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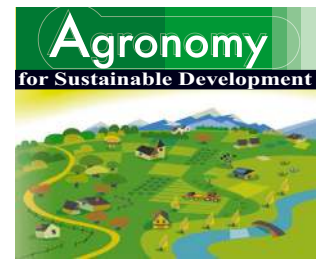
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Review article

Climate change in Europe. 1. Impact on terrestrial ecosystems and biodiversity. A review*

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(Accepted 14 November 2008)

Abstract – Ecosystems have an essential role in providing services to humankind such as nutrient cycling, pest control, pollination, quality of life, and hydrological, atmospheric and climatic regulation. About 60% of the world's known ecosystems are currently used unsustainably. In Europe, the richness and abundance of biodiversity is undergoing significant decline, partly due to climate change. This article outlines the impacts of climate change on biodiversity by showing both observed and projected changes in the distribution and phenology of plants and animals (phenology refers to changes in the timing of seasonal events). The four major findings are the following. (1) Concerning the distribution of plant species, climate change is responsible for the observed northward and uphill distribution shifts of many European plant species. By the late 21st century, distributions of European plant species are projected to have shifted several hundred kilometres to the north, forests are likely to have contracted in the south and expanded in the north, and 60% of mountain plant species may face extinction. The rate of change will exceed the ability of many species to adapt. (2) Concerning plant phenology, the timing of seasonal events in plants is changing across Europe due to changes in climate conditions. For instance, 78% of leaf unfolding and flowering records show advancing trends. Between 1971 and 2000, the average advance of spring and summer was 2.5 days per decade. The pollen season starts on average 10 days earlier and is longer than 50 years ago. Trends in seasonal events will continue to advance as climate warming increases in the years and decades to come. (3) Concerning the distribution of animal species, Europe's birds, insects, and mammals are moving northwards and uphill in response to observed climate change. Rate of climate change, habitat fragmentation and other obstacles will impede the movement of many animal species. Distribution changes are projected to continue. Suitable climatic conditions for Europe's breeding birds are projected to shift nearly 550 km northeast by the end of the century. Projections for 120 native European mammals suggest that up to 9% face extinction during the 21st century. (4) Concerning animal phenology, climatic warming has caused advancement in the life cycles of many animal groups, including frogs spawning, birds nesting and the arrival of migrant birds and butterflies. Seasonal advancement is particularly strong and rapid in the Arctic. Breeding seasons are lengthening, allowing extra generations of temperature-sensitive insects such as butterflies, dragonflies and pest species to be produced during the year. These trends are projected to continue as climate warming increases in the decades to come. Populations may explode if the young are not exposed to normal predation pressures. Conversely, populations may crash if the emergence of vulnerable young is not in synchrony with their main food source or if shorter hibernation times lead to declines in body condition.

climate change / biodiversity / temperature / plant / animal / phenology / pollen season / insect / bird / leafing date / reptile / amphibian / butterfly

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1. INTRODUCTION

Climate change is an important driving force in the distribution and functioning of natural systems (Parmesan and Yohe, 2003). Europe's biodiversity (its species, habitats and ecosystems) has been modified repeatedly during past glacial and inter-glacial periods, with some species recolonising the continent from ancient *refugia*. Today, ecosystems have an essential role in providing services to humankind such as nutrient cycling, pest control, pollination, quality of life, and hydrological, atmospheric and climatic regulation (Díaz et al., 2006; IPCC, 2007). Impoverishment of Europe's biodiversity may affect the delivery of ecosystem services with potentially serious consequences (Lovejoy and Hannah, 2005). Maintaining and enhancing healthy ecosystems are an important element in climate change mitigation and adaptation actions.



Photo: © European Environment Agency

About 60% of the world's known ecosystems are currently used unsustainably (Reid et al., 2005). In Europe, the richness and abundance of biodiversity is undergoing significant decline. This is in large part due to changes in land use and management, which are resulting in degradation of (semi-)natural

habitats, declines in traditional agricultural and forest management on which many habitats depend, and now large-scale land abandonment. Urbanisation, industrialisation, modification of rivers and watercourses, fragmentation of habitats by infrastructure and growing pressure from public access to the countryside for tourism and recreation are also causing widespread biodiversity losses (Millennium Ecosystem Assessment, 2005).

It is likely that these losses of biodiversity will be exacerbated by climate change. Projections suggest that between one fifth and one third of European species could be at increased risk of extinction if global mean temperatures rise more than 2 to 3 °C above pre-industrial levels (Lovejoy and Hannah, 2005; IPCC, 2007). A combination of climate change and the drivers of change outlined above will reduce the adaptive capacity (and resilience) of many species, possibly resulting in different ecosystems and landscapes across Europe. Local and regional extinctions are likely (McKinney and Lockwood, 1999). Species at greatest threat include specialists, those at the top of the food chain, those with latitudinal and altitudinal restrictions, and those with poor dispersal abilities.

The European Commission, through its target to 'halt the loss of biodiversity by 2010 – and beyond', is addressing observed and projected declines in biodiversity and their consequences for human well-being. As part of this process, reducing the impacts of other drivers of change will enhance the ability of species to adapt to climate change (IPCC, 2007). But new areas for conservation are also needed, together with measures to improve connectivity, thus facilitating species movement in fragmented landscapes. As such, the robustness of the European ecological network of Natura 2000 sites should be strengthened, including through more widespread implementation of Article 10 of the Habitats Directive (which relates to the network's coherence).

This section outlines the impacts of climate change on biodiversity by showing both observed and projected changes in the distribution and phenology (changes in the timing of seasonal events) of plants and animals, and the implications for communities.

2. DISTRIBUTION OF PLANT SPECIES

Key messages

- Climate change, in particular milder winters, is responsible for the observed northward and uphill distribution shifts of many European plant species. Mountain ecosystems in many parts of Europe are changing as pioneer species expand uphill and cold-adapted species are driven out of their ranges.
- By the late 21st century, distributions of European plant species are projected to have shifted several hundred kilometres to the north, forests are likely to have contracted in the south and expanded in the north, and 60% of mountain plant species may face extinction.
- The rate of change will exceed the ability of many species to adapt, especially as landscape fragmentation may restrict movement.

2.1. Relevance

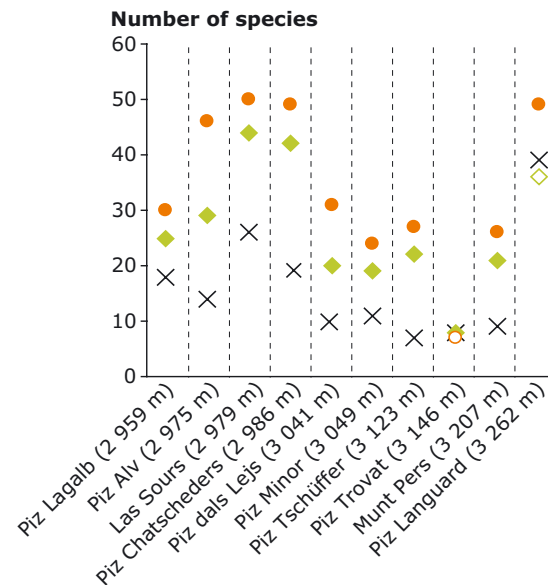
The rate of climate change is likely to exceed the adaptive capacity of some wild plant species (IPCC, 2007), whilst others are expected to benefit from changing environmental conditions (Sobrino Vesperinas et al., 2001). Consequently, the composition of many plant communities is changing to the extent that completely new assemblages are appearing. In addition, there is a parallel change in plant distribution and the increased threat of extinction of species at the edge of their geographical and altitudinal ranges – particularly poorly-dispersing endemics. The ecological implications of these changes and the effects on the services that these ecosystems provide are not always clear. Together with the emergence of invasive non-native species, these factors will have challenging consequences for long-term biodiversity conservation (Gitay et al., 2002) and the ability of Europe to meet its target to halt biodiversity loss, not least in relation to the favourable status of Natura 2000 sites.

The adaptive capacity of species is linked to genetic diversity and this too might change under climate change; sensitive and valuable relic populations will be particularly affected.

2.2. Past trends

Warmer temperatures in the past 30 years have significantly influenced seasonal patterns across Europe. As evidenced during glacial and inter-glacial periods, the predominant adaptive response of temperature-sensitive plant species has been to shift distributions, resulting in northward and altitudinal movements. One such climate-limited species is holly (*Ilex aquifolium*), which has expanded in southern Scandinavia in a manner consistent and synchronous with recorded regional climate changes, linked in particular with increasing winter temperatures (Walther et al., 2005).

Mountain ecosystems are particularly vulnerable to climate change (IPCC, 2007). There has been a general increase in



Note: Endemic, cold-adapted species are declining as pioneer species drive them out of their characteristic niches due warming conditions. ×: 1900s; ◇: 1980s; ●: 2003; open symbols indicate a (temporary) decrease in species number (Piz Trovat, Piz Languard).

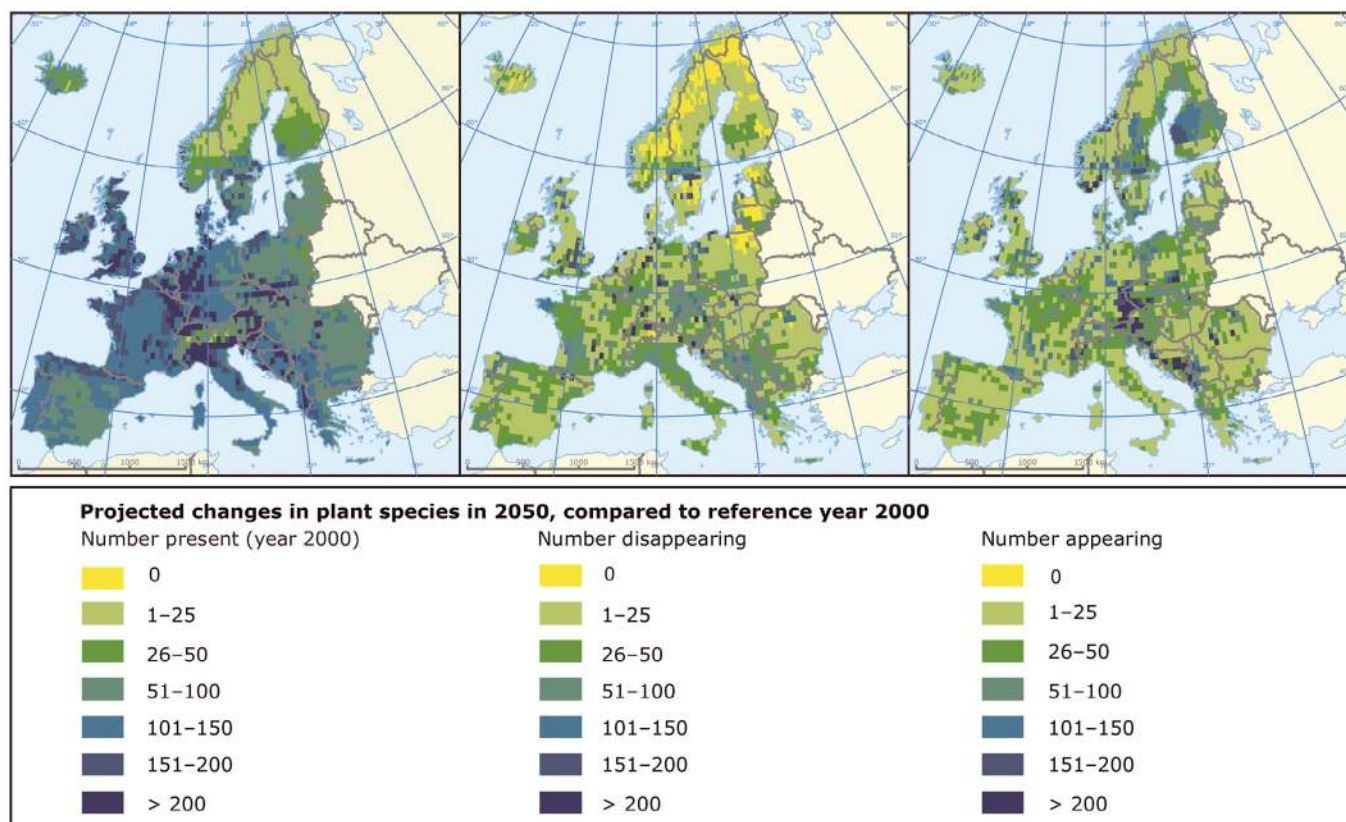
Source: Walther et al., 2005.

Figure 1. Increase in species richness on Swiss Alpine mountain summits in 20th century.

mountain summit species in Europe since the Little Ice Age in the 18th century. In Switzerland, for example, the uphill shift of Alpine plants showed an accelerating trend towards the end of the 20th century that is likely to be linked with the extraordinarily warm conditions of the 1990s (Walther et al., 2005) (Fig. 1). Evidence also emerged of declines in cold-adapted species as warming conditions and pioneer species drove these from their characteristic niches. Similar observations are expected from current European monitoring programs (e.g. GLORIA) for which results will be available by the end of 2008. In the Swedish Scandes, the tree line of the Scots pine (*Pinus sylvestris*) rose by 150–200 metres as warmer winters significantly lowered mortality and increased rates of establishment. Observations from other continents show that uphill tree line migration is a global phenomenon that could become a major threat to biodiversity in high mountains (Kullman, 2006, 2007; Pauli et al., 2007).

2.3. Projections

Projections indicate that, by the late 21st century, the potential range of many European plant species may shift several hundred kilometres in a northerly direction. This is several times faster than past rates as estimated from the Quaternary record or from historic data (Huntley, 2007). The distribution of tree species is also likely change significantly, with



Note: Results for stable area per grid cell, using the EuroMove model with HadCM2 A2 climate scenario.

Source: Based on Bakkenes et al., 2006.

Figure 2. Projected changes in number of plant species in 2050.

forests expanding in the north and contracting in the south, and broadleaved species replacing native coniferous species in western and central Europe (IPCC, 2007). Modelling of late 21st century distributions of 1350 European plant species under a range of scenarios led to the conclusion that more than half will be at the edge of their geographic and altitudinal ranges and could become threatened by 2080, with high risks of extinction (Thuiller et al., 2005). The greatest changes are projected for endemic plant species in Mediterranean, Euro-Siberian and many mountain regions. Mountain communities may face up to a 60% loss of plant species under high emission scenarios, reversing the 20th century trend outlined above (Thuiller et al., 2005; IPCC, 2007).

Bakkenes et al. (2006) obtained similar results from modelling stable areas of plant species distribution for this century under different climate change scenarios (Fig. 2). This study suggests that 10–50% of plant species in European countries are likely to disappear by 2100 from their current location in the absence of climate change mitigation. Again, species in southeast and southwest Europe are likely to be worst affected. This number will be higher if migration is restricted due to continuing fragmentation or if there is competition with invasive species.

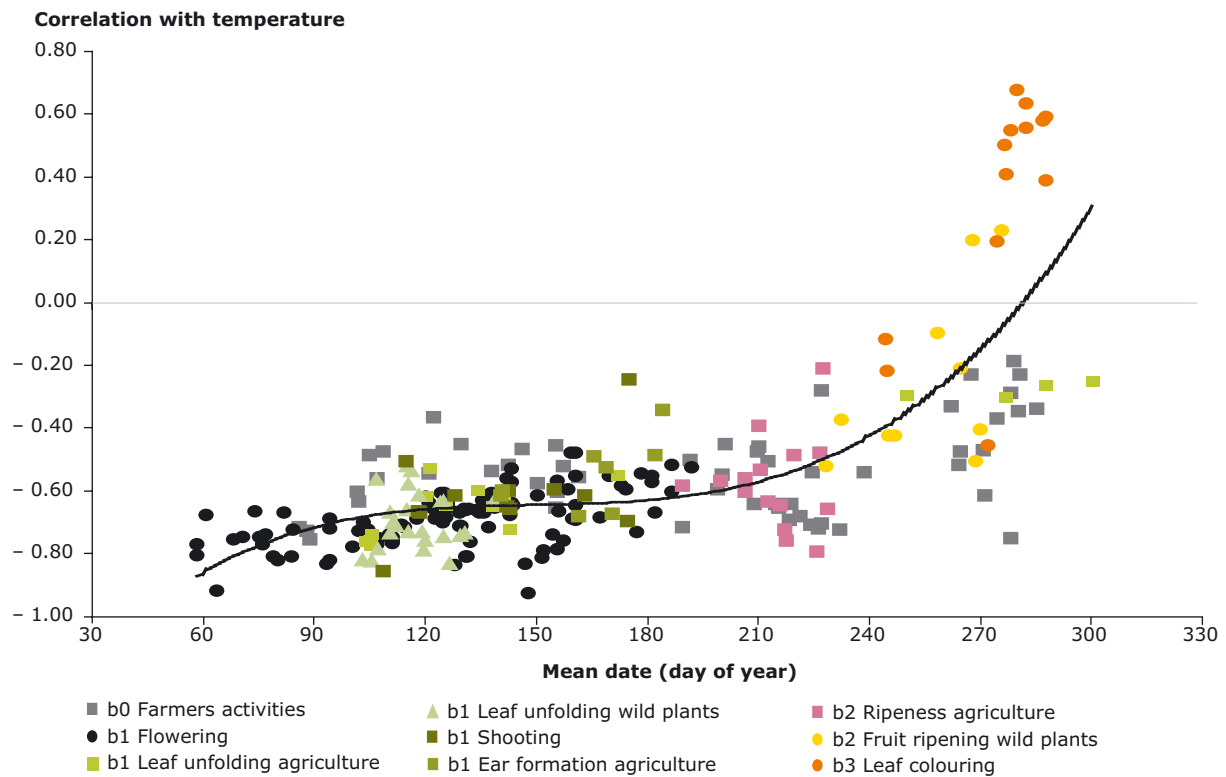
3. PLANT PHENOLOGY

Key messages

- The timing of seasonal events in plants is changing across Europe, due mainly to changes in climate conditions; 78% of leaf unfolding and flowering records show advancing trends and only 3% a significant delay. Between 1971 and 2000, the average advance of spring and summer was 2.5 days per decade.
- As a consequence of climate-induced changes in plant phenology, the pollen season starts on average 10 days earlier and is longer than 50 years ago.
- Trends in seasonal events will continue to advance as climate warming increases in the years and decades to come.

3.1. Relevance

Phenology is the study of changes in the timing of seasonal events such as budburst, flowering, dormancy, migration and hibernation. Some phenological responses are triggered principally by temperature, while others are more responsive to



Note: In a study of 254 national records across nine countries, most phenological changes correlated significantly with mean monthly temperatures of the previous two months. The earlier a spring event occurred, the stronger the effect of temperature.

Countries included: Austria, Belarus/northern Russia, Estonia, Czech Republic, Germany, Poland, Slovenia, Switzerland, Ukraine/southern Russia. Phenophase groups included: (b0) Farmers activities, (b1) Spring and summer with different leafing, shooting and flowering phases, (b2) Autumn fruit ripening and (b3) Leaf colouring of deciduous trees in fall.

Source: Menzel et al., 2006.

Figure 3. Phenological sensitivity to temperature changes.

day length (Menzel et al., 2006). Changes in phenology are linked with the growing season and affect ecosystem functioning and productivity.

Farming, forestry and gardening, as well as wildlife, are affected. The timing of tilling, sowing and harvesting is changing, fruit is ripening earlier due to warmer summers (Menzel et al., 2006), and grass in municipal parks and on road verges requires cutting more frequently and for longer.

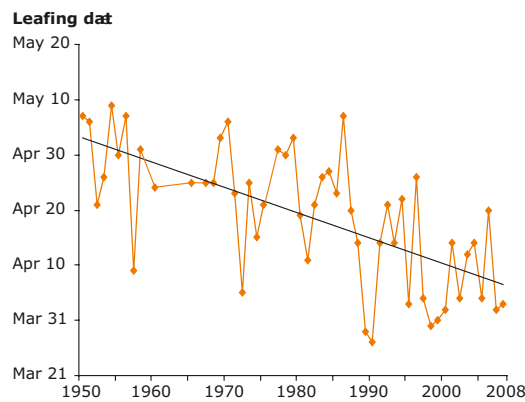
Changes in flowering have implications for the timing and intensity of the pollen season; this is showing an advancing trend as many species start to flower earlier. Allied to this, the concentration of pollen in the air is increasing (Nordic Council, 2005).

3.2. Past trends

There is clear evidence of changing phenology across Europe in recent decades (Parmesan and Yohe, 2003; Root et al., 2003; Menzel et al., 2006) (Fig. 3). Overall, 62% of the observed variability in the timing of life cycle events can be explained by climate (van Vliet, 2008). However, variability dif-

fers between events, with those occurring earlier (i.e. spring) being more variable than later events (Menzel et al., 2006). For example:

- 78% of all leaf unfolding, flowering and fruiting records across Europe show an advancing trend and only 3% a significant delay. The average advance of spring/summer phenological events is occurring at a rate of 2.5 days per decade (Menzel et al., 2006).
- The pollen season currently starts on average 10 days earlier and is of longer duration than 50 years ago.
- In Britain, the first flowering date for 385 plant species has advanced by 4.5 days on average during the past decade in comparison with the previous four decades (Fitter and Fitter, 2002); oak leafing has advanced three weeks in the last 50 years (DEFRA, 2007) (Fig. 4).
- In the Arctic, rapid climate-induced advancement of spring phenomena (e.g. flowering, egg laying) has been observed during the last 10 years. The strong responses of Arctic ecosystems and large variability within species illustrate how easily biological interactions can be disrupted by climate change (Høye et al., 2007).



Note: Annual observations (connected by straight lines); black line: average change in leafing date (showing advancement).

Source: Nature's Calendar, the United Kingdom.

Figure 4. Oak (*Quercus* sp.) leafing date in Surrey (United Kingdom) 1950–2008.

3.3. Projections

Phenological changes will alter growing seasons, ecosystem production, population-level interactions and community dynamics (Fitter and Fitter, 2002). Different species show different phenological responses; for example, annuals and insect-pollinated species are more likely to flower early than perennials and wind-pollinated species (Fitter and Fitter, 2002). Ecological research is evaluating these response thresholds to better understand what the wider effects might be. While advancing trends in seasonal events will continue as climate warming increases in the years and decades to come, it is uncertain how different species will respond when temperature thresholds are reached and whether linear relationships between temperature and growing season will be realised in the future.

4. DISTRIBUTION OF ANIMAL SPECIES

Key messages

- Europe's birds, insects, mammals and other groups are moving northwards and uphill, largely in response to observed climate change. But rates of distribution change are not necessarily keeping pace with changing climate.
- A combination of the rate of climate change, habitat fragmentation and other obstacles will impede the movement of many animal species, possibly leading to a progressive decline in European biodiversity.
- Distribution changes are projected to continue. Suitable climatic conditions for Europe's breeding birds are projected to shift nearly 550 km northeast by the end of the century, with the average range size shrinking by 20%. Projections for 120 native European mammals suggest that up to 9% (assuming no migration) risk extinction during the 21st century.

4.1. Relevance

The northward shift in distribution of animal species has a range of potential consequences for agriculture (livestock and crops), human health, as well as for biodiversity and its conservation (Sparks et al., 2007). The distribution of many animal species will be particularly affected by climate change if landscape fragmentation impedes their movement to more suitable climatic conditions. This will also affect the ability of Europe to meet its biodiversity target (above). In addition, warmer conditions, particularly warmer winters, are allowing the establishment of new pest species such as the European corn borer (*Ostrinia nubilalis*), American bollworm (*Heliothis armigera*), gypsy moth (*Lymantria dispar*) and some migratory moths and butterflies (see Sect. 5). Health risks associated with vector-borne diseases are linked to invasions of species such as ticks and mosquitoes.

4.2. Past trends

The northward and uphill movement of a wide variety of animal species has been observed over recent decades across Europe. These observations are partly attributable to observed changes in climatic conditions, whilst others are triggered more by land-use and other environmental changes.

In Britain, 275 of 329 animal species analysed over the last 25 years shifted their ranges northwards by 31–60 km, 52 shifted southwards, and two did not move (UKCIP, 2005; Hickling et al., 2006) (Fig. 5). However, many species, including butterflies, are failing to move as quickly as might be expected under the current rate of climate change (Warren et al., 2001).

Climate change has also already influenced the species richness and composition of European bird communities (Lemoine et al., 2007; Gregory et al., 2008). A recent study of 122 terrestrial bird species indicated that, from around 1985, climate change has influenced population trends across Europe, with impacts becoming stronger over time (Fig. 6). The study shows that 92 species have declined their populations because of climate change, whereas 30 species have generally increased (Gregory et al., 2008).

In a study of 57 non-migratory European butterflies, 36 had shifted their ranges to the north by 35–240 km and only two had shifted to the south (Parmesan et al., 1999). The sooty copper (*Heodes tityrus*), for example, spread north from Catalonia and by 2006 had established breeding populations on the Baltic coast (Parmesan et al., 1999). In Spain, the habitat of 16 mountain-restricted butterflies reduced by about one third over the last 30 years; lower altitudinal limits rose on average by 212 m – in line with a 1.3 °C rise in mean annual temperature (Wilson et al., 2005).

In Germany, the once rare scarlet darter dragonfly (*Crocothemis erythraea*) has spread from the south, paralleling observed changes in climate, and is now found in every federal state (Ott, 2007). Similarly, the spread of the comma butterfly in the Netherlands has been linked to recent climate change patterns.

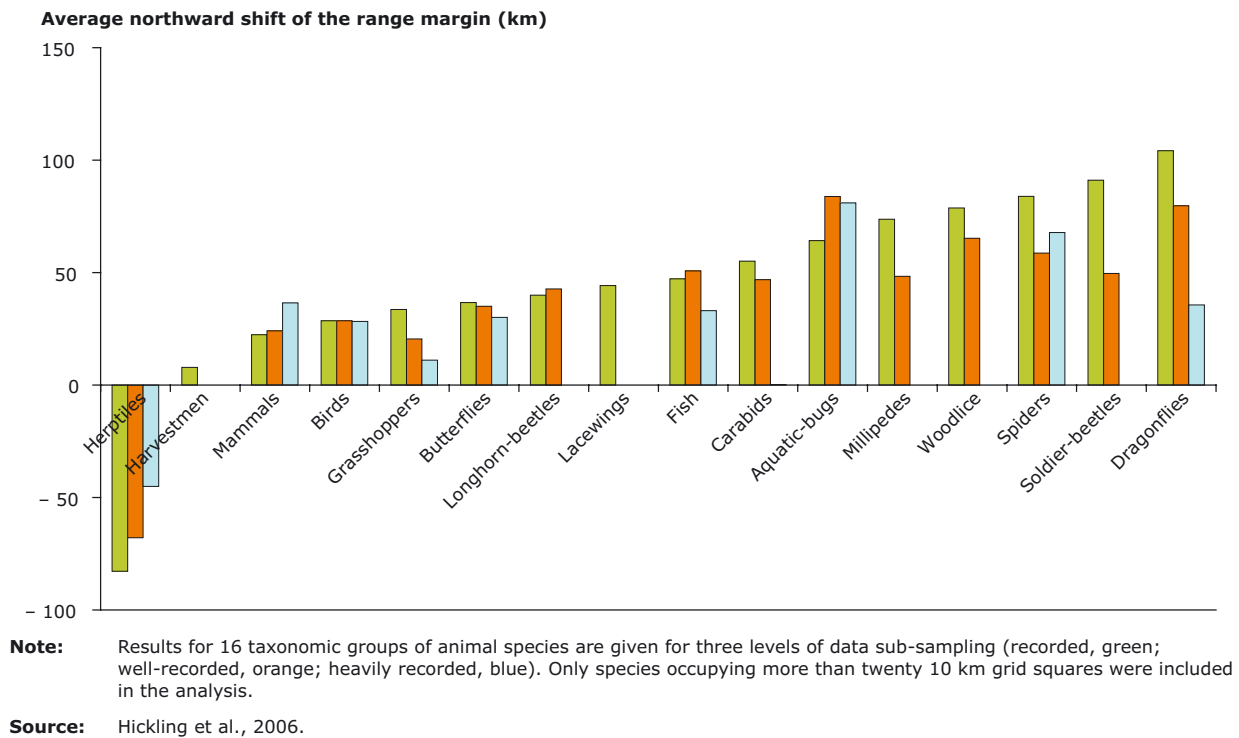
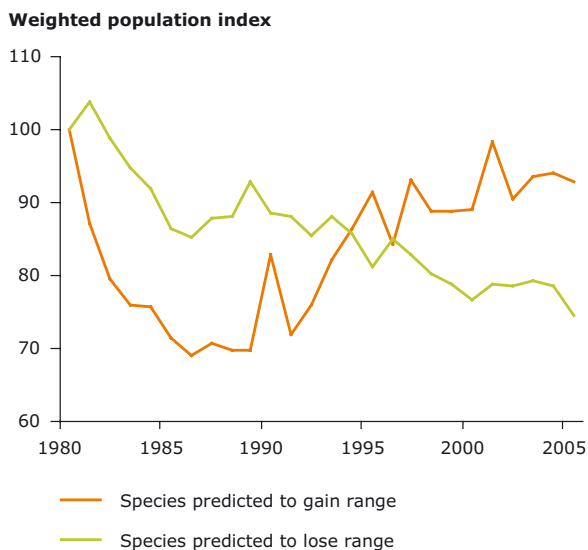


Figure 5. Latitudinal shifts in northern range margins in the United Kingdom for selected groups of animal species over the past 40 years.



Note: Weighted composite population trends under climate change were modelled as an index for two groups of widespread European land birds for 1980 to 2005, using climate envelope models. The index is set to 100 in 1980. The orange line shows the modelled weighted composite trend of 30 bird species. It shows an increase of their geographical range in the study region. The green line shows the modelled trend of 92 species that have lost range. Range changes were modelled by averaging using three global climate models and two emissions scenarios.

Source: Gregory et al., 2008.

Figure 6. Impact of climate change on populations of European birds, 1980–2005.

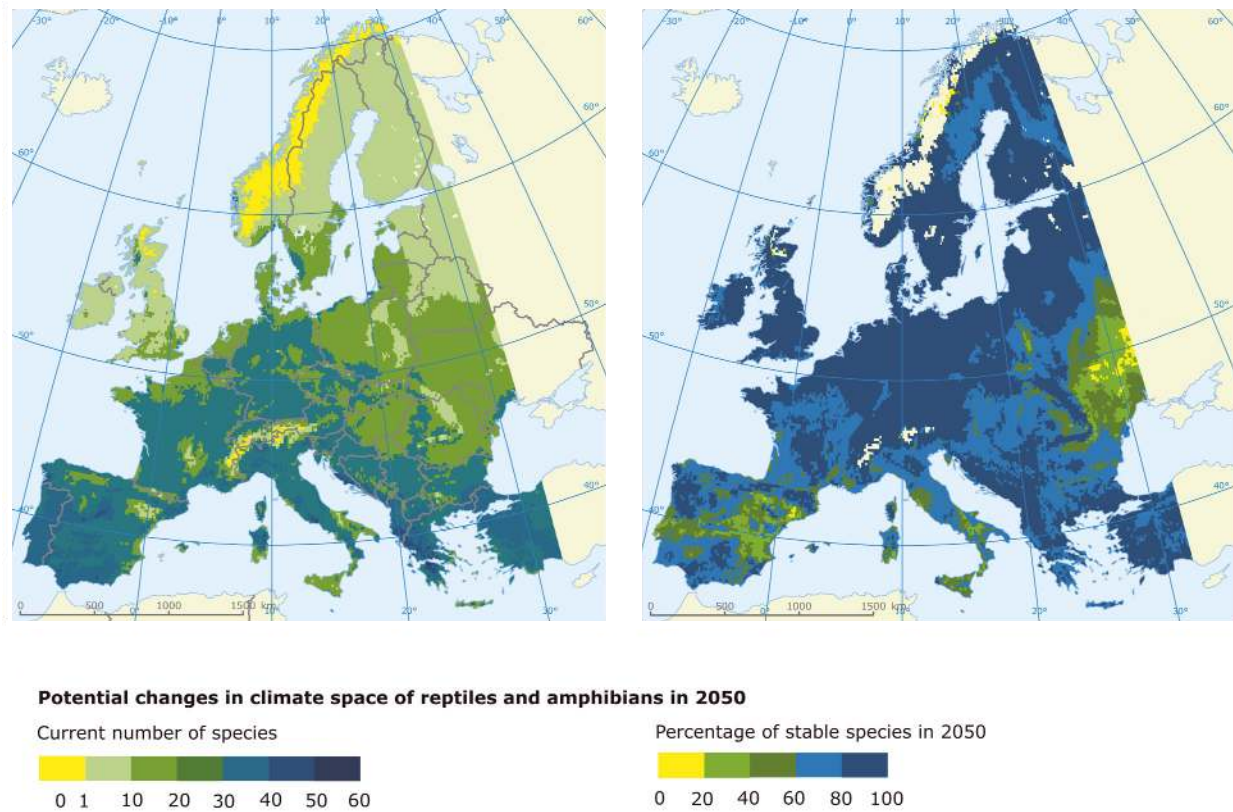
4.3. Projections

Projections suggest that the northward and uphill movement of many animal species will continue this century. Widespread species may be less vulnerable, while threatened endemics – already under pressure – will be at greatest risk, although there will be spatial variation (Levinsky et al., 2007; Lemoine et al., 2007). An important constraint will be the ability of species to move. This ability represents a significant research challenge, especially in the context of the effectiveness of ecological networks under a fast-changing climate.

The limited dispersal ability of many reptile and amphibians, coupled with the fragmentation of ecological networks, is very likely to reduce the ranges of many species (Hickling et al., 2006; Araújo et al., 2006), particularly those in the Iberian Peninsula and parts of Italy (Fig. 7).

A study of 120 native terrestrial mammals projected that species richness is likely to reduce dramatically this century in the Mediterranean region, but increase towards the northeast and in mountainous areas such as the Alps and Pyrenees, assuming that movement through fragmented landscapes is possible.

Under a 3 °C climate warming scenario (above pre-industrial levels), the ranges of European breeding birds are projected to shift by the end of the 21st century by about 550 km to the northeast, with average range size being 20% smaller. Arctic, sub-Arctic, and some Iberian species are projected to suffer the greatest range losses (Huntley et al., 2008). In polar regions, projected reductions in sea ice will drastically reduce habitat for polar bears, seals and other ice-dependent



Note: Projected data based on the Generalised Linear Model map using the HadCM3 A2 scenario for the 2050s are compared with the current situation.

Source: Bakkenes, 2007, based on Araújo et al., 2006.

Figure 7. Projected impact of climate change on the potential distribution of reptiles and amphibians in 2050.

species (IPCC, 2007). In addition to climate change, these top predators will also be affected by declining fish stocks.

5. ANIMAL PHENOLOGY

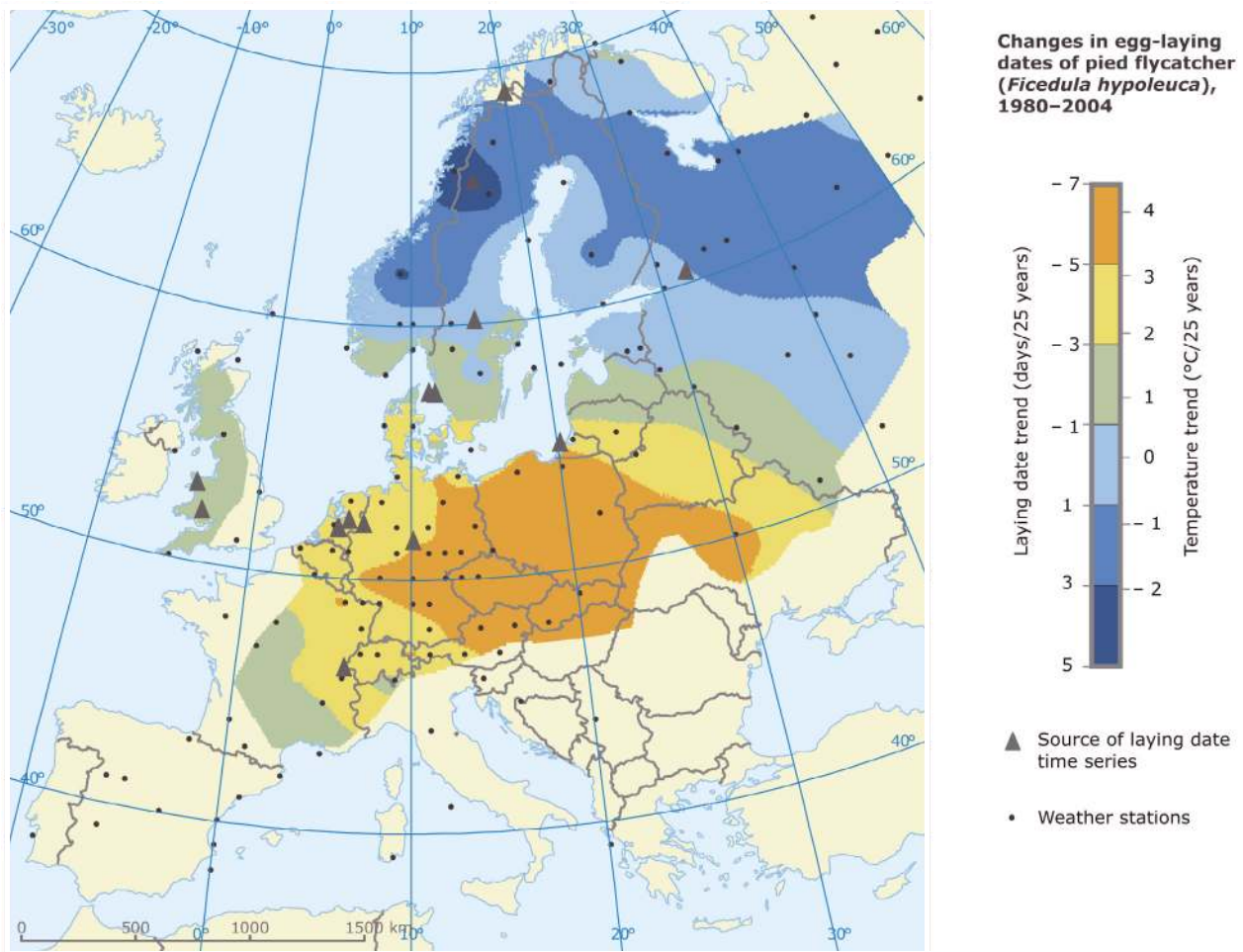
Key messages

- Climatic warming has caused advancement in the life cycles of many animal groups, including frogs spawning, birds nesting and the arrival of migrant birds and butterflies. Seasonal advancement is particularly strong and rapid in the Arctic.
- Breeding seasons are lengthening, allowing extra generations of temperature-sensitive insects such as butterflies, dragonflies and pest species to be produced during the year.
- These trends are projected to continue as climate warming increases in the decades to come. Populations may explode if the young are not exposed to normal predation pressures. Conversely, populations may crash if the emergence of vulnerable young is not in synchrony with their main food source or if shorter hibernation times lead to declines in body condition.

5.1. Relevance

Climate warming affects the life cycles of many animal species, particularly those such as butterflies, dragonflies and damselflies that are sensitive to temperature. Milder springs are allowing earlier onset of breeding and extra generations to emerge during the year. Furthermore, populations may explode if the young are not exposed to normal predation pressures. Conversely, populations may crash if the emergence of vulnerable young is not in synchrony with their food source or if shorter hibernation times lead to declines in body condition – as evidenced in the lower survival rates of some amphibians (Reading, 2007).

Insect pests are likely to become more abundant as temperatures increase (Cannon, 1998). As the impacts of climate change on ecosystems favour generalists, and as warmer temperatures increase insect survival and reproduction rates, more frequent, severe and unpredictable pest outbreaks may occur (McKinney and Lockwood, 1999). In temperate regions, milder winters are allowing increased rates of winter survival (Bale et al., 2002) and it has been estimated that, with a 2 °C temperature increase, some insects could undergo up to five additional life cycles per season (Yamamura and Kiritani, 1998).



Note: Dots: weather stations used to calculate changes in local egg-laying dates (derived from temperature data); triangles: location of pied flycatcher laying date time series.

Source: Both and Marvelde, 2007.

Figure 8. Changes in egg-laying dates (1980–2004) of the pied flycatcher (*Ficedula hypoleuca*).

5.2. Past trends

As spring temperatures increased in Europe over the past 30 years, many organisms responded by advancing the timing of their growth and reproduction.

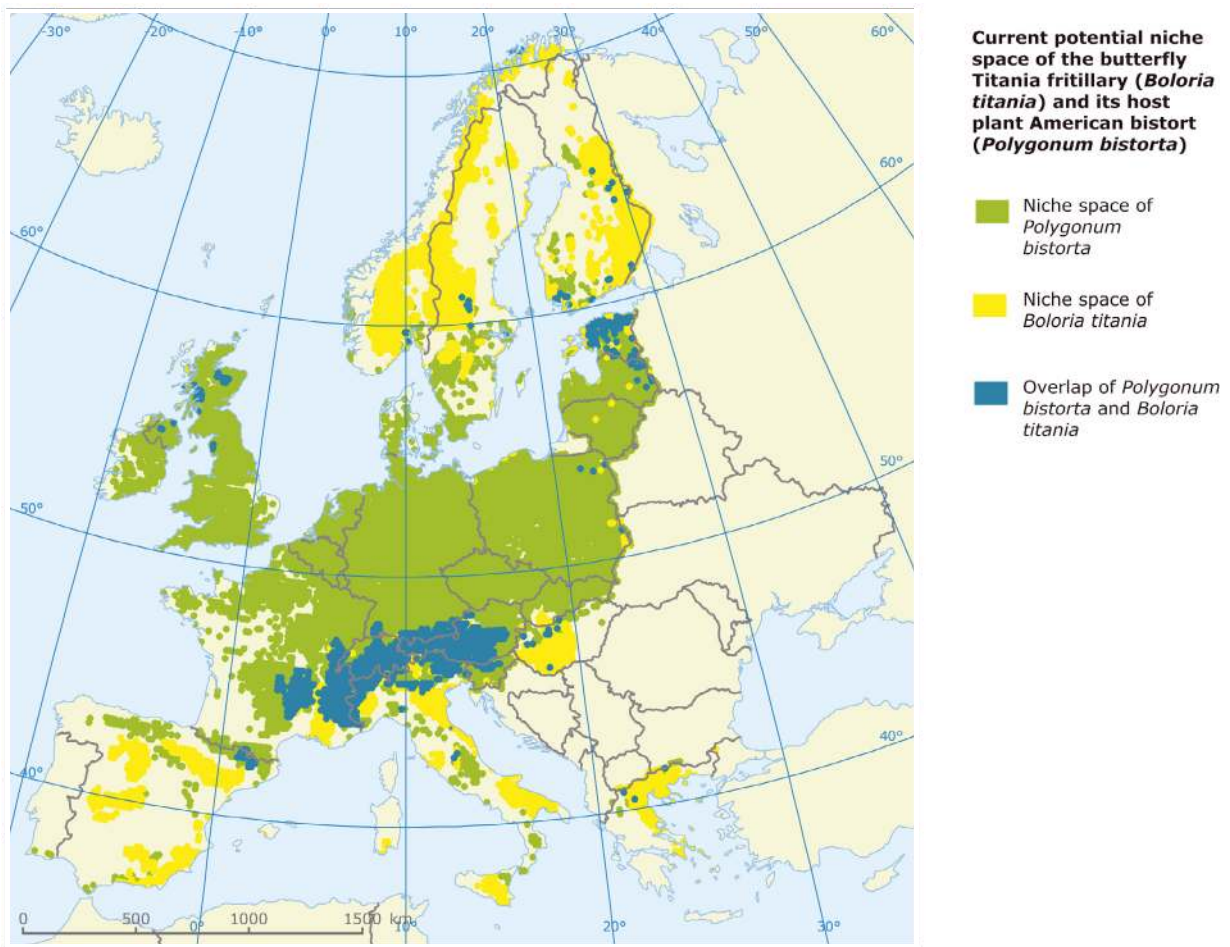
A study in Britain (Crick and Sparks, 1999) analysed 74 258 records for 65 bird species from 1971 to 1995. The study showed significant trends towards earlier (8.8 days on average) laying dates for 20 species (31%), with only one species laying significantly later. The effects, however, are not necessarily uniform. The predicted egg-laying date for the pied flycatcher (*Ficedula hypoleuca*), for example, shows significant advancement during the period 1980 to 2004 in western and central Europe, but delays in northern Europe (Fig. 8); both are strongly driven by temperature trends (Both and Marvelde, 2007).

Strong and rapid phenological changes have been observed in the high latitudes in response to warming of the region

occurring at twice the global average rate (Høye et al., 2007). The date of snowmelt in northeast Greenland has advanced by an average of 14.6 days since the mid 1990s, resulting in earlier egg-laying dates for birds in the region.

5.3. Projections

The future impacts of climate change on animal phenology are poorly understood, but could include increasing trophic mismatch and disturbance to ecosystem functioning. The trend towards warmer springs may continue to induce earlier breeding and migration activity. Unpredictable cold snaps are likely to cause high mortality amongst early movers. Meanwhile, species whose life cycles are calibrated according to day length, and which do not respond so readily to changing temperatures, will not be able to exploit earlier spring resources unless they can adapt.



Source: Schweiger et al., in press.

Figure 9. Current potential niche space of the butterfly *Boloria titania* and its host plant *Polygonum bistorta*.

6. SPECIES-ECOSYSTEM RELATIONSHIPS

Key messages

- The stability of ecosystems and, therefore, the services that they provide, will become increasingly affected by climate change due to species-specific responses and, thus, the disruption of established biotic interactions.
- The changing range of host species has major implications for range expansions of species and places additional pressures on those of conservation importance.

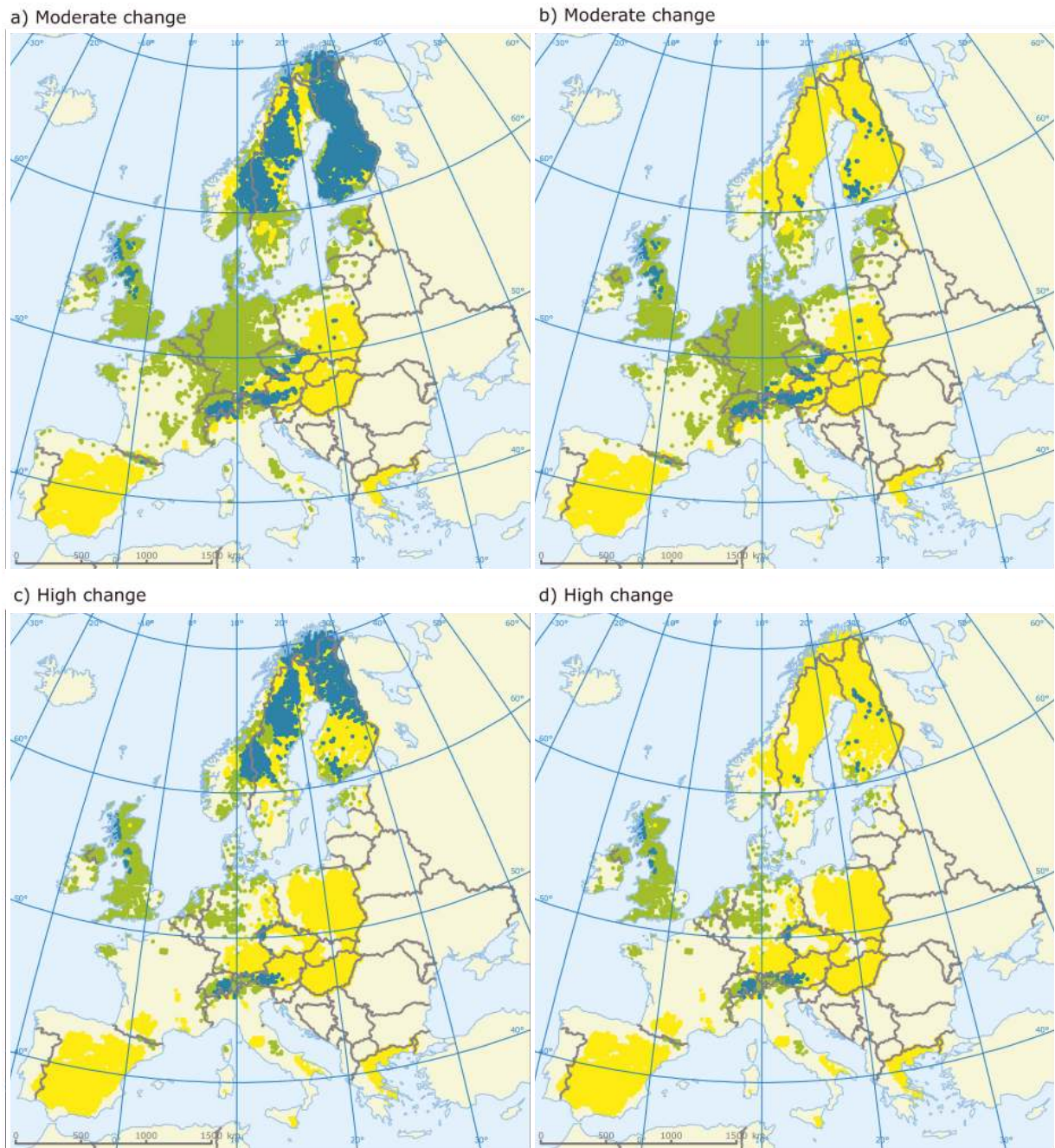
6.1. Relevance

Suitable climate is an important factor in determining the distribution of species and the composition and stability of ecosystems. For many animal species, a major constraint on successful colonization of new areas is the absence of ecologically-linked host plants (Schweiger et al., in press).



Sooty copper (*Heodes tityrus*)

Photo: © Guy Padfield, <http://www.guypadfield.com>



Relationship between projected distribution space of the butterfly *Titania fritillaria* (*Boloria titania*) and its host plant American bistort (*Polygonum bistorta*) for moderate (a, b) and high (c, d) climate change scenarios for 2080 under the assumption of unlimited (a, c) and no (b, d) dispersal of its host plant

■ Niche space of *Polygonum bistorta*
 ■ Niche space of *Boloria titania*
 ■ Overlap of *Polygonum bistorta* and *Boloria titania*, which is the butterfly's potential future niche space

Note: Global change scenarios based on storylines developed within the EU-funded project ALARM (Settele et al., 2005; Spangenberg, 2007; www.alarmproject.net).

Source: Schweiger et al., in press.

Figure 10. Relationship between projected distribution space of the butterfly *Titania fritillaria* (*Boloria titania*) and its host plant American bistort (*Polygonum bistorta*) for 2080.

Advancements in spring activity may result in asynchrony between food sources and breeding, causing starvation of young that emerge too early, and the disruption of predator-prey relationships.

This so-called trophic mismatch has been demonstrated for various animal groups, including birds (Both et al., 2006), and in some cases is causing crashes or explosions in populations. Additionally, extreme events such as floods, drought and fire can disrupt ecosystems, preventing growth of key plant species and limiting nesting, breeding and feeding opportunities for animals.

6.2. Past trends

Many butterfly species are moving northward (see Sect. 4), but often with overall declines in abundance and range size (Warren et al., 2001). Biotic interactions are important factors in explaining the distributions of butterflies, because they are often host-specific. For example, many parts of Europe are climatically suitable for the butterfly *Titania fritillaria* (*Boloria titania*) (Fig. 9) and the species may even be able to migrate quickly in response to climate change. However, an important constraint to range expansion is the presence of its host plant American bistort (*Polygonum bistorta*) (Schweiger et al., in press). Likewise, the current distribution of the clouded Apollo (*Parnassius mnemosyne*) is explained not only by climate suitability, but also by the presence of its *Corydalis* host plant (Araújo and Luoto, 2007).

Climate change has also had a disruptive effect on Scottish seabird communities and their food webs. During 2004 and 2005, major population crashes have been observed. In Shetland, over 1000 guillemot nests and 24 000 nests of the Arctic tern were almost entirely deserted, and on the nearby island of Foula, the world's largest colony of great skuas saw only a few living chicks. The cause was a drastic reduction in the populations of sandeel, their principal food source. The disappearance of the sandeel was due, in turn, to the northward movement of cold-water plankton on which these fish feed. The plankton's range had shifted because the waters between Britain and Scandinavia had become too warm for it to survive there. Since 1984, some seabird species around Scotland have decreased by 60–70% (CEH, 2005).

6.3. Projections

The response to climate change of the butterfly *Titania fritillaria* (*Boloria titania*) and its host plant American bistort (*Polygonum bistorta*) is likely to lead to a reduction in range overlap and, thus, an uncertain future for this specialist butterfly (Fig. 10). Played out on a larger scale, these trophic mismatches benefit generalists at the expense of specialists, putting additional pressures on the capacity of ecosystems to provide certain services and on species of conservation importance (McKinney and Lockwood, 1999; Reid et al., 2005; Biesmeijer et al., 2006).

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