on coarse-scale climatic associations. Approaches to modelling changes to butterfly distributions under climate change have begun to take the key step of concomitantly modelling changes to the distributions of the specific host plants of the species (Araújo & Luoto 2007, Schweiger et al. 2008), with the result that the future potential distributions of the butterfly species are much smaller (but more realistic) than if modelled without consideration of the availability of host species.

Nevertheless, modelling future areas of suitable climate space for species, based on their current associations and future scenarios of climate change, allows very general conclusions to be drawn about the likely effects of climate change on species range sizes, the relative vulnerability of particular groups of species, and the relative effects of different scenarios of climate change or carbon emission levels (e.g. Settele et al. 2008). This approach has now been carried out for 293 of the c. 450 European butterfly species, the remainder being considered too highly restricted to produce workable models (see Box 1). In these models, under a relatively conservative climate change scenario based on a mean temperature increase by 2080 of 2.4°C (SEDG) 48% of butterfly species were estimated to suffer more than 50% reductions in their distribution size, but only 3% of species more than a 95% reduction. Under a scenario of 4.1°C temperature increase by 2080 (GRAS), 78% of species suffered greater than 50% declines, whilst 24% suffered 95% reductions in distribution. These estimates assume that species fail to colonize regions which become climatically suitable: evidence from observed changes to date suggests that such a scenario may be more realistic for most species than the assumption that they will colonize suitable climates as they become available (Warren et al. 2001, Menéndez et al. 2006). The implications of Settele et al.'s (2008) models for Bern Convention species are considered in section 4 below.

Box 1. The Climatic Risk Atlas of European Butterflies (Settele et al. 2008)

Rationale

The atlas models climate associations for 294 of the *c.* 450 European butterfly species, and then projects the distributions of suitable climate space for these species based on climate change scenarios for 2050 and 2080. The main objectives were to:

1. Provide visual evidence for discussions on climate change risks and impacts on biodiversity, and thus contribute to communication of climate change risks.
2. Present data on a large taxonomic group which could help prioritise conservation efforts under climate change.
3. Reach a broader audience for scientific predictions of climate change impacts on biodiversity.

The climate change scenarios

These were developed as part of the EU project ALARM (Assessing LARge-scale environmental Risks for biodiversity with tested Methods). Three scenarios of change were employed:

1. Sustainable Europe Development Goal (SEDG): focused on achievement of sustainable development by integrating economic, social and environmental policies. Policy aims to stabilise atmospheric greenhouse gas concentrations and end biodiversity loss. SEDG approximates to IPCC B1 scenario, with mean expected temperature rise of 2.4°C by 2080.
2. Business As Might Be Usual (BAMBU): a continuation of known and foreseeable socio-economic and policy trajectories. Environmental policy is perceived as a technological challenge, tackled by innovation, market incentives and some regulation. BAMBU approximates to IPCC A2 scenario, with mean expected temperature rise of 3.1°C by 2080.
3. GRowth Applied Strategy (GRAS): economic growth based on free trade is actively pursued by governments. Environmental policy focuses on damage repair and some limited scope preventative action, based on cost-benefit calculations. GRAS approximates to IPCC scenario A1F1, with mean expected temperature increase of 4.1°C by 2080.

The bioclimate models

The following variables were used to model the climate niche of all species:

1. Accumulated growing degree days until August, a measure of temperature availability.
2. Soil water content for the upper horizon, a measure of water availability and near surface microclimate.
3. Range in annual precipitation, reflecting continentality and oceanicity.
4. Range in annual temperature, reflecting continentality and oceanicity.

50 x 50 km² butterfly distribution data were related to climate data from 1971-2000. Climate projections for 2021-2050 and 2051-2080 were used to make predictions of climate niche space for the species in 2050 and 2080 respectively. The results are based on changes to modelled climate niche space, compared with estimated niche space in 1971-2000.

Two alternative assumptions are made about the ability of species to shift their distributions:

1. Full Dispersal: the total area of niche space in 2050 or 2080 will be occupied.
2. No Dispersal: only the area of niche space which overlaps with the current modelled niche will be occupied.

Based on recent changes to butterfly species distributions, observed changes for many species will be somewhere between the two dispersal scenarios, but closer to the No Dispersal scenario particularly for habitat specialists (Warren et al. 2001, Menéndez et al. 2006).

Box 1 continued. The Climatic Risk Atlas of European Butterflies.

The climate risk categories

These were derived based on:

1. The accuracy of climate variables at predicting current species distributions (based on the AUC technique, with AUC > 0.75 showing moderate to good accuracy, and AUC < 0.75 showing only limited accuracy).
2. Estimated changes to niche space from 2000 to 2080, based on the No Dispersal assumption.

Risk categories were as follows:

1. PR – Potential Climate Risk – only limited model accuracy (AUC <0.75)

All other categories have moderate to high model accuracy (AUC >0.75).

2. LR – Lower Risk – <50% maximum estimated decline in niche space due to climate change in any of the climate change scenarios.
3. R – Climate Change Risk – 50-70% maximum estimated decline.
4. HR – High Risk – 70-85% maximum estimated decline.
5. HHR – Very High Risk – 85-95% maximum estimated decline.
6. HHRH – Extremely High Risk - >95% maximum estimated decline.

The distributions of species which are currently restricted to localized areas such as mountain ranges or islands may show little or no geographical overlap with locations that are predicted to be climatically suitable in the future (e.g., Ohlemüller et al. 2006, 2008), and may find it near-impossible to colonize regions which are predicted to become climatically suitable. Species with very narrow climatic tolerances and hence restricted geographical distributions will be least able to survive climate change, unless their populations can adapt to changing conditions, or unless very fine scale variation in microtopography or vegetation allows them to persist in or near their current geographic ranges.

3.2 Interactions of climate change with additional threats to invertebrate biodiversity

For butterflies, habitat loss and fragmentation already appear to have constrained the ability of species to expand their distributions to occupy favourable climates as they become available (Warren et al. 2001, Menéndez et al. 2006). The rate at which the silver-spotted skipper butterfly *Hesperia comma* has been able to expand its distribution through landscapes at its northern range margin in Britain can be predicted fairly accurately by the degree of habitat fragmentation, and its effects on the dynamics of colonization and local population extinction in the species (“metapopulation dynamics”) (Wilson et al. 2009). Whilst these conclusions prompt concern about the probable inability of species to shift their distributions through highly modified landscapes, they do at least suggest that it will be possible to identify which landscapes might have the best chance of being successfully managed to promote range shifts.

Pollution in the terrestrial environment may cause direct loss of habitat for species (imposing constraints on range shifts), or may reduce the favourability of habitat. Patterns of nitrogen deposition in northern Europe appear to be correlated with declines in population densities and distributions for butterflies whose immature stages are active in spring. It has been suggested that nitrogen deposition coupled with longer annual growing seasons have led to changes in plant competitive interactions, leading to the overgrowth of the sheltered, warm microhabitats which these butterfly species require (WallisDeVries & Van Swaay 2006). Encouragingly, freshwater invertebrate communities in chalk streams in Britain appear to be able to withstand negative impacts of climate change as long as pollutant discharges into the streams are minimised and water quality is maintained (Durance and Ormerod 2009).

Changes to climate conditions can alter the effects of emergent disease on invertebrate populations. High seawater temperatures in the north-western Mediterranean have been linked to mass mortality in benthic macroinvertebrate communities, particularly in gorgonians and sponges (Bally and Garabou 2007, Garabou et al. 2009). In France, mortality from the marine bacterial pathogen *Vibrio harveyi* in Abalone *Haliotis tuberculata* has increased linked to climate warming (Travers et al. 2009).

Species which have high reproductive rates, generalist habitat requirements, and are highly dispersive may be able to colonize regions rapidly as they become climatically favourable. Given these considerations, there is likely to be an increased opportunity for cosmopolitan or outbreak species such as many agricultural or forestry pests (e.g. Battisti et al. 2005 2006) or disease vectors to expand their distributions. The attributes of invasive alien species, and how these may be affected by climate change, are reviewed in detail in Capdevila-Argüelles & Zilletti (2008), Hellmann et al (2008), and Pejchar and Mooney (2009). The following section provides a discussion of the possible effects of climate change on the provision of ecosystem services and disservices by invertebrates.

3.3. Climate change and invertebrate ecosystem services

Invertebrates play important roles in providing direct ecosystem “services” (benefits) and “disservices” (costs) for human societies, and also have major effects on the functioning of ecosystems. Changes to invertebrate distributions, abundance and population dynamics caused by climate change therefore have the capacity to have important ecological and socio-economic effects. Examples of these effects include changes to the prevalence of human and livestock diseases caused or vectored by invertebrates, changes to the distributions or abundance of agricultural or forest pests, changes to the abundance and community composition of decomposers involved in nutrient cycling, and changes to the abundance and diversity of pollinators. A brief review is provided below of the evidence that these ecosystem services are being, or will be, affected by climate change.

There has been considerable debate about the potential for climate change to shift the global distributions, prevalence and virulence of vector-borne diseases, particularly those such as malaria, Yellow fever, Dengue, arboviruses and West Nile Virus which are vectored by mosquitoes (e.g., Epstein et al. 1998, Russell 1998, Sutherst 1998, Reiter 2001 2008). Changes to the distribution, abundance or life cycles of the invertebrate vectors of pathogens could play important roles in determining the frequency and distribution of future disease outbreaks, as could direct effects of climate warming on pathogen survival, development and seasonality. However, at present there is relatively little evidence for direct climate-driven changes to the spatial or temporal pattern of invertebrate-borne diseases (Harvell et al. 2002). Recent climate-based models of the future distributions of *falciparum* malaria show rather few predicted changes from the current distribution (Rogers and Randolph 2000). Furthermore, evidence that malaria has expanded its distribution to higher elevations in the East African highlands appears mainly to reflect increased antimalarial drug resistance and decreased mosquito control activities, in the absence of significant changes to meteorological conditions (Hay et al. 2002a, b). In contrast, the spread of Bluetongue Virus (BTV) into southern and central Europe since 1998 seems to be related to increased virus persistence during milder winters, northward expansion of its vector, the biting midge *Culicoides imicola*, and transmission by other indigenous European *Culicoides* species beyond the former geographic range of BTV (Purse et al. 2006). Increased understanding of the ecology of pathogens, their vectors and their hosts is needed to determine their sensitivity to climate change and other environmental changes (Reiter 2001 2008). Systematic sampling along latitudinal and elevational gradients could help to elucidate effects of climate change on the distributions of vector species (Kovats et al. 2001).

Changes to the composition of soil invertebrate communities can lead to important changes in nutrient cycling, including carbon turnover (Bradford et al. 2002 2007). Two years of soil warming of +3.5°C led to marked changes in the invertebrate faunal composition of experimental mesocosms in southern Scotland (2°W, 55°N), which could profoundly alter ecosystem carbon function (Iglesias Briones et al. 2009). In contrast, simulated warming had little effect on the soil microarthropod community in nutrient poor alpine *Dryas* heath in south Norway, whereas nutrient addition significantly altered community composition (Hågvar and Klanderud 2009). Further research into the

effects of climate change on soil invertebrates will be valuable to determine the capacity of ecosystems to adapt to climate change, and their potential role in carbon storage.

Invertebrate pests have important ecological and socio-economic effects on agricultural and forest systems, which are likely to be highly sensitive to climate change given the direct and indirect effects of climatic conditions on invertebrate demography and distributions (Harrington 2002, Sutherst et al. 2007). Information from across Europe has been used to model how the phenology of aphid populations, including many important crop pests, will be affected by climate change (Harrington et al. 2007). Forest insect herbivores influence levels of forest defoliation, forest disturbance regimes (e.g. by providing fuel for forest fires), and therefore affect forest nutrient cycling, productivity, carbon sequestration and biodiversity. Consequently, the effects of climate change on forest insect pests could have important ecological and economic impacts, and research on these is vital to adapt future forest management to climate change (Ayres and Lombardero 2000, Logan et al. 2003). Changes to the distributions, abundance and dynamics of forest invertebrate pests have begun to be documented, and models developed of their responses to climate change. The distribution of the pine processionary moth *Thaumetopoea pityocampa* in Europe has expanded polewards and uphill in response to recent climate warming (Hóðar et al. 2003, Battisti et al. 2005 2006) to the extent that the species has become an exemplar system for ecological modelling of the responses of pest species to climate change (Robinet et al. 2007, Netherer and Schopf 2009). In north America, models have been developed linking recent warming to the range expansion and increased outbreak frequency and severity of the mountain pine beetle *Dendroctonus ponderosae* (Carroll et al. 2003 2006, Aukema et al. 2006). Tree mortality during mountain pine beetle outbreaks reduces forest carbon uptake, and increases carbon emissions from decaying dead trees, potentially converting Canadian forests from carbon sinks to large net carbon sources (Kurz et al. 2008), and emphasising the importance of forest invertebrate dynamics both for climate change mitigation and adaptation.

Approximately one third of global crop production and 60-90% of plant species require animal pollinators, many of them invertebrates (Klein et al. 2007, Kremen et al. 2007). Climate change has the potential to decouple plant-pollinator interactions by altering the distributions or phenology of plants or their pollinators, but there is limited evidence that such changes have yet occurred, or of how they might affect plant-pollinator networks in the future (Hegland et al. 2009). In Spain, the phenology of pollinator insects including the honey bee *Apis mellifera* has advanced to a greater extent than plant phenology, leading to potential temporal mismatches (Gordo and Sanz 2005 2006). A warm spring in Japan in 2002 reduced seed-set from two plant species usually pollinated by bumble bees, because plant phenology advanced more than that of the bumble bees; whereas two fly-pollinated species in the same region showed comparably early flowering but no reduction in seed-set (Kudo et al. 2004). Memmott et al. (2007) used highly-resolved information on phenology and species interactions in a network of 1420 pollinators and 429 plant species from western Illinois (USA) to predict that climate-related phenological shifts could reduce the floral resources available to 17-50% of pollinator species. Maintaining high plant and pollinator diversity in heterogeneous landscapes may therefore be vital to act as a buffer against potential climate-related phenological changes to current plant-pollinator interactions (Kremen et al. 2007, Hegland et al. 2009, Winfree and Kremen 2009).

4. VULNERABILITY OF BERN CONVENTION INVERTEBRATES TO CLIMATE CHANGE

Berry (2008) provides an overview of existing information on the vulnerability of Bern Convention habitats and species to climate change. Vulnerability incorporates the components of levels of exposure to climatic changes, sensitivity to those changes, and the scope and limitations of adaptation to those changes, either autonomously by the species concerned, or following planned, societal adaptation (IPCC 2007, summarised in Berry 2008; see Box 2). Here I address available evidence for the vulnerability of Bern Convention invertebrate taxa to climate change. There are few examples of evidence for the direct effects of climate change on Bern Convention Invertebrates, and vanishingly few outside the Lepidoptera. However, recent research on the habitat associations or distributions of a number of taxa provide clues regarding their likely vulnerability.

Box 2. The terminology of climate change vulnerability (IPCC 2007, Berry 2008)

Vulnerability

The degree to which a system is susceptible to, and unable to cope with, adverse effects of climate change. Vulnerability is a function of *exposure* to climate change, *sensitivity* to climate change, and the adaptive capacity of the system (*adaptation*). High vulnerability reflects high exposure, high sensitivity, and low adaptive capacity.

Exposure

The character, magnitude, and rate of climate change and variation to which a system is exposed. The types of exposure of most concern are high changes to temperature, precipitation, sea level rise, increased frequency or magnitude of extreme events, and changes to disturbance regimes such as fire. Different regions or habitats may experience different levels of change in exposure to these variables.

Sensitivity

The degree to which a system is affected, either adversely or beneficially, by climate change. Species near thresholds of climate tolerance (e.g. at range margins) may be highly sensitive, as may species with highly localized distributions, which suggest a small niche breadth.

Adaptation

The adjustment in natural or human systems in response to actual or expected climate stimuli or their effects, which moderates harm or exploits beneficial opportunities.

Autonomous (or *spontaneous*) adaptation refers to responses by species which enable them to persist, including genetic adaptation, adjustments to phenology or physiology, or colonization of regions which become climatically favourable. A range of factors can contribute to a weak adaptive capacity (e.g., small population or distribution size, limited dispersal ability, low genetic diversity, highly specific habitat requirements or biotic interactions). *Planned* (or *societal*) adaptation includes human management and policy actions aimed at increasing the autonomous adaptive capacity of species.

4.1 Lepidoptera

Butterflies have by far the most detailed distribution data of any invertebrate group, and this information has been used to produce bioclimate models for fifteen of the 23 Bern Convention butterfly species. Nine of these species are categorised as having High, Very High, or Extremely High climate change risk, indicating that more than 70% of the current European distributions of the species are predicted to be climatically unfavourable by 2080 in at least one climate change scenario (see Table 1). Four species were categorised as experiencing climate change Risk, because more than 50% of currently suitable grid cells are predicted to be unsuitable by 2080 in at least one scenario. Only one species (the scarce fritillary *Euphydryas maturna*) did not achieve modelled losses of >50% in any 2080 scenario (Lower Climate Change Risk), whilst the current distribution of the marsh fritillary (*Euphydryas aurinia*) was only considered to be explained by climate conditions to a limited extent (Potential Climate Change Risk).

Table 1. Modelled climate risk for Bern Convention species of butterfly (after Settele et al. 2008)

	Model accuracy (AUC)	Climate Risk Category	Mean 2080 modelled change (%)*	
			Full dispersal	No dispersal
<i>Apatura metis</i>	0.98	HHR	+47	-71
<i>Coenonympha hero</i>	0.88	HHR	-44	-76
<i>Coenonympha oedippus</i>	0.95	R	+161	-50
<i>Euphydryas aurinia</i>	0.72	PR	-24	-41
<i>Hypodryas maturna</i>	0.79	LR	+46	-37
<i>Lopinga achine</i>	0.81	R	+58	-43
<i>Lycaena dispar</i>	0.88	R	+54	-41
<i>Maculinea arion</i>	0.77	R	-17	-52
<i>Maculinea nausithous</i>	0.91	HHHR	-45	-84
<i>Maculinea teleius</i>	0.84	HHR	-26	-74
<i>Melanargia arge</i>	0.98	HR	+119	-64
<i>Papilio alexanor</i>	0.94	HHR	-53	-77
<i>Parnassius apollo</i>	0.8	HR	-51	-66
<i>Parnassius mnemosyne</i>	0.77	HR	-18	-65
<i>Zerynthia polyxena</i>	0.85	HR	+80	-59

* Mean modelled change is shown as the mean of the three climate change scenarios (SEDG, BAMBU, GRAS). Differences among scenarios are shown in Fig 1.

Three important conclusions can be drawn from Settele et al.'s (2008) models for Bern Convention species of butterfly:

1. Increases in temperature by 2.4°C (SEDG scenario), 3.1°C (BAMBU scenario) or 4.1°C (GRAS scenario) lead to marked and significant differences in the predicted distribution sizes of Bern Convention butterfly species. In both 2050 and 2080 the highest warming scenario (GRAS) leads to consistently lower modelled distribution sizes than both other scenarios. In 2080, the intermediate scenario (BAMBU) leads to consistently reduced distribution sizes relative to the most conservative scenario (SEDG) (Fig. 1). Therefore mitigation of climate change by reduction of greenhouse gas emissions represents a real and necessary action for the conservation of these species.
2. Successful colonization of regions beyond current species distributions which become suitable in the future would lead to marked increases in potential distribution sizes for all Bern Convention species, relative to the "No Dispersal" scenario (Fig. 1). Given the fact that most Lepidoptera listed by the Convention have highly specialist habitat requirements, and fragmented distributions of habitat, it is unlikely that they will be able to expand their distributions autonomously to colonize regions that become climatically favourable. Therefore estimates of future distribution sizes based on the No Dispersal scenario are likely to be more realistic for these species than those assuming Full Dispersal. Therefore conservation intervention in the form of assisted colonization may become an appropriate technique for those species which are likely to suffer the most severe reductions in distribution size.
3. The nine Bern Convention butterfly species with highest climate change risk occur in a range of biotopes, including central European meadows (*Coenonympha hero*, *Maculinea nausithous*, *Maculinea teleius*), Mediterranean grasslands (*Melanargia arge*, *Papilio alexanor*, *Zerynthia polyxena*), meadows in mountains or at high latitudes (*Parnassius apollo*, *Parnassius mnemosyne*), and riverine woodlands in eastern Europe (*Apatura metis*). At least in terms of species sensitivity, it does not appear that ecological communities associated with some habitats are necessarily more at risk than others. Protection and management of a wide range of natural and semi-natural habitats will therefore be vital.

Many Lepidoptera listed by the Bern Convention possess other features which imply high climate change sensitivity, or reduced capacity for adaptation (see Box 2). All eight butterfly species not modelled by Settele et al. (2008) are European endemics, generally with extremely restricted distributions to islands or mountain ranges. Given their often small distributions or population sizes, and their isolation to narrow suitable regions, these species have very little opportunity for latitudinal range shifts. There may be some limited scope for elevational range shifts for mountain-dwelling species. Movement patterns have been quantified for *Erebia sudetica* in the Czech Republic (Kuras et al. 2003), whilst habitat requirements for *Erebia calcaria* have been modelled in Slovenia (de Groot et al. 2009). Research projects such as these will be extremely valuable in identifying the factors limiting species distributions, and the potential role of habitat fragmentation in constraining species range shifts in response to climate change.

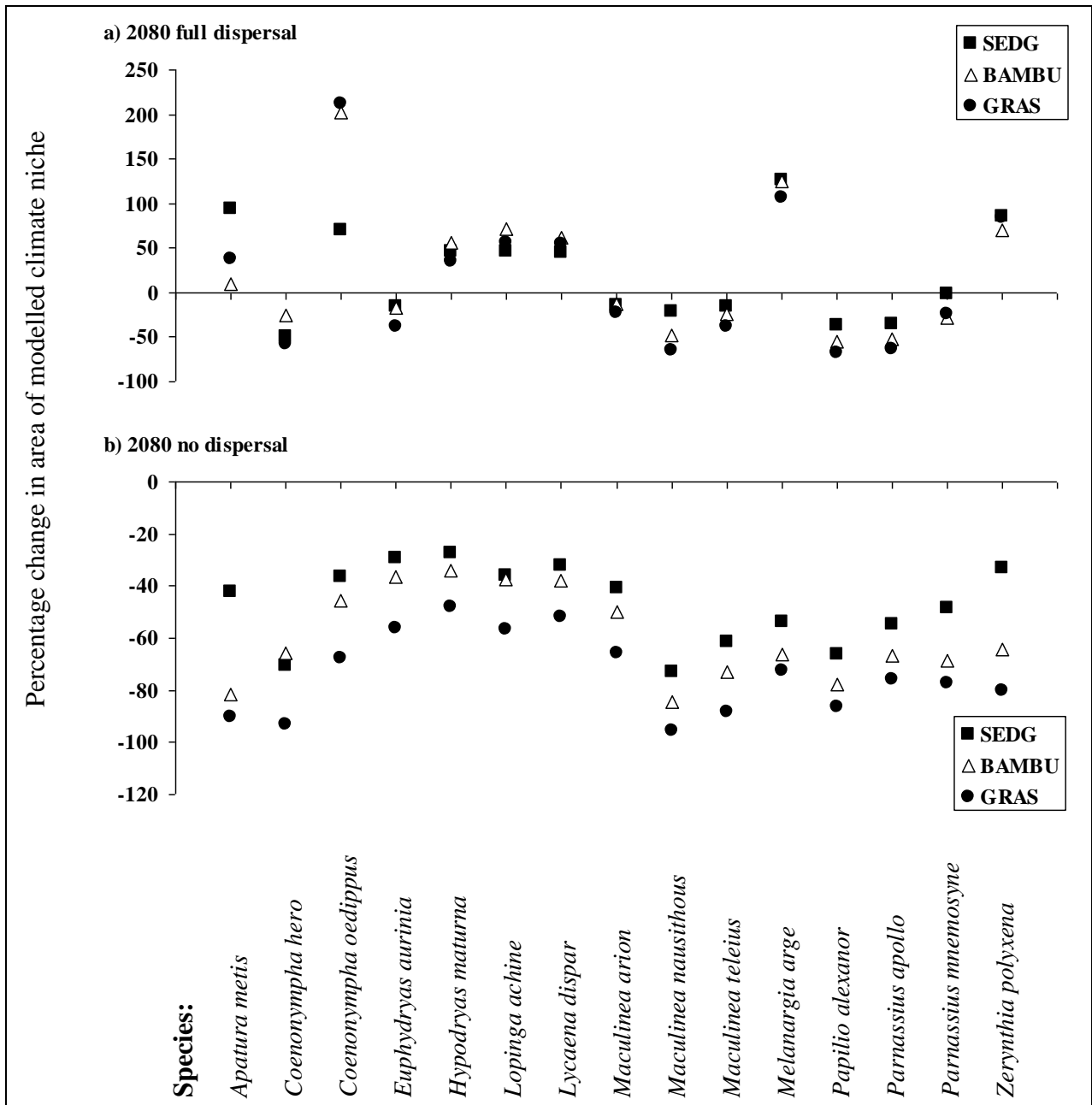


Figure 1. Modelled changes to the European climate niche space for butterflies listed by the Bern Convention (adapted from Settele et al. 2008; see Box 1). Data show percentage change in modelled niche space between 2000 and 2080, assuming either full dispersal (a) or no dispersal (b), and are shown for three climate change scenarios, for 2.4°C increase (SEDG, squares), 3.1°C increase (BAMBU, triangles), and 4.1°C increase (GRAS, circles).

The butterflies listed by the Bern Convention generally have highly specialist or fragmented habitat distributions and limited dispersal capacities, suggesting that they would be unlikely to expand their ranges in response to climate change. The distributions of habitats for some of the species can be predicted by the effects of climatic conditions and/or landcover (e.g., for *Parnassius mnemosyne* see Heikkinen et al. 2005 2007, Luoto et al. 2007; for *Maculinea nausithous* see Jiménez-Valverde et al. 2008). Research into dispersal capacity suggests that distances of 10-50 km between habitat areas would almost certainly prevent natural colonizations (e.g., for *Parnassius apollo* see Brommer and Fred 1999; for *Parnassius mnemosyne* see Meglecz et al. 1999, Valimaki and Itamies 2003; for *Coenonympha hero* see Cassel-Lundhagen & Sjogren-Gulve 2007 2008).

Fine-scale information on habitat use also suggests the potential sensitivity of species to climate change. The *Maculinea* species have intimate associations with host ant species, whose distributions in turn depend on local microclimate variation (e.g. Thomas et al. 1998, Mouquet et al. 2005). Larvae in both *Parnassius apollo* and *P. mnemosyne* appear to thermoregulate by moving between areas of litter, bare ground and more shaded vegetation (Valimaki and Itamies 2005, Ashton et al. 2009), whilst winter flooding may be a significant source of larval mortality in *Lycaena dispar* (Nicholls & Pullin 2000 2003). Changes to climate conditions may mean that there are changes to the microhabitat types which satisfy the microclimate requirements of species, so monitoring of habitat use and population responses to habitat management may be important. In the case of *Parnassius apollo*, local extinctions have already been linked to climate warming in France (Descimon et al. 2006) and Spain (Wilson et al. 2005, Ashton et al. 2009), with the low elevation limits of the species shifting markedly uphill in both regions. “False-spring events” in France appear to have resulted in the early emergence of *P. apollo* larvae from winter diapause, leading to their starvation when conditions later became too cold for feeding activity (Descimon et al. 2006). The very small populations of *P. apollo* which remain in some parts of its distribution may have led to inbreeding depression which render the species less able to adapt to changing conditions; however, reintroductions for this species have been carried out in Poland, with some measure of success (Adamski & Witkowski 2007). Understanding how climatic conditions influence the availability of resources for threatened species is vital to manage habitat successfully for species conservation. In the case of the myrmecophilous species *Maculinea arion*, management of sward structure in order to provide suitable microclimates for the larval host ants (*Myrmica sabuleti*) was an essential step for the reintroduction of the species to the UK (Thomas et al. 2009). Continued appropriate management has allowed reintroduced populations to survive in the UK and colonize additional suitable habitat nearby, in an exemplary example of how detailed ecological knowledge and habitat management can result in successful landscape-scale conservation (see also Settele and Kühn 2009).

4.2 Other Insecta

A number of narrow range European endemic species are likely to have very limited scope for range expansion to future climatically favourable regions (e.g., *Coenagrion freyi* (Odonata), *Cordulegaster trinacriae* (Odonata), *Baetica ustulata* (Orthoptera), *Carabus olympiae* (Orthoptera)). *Carabus olympiae* is known to have a restricted habitat distribution in the Italian alps, and increased conversion of beech woodland or scrub to pasture would likely prevent the species from being able to colonize locations outside its current narrow range (Negro et al. 2007 2008). A few cases of possible interactions between climate and habitat associations have been studied: *Saga pedo* (Orthoptera) is known to be restricted to steep south-west facing slopes at its northern range limit (Kristin & Kanuch 2007); *Cerambyx cerdo* (Coleoptera) uses insulated tree trunks in central Europe, so semi-open pasture landscapes favour the survival of this saproxylic beetle which acts as an ecosystem engineer by creating habitat for many other threatened beetles (Buse et al. 2007 2008). Identifying and maintaining suitable habitats for such species will be vital for their conservation: there is a great need for further information regarding the habitat requirements of non-lepidopteran Bern Convention insects, and whether these habitat requirements vary across the latitudinal or elevational ranges of species. A safety-first approach to habitat management in the mean time would be to maintain heterogeneous conditions (see 5.2.4. below).

Considerable autecological work has been carried out on the beetle *Osmoderma eremita*. This species is sensitive to increases in air temperature (Renault et al. 2005) and has extremely limited dispersal (Hedin et al. 2008). In fragmented habitats, *O. eremita* rarely moves between woodlands, and

persistence within woodlands is dependent on aggregations of old growth oak trees (Ranius 2000 2007). Conservation of highly sedentary, habitat specialist species which are sensitive to climate represents a significant challenge under climate change, but the information on habitat requirements such as exists for *O. eremita* is a vital first step.

4.3 Other Arthropoda - Arachnidae

The distribution of the Iberian endemic spider *Macrothele calpeiana* appears to be determined mainly by climate variables, with the species occurring in regions with high precipitation and high precipitation periodicity, but absent from regions where temperatures reach extremes (Jiménez-Valverde & Lobo 2006). The distribution model developed for the species proved accurate at identifying a region of southern Portugal in which populations of *M. calpeiana* occurred but had not previously been found (Jiménez-Valverde et al. 2007). This example shows the value of distribution data for developing models which might help to pinpoint previously unrecorded localities for rare species. Further modelling of climate scenarios may be helpful in estimating the sensitivity of *M. calpeiana* to climate change; the models also suggest that the species may require forest cover in order for populations to persist, or shift their range as the climate warms.

4.4 Mollusca

Many Bern Convention listed molluscs are narrow range endemics (e.g., to the Mediterranean or to Madeira) and are therefore likely to be vulnerable to climate change. Efforts to reintroduce the Mediterranean endemic limpet *Patella ferruginea* have been hampered by high rates of mortality of transplanted individuals (Espinosa et al. 2008), suggesting that assisted colonization may be a difficult technique to adopt for this species.

4.5 Anthozoa

The warm-water coral *Astroides calycularis* has recently colonized the eastern Adriatic sea from its previous range limit in the south-western Mediterranean, related to increases in water temperature and changes to surface water currents (Kruzic et al 2002, Grubelic et al. 2004, Bianchi 2007). This range expansion is indicative of the colonization of the Mediterranean by species (from the Atlantic or Red Sea) with predominantly sub-tropical biogeographic associations (Bianchi 2007).

5. ADAPTING INVERTEBRATE CONSERVATION TO CLIMATE CHANGE

Invertebrates are shifting their ranges to accompany recent climate warming, and conservation faces the key challenge of preventing species being lost from climatically-deteriorating parts of their range before they can colonize regions or habitats that become more favourable. This challenge is compounded particularly by habitat fragmentation. The foregoing discussion shows that species are likely to respond to climate change in individualistic ways, leading to sometimes unpredictable changes in distribution and abundance patterns, phenology and interactions between species. Conservation programmes may need to be similarly flexible and dynamic as a result, but certain general guidelines can be drawn.

5.1 Species sensitivity

Climate change disproportionately threatens species with small or isolated populations or distribution sizes, narrow habitat requirements, and poor dispersal abilities. These traits increase the risk that climate variation will result in declines in population size and local extinctions, whilst reducing the ability of species to exploit novel resources or colonize climatically suitable locations. These characteristics typify Bern Convention invertebrates, and suggest that climate change is most likely to increase the vulnerability of species that were already most threatened by other drivers of change.

5.2 The scope for planned adaptation

Species vulnerability could be high in regions or environments where exposure to climate change is extreme, or for species with high sensitivity based on their ecological traits (distributions, niche breadths, threats from other environmental drivers). These features of exposure or sensitivity imply that there are strong limitations to autonomous adaptation through evolutionary responses or

distribution change. Planned or societal adaptation therefore may be necessary for the conservation of highly vulnerable species, to overcome the barriers to autonomous adaptation. Some general guidelines for invertebrate conservation are provided below (see also Hopkins 2007, Mitchell et al. 2007 for general guidelines for adapting conservation to climate change).

5.2.1. Prioritization of regions, taxa or biotopes

Priority conservation management may be required in habitats or regions whose biodiversity is particularly sensitive to the effects of climate change. These regions or habitats can be identified by the modelling of species or biome responses to climate change (e.g. Hannah et al. 2002). At international scales, centres of endemism or biodiversity hotspots may represent concentrations of species that are especially vulnerable to changes both in land-use and climate (Myers et al. 2000). High latitudes and elevations will experience the greatest exposure to temperature change, potentially shifting the suitable climate space for species to locations far outside their current ranges. Montane areas will be particularly vulnerable because they support a disproportionate number of rare or endemic species (e.g. eight Bern Convention butterfly species are either entirely or almost entirely restricted to mountainous regions), and because they often represent the lower latitudinal margins of species ranges, which are especially sensitive to climate warming and which may be important reservoirs of genetic variability (Hampe & Petit 2005). Conversely, mountainous areas may present opportunities for conservation, since (i) they often retain comparatively intact habitats relative to lowland landscapes, (ii) steep elevational gradients may allow species ranges to track changing climates more quickly and over smaller distances than in the lowlands, and (iii) small-scale topographical variation may allow survival and adaptation in localized refugia. Mediterranean biomes may require special attention because of the lack of opportunity for species adapted to hotter and drier conditions to colonize these regions as climate warming proceeds. The invertebrate fauna of wetlands, including peatlands, ponds, lakes and rivers, may also be vulnerable to climate change impacts (e.g. for Odonata, Ott 2007). Minimizing the other threats to species in these regions may increase the likelihood that they will survive climate change.

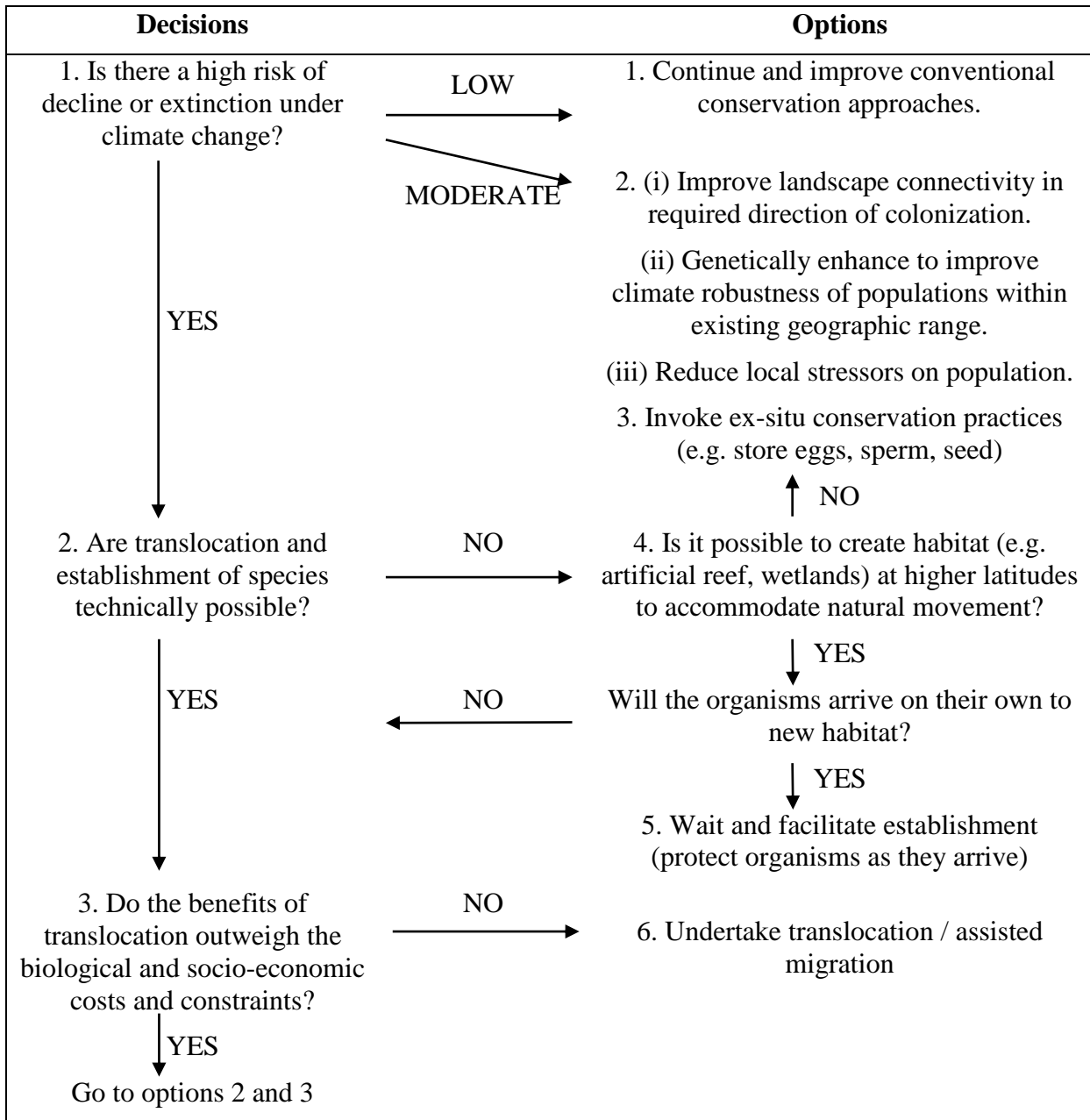
5.2.2. Landscape-scale conservation

At regional scales, landscape-scale habitat management of reserve networks and the wider environment will be important both to maintain current populations of species and to increase their likelihood of colonizing locations or habitats that become more favourable. Such an approach has been successfully employed for the butterfly *Hesperia comma* in England where grassland management in agri-environment schemes has allowed the species at least partially to overcome the constraints of habitat fragmentation on its range expansion (Davies et al. 2005, Wilson et al. 2009). Climate-related changes in the habitat associations of *H. comma* meant that it was able to colonize many areas of grassland which would not previously have been defined as ideal habitat for the species (Davies et al. 2006). Thus, site protection or management may benefit species that are present not only at a site itself but in the surrounding landscape; and changes to habitat use by species under climate change may allow them to colonize locations which would formerly have been considered unsuitable.

5.2.3. Assisted colonization

Management of the wider landscape to increase connectivity between populations will be least feasible for very sedentary species whose current distributions are very small or very isolated from locations that are expected to be suitable in the future. In this context, management of remnant networks of natural habitat combined with population translocations, or “assisted colonization”, could be more cost effective than the creation of wildlife corridors linking highly modified landscapes (Hulme 2005). Using bioclimate modelling approaches could help to identify the regions and taxa in which introductions would have the best chance of success. Introductions of insect species into suitable habitats beyond their current range have been successful on a number of occasions (e.g. Menéndez et al. 2006). However, the scope of population translocations as a conservation tool may be limited to a relatively small number of flagship species by their cost and requirement for very detailed ecological data (e.g., see Thomas et al. 2009). Hoegh-Guldberg et al. (2008) propose a decision framework for identifying appropriate systems in which to employ assisted colonization (see Box 3), in order to ensure that species translocations do not cause more problems than they solve, either for the focal species or for those in the locations to which they are introduced.

Box 3. A decision framework for the application of assisted colonization to the conservation of species under climate change (adapted from Hoegh-Guldberg et al. 2008).



5.2.4. Management for heterogeneity

The maintenance of habitat heterogeneity at local and landscape scales may favour species persistence for two reasons.

First, the habitat associations of species change with climate over time (Davies et al. 2006) and over species' geographic ranges (Thomas 1993, Thomas et al. 1998 1999). In addition, the habitat conditions or management practices that benefit species may change between seasons (Roy & Thomas 2003) or years (Kindvall 1996, Sutcliffe et al. 1997), depending on prevailing abiotic conditions, and the provision of a variety of habitat or micro-habitat types will allow species to exploit the microhabitats that are most favoured at a particular time. Careful monitoring may be increasingly necessary to detect the relationships of climate with the population sizes and habitat associations of species, and to ensure that habitat is not managed according to outdated prescriptions.

Second, habitat heterogeneity could act as a buffer against extreme conditions, allowing populations to survive in some locations or habitats when others become temporarily unfavourable or uninhabitable. For example, habitats with greater variation in topography or humidity support more persistent populations of the bush cricket *Metrioptera bicolor* (Kindvall 1996), and habitat heterogeneity has also been shown to be vital to permit population and metapopulation persistence of the butterfly *Euphydryas editha* in California (Singer & Thomas 1996, Thomas et al. 1996).

5.3 Monitoring, research and policy implications

There is a need for monitoring and research into both the sensitivity of species to climate change and the scope for adaptation, either by the species themselves or through planned conservation or policy interventions.

Sensitivity. Information on species sensitivity is needed to prioritise species, habitats and regions for planned adaptation to climate change.

Excellent Europe-wide information on the distributions of butterflies has allowed the development of models as a first step to compare the likely sensitivity of different species to climate change, and differences in the impacts of different climate change scenarios (Settele et al. 2008). For a well-known group like the butterflies, information on habitat requirements or host plant associations can then be used to increase the realism of modelled changes to species distributions (Araújo & Luoto 2007, Schweiger et al. 2008). These kind of approaches could now be employed for many other threatened butterfly species, and ground-truthed with empirical information about the effects of climate, habitat and biotic interactions on the population dynamics and distributions of species, in order to strengthen support for the impacts of climate change, and to allow further development of models to predict the effects of climate change on species distributions.

For the many species of invertebrate for which comparatively little is known about distribution or habitat associations, there is a great need to collect this basic ecological data. Distribution modelling approaches can then be used to predict locations where the focal species may occur, and to hint at the climatic or habitat requirements or tolerances of species (e.g. Jiménez-Valverde & Lobo 2006). Such approaches can help to target distribution surveys for poorly documented species or regions (Jiménez-Valverde et al. 2007 2008).

Adaptive capacity. Where prior information exists about the distribution, population size, or habitat associations of species, continued monitoring allows the detection of responses to environmental change. Such information may be vital to determine whether and how species are shifting their distributions, by testing for extinctions at warm range margins or expansions at cool range margins, and whether these processes keep track of or lag behind climate change.

Monitoring of population sizes and habitat associations will help to determine whether habitat is being managed successfully for species in a changing climate. Exemplar systems need to be developed which show the roles of habitat availability in facilitating or constraining species range shifts under climate change, if possible employing historical datasets to test the predictions of models of distribution change (e.g. Wilson et al. 2009). Information on the systems or species for which local and landscape-scale management of habitat have respectively permitted population increases or range expansions may be vital to draw conclusions about best practice for adapting conservation to climate change.

The current dialogue about the possible role of assisted colonization in facilitating species responses to climate change (Hoegh-Guldberg et al. 2008) also requires a firm evidence base from successful and unsuccessful reintroduction programmes (e.g. Adamski & Witkowski 2007, Espinosa et al. 2008, Thomas et al. 2009), to help provide information about the feasibility and consequences of the approach.

Finally, documentation and publicity about observed responses of invertebrates to climate change (and their ecological consequences) will be vital to impress upon policy makers and the general public: a) the effects of climate change on natural systems; and b) the potential benefits and wide-reaching impacts of climate change mitigation and planned adaptation.

Further scientific information on the vulnerability of species and systems to climate change should be used to guide policy regarding climate change mitigation and adaptation. The most comprehensive assessment of potential climate change impacts on an invertebrate group in Europe (carried out for butterflies by Settele et al. 2008) identifies the potentially profound impacts on species distributions of the magnitude of predicted warming. Mitigation is therefore a pressing need. Warren (2008, Foreword in Settele et al. 2008) also suggests the following policy considerations to ensure that habitat networks are available for species to shift their distributions as the climate warms:

- Shifts in Common Agricultural Policy (CAP) funding to reward delivery of biodiversity.
- Better resourced and targeted agri-environment schemes, and targeting of Less Favoured Area (LFA) payments to sustain High Nature Value (HNV) farming.
- Full implementation of the EU Habitats' and Species Directives with proper protection and management of Natura 2000 sites across Europe.
- New initiatives to resource creation of habitat networks to support biodiversity and help mitigate the adverse effects of climate change.

6. MAIN CONCLUSIONS AND RECOMMENDATIONS

Changes to the life history, population dynamics, distributions and diversity of invertebrates have been observed in response to recent climate change. To minimise losses in invertebrate biodiversity resulting from these changes, there is a need for conservation policy and practice to increase the adaptive capacity of natural and managed systems.

Narrow range endemics are particularly vulnerable to climate change and may have little opportunity to shift their distributions naturally to track suitable climate space. Documenting and conserving the current distributions and habitats for these species is vital if they are to have any chance of surviving climate change. Regions which support populations of many narrow range endemic species and species which are unlikely to be able to shift their distributions naturally in response to climate change include Atlantic and Mediterranean islands, and southern and central European mountain ranges.

PROPOSED ACTIONS :

Conserve heterogeneity

I.1. Maintain and actively manage large areas and networks of heterogeneous habitat, in order to: (i) protect large populations with low chances of local extinction; (ii) be prepared for changes to the habitat associations of species in a changing climate; and (iii) act as insurance against extreme climatic or climate-related events (e.g. fire).

Conserve existing populations

I.2. Conserve existing populations of threatened species in a range of habitats and locations across their geographic ranges. Focus efforts to conserve existing populations of species on existing high biodiversity and protected area networks, such as Emerald and Natura 2000 sites across Europe.

Minimise threats to vulnerable systems

I.3. Minimise threats which interact with climate change to threaten invertebrate biodiversity, including land-use intensification, abandonment of traditional farming and forestry, wetland drainage, urbanisation, pollution, and the spread of alien invasive species. As a priority, minimise these threats in systems which support the most vulnerable invertebrates, including:

- *Biotopes*: Mountains, natural and semi-natural grasslands, old growth forests, the Mediterranean biome, wetlands (including peatlands, freshwater lakes, ponds and rivers) and marine benthic systems.
- *Regions*: Atlantic and Mediterranean Islands, and southern and central European mountain ranges.

Facilitate range shifts

I.4. Establish or maintain landscape-scale networks of natural and semi-natural habitat in order to increase the chances that species can shift their distributions naturally, because many invertebrates will need to expand their distributions to higher latitudes or elevations in order to survive climate change.

I.5. Achieve landscape-scale ecological networks through measures including protection and active management of existing habitats, restoration of degraded habitats, and sustainable management of areas separating existing protected areas.

I.6. Consider assisted colonisation by planned conservation interventions for the conservation of species whose current distributions are unlikely to support them in the long term, and which are unlikely to reach identifiably suitable habitat and climatic conditions outside their current ranges.

Monitor and research

I.7. Undertake increased monitoring and research into the responses of invertebrates and ecological systems to climate change, which is crucial to provide an evidence base for making decisions about policy and management, including the following key areas:

- Document species distributions, habitat requirements, and climate associations for poorly known species and regions as baseline data to predict likely responses to climate change and other environmental drivers, and to permit recommendations to be made regarding their conservation.
- Test the independent and interacting roles of climate change and other threats in driving observed changes to the population dynamics and distributions of species, which will help to identify underlying causes, project future ecological responses, and prioritise systems and approaches for adaptive management.
- Monitor responses to climate change by invertebrates in order to detect changes to the relative vulnerability of different species, and to ensure that resources are focused towards priority species and systems.

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