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Climatic change and the conservation of European biodiversity: Towards the development of adaptation strategies

- FINAL VERSION -

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EXECUTIVE SUMMARY

Introduction – Prepared for the 'Group of Experts on Biodiversity and Climate Change' of the Bern Convention, this 'Discussion Paper' focuses upon the principles that must underpin the development of adaptation strategies for biodiversity conservation in the face of climatic change, as well as providing the background evidence from which these principles emerge.

Context – Predicted 21st century climatic change – Europe is projected on average to experience warming greater than the global mean warming. Winter warming is projected to be greatest in the north, where the December–January–February (DJF) mean warming is likely to be approximately double the global mean warming, whereas during the summer months warming is projected to be greatest in the south, where the June–July–August (JJA) mean warming is again likely to be approximately double the global mean warming in many areas, and as much as three times the global mean warming in some areas. Seasonal temperature extremes are projected to increase even more markedly, with annual minimum temperature increases of $6 - 18°C$ projected for central and eastern Europe and annual maximum temperature increases of $6 - 12°C$ projected for areas south of *ca*. 50° N. Annual precipitation is projected to increase in the north but to decrease in the south, with greatest changes in the summer in the south (JJA precipitation projected to decrease by > 40 % south of 40° N) and in the winter in the north (DJF precipitation projected to increase by 20 – 50 % north of 40° N). Such changes can be placed in context by comparing them to the present spatial gradients or to past climatic changes. During the Quaternary geological period, the difference in global mean temperature between glacial and interglacial stages is comparable in magnitude to the upper end of the range of possible global mean warming projected by the IPCC in their Fourth Assessment Report, whilst at the lower end of this range the warming results in conditions at least as warm as any during the past two million years. The projected rate of global mean warming exceeds by at least an order of magnitude the rate of global warming during the most rapid large magnitude events of the Quaternary period.

Species' responses to past climatic changes – Species' principal response to past rapid climatic changes was a spatial response, their geographical range changing as the area in which their climatic tolerances and/or requirements were met shifted. This spatial response was complemented by adaptive genetic responses of the population at any given locality as the climatic conditions at that locality changed. Species unable to achieve a sufficient spatial and/or adaptive response suffered extinction, at least regionally and in some cases globally. The magnitude of the spatial response required was less in regions of high topographic diversity, where species could shift elevation or utilise areas of contrasting topography, especially aspect and slope. In areas of lower relief, species' range boundaries shifted by between a few hundred and *ca*. 2000 km in response to the climatic change from the last glacial stage to the Holocene. Such extensive range boundary shifts took place at long-term average rates of $200 - 500$ m yr^{-1}, exceptional taxa achieving rates of as much as $1 - 2$ km yr^{-1}. Species' spatial responses were individualistic. Evidence of species' responses to 20th century climatic change complements the Quaternary record and provides independent evidence of the importance of the spatial response and of its rate, which has averaged 610 m yr^{-1}.

Ecosystems and climatic change – The individualistic response of species to climatic change renders species assemblages (communities) and ecosystems impermanent. A sustained climatic change results initially in quantitative changes in the relative abundance of component species, followed by qualitative changes in species composition. As species composition changes so too, in many cases, do the structural and functional attributes of the ecosystem. Species composition changes often are facilitated by some form of disturbance of the present ecosystem. Changes in the functional attributes of ecosystems often affect their ability to deliver various of the ecosystem services upon which human society depends. Combinations of environmental conditions without a present analogue are characterized by species assemblages and ecosystems without analogues amongst those found today. An important minority of ecosystems depend upon a physical habitat that itself is threatened by global climatic change, notably the ecosystems of the Arctic sea ice and of many coastal wetland areas.

Species' potential responses to projected climatic change – 'Climate envelope' models of various types can be used to simulate species' potential distributions under a given scenario of

projected future climatic conditions.   Although subject to criticism by some, such models of the relationship between a species' realized geographical range and biologically relevant climatic variables nonetheless offer valuable insight into the magnitude and rate of species' potential spatial responses to projected climatic change.   Although rarely highlighted, the principal limitation of such models arises from the frequency with which future combinations of environmental conditions are without a current analogue.   Such models only portray species' potential future geographical ranges; the dynamics of species' range shifts, and the time scales over which these potential range shifts might in practice be achieved, are simulated using a separate class of dispersal or 'migration' model.   Work to combine the two classes of model is a current topic of active research.

Application of 'climate envelope' models to various European taxa leads to important conclusions about the rates and magnitudes of species' potential range shifts.   By the late 21st century, the mean potential range shift relative to the late 20th century is by a distance of several hundred kilometres in a north-eastward direction, although some individual species' potential ranges are displaced in quite disparate directions and by distances in excess of 2000 km.   The mean rate of potential range shift is between a few times and more than an order of magnitude faster than past rates of range shift estimated from the Quaternary record or from historical data.   Species' on average have future potential ranges of smaller extent than their present ranges;   as a result, the mean number of species potentially occurring in an area is reduced.   Some species that occur today in Europe have no potential range in the continent by the end of the present century, and for a larger number their potential range does not overlap their present range.   A small but significant proportion of European species are as a result likely to face a substantial threat of eventual extinction in Europe, and in some cases of global extinction.   A much larger proportion of species are likely to suffer substantial loss of genetic diversity as a consequence of a combination of range and population reductions resulting from their failure to adjust their geographical ranges sufficiently rapidly.   Species at most heightened risk of eventual extinction will include those that already are rare and/or threatened, those with limited geographical ranges, and some migratory species.   Species not present in Europe today as 'natives' but found in adjacent regions are likely to find suitable climatic conditions in Europe in the future.

Implications for biodiversity conservation strategies – Adaptation strategies must be developed that take into account the implications arising from the evidence presented above. Adaptation strategies alone, however, will be insufficient; stringent mitigation measures also will be necessary if the rate and eventual magnitude of climatic change are not to exceed the resilience threshold of the biosphere.

In particular, adaptation strategies must take account of:

• Species' spatial response to climatic change;	*[Recommendation 1]*
• The need to facilitate, rather than to hinder, gene flow through species' populations to enable the adaptive component of their response to climatic change;	*[Recommendation 2]*
• Species' individualism and the consequent impermanence of species assemblages and ecosystems;	*[Recommendation 3]*
• The vital role of protected areas in any successful adaptation strategy;	*[Recommendation 4]*
• The absolute need to render landscapes 'permeable' to species as they adjust their spatial patterns of distribution.	*[Recommendation 7]*

In order to achieve this, and to be effective, adaptation strategies must incorporate:

• Re-evaluation of the management goals of protected areas;	*[Recommendation 1]*
• The need to maintain legal protection for protected areas that in future may not support the species or ecosystems that led to their initial designation;	*[Recommendation 1]*
• A re-evaluation of the concept of a 'native' species;	*[Recommendation 1]*
• Implementation of management, of protected areas and the wider landscape, that will facilitate species' potential future range changes;	*[Recommendation 1]*
• Measures designed to minimise loss of intra-specific genetic diversity, especially that component of such diversity concentrated near the 'trailing	*[Recommendation 2]*

edge' of species' European distributions;   [*Recommendation 3*]
- Measures designed to facilitate community and ecosystem changes;
- Management practices designed to facilitate ecosystem dynamic processes upon which realisation of community and ecosystem changes often depends;   [*Recommendation 3*]
- Continued protection and appropriate management of existing protected areas;   [*Recommendation 4*]
- Identification, using a 'coarse filter' approach, of gaps in the existing network of protected areas;   [*Recommendation 4*]
- Augmentation of the existing protected areas network to maximise representation of the range of combinations of environmental conditions and physical habitats, as well as to minimise the occurrence of large spatial gaps in the network.   [*Recommendation 4*]
- Implementation of appropriate management of the wider landscape and development of a landscape structure that will facilitate species' spatial responses to climatic change;   [*Recommendation 4*]
- Exploitation of buffer zones to enhance the effectiveness of protected areas;   [*Recommendation 5*]
- Development of landscapes that provide functional networks of habitat 'stepping stones' ensuring connectivity between the protected areas that will form the major nodes in these functional networks, the 'stepping stones' being of varying sizes and separations and providing appropriate representation of the range of physical habitats characteristic of the landscape;   [*Recommendation 7*]
- Implementation of management of the 'matrix' of the wider landscape in ways that are less intensive and that favour the maintenance or enhancement of fine-scale heterogeneity;   [*Recommendation 8*]
- Exploitation of existing, and development of new, incentive schemes for land-owners that promote the desired lower intensity land management, increased fine-scale heterogeneity and provision of habitat 'stepping stones'.   [*Recommendation 9*]

In addition, adaptation strategies must recognise that continuous corridors are neither a necessary part of achieving landscape connectivity nor a viable option in most parts of Europe on the scale necessary to render them an effective response to climatic change. [*Recommendation 6*]   Adaptation strategies also must recognise the scale mismatch between viable buffer zones and species' potential spatial responses to climatic change;   buffer zones are valuable in enhancing the effectiveness of protected areas, but offer little or nothing specifically in relation to adaptation to climatic change.

Strategies for adaptation   –   In addition to the implications outlined above for the development of adaptation strategies, such strategies also must have a number of further attributes.

In relation to species' dynamic and individualistic responses to climatic change, adaptation strategies must also:

- Implement management of both protected areas and 'stepping stones' that accelerates community and ecosystem transformation;   [*Recommendation 10*]
- Implement management, especially of protected areas, that will maximise populations of rare or threatened species found therein, even in the case of sites near the 'trailing edge' of a species' range where it is unlikely to persist in the longer term but where elements of the species' intra-specific genetic diversity important to its ability to adapt to climatic change elsewhere in its range are likely to be concentrated;   [*Recommendation 10*]
- Combine and balance the foregoing requirements;   [*Recommendation 10*]

- Develop a new holistic approach to the legal framework for the protection of an overall functional network of protected areas and the associated 'stepping stones' required to render the landscape permeable, taking a continental scale view rather than a national focus;   [*Recommendation 11*]
- Adopt the concept of a 'potential native' species and provide equivalent protection for all such species.   [*Recommendation 12*]

In relation to the importance of maintaining and augmenting the existing protected area network, adaptation strategies must also:

- Address as a matter of urgency the need to amend the legal basis for the designation of many protected areas so as to ensure continuity of protection of these sites that will be vital to any successful adaptation strategy;   [*Recommendation 11*]
- Take the steps necessary to increase the extent of the protected area in order that the often conflicting management practices required to facilitate change, on the one hand, and to maximise populations of rare and threatened species, on the other, can be accommodated;   [*Recommendations 13 & 15*]
- Target increases in the extent of the protected area such that the additional area, whether in the form of extensions to existing protected areas or of additional newly designated protected areas, offers the greatest flexibility and potential for species to adjust their distributions within the landscape in response to climatic change, e.g. by adding areas that extend to the highest elevations in the local landscape, that offer a high degree of topographic diversity, that maximise the range of physical habitats represented and/or that maximise the extent of the physical habitat and ecosystem that is dominant within the landscape.   [*Recommendation 14*]

In relation to the requirement to ensure connectivity of the protected area network through appropriate management of the wider landscape, adaptation strategies must also:

- Take the steps necessary to retain as many as possible of the remaining fragments of unaltered or semi-natural habitat in the landscape, especially of western Europe, in order that they may serve as 'stepping stones' and contribute to rendering the landscape permeable;   [*Recommendation 16*]
- Make the necessary provisions to encourage the creation of habitat 'stepping stones' in landscapes where past land management practice has led to the absence of sufficient suitable patches of unaltered or semi-natural habitat that may be managed for this purpose;   [*Recommendation 9*]
- Ensure that the legal protection afforded to species applies wherever in the landscape they may be present, and that the default status of species is that they are protected from disturbance or destruction wherever they may occur.   [*Recommendation 17*]

Although translocations and captive-breeding programs must not be ruled out as potential components of an adaptation strategy, they should be considered only as options of last resort, and will be impractical on any large scale, being viable only principally for extremely rare or threatened species.   [*Recommendation 19*].

Given the potential scale of species' responses to climatic change, adaptation strategies must be international, and preferably sub-continental or continental, in scope. [*Recommendation 18*].

Conclusion – Projected climatic changes are, relative to past changes, large in magnitude, at least an order of magnitude more rapid and leading to a destination without precedent in the past ten million or more years. Species' potential range shifts in response to these changes are large, range boundaries potentially shifting 500 – 1000 km in many cases. Because these responses are individualistic, conservation efforts must focus upon species and upon the provision of functional networks encompassing the full range of physical habitats found within a region; communities and ecosystems should not in themselves be a focus for conservation efforts. Maintaining and augmenting the existing protected area network will be vital to any successful strategy for biodiversity conservation in the face of climatic change. This enhanced network of protected areas must be embedded within landscapes that are managed to ensure their permeability to species making adjustments to their spatial distributions. The provision of habitat 'stepping stones' is seen as the primary mechanism for rendering landscapes permeable. The challenges and opportunities that the development of such adaptation strategies presents must be addressed internationally if the resulting strategies are to be effective.

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I.   INTRODUCTION

This paper has been prepared for the 'Group of Experts on Biodiversity and Climate Change' of the Bern Convention for discussion at their meeting in June 2007.   The principal focus of the paper is upon the principles that ought to underpin the development of adaptation strategies that will maximise the conservation of biodiversity in the face of climatic change, and what these principles may mean in practice;   these topics are dealt with in sections 6 and 7 of the paper.   In order to illustrate the basis from which these underpinning principles have been developed, however, the paper begins with four sections summarising essential background material, a thorough understanding of which is essential to the development of appropriate adaptation strategies.   These background sections deal in turn with: the climatic changes predicted by the end of the present century;   evidence from studies of the Quaternary geological period, as well as of the more recent past, showing how species have responded to past climatic changes;   a discussion of how ecosystems are affected by climatic change;   and an outline of the expected responses of species to projected 21st century climatic changes.   The sixth section then sums up the key implications of this background material for the development of biodiversity conservation strategies.   The seventh section deals with the principles and potential practical approaches to adaptation, and is followed by the final concluding section summarising the key elements that it is proposed ought to be part of any adaptation strategy.

II.   CONTEXT – PREDICTED 21ST CENTURY CLIMATIC CHANGE

Before considering potential adaptation strategies to maximise the conservation of European biodiversity in the face of predicted climatic changes, it is essential to understand how the climate of Europe is expected to have changed by the end of the present century, and the extent to which different regions of Europe may experience climatic changes that differ in important respects.   It is also important to consider the predicted climatic changes in the context of past changes, because such contextual background can assist in assessing the resilience of the biosphere to predicted 21st century climatic changes.

Successive scientific reports from the Intergovernmental Panel on Climate Change (IPCC) have provided estimates of the range of potential increase in the global mean temperature by the end of the present century (IPCC, 1990, 1995, 2001, 2007).   The most recent report (IPCC, 2007) considers that the most likely global mean temperature increase this century (2090–99 relative to 1980–99) is 1·8°C for the low emission B1 scenario and 4·0°C for the high emission A1FI scenario (Leggett *et al.*, 1992; Nakicenovic & Swart, 2000), with likely ranges of 1·1 – 2·9°C and 2·4 – 6·4°C respectively.   This report also estimates that there has been an increase of 0·74°C (uncertainty range 0·56 – 0·92°C) in global mean surface temperature during the 20th century (1906–2005);   furthermore, the rate of warming has accelerated during the century.   In terms of biodiversity conservation and adaptation measures, the IPCC (2007) also reports that global mean temperature is expected to continue to increase at a rate of *ca*. 0·2°C per decade for the next two decades regardless of future emission levels; thereafter, the extent and rate of warming are determined by the emission levels and hence by the stringency of internationally agreed and implemented mitigation measures.

Global mean temperature, however, is to some extent a misleading value to consider.   The IPCC (2007) reports that warming is expected to be greater in general over the continents than over the oceans, and greatest over the high northern latitudes.   Snow cover is expected to be reduced in extent and duration, whilst the extent of Arctic sea ice will decline;   in some scenarios late-summer sea ice in the Arctic basin has almost disappeared by the end of the century.   Precipitation is very likely to increase in high latitude areas, with decreases likely in sub-tropical land areas.   It is also considered very likely that a range of extreme climatic events, including heat waves and episodes of heavy precipitation, will become more frequent.

Although the full regional implications of the results presented in the IPCC Working Group 1 Fourth Assessment Report (IPCC, 2007) are not yet available at the time of writing, the results from climate projections made for the Third Assessment Report (Cubasch *et al.*, 2001) can be used to provide a valuable guide as to what can be expected in Europe.   In addition, various regional climate modelling studies (e.g. Räisänen *et al.*, 2004) provide further insight.   Overall, the results presented by Räisänen *et al.* (2004) indicate that Europe can be expected to experience warming of a greater

magnitude than the global mean.   For general circulation model (GCM) scenarios giving 21st century global mean warming of 2·3 – 2·6°C for the SRES B2 scenario and 3·2 – 3·4°C for the A2 scenario, annual mean temperatures across Europe increased by 2 – 4°C and 2 – 6°C respectively (2071–2100 relative to 1961–90).   These are equivalent to mean rates of temperature increase of 0·18 – 0·36°C per decade and 0·18 – 0·55°C per decade respectively.   Seasonal temperatures showed even greater increases.   Simulated warming was greatest in winter in the north, where the DJF (December–January–February) mean temperature increased by 4 – 6°C over much of Fennoscandia, whereas warming was greatest in summer in the south, where JJA (June–July–August) mean temperature increased by 4 – 6°C over large areas in most scenarios, and by as much as 10°C in some scenarios and areas.   Temperature extremes were simulated to increase to an even greater extent, annual maximum temperature increased by 6 – 12°C across most of Europe south of *ca*. 50° N, whilst annual minimum temperature increased by 6 – 18°C throughout most of Europe east of the Greenwich Meridian.
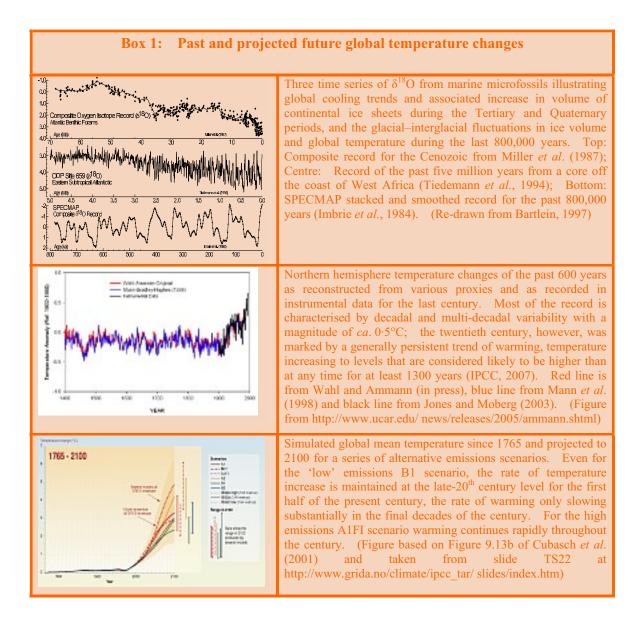
Turning to precipitation, the results presented by Räisänen *et al.* (2004) showed a very marked contrast between southern and northern Europe, both in terms of total annual precipitation and in terms of seasonal precipitation.   Annual precipitation was consistently simulated to decrease, by 10 – 40 %, across most of southern Europe, with slight increases in south-east Europe for only one of the scenarios examined, whereas increases of 10 – 40 % were simulated for areas north of *ca*. 60° N. During the summer season, JJA precipitation decreased by > 40 % across most of Europe south of *ca*. 40° N in most scenarios, whereas JJA precipitation increased in most areas north of *ca*. 60° N. Winter season (DJF) precipitation increased even more markedly in northern Europe, by 20 – 50 % in most areas north of *ca*. 40° N, whilst southern Europe was simulated to have only small changes, with increases or decreases of < 10 % in most areas for most scenarios.   Maximum one-day precipitation increased across many parts of Europe, by > 20 % in many areas, but with no clear large-scale geographical pattern.

Windiness showed a general tendency to increase in north-eastern Europe, by up to 12 % in some scenarios, but to decrease in the south and west, although generally by only 4 – 8 %.   Extreme wind events showed a similar pattern, being characterised by up to 15 % higher extreme wind speeds in northern Europe but up to 11 % lower extreme wind speeds in the south-west.   This pattern relates to the more northerly position simulated for the predominant storm track by the end of the century.

One way to contextualise these simulated climatic changes is to compare them with the magnitude of the spatial gradients in the present climate of Europe.   The simulated increase of 4 – 6°C in DJF mean temperature in Fennoscandia is equivalent to the present (1961–90) difference in DJF mean between Helsinki and Bucharest, or between Copenhagen and Dublin, whilst the simulated increase of 4 – 6°C in JJA mean temperature in southern Europe is equivalent to the present difference between Bordeaux and Madrid.   The simulated increases and decreases in precipitation do not generally translate into such large spatial displacements, mainly because the spatial patterns in precipitation are more regional in scale, whereas those in temperature are more clearly continental in scale.   Nonetheless, the increase in DJF precipitation simulated in northern Europe equates to westward shifts of at least a few hundred kilometres in most regions, whilst the decrease in JJA precipitation simulated in the south equates generally to a similar magnitude of displacement, usually in a southward direction.   In south-western Europe, however, the simulated decrease in JJA precipitation is equivalent to a spatial displacement of similar magnitude to that implied by the simulated increase in JJA mean temperature.

An alternative and in may ways more telling way to contextualise the simulated changes is to compare their rate and magnitude, as well as the potential future climate of Europe, with evidence of past climate and past rapid climatic changes [Box 1].   The Quaternary geological period spans approximately the last two million years, the transition from the preceding Tertiary period being marked by a global cooling event (Bartlein, 1997).   Superimposed upon a general long-term cooling trend during the Quaternary have been a series of marked fluctuations in global climate on time scales of tens to hundreds of thousands of years.   For the past *ca*. 800,000 years the predominant fluctuations have had a periodicity of *ca*. 100,000 years (EPICA community members, 2004) and have been of larger magnitude than previously.   These fluctuations characterise the Quaternary "Ice Age",

representing alternations between interglacial conditions, broadly similar to the present in global climatic terms, and glacial conditions, when global mean temperature is estimated to have been *ca*. 5 – 7°C cooler than that of the recent past (Kutzbach *et al.*, 1998).

Box 1: Past and projected future global temperature changes	
	Three time series of $\delta^{18}O$ from marine microfossils illustrating global cooling trends and associated increase in volume of continental ice sheets during the Tertiary and Quaternary periods, and the glacial–interglacial fluctuations in ice volume and global temperature during the last 800,000 years. Top: Composite record for the Cenozoic from Miller *et al.* (1987); Centre: Record of the past five million years from a core off the coast of West Africa (Tiedemann *et al.*, 1994); Bottom: SPECMAP stacked and smoothed record for the past 800,000 years (Imbrie *et al.*, 1984). (Re-drawn from Bartlein, 1997)
	Northern hemisphere temperature changes of the past 600 years as reconstructed from various proxies and as recorded in instrumental data for the last century. Most of the record is characterised by decadal and multi-decadal variability with a magnitude of *ca*. 0·5°C; the twentieth century, however, was marked by a generally persistent trend of warming, temperature increasing to levels that are considered likely to be higher than at any time for at least 1300 years (IPCC, 2007). Red line is from Wahl and Ammann (in press), blue line from Mann *et al.* (1998) and black line from Jones and Moberg (2003). (Figure from http://www.ucar.edu/ news/releases/2005/ammann.shtml)
	Simulated global mean temperature since 1765 and projected to 2100 for a series of alternative emissions scenarios. Even for the 'low' emissions B1 scenario, the rate of temperature increase is maintained at the late-20th century level for the first half of the present century, the rate of warming only slowing substantially in the final decades of the century. For the high emissions A1FI scenario warming continues rapidly throughout the century. (Figure based on Figure 9.13b of Cubasch *et al.* (2001) and taken from slide TS22 at http://www.grida.no/climate/ipcc_tar/ slides/index.htm)

Even the warmest of interglacial stages, which was probably the last or Eemian interglacial, *ca*. 127 – 110 thousand years ago (Brauer *et al.*, 2007), had a global mean temperature no more than 1 – 2°C warmer than the recent past (Overpeck *et al.*, 2005). Thus, in terms of magnitude, the projected increase in global mean temperature this century is unlikely to exceed the magnitude of the shift in global mean temperature between the last glacial maximum, *ca*. 21,000 years ago, and the middle of the present interglacial stage, *ca*. 6000 years ago. In terms of 'destination', however, even at the lower end of the uncertainty range given by IPCC (2007) (*ca*. 1·84°C warming between 1906 and 2090-99), the projected increase represents warming at least equivalent to the warmest part of the past two million years; an increase near the middle of the projected range, i.e. *ca*. 3·6°C warming between 1906 and 2090-99, would result in global temperatures without precedent during the Quaternary and probably unparalleled also during the late-Tertiary, whilst any increase greater than this leads to a destination without an analogue during at least the past ten million years of earth history.

The most rapid large magnitude changes in global mean temperature of the recent geological past are the so-called glacial terminations, the most recent of which occurred between *ca*. 15,000 and 9000 years ago. Although the rapidity of the increase in global mean temperature has been a subject of debate, with conflicting views expressed (see e.g. Overpeck *et al.*, 2003; 2005), the most recent consensus is that the most rapid past large magnitude global warming events were at least an order of magnitude less rapid than the warming projected for the present century (Jansen *et al.*, 2007). Thus both the 'destination' and the rate of the changes in global climate projected for the present century are very likely to be without any precedent in recent earth history – and hence unprecedented during the 'evolutionary lifetime' of most species on earth today, ourselves included.

III. Species' responses to past climatic changes

Species' distribution patterns are determined by a hierarchy of interacting factors operating at different temporal and spatial scales. The restriction of some major taxonomic groups to a single continent or hemisphere reflects the relationship between their evolutionary history and the plate tectonic movements of the continents on the earth's surface over the geological long-term of tens to hundreds of millions of years. The vicariant patterns of distribution in different parts of southern Europe, or on the islands of the Mediterranean, seen amongst species in some taxonomic groups, probably reflects independent evolution in these areas during the late-Tertiary and Quaternary from ancestral species more widespread in the region earlier in the Tertiary (see e.g. Blondel *et al.*, 1996; Randi, 1996). Such historical factors interact principally with current climate to determine species' present distribution patterns at sub-continental to continental scales. At more local spatial scales, factors such as geology, topography and land-use interact with the macroclimate to determine how species are distributed within a region or landscape. Shorter-term historical factors, including natural and anthropogenic disturbance, historical land-use and extreme climatic events, also play a part in determining species' patterns of occurrence at these more local spatial scales.

Given the magnitude of projected future climatic changes, as discussed above, and the predominant role of climate, along with long-term historical factors, in determining species' sub-continental to continental scale distribution patterns, it is at this scale that insight is needed into the potential responses of species to climatic change. Given also the rapid large magnitude climatic changes that have characterised the fluctuations between glacial and interglacial conditions over the past 800,000 years, the record of species' responses to those past changes can provide the insight that we seek.

The Quaternary fossil record provides ample evidence of how the members of many different taxonomic groups of terrestrial organisms responded to past climatic changes. The most valuable part of this record, however, is that extending from the last glacial maximum, *ca*. 21,000 years ago, to the present. This is because this interval spans the most recent glacial termination, is within the range of radiocarbon dating, enabling the rates of change to be better assessed than for any earlier glacial termination, and is represented by hundreds of sedimentary records throughout Europe, as well as hundreds more from the other continents. Furthermore, in the case of Europe these records include many from areas covered by the ice sheets of the last glacial stage, areas where glacial erosion

has often removed, or glacial deposition buried, sediments deposited during earlier stages of the Quaternary.
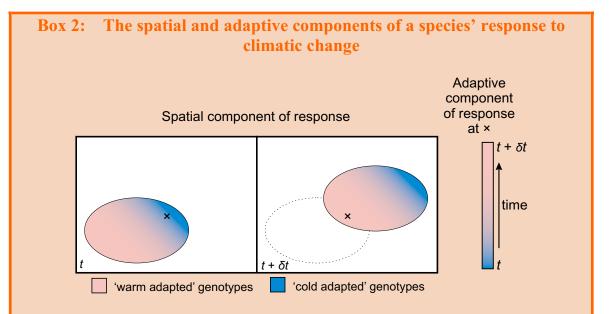
Studies of the fossil pollen and spores of higher plants preserved in peats and lake sediments have allowed mapping of the distribution and abundance patterns of individual European plant taxa (Huntley & Birks, 1983; Huntley, 1988) and of the patterns in the vegetation of Europe (Huntley, 1990b; 1990c) since the last glacial. More recently, complementary data from genetic studies of species across their European ranges have provided improved understanding of tree species' past distribution patterns and their responses to Quaternary climatic changes (see e.g. Brewer *et al.*, 2002; Heuertz *et al.*, 2006; Magri *et al.*, 2006; Palme & Vendramin, 2002; Palme *et al.*, 2003; Petit *et al.*, 2002a; Scotti *et al.*, 2000; Vendramin *et al.*, 1999). These data, along with the parallel but less abundant fossil evidence for members of other taxonomic groups, reveal that the principal large scale response of species to past climatic changes was a spatial response: Species shifted their geographical distribution as the climate changed, apparently occupying those areas where, at any given time, their climatic tolerances and/or requirements were satisfied (Graham & Grimm, 1990; Huntley, 1991).

In the past, this spatial response often has been contrasted with an *in situ* adaptive evolutionary response, seen as the alternative way a species might respond to climatic change (e.g. Huntley *et al.*, 1997a). Furthermore, the Quaternary fossil record has provided evidence, at least for a handful of species, that can be interpreted as indicating adaptive morphological evolution in response to climatic fluctuations on multi-millennial time scales (e.g. Rousseau, 1997; Smith *et al.*, 1995). In these examples, however, that record adaptive evolutionary response of a species in one region, the range of morphology seen amongst the fossils falls within the overall range found today across the species' geographical range. This underlines the argument put forward by Bradshaw and McNeilly (1991), on the basis of previous extensive work on evolutionary adaptation of plant species to heavy-metal contaminated soils (see e.g. Symeonidis *et al.*, 1985; Wu *et al.*, 1975), that species' capacity to adapt to climatic change will be constrained by their inherent genetic variance. Recent experimental studies of species' responses to short-term climatic fluctuations (e.g. Franks *et al.*, 2007; see also Huntley, 2007) have provided further evidence in support of this argument. Only exceptionally has evidence been found of a species displaying previously unrecorded morphological evolution during its post-glacial range expansion (Hellberg *et al.*, 2001); such exceptions are not unexpected, however, and may reflect either the selection of genotypes arising from 'new' mutations or the selection of previously 'hidden' genetic variance. In reality, for most species, adaptive evolutionary responses such as those recorded for *Pupilla muscorum* (Rousseau, 1997) or *Neotoma cinerea* (Smith *et al.*, 1995) are the local complement to, and a consequence of, the species' overall spatial response to climatic change, rather than some separate and contrasting response [Box 2]. Only over much longer time scales, typically of hundreds of thousands of years, and hence spanning several glacial–interglacial cycles, have new species evolved adapted to the new environmental opportunities offered as a result of the long-term trends in the global environment during the Quaternary (Lister, 2004).

The Quaternary fossil record also provides evidence of the fate of species that were unable to achieve a sufficient spatial and/or adaptive response to past rapid climatic changes of large magnitude: Such species suffered regional or global extinction (Stuart, 1993; Stuart *et al.*, 2004). Although the extent to which human hunting pressures may have contributed to the extinction of some Pleistocene mammals, by exacerbating the stresses they faced already as a result of the rapidly changing climate, is still a matter of debate (Barnosky *et al.*, 2004), the role of rapid large magnitude climatic changes is likely to have been important in most cases (see e.g. Guthrie, 2006). The demonstration that an important forest tree of south-eastern North America became extinct during the last glacial termination (Jackson & Weng, 1999) reinforces the important role of climatic change in such extinctions. Such extinctions can result from several different mechanisms (Huntley, 1999; Overpeck *et al.*, 2003) that generate spatial and/or temporal discontinuities in the availability of, or major reductions in the extent of, areas offering the conditions to which the species is adapted.

In addition to providing evidence of the primary role of the spatial response of species to past climatic changes, the Quaternary fossil record also enables estimates to be made of the rates and magnitudes of this response. The magnitude of the spatial response, in terms of the overall displacement of species' range boundaries, varied according to the extent to which species were able

to exploit, or in some cases perhaps were limited to exploiting, topographically varied landscapes that offered sites with contrasting local climatic conditions in relative proximity to one another (McGlone, 1997, 1988; Thompson, 1988), as opposed to facing the necessity to shift across extensive relatively low relief areas (Huntley, 1988; Webb, 1988). In a European context, this means that many species probably were able to persist through both glacial and interglacial stages in parts of southern Europe (Bennett *et al.*, 1991), because they were able to take advantage of the relatively high relief, occupying topographically contrasting sites during glacial as opposed to interglacial stages. Some such species, especially perhaps those restricted to individual Mediterranean islands, may as a result have been able to persist through Quaternary climatic fluctuations without any substantial shift in their overall geographical distribution. Over most of the European continent, however, and especially in areas north of the principal mountain ranges, that extend from the Cantabrians in the west to the Carpathians in the east, as well as in areas that were directly affected by the last glacial ice sheets, species' range boundaries shifted by one to two thousand kilometres in response to the climatic changes marking the transition from the last glacial stage to the post-glacial or Holocene (Huntley & Birks, 1983; Huntley, 1988). For many species this shift in range boundary represented a range expansion from a much more limited area of distribution during the glacial; others, however, especially species that today are limited to Boreal or Arctic areas of Europe, shifted their entire range. It also is relevant to note that the present distributions of temperate species in Europe probably are close to their maximum Quaternary extent, whereas those of Boreal, Arctic and montane species probably are close to their minimum Quaternary extent.

Box 2:   The spatial and adaptive components of a species' response to climatic change

The rectangular area represents a continental region, within which the species' area of geographical distribution is represented by the shaded ellipse. The graded colour of the shading represents clinal variation in the species' adaptation to temperature. The shaded ellipse is displaced between times t (left-hand panel) and $t + \delta t$ (right-hand panel), its former position at time t being indicated on the panel for time $t + \delta t$ by the dotted outline. This displacement represents the spatial component of the species' response to a climatic change between times t and $t + \delta t$. The symbol × signifies a fixed location that falls within the species' geographical distribution at both times t and $t + \delta t$. At this location the adaptive component of the species' response to climatic change results in natural selection progressively favouring more warm adapted genotypes. (Re-drawn from Huntley *et al.*, 2006; see also Huntley *et al.*, in press)

Turning to the rate at which species realised their range or range boundary shifts made in response to the climatic changes of the last glacial termination, the most abundant evidence upon which to assess these rates comes once again from the numerous studies of the pollen and spores of higher plants preserved in peats and lake sediments.   Mapping of such data has enabled estimates of these rates to be made for eastern North America (Davis, 1976) and Europe (Huntley & Birks, 1983; Huntley, 1991, 1988).   The results suggest that for most trees, the group best represented in the pollen records from these regions, the long-term average rates of range boundary displacement were **$200 – 500$ m yr^{-1}, with exceptional examples from both continents of taxa that achieved rates of as much as $1 – 2$ km yr^{-1}** (Huntley & Birks, 1983; Ritchie & MacDonald, 1986).   Although a number of recent studies have used evidence from macrofossils (e.g. fruits, seeds) to demonstrate that tree taxa were locally present up to a millennium before their pollen increased in abundance (Kullman, 1998a, b), indicating that the rates inferred from the palynological evidence may be under-estimates, the results of these studies imply only modestly higher rates, given that range boundary adjustments took place over several millennia.   Furthermore, similar macrofossil evidence indicating that some temperate taxa may have had glacial areas of distribution that extended north of the main European mountain chains (Kullman, 1998a; Stewart & Lister, 2001; Willis *et al.*, 2000; Willis & van Andel, 2004), and perhaps even isolated areas of persistence in northern Europe (Kullman, 2006), imply that the magnitude of the range boundary adjustments estimated from the palynological evidence may be over-estimates, in which case their potential rates of adjustment to future projected climatic changes also will be over-estimated.   On balance, long-term average rates of range boundary adjustment by trees in the range $2 – 20$ km per decade are consistent with the available evidence.   The more limited evidence for other taxonomic groups indicates rates of range boundary adjustment of a similar magnitude (e.g. Preece, 1997).   The issue of the extent to which species' rates of range boundary adjustments lagged behind the climatic changes to which they were a response was long debated (Davis, 1989; see e.g. Davis, 1984; 1986; Pennington, 1986).   Prentice *et al.* (1991b), however, demonstrated that, in eastern North America, the apparently lagging responses of some tree taxa, discussed by previous authors, reflected the differing climatic tolerances and requirements of these taxa, and hence their different opportunities to respond as the climate continued to change during the Holocene   Furthermore, in areas of high relief, where species' responses can be realised mainly through local adjustments of the elevation range or topographic positions that they occupy, high temporal resolution analyses have now shown no evidence of lags, nor of differential rates of response between vegetation and aquatic invertebrates (Ammann *et al.*, 2000).

A further key conclusion from studies of species' responses to past climatic changes is that these responses were individualistic: Each species exhibited its own unique patterns, rates and magnitudes of distribution change in response to the changes in climate (see e.g. FAUNMAP Working Group, 1996; Graham & Grimm, 1990; Huntley & Birks, 1983; Huntley, 1991).   This has important implications when considering the interactions between ecosystems and climatic change.   It also informs the approaches used to simulate the potential impacts of projected 21st century climatic changes on species and biodiversity.

In addition to the important evidence from studies of the Quaternary of the nature of species' responses to past climatic changes, of the individualism of these response, and of the rates and magnitudes at which the spatial component of these responses were achieved, an understanding of the Quaternary history of Europe also provides important insight into present patterns of biodiversity across the continent.   The most obvious and long-standing of these insights relates to the importance of high relief areas of southern Europe, especially in the Iberian Peninsula, Italy and the Balkans. These areas are important firstly because many species that remain restricted to these areas today were able to persist there also during glacial stages, and secondly because of the scope that they have offered for vicariant evolution in many species groups.   However, it also is apparent that many species that today have more extensive distributions in the temperate zone of Europe had their glacial areas of distribution principally in these regions, and have in many cases also persisted in these regions during the post-glacial and earlier interglacial stages (Bennett *et al.*, 1991).   As a result of the relative stability of the populations in these regions, and the contrasting impact of the multiple founder effects that have characterised the process of Holocene range expansion leading to the species' wider present area of distribution (Ibrahim *et al.*, 1996), the genetic diversity of the southern populations of many species represents a highly disproportiate fraction of the species' overall genetic diversity

(Hampe & Petit, 2005; Petit *et al.*, 2003).   Furthermore, in the case of those temperate species that have long been present in two or more of these regions, unique components of the species' overall genetic diversity are now often associated with each region (Hewitt, 1996, 1999; Santucci *et al.*, 1998), probably as a reflection of allopatric genetic divergence during the Pleistocene, and especially perhaps during glacial stages (cf. Knowles, 2001).

The evidence of species' responses to climatic change from studies of the Quaternary is now being complemented by evidence from studies of the responses of species to the climatic changes that have characterised the past century, and that have accelerated in rate since *ca*. 1950.   As expected, given the evidence from the Quaternary, many species are showing evidence of spatial responses to the climatic changes (see e.g. Franco *et al.*, 2006; Hill *et al.*, 2002; Parmesan *et al.*, 1999; Root *et al.*, 2003; Thomas & Lennon, 1999; Thomas *et al.*, 2006).   Parmesan and Yohe (2003) reported, on the basis of an extensive meta-analysis of studies of species' responses to recent climatic change, that species were on average shifting their range boundaries at *ca*. 6·1 km per decade.   This figure, strikingly, falls within the range expected on the basis of evidence from studies of the Quaternary.   In contrast to the conclusions from the record of species' responses to Quaternary climatic changes, however, there also is mounting evidence that many species' have failed to shift their ranges as quickly as they potentially might have done in response to the climatic changes of the past half century, given the rates at which climate has been changing.   Although Parmesan *et al*. (1999) concluded that in general European butterflies exhibited poleward shifts, especially of their northern range boundaries, of similar magnitude to that expected in response to recent climatic warming, a more detailed analysis of butterflies in Great Britain (Warren *et al.*, 2001) subsequently provided clear evidence that many species' range boundary adjustments were lagging the climatic changes.

In addition to the evidence of spatial responses to recent climatic changes, a large number of species has also been shown to be exhibiting phenological responses (Parmesan & Yohe, 2003; Root *et al.*, 2003).   Such responses, especially earlier arrival of migrants in spring and earlier dates for key stages of the annual reproductive cycle, reflect triggering of these annual activities by spring temperature.   However, not all organisms use temperature as a trigger; many instead use day length.   Day length, however, is not changing as climate changes, with the potential result that species' interactions may be disrupted if one of a pair of interacting species responds to spring temperature increases with earlier onset of key life-cycle stages whereas the other, responding to day length, shows no advance in the timing of its activities.

The spatial and phenological responses already apparent are only two of a hierarchy of responses that species can be expected to exhibit when examined across the full range of scales from patch *via* landscape and regional to continental [Box 3].   Monitoring of these and other responses that can be expected to be apparent at individual sites, within regions or countries, or continent-wide, will be important to provide evidence of the extent and rapidity with which climatic change is impacting upon the biosphere.

Box 3: The 'hierarchy' of species' responses to climatic change

Species' responses to climatic change can be classified in various ways; furthermore, how a species is perceived to respond to climatic change will depend upon where, within its overall geographical distribution, and also at what temporal and spatial scales, it is examined. The 'hierarchy' of responses proposed here comprises five general categories of response that to some extent operate at progressively larger spatial and/or longer temporal scales. These should not be considered as alternatives or as competing responses, however, but as components of an overall response by species to climatic change; the apparent relative importance of each component simply changes according to the spatial and/or temporal scale at which the response is observed.

Behavioural responses: Species may alter their behaviour in various ways as climate changes. The phenological changes exhibited by many species in response to the climatic changes of the past half century are in many cases likely principally to be behavioural responses. These changes are apparent for species' life-cycle stages that are triggered by temperature (see e.g. Both *et al.*, 2005). Typically such responses are manifested in Europe as earlier onset of various life-cycle stages in spring and/or later onset of stages in the autumn. Behavioural responses may also underlie changes in migratory strategy seen in some birds, whilst species that use behavioural mechanisms to regulate their temperature will also exhibit changes in behaviour as climate changes. Behavioural responses are often apparent even in response to inter-annual climatic variability and may occur throughout a species' range.

Population dynamic responses: It is likely that for many species climatic effects operate principally through the sensitivity of various stages of their life-cycle to some aspect(s) of climate. Thus breeding success, number of offspring/propagules produced, survival to adulthood and adult survival all may be influenced by climatic conditions. Examples where such sensitivity has been demonstrated include the dependence upon temperature during the flowering period for successful fertilisation in *Tilia cordata* (Pigott & Huntley, 1981) and the impact of low temperatures on over-winter survival of the eggs of *Epirrita autumnata* (Tenow & Nilssen, 1990), although such effects have been inferred for many more species (see e.g. Cowley & Siriwardena, 2005; Rodel *et al.*, 2004; Steen *et al.*, 2006). Positive population responses can be expected towards the 'leading edge' of a species' distribution relative to a climatic change, and *vice versa*. Although a single extreme season may elicit an obvious and more or less immediate population response in some species, population responses for most species that live longer than one year are likely only to become apparent over a period of several years, or even longer in the case of long-lived species.

Adaptive genetic responses: Climatic change may exert selective pressures favouring genotypes within a species' population that are better-adapted (e.g. physiologically, behaviourally or morphologically) to the new conditions. Thus at least some phenological responses have been shown to be genetically controlled (see e.g. Franks *et al.*, 2007), as have some observed changes in migratory strategy (see e.g. Berthold *et al.*, 1992). The extent of such responses, however, will vary amongst species according to their inherent genetic variance (Bradshaw & McNeilly, 1991; Huntley, 2007). The extent to which such responses will be apparent will also vary according to the location examined; the greatest magnitude of response is likely to be seen at locations close to the 'leading edge' of a species' distribution relative to a climatic change, whereas most species are unlikely to exhibit any adaptive response at locations close to the 'trailing edge' of their distribution. Where they occur, however, such responses may be achieved within only a few generations, although how long this represents will depend upon the longevity and/or age at first breeding of the species examined.

Spatial responses: These responses result from the effects of climatic change on species' population dynamics combined with species' inherent dispersal behaviour. A proportion of individuals disperse beyond the species' effective climatic limits; under stable climatic conditions these individuals will fail to breed and/or fail to survive. Under changing conditions, however, individuals dispersing beyond the 'leading edge' of the species' distribution relative to the climatic change will find suitable conditions and thus will survive to establish populations beyond the species' previous range limit. Conversely, individuals close to the 'trailing edge' of the distribution, but within the previous range limit, will experience unsuitable conditions, resulting in breeding failure and or failure to survive. The net effect is an overall shift in the species' distribution. Such shifts may be manifested with respect to elevation, locally within topographically complex landscapes, or at regional – continental scales. Evidence from the Quaternary, along with evidence of species' responses to recent climatic change, indicates that such responses will become apparent over time scales of no more than decades, at least in the case of more mobile species.

Macro-evolutionary responses: As Lister (2004) has argued, only long-term ($> 10^5$ years) persistent climatic trends in the past led to the evolution of new species adapted to the new conditions. Thus, for example, the mammoth lineage (*Mammuthus* spp.) exhibited evolution during the Quaternary that culminated in the Woolly Mammoth (*Mammuthus primigenius*), a cold-adapted species able to exploit the steppe–tundra habitat that was extensive during late-Quaternary glacial stages

IV. ECOSYSTEMS AND CLIMATIC CHANGE

A primary consequence of the individualism of species' responses to climatic change is that the assemblages of species found at any time, and recognised as communities or ecosystems, are impermanent (Huntley, 1996; West, 1964). Thus the Quaternary fossil record provides abundant evidence that, when past combinations of climatic and other conditions were without a contemporary analogue, the composition of the communities or ecosystems of that time also were without an analogue among present-day communities and ecosystems (Graham & Grimm, 1990; Graham, 1997; Graham, 1992; Huntley, 1990a; Overpeck *et al.*, 1985; Overpeck *et al.*, 1992).   Thus it can be argued that, at least with respect to their species composition. ecosystems do not respond to climatic change, only their component species exhibiting responses.   Nonetheless, changes in ecosystem composition and structure can be observed, although these are manifestations of the individualistic responses of the species of which those ecosystems are comprised.

Initially, the relative abundances of the component species present in the ecosystem can be expected to change as climatic change differentially affects their population dynamics. Species favoured by the change will increase in relative abundance, whereas those disadvantaged by the change will decrease in relative abundance. Such shifts in relative abundance may be manifested relatively rapidly;   even in stands dominated by herbaceous perennials, the relative abundance of the various plant species, in terms of their above-ground biomass, has been shown to vary between years in response to inter-annual climatic variations (Dunnett *et al.*, 1998). Such changes may reflect either direct or indirect effects of the climatic change upon the species exhibiting a response;   a predatory species, for example, may exhibit a response as a result of a change in prey abundance and/or availability rather than because the climatic change has any direct physiological or other impact upon the species itself (see e.g. Buse *et al.*, 1999). Furthermore, such indirect effects may often reflect, or be exacerbated by, differential phenological responses by interacting species at different trophic levels (see e.g. Visser *et al.*, 1998; 2004; 2006).   It is important to note at this point, however, that such indirect responses mediated through inter-specific interactions do not conflict with the individualism of species' responses, because the majority of such interactions are non-specific (Huntley *et al.*, 1997b).   Given also that the majority of specialised interactions are not obligate for both interacting species, it is only in the small minority of highly specialised and jointly obligate interactions that interacting species potentially will show a joint response to climatic change.

Such quantitative changes in the composition of the ecosystem will be complemented by qualitative changes in composition.   Taxa previously absent will invade the ecosystem when climatic conditions change sufficiently to enable them to do so, even if initially the ecosystem acts principally as a sink for dispersing individuals from source populations in climatically more favourable areas nearby. In parallel to this, taxa for which conditions are no longer suitable will be lost from the ecosystem.   The rates both of the recruitment of new taxa and of the loss of taxa initially present will be determined in part by the rate of change of climatic conditions and in part by the life-history characteristics of the taxon and how these respond to climate.   Thus, long-lived plant taxa, especially trees, may persist long after conditions either are no longer suitable to sustain their regeneration or else would favour a different competitive outcome following a disturbance (Prentice *et al.*, 1991a, 1993). Shorter-lived taxa are likely to be lost much more rapidly, especially if the altered climate impacts strongly and negatively upon a critical life-history stage.   Similarly, longer-lived taxa, that typically take longer to reach reproductive maturity, often produce fewer offspring or propagules than short-lived taxa and depend upon rare long-distance dispersal events over distances often in excess of ten kilometres, are likely to colonise newly-suitable ecosystem patches more slowly than will shorter-lived taxa.   Expressing this in terms of reproductive strategies, K-selected taxa can be expected in general to colonise newly available areas more slowly than will r-selected taxa.   In terms of Grime's (1978) model of plant strategies, R-strategists (ruderals) are likely to colonise more rapidly than C-strategists (competitors) with S-strategists (stress tolerators) likely to be those that will respond least rapidly.

Structural changes in ecosystems will occur where these are the consequence of the compositional changes.   Thus, for example, if conditions change in a way that allows tree taxa to colonise an

ecosystem that previously was dominated by herbaceous species, then inevitably a structural change will take place. Such structural changes will often, in turn, result in a cascade of further compositional changes: For example, light-demanding herbaceous plants may be replaced by shade-tolerant taxa; grazing herbivores may be replaced by browsing species; ground-nesting birds feeding predominantly by picking invertebrates from the ground surface or short vegetation may be replaced by species that nest in the tree canopy or in tree-holes and that feed predominantly upon invertebrates gleaned from leaves in the tree canopy. These latter changes may not in themselves be direct consequences of the climatic change, and of how this interacts with the tolerances or requirements of the species in question, but are certainly indirect consequences of the climatic change. Often these indirect mechanisms may have consequences at least as important and far-reaching as the direct effects of the climatic change.

These changes in ecosystem composition, and especially in ecosystem structure, in many cases have important implications for the interactions between the biosphere and the climate system, as well as for ecosystem services upon which society depends. Although a detailed discussion of these effects is not appropriate here, their potential importance must not be overlooked. A change from tundra to taiga in Arctic Europe, for example, would have important implications in terms of the snow–albedo feedback that would lead to further warming, whilst the same change also has the potential to result in the accelerated decomposition of organic matter stored in the soils of the present tundra (Sjogersten & Wookey, 2002), again leading to a possible positive feedback as this decomposition process releases carbon dioxide to the atmosphere. The potential simplification and reduced biodiversity in ecosystems that lose species as a result of climatic change more rapidly than potential new species are recruited may well result in reduced biomass and hence reduced carbon dioxide uptake by these ecosystems (Diaz *et al.*, 2006; Fargione *et al.*, 2007; Lambers *et al.*, 2004; Loreau *et al.*, 2001; Reich *et al.*, 2001; Reich *et al.*, 2004; Symstad *et al.*, 2003; Tilman *et al.*, 2001; Tilman *et al.*, 2006); such carbon dioxide uptake is a vital ecosystem service upon the maintenance of which society depends.

Before leaving the subject of ecosystems and climatic change, it should be noted that some ecosystems depend for their continued existence upon physical habitats that themselves are at risk as a result of projected climatic changes. Globally perhaps the most threatened this century is the habitat provided by the sea ice of the Arctic basin (IPCC, 2007). This is relevant to European biodiversity because the seasonal sea-ice at present extends into the Barents Sea and supports a unique component of that biodiversity, including *Pagophila eburnea* (Ivory Gull), *Ursus maritimus* (Polar Bear) and several species of seal that use the sea-ice during the breeding season. The melting of permafrost in Arctic Europe will similarly result in loss of habitats such as those provided by palsa mires (Fronzek *et al.*, 2006). Elsewhere in Europe, the threat to wetlands, especially in the south where the combination of higher summer temperatures and reduced precipitation will result in the greatest tendency towards drying of such systems, has potentially severe implications for biodiversity. In this case, furthermore, the threat from climatic change adds to the considerable pressures faced by this habitat already from human water resource demands and drainage to provide agricultural land.

V. SPECIES' POTENTIAL RESPONSES TO PROJECTED CLIMATIC CHANGE

Given the evidence of how species' responded to past rapid climatic changes of large magnitude, and especially of the predominant role played by individualistic spatial responses, many studies have applied models of various types to simulate species' potential future distributions given scenarios of projected future climate. Collectively, these models can be referred to as 'climate envelope' models, although the methods used to fit the models, and the climatic or bioclimatic variables selected for inclusion in the models, vary widely. Although different models fitted to data for the same species using the same climatic dataset can give quite different projections of potential future species' distributions (see e.g. Araujo *et al.*, 2005b), leading some authors to recommend an approach that applies a series of alternative modelling techniques and then uses 'expert opinion' to select that which is viewed as the 'most accurate' (Thuiller, 2003) or an approach that identifies and selects the most 'consensual' simulations (Araujo *et al.*, 2005a), most of the discrepancies between models are likely to result from the disparate selections of variables made by different techniques. Where fundamentally different modelling approaches have been used but applied to the same or a closely similar set of

bioclimatic variables, the latter selected on the basis of their known physiological relevance to the group of taxa being modelled, the resulting simulations of potential future ranges are extremely similar (compare the results presented for several taxa in Huntley *et al.* (1995) and Huntley (1995) with those for the same taxa presented in Sykes *et al.* (1996) and Sykes (1997)).   Furthermore, the robustness of the modelling approach also has been demonstrated by studies examining a species' ranges in its native area of occurrence and in an area to which it was introduced (Beerling *et al.*, 1995), and by studies of species' historical and present geographical distributions (Araujo *et al.*, 2005b; Hill *et al.*, 1999).

The use of such models has, however, been criticised by various authors (see e.g. Davis *et al.*, 1998a; Davis *et al.*, 1998b; Lawton, 2000) who draw attention to some of the inherent assumptions of such models, although it also should be noted that others have presented strong counter-arguments (see e.g. Hodkinson, 1999; Pearson & Dawson, 2003).   The most contentious of the assumptions made by climate envelope modelling has been that relating to the individualism of species' responses. It is argued by the critics that as the group of other species with which a target species interacts changes, as a consequence of individualism, then the realised climatic range of the target species will, as a result of changes in competitive interactions in particular, be altered.   However, the evidence to support this argument is drawn from microcosm experiments with very small numbers of interacting species.   In reality, species interact as part of a much larger assemblage in an ecosystem, and do so with a different set of species in different parts of their present geographical ranges.   The magnitude of any inaccuracies in simulated potential future ranges resulting solely from changes in the composition of species assemblages is thus likely to be small relative to other sources of inaccuracies. The real problem, although is has rarely been the focus of criticisms of the use of climate envelope models, is that of making simulations of species' potential future ranges for combinations of conditions without a contemporary analogue.   In this context we should note that, even if a future climate is analogous to a present climate, it is likely to be located at a different latitude, and there also will be a higher atmospheric concentration of CO_2, both factors that act in concert with climatic conditions to determine species' performance and hence distribution and abundance patterns.   When examining simulations of species' potential future ranges made using climate envelope models, the uncertainties arising from the no-analogue character of future conditions (Williams *et al.*, 2007) should always be borne in mind.

A second area of criticism of climate envelope models relates to their failure to include any simulation of the dynamics of the simulated potential range changes.   Whilst this clearly is a limitation of the present state-of-the-art in such modelling, a separate series of models has been developed by various workers to simulate these dynamics (see e.g. Allen *et al.*, 1991; Carey, 1996, 1998; Collingham *et al.*, 1996; del Barrio *et al.*, 2006; Hanski & Thomas, 1994; Hanson *et al.*, 1990; Hengeveld, 1989; Hengeveld & van den Bosch, 1997; Johnson *et al.*, 1981; Pease *et al.*, 1989; Pulliam *et al.*, 1992).   Such models typically simulate the species' population dynamics and dispersal and have been used to explore the extent to which species' recorded recent range changes have tracked or lagged behind the potential range changes made possible by recent climatic warming (Warren *et al.*, 2001), to simulate the spread of alien invasive species (Collingham *et al.*, 1997; Wadsworth *et al.*, 2000), and to explore how landscape patterning and habitat fragmentation may affect species' ability to shift their geographical ranges (Collingham & Huntley, 2000; Hanson *et al.*, 1990; Hill *et al.*, 2001).   An important area of ongoing and future research is the integration of climate envelop and range dynamic models so as to provide simulations of the potential dynamic response of species to climatic change (see e.g. del Barrio *et al.*, 2006).

Notwithstanding their acknowledged assumptions and limitations, climate envelope models provide important insight into the potential magnitude and character of species' potential responses to projected future climatic changes (Pearson & Dawson, 2003).   Whilst the choice of fitting method and of variables remains an area of active scientific debate, and the details of the simulated potential future ranges of individual species, even for the same projected future climate scenario, remain uncertain, the results presented to date for a variety of taxonomic groups (see e.g. Araujo *et al.*, 2006; Hill *et al.*, 2003; Huntley *et al.*, 1995; Huntley, 1995; Huntley *et al.*, 2004; Huntley *et al.*, 2006; Huntley *et al.*, in press; Midgley *et al.*, 2003; Sykes *et al.*, 1996; Sykes, 1997; Thuiller, 2003; Thuiller *et al.*, 2006) are consistent in several important respects, allowing important conclusions to be reached

that are relevant to biodiversity conservation in Europe, as well as more generally. These conclusions include:
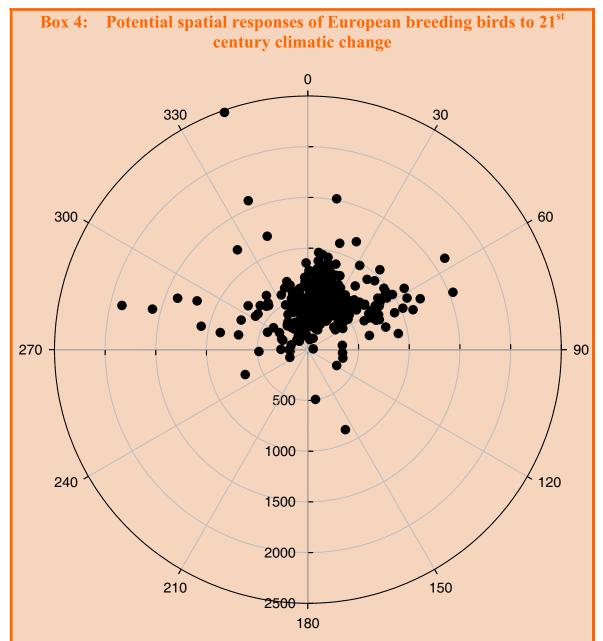
- European species' potential geographical distributions shift by several hundred kilometres, or even more than a thousand kilometres, by the end of the century.

- The overall trend in Europe is for species' future potential ranges to be displaced north-eastwards relative to their present ranges, although some individual species' range displacements are in quite disparate directions [Box 4].

- The rate of potential range displacement averages *ca*. 24 – 81 km per decade, depending upon the emissions scenario and GCM considered;   these rates are at least several times, and up to more than an order of magnitude, faster than rates estimated from the Quaternary fossil record (e.g. Huntley, 1991) or reported from studies of recent range adjustments (e.g. Parmesan & Yohe, 2003).

- Most species' potential future range in Europe is smaller in extent than its present range.

- The overlap between a species' potential future range and its present range is often less than half the extent of its present range by the end of the century, even for more moderate scenarios of climatic change.

- As a consequence of the general trend for species' ranges to decrease in extent, so too does the average number of species potentially present in a 50 km or $0.5°$ grid cell decrease.

- Some species currently found in Europe have no potential range in Europe by the end of the century, including some species endemic to the continent.

- Some species have no overlap between their potential future range and their present range by the end of the century, even for more moderate scenarios of climatic change.

A small but significant proportion of species occurring in Europe today are likely to face a substantial threat of eventual extinction as a consequence of 21st century climatic change.

One of the areas of greatest uncertainty in these simulations is the extent to which the dynamics of species' range boundary adjustments will enable species to realise the simulated shifts in their potential ranges. Because of this uncertainty, results often are presented for what might be considered as two of the four possible end members of the range of potential outcomes. The two cases generally considered are sometimes referred to as the 'universal dispersal' (or 'perfect dispersal') and 'dispersal failure' cases (Thomas *et al.*, 2004b). In the 'universal dispersal' case, species are assumed to realise fully their potential future range, dispersing into all newly-suitable areas whilst failing to persist in those parts of their present range that are no longer climatically suitable. In the 'dispersal failure' case, species are assumed to persist only in the area of overlap between their potential future and present ranges, failing to disperse into any newly-suitable areas whilst at the same time failing to persist in those parts of their present range that are no longer climatically suitable.
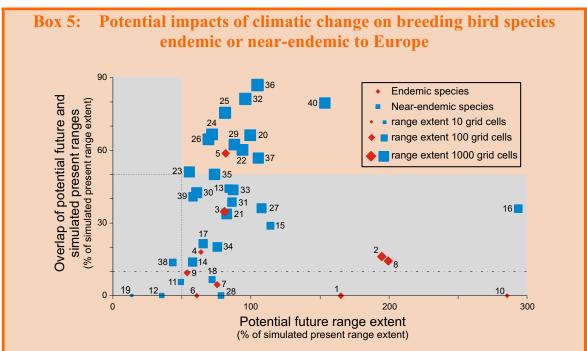
The other two possible end members generally are not considered because they are argued to be highly unlikely to be realised. The first of these, which might be labelled as the 'historical' end member, assumes that species' ranges do not change in response to the climatic change, species failing to disperse into any newly-suitable areas whilst at the same time persisting even in those parts of their present range that are no longer climatically suitable. Not only is persistence in areas that are no longer climatically suitable a highly unlikely outcome, at least over time scales beyond the generation time of the organism in question, but this possibility conflicts both with evidence from the Quaternary and with evidence of species' responses to recent climatic changes (Parmesan, 1996; Parmesan *et al.*, 1999), including evidence of range boundary retreat from areas that no longer are climatically suitable (Franco *et al.*, 2006; Thomas *et al.*, 2006). The last of the possible end members, which might be labelled 'universal persistence', assumes that species realise fully all potential range gains whilst persisting throughout their present range, in other words dispersing into all newly-suitable areas whilst at the same time persisting even in those parts of their present range that are no longer climatically suitable. Once again, the proposed persistence in areas that are no longer climatically suitable is both

highly unlikely and at odds with the evidence from past and recent range changes.   Neither of these alternatives will be considered further here.

Box 4:   Potential spatial responses of European breeding birds to 21st century climatic change

Simulated range shifts of European breeding birds are illustrated above by means of a polar plot of the geodesic distances and azimuths between the centroids of each species' distributions as simulated for the present climate (1961–90) and for a projected future climate scenario (2070-99).   The latter scenario was derived from a simulation made for the SRES B2 emissions scenario using the Hadley Centre HadCM3 general circulation model (Gordon *et al.*, 2000; Johns *et al.*, 2001).   The angular placement of each point reflects the bearing of the initial azimuth from the centroid of the present to the centroid of the potential future simulated range.   The distance of the point from the centre of the plot represents the geodesic distance (km) between the centroids of the present and potential future ranges.   For this particular potential future climate scenario the mean geodesic distance is 545 km, the range of values being 54 – 2477 km, and the mean azimuth is 9·3°.   The mean displacement of the centroid is equivalent to a mean rate of range adjustment of 50 km per decade, with the range being 5 – 227 km per decade.   (Re-drawn from Huntley *et al.*, in press)

Boxes 4 and 5 present results from modelling of the potential impacts upon the distributions of birds breeding in Europe (Huntley *et al.*, in press) that illustrate some of these conclusions.

Box 5: Potential impacts of climatic change on breeding bird species endemic or near-endemic to Europe

A plot of the overlap of the potential future and simulated present ranges against the relative extent of the potential future range for the 40 species of bird breeding in Europe and either endemic or near-endemic to the region. Near-endemic species are those with > *ca*. 90 % of their range and/or population within Europe, Europe being defined as it is by the European Bird Census Council (see Hagemeijer & Blair, 1997). Simulated potential future ranges are for a future climate scenario (2070–99) derived from a simulation made for the SRES B2 emissions scenario using the Hadley Centre HadCM3 general circulation model (Gordon *et al.*, 2000; Johns *et al.*, 2001). Numbers identify the species (see below). The size of the symbols is proportional to the log of the simulated present range extent. Species considered to be most at risk from climate change are those with low values of overlap or relative future range extent or both. Zones with overlap and/or relative extent less than 50 % are shaded and bounded by dotted lines. The dot-dashed line bounds the zone with overlap less than 10 %.

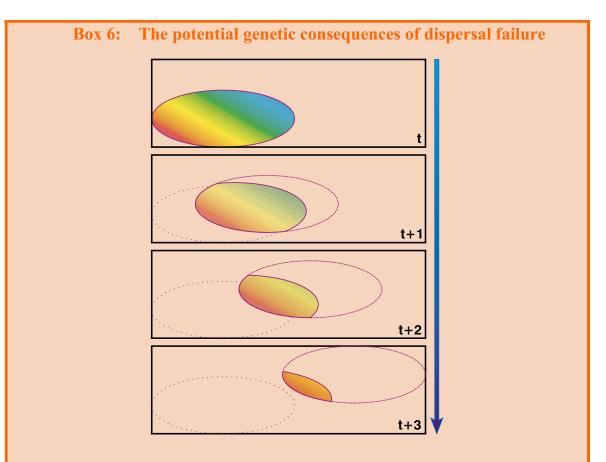| Endemic species		13	*Phalacrocorax aristotelis*	27	*Turdus torquatus*
1	*Aquila adalberti*	14	*Milvus milvus*	28	*Acrocephalus paludicola*
2	*Alectoris graeca*	15	*Accipiter brevipes*	29	*Acrocephalus palustris*
3	*Alectoris rufa*	16	*Falco eleonorae*	30	*Hippolais icterina*
4	*Stercorarius skua*	17	*Porzana parva*	31	*Sylvia undata*
5	*Anthus petrosus*	18	*Larus melanocephalus*	32	*Sylvia atricapilla*
6	*Sylvia balearica / S. sarda*	19	*Larus audouinii*	33	*Regulus ignicapillus*
7	*Cyanopica cyanus*	20	*Picus viridis*	34	*Ficedula albicollis*
8	*Passer × italiae*	21	*Dendrocopos medius*	35	*Parus cristatus*
9	*Serinus citrinella*	22	*Lullula arborea*	36	*Parus caeruleus*
10	*Loxia scotica*	23	*Anthus pratensis*	37	*Certhia brachydactyla*
Near-endemic species		24	*Prunella modularis*	38	*Sturnus unicolor*
11	*Calonectris diomedea*	25	*Erithacus rubecula*	39	*Loxia pytyopsittacus*
12	*Puffinus yelkouan*	26	*Saxicola rubetra*	40	*Emberiza cirlus*

(Figure re-drawn from, and text after, Huntley *et al.*, in press)

The issue of the proportion of species that may be at risk of extinction as a result of projected 21st century climatic changes (Thomas *et al.*, 2004c; 2004b) is one that has sparked considerable debate (Buckley & Roughgarden, 2004; Harte *et al.*, 2004; Lewis, 2006; Thomas *et al.*, 2004a; Thuiller *et al.*, 2004). Although only a relatively small proportion of European species either have no potential future range in Europe or no overlap between their potential future and present ranges, a substantial proportion of species have potential future ranges much smaller than their present ranges. Such

range reductions inevitably will be paralleled by reductions in population size of the species. Furthermore, species that either fail to disperse into newly suitable areas, or disperse into these areas more slowly than these areas become available, also are likely to suffer genetic impoverishment, as genotypes adapted to the climatic conditions of the leading edge of their distribution are lost because the species fails to realise its potential range expansion into such climatic areas sufficiently quickly (Overpeck *et al.*, 2003) [Box 6]. Although making a reliable quantitative assessment of the proportion of species that may be committed to extinction in the longer term as a consequence of the combined effects of range reduction, population reduction and genetic impoverishment, remains contentious (Lewis, 2006), the estimate made by Thomas *et al*. (2004b), that 15 – 37 % of the species they examined were likely to be committed to extinction if climatic changes of the magnitude projected by 2050 came to pass, cannot be ignored. Perhaps even more important than these actual figures, however, is the clear demonstration given by Thomas *et al*. (2004b) that, whatever the actual proportion of species at risk, this proportion increases rapidly for more extreme climatic change scenarios. Furthermore, the low end scenarios considered by Thomas *et al*. (2004b) had global mean warming of only $0·8 – 1·7°C$, whilst their mid-range scenarios had global mean warming of $1·8 – 2·0°C$ and their high-end scenarios had global mean warming of $2·0 – 3·0°C$. These scenarios thus span an overall range from $0·8 – 3·0°C$, compared to the most recent IPCC assessment of the uncertainty range for global mean warming by the end of the present century of $1·1 – 6·4°C$ (IPCC, 2007). Even if Thomas *et al*. (2004b) over-estimated the proportion of species committed to extinction, they did so for global warming scenarios that were all less than the midpoint $(3·75°C)$ of what is now considered the potential range of warming by the end of the present century. They also took no explicit account of the potential 'extinction debt' already accrued in some regions as a consequence of human land-use practices (see e.g. Hanski, 2000; Hanski & Ovaskainen, 2002); the possibility that 20th century climatic change has added to such extinction debts also apparently has not yet been examined.

Whatever the actual proportion of species that may be at risk of extinction this century, or committed to extinction in the longer term as a result of 21st century climatic changes, some general conclusions can be reached about the characteristics of species that render them more vulnerable to such threat. In particular, species that have a limited geographical range at present are more likely to have a potential future range that has little or no overlap with that present range, and thus to face greater additional threat as a result of climatic change. Such restricted range species will include many that are considered threatened or vulnerable because of their limited range and/or population. Thus the additional risk as a result of climatic change will tend to be greatest for species that already are at risk for non-climatic reasons. From a European perspective, species that also are endemic to the region, or nearly so, are at greatest risk of global extinction as a consequence of climatic change [Box 5].

Migratory species also face additional risk as a result of climatic changes that will affect both their breeding and non-breeding ranges; in many cases such species also depend upon key areas as migratory staging posts and these areas too will be affected by climatic change. Of migratory species breeding in Europe a large proportion are trans-Saharan migrants that winter from the Sahel south to the Cape of Good Hope in some cases. There is evidence already that some such species' European breeding populations have decreased over recent decades, apparently principally as a consequence of climatic changes in the semi-arid areas of sub-Saharan Africa where they spend the non-breeding season (Sanderson *et al.*, 2006). Furthermore, not only may the areas suitable for use by migratory species during different parts of their annual cycle decrease in extent and/or suitability, but in some cases key staging posts may be lost and/or the distance between breeding and non-breeding areas increased. It also is important to remember that a significant proportion of migratory birds wintering in Europe are shorebirds whose wintering habitats are vulnerable also to negative impacts as a result of rising sea-levels associated with climatic change; such impacts will exacerbate the effects of habitat loss that already have discernible impacts upon some such species (see e.g. Burton *et al.*, 2006). Similar threats are faced by the many shore-birds and other wetland birds that breed in Europe but winter in coastal wetlands, notably on the west African coast.

Box 6:   The potential genetic consequences of dispersal failure

Schematic to illustrate the potential loss of genetic diversity as a consequence of rapid climatic change. Each rectangular panel represents the same geographical space, the four panels representing successive steps along a time-series of climatic change that advances downwards, as indicated by the arrow.   The ellipse in each panel represents the climatically determined potential range of the species in that geographical area at that time.   As a consequence of climatic change the species' potential range shifts north-eastwards with time. The shaded area in each panel indicates the area where the species is present at that time step, i.e. its realized range.   At time *t* the species fully occupies its potential climatically-determined range, as indicated by the shading of the entire ellipse.   Thereafter the area occupied by the species progressively diminishes in size through time, because the rate at which the species' is able to adjust its geographical distribution is less than the rate required to realize fully its potential range in the newly-suitable area, whereas it is unable to persist in areas of its former range that are no longer climatically suitable.   The species' realized range thus becomes progressively more restricted to the south-western part of its potential range.   The spectrum of shading across the species' realized ranges represents clinal adaptive genetic variation in some character(s) related to the principal climatic gradient spanned by the species' realized range at time *t*.   It is assumed that gene flow through the species' population is sufficiently rapid that there is no lag in allele 'migration' relative to the rapid climatic change.   At time *t* the full range of genotypes (from red to blue) is present along the climatic gradient across the species' realized range.   As the realized geographic range decreases in extent, however, it also decreases with respect to its range along the climatic gradient with respect to which the species exhibits clinal variation.   Thus at time step *t+1* the species no longer occupies that part of the climatic gradient to which the blue genotypes are adapted, with the result that they are lost from the population.   By time step *t+3* only genotypes close to the red extreme of the cline are able to persist within the species' realised geographic range.   The extent to which such loss of diversity may be irreversible depends upon the underlying genetics;   if alleles associated with the blue genotype are not maintained in populations at the opposite end of the cline then the loss effectively will be irreversible, at least in the short-term.   Furthermore, it should be noted that, were allele 'migration' to lag the climatic change as much as does the adjustment of the species' geographical range, then the genotypes able to occupy the 'realized range' at time *t+3* previously would have become extinct.   Such a loss of 'trailing edge' genotypes has potentially particularly serious consequences for temperate species of Europe, in many of which the majority of their genetic diversity is found in populations near the southern edge of their range (Hampe & Petit, 2005).   In addition, loss of genotypes adapted to the red climatic extreme of the range tolerated by the species would, in the example illustrated, greatly enhance the risk of extinction of the species as a consequence of climatic change.   (Re-drawn from Overpeck *et al.*, 2003)

Not all of the potential impacts upon migratory species are negative, however. Some migrants may benefit from reduced migratory distances if climatic change results in greater proximity between areas suitable for use during the breeding and non-breeding seasons. Amongst species that winter in Europe but breed in the Arctic, the milder winters projected for northern Europe may enable them to winter closer to their breeding areas, whilst species breeding in Europe but spending the non-breeding season in sub-Saharan Africa may in future find suitable non-breeding season conditions in areas around the Mediterranean basin, possibly including parts of southern Europe.

An often overlooked consequence of the likely responses of species to projected climatic change is the arrival in Europe, without human intervention in their dispersal, of species that are not at present considered as native to the region. The most obvious source for such species is northern Africa, especially as the projected future climate of southern Europe is warmer and drier than the present climate and more similar to that of Africa north of the Sahara. Some species of Turkey and the Middle East may also in future find suitable climatic conditions in eastern Europe. In addition, some of the many species already introduced to Europe from other continents may find the projected future climate of Europe more favourable for their naturalisation and may become 'invasive'.

Finally, an important consequence of the contrast between the destination of the projected climatic change and the direction in which climate has fluctuated during the Quaternary is that the southern populations of many temperate species, that harbour a disproportionate proportion, and often novel components, of the genetic diversity displayed by those species, are the populations at greatest and earliest risk of succumbing to the negative impacts of climatic change (Hampe & Petit, 2005) [Box 6].

IV. Implications for biodiversity conservation strategies

The preceding four sections have presented an outline of the background evidence and provided the context in which strategies must be developed for the conservation of biodiversity in a world subject to rapid large magnitude climatic change. They also have presented evidence of the potential consequences, in terms of species' extinction and reduced ecosystem services, if such measures are not successfully developed and implemented in the very near future. The present section aims to draw out and focus the key implications that emerge from consideration of this background evidence, and that must inform the development of adaptation strategies. Before turning to summarise these implications, however, it is vital to emphasise that, whilst such adaptation strategies are essential, they alone are insufficient to ensure that ecosystems and biodiversity are not damaged irreparably by 21st century climatic changes. Stringent mitigation measures also are required to ensure that the rate and eventual magnitude of the climatic change does not exceed the resilience threshold of the biosphere. Although this threshold is not well understood, attempts can be made to estimate it from the evidence presented above of past climatic changes and of the biospheric response to these changes [Box 7].

1. Species' geographical distributions respond dynamically to climatic changes

In many respects the most fundamental response to climatic change is that of species adjusting their geographical distributions according to the interaction between their inherent climatic tolerances and/or requirements and the changing climate. The palaeoecological record shows that such range adjustments have in the past been of a magnitude similar to that simulated as the potential response of species to projected 21st century climatic changes: i.e. species' range boundaries have in the past shifted across Europe by distances of between several hundred and two thousand kilometres, just as the potential shifts in species' ranges simulated for the present century range from tens to more than two thousand kilometres [Box 4]. The scale of these potential future range changes poses a number of challenges to current conservation management goals and practices.

Firstly, many individual protected areas have as a principal reason for their establishment the protection of one or more rare or threatened species, or of a representative assemblage of species viewed as characteristic of a given habitat and region. Often the management of such protected areas has amongst its goals the maintenance or even increase in the population(s) of the rare or threatened species that form part of the basis for its establishment, and management practices are implemented that seek to ensure the achievement of this goal. Species may of course be inherently rare, or their

rarity may result from direct anthropogenic pressures such as hunting or persecution, or from indirect anthropogenic pressures, such as land-use practices that have led to loss and/or fragmentation of habitat.   In many cases, however, a species is rare in a particular region because that region is at the margin of the species' geographical distribution.   In some such cases climatic change may be favourable to the species, if the range margin in question is at the 'leading edge' of the species' distribution with respect to climatic change, but in other cases climatic change will be unfavourable for the species because the range margin in question is at the 'trailing edge' of the species' distribution with respect to the climatic change.   The latter will typically arise in Europe where the target species' is close to its southern or south-western range margin.   In such cases the eventual loss of that species from the protected area will often be inevitable.   More generally, a proportion of all the species currently present in any protected area can be expected no longer to be sustainable in that area in the future as a consequence of climatic change.   On the other hand, a complementary group of species that are not currently present in the area can be expected to find suitable climatic conditions there in the future.   In some cases the current management strategy for the area may lead to practices being implemented that actively discourage the establishment of such 'invading' species;   such strategies are inimical to the long-term conservation of biodiversity in a world of climatic change.

Secondly, and at the wider geographical scales of nations, and of the European continent as a whole, species often are categorised as 'native' as opposed to 'alien', with conservation measures being targeted at native species, whereas alien species are considered to be undesirable and often are subject to measures that aim to limit their spread or even to bring about their eradication from areas where they are not considered native.   Given the scale of species' potential range boundary adjustments, however, species native at present in parts of southern Europe have the potential in future to become native components of the ecosystems of countries further north and east in Europe from which they are currently absent.   It is essential to avoid such 'invading' species being considered as aliens in the countries to which their range may newly extend in future (cf. the situation in Canada where species extending their ranges north from the USA would be classified as 'alien species' under present legislation, see Scott & Lemieux, 2005).   There thus is a need for a recognition that all species native to Europe should be afforded any necessary protection in future even in countries or regions where they have not historically been present as natives.   This principle, however, must extend beyond the species native to Europe today.   The magnitude of species' potential range adjustments makes it inevitable that some species today absent from Europe as natives, but native in adjacent regions, such as northern Africa, Turkey or the Middle East, will have potential future ranges that include parts of Europe where the climate in future is similar to the present climate of those adjacent regions.   These species too must be afforded any necessary protection in whatever parts of Europe may in future lie within their potential range.

> *Recommendation 1: Adaptation strategies must recognise the dynamism of species' geographical ranges. This will require a re-evaluation of the management goals of protected areas, as well as of the basis for maintaining the protection of areas that in future may no longer support one or more of the species whose local conservation was a primary reason for the initial recognition of the protected area. A re-evaluation of the use of the concept of 'native' species in setting conservation priorities also will be required, both at the level of individual countries and at the European scale. In addition, strategies will be required that aim to facilitate the achievement by species of the potential future range changes required as they adjust to the projected climatic changes.*

Box 7 – Assessing biospheric resilience

The resilience of the biosphere to the effects of climatic change, or in other words, its capacity or ability to recover to its former state after climatic change ceases, is in some senses not a useful concept.   If the end point of climatic change is a global mean temperature warmer than that of the recent past, then the biosphere inevitably will be altered and will not return to its former state.   Nonetheless, the concept can perhaps usefully be applied in relation to some important or valued properties of the biosphere, such as ecosystem function or regional biodiversity.

From the point of view of biodiversity conservation, and the resilience of biodiversity to climatic change, the key consideration is to attempt to assess how much climatic change can be accommodated before biodiversity loss is irreversible.   Irreversible biodiversity loss might be considered to have occurred when a species becomes extinct, or part of the adaptive genetic variance of that species is lost.   In their synthesis of the potential impacts of climatic change on the bird species breeding in Europe, Huntley *et al*. (in press) found that 1·4 – 4·9 % of species had no simulated climatically suitable area in Europe by the end of the present century;   this suggests that for this range of climatic change scenarios, irreversible biodiversity loss will occur in Europe this century.   However, even the 'worst case' of *ca* 5 % loss in these scenarios might be considered acceptable by some – it is after all within the widely accepted uncertainty band used by biologists to assess the significance of their results.   However, a more relevant measure, in terms of resilience, is the extent of the overlap between species' present and potential future ranges.   Given evidence of the disparity between the rates at which species have in the past adjusted their ranges (Huntley, 1991) and the projected rate of climatic change (IPCC, 2007), the long-term survival of many species, and the maintenance of their adaptive genetic variance, will depend upon their persistence in this area of overlap.   This persistence will be vital to allow their subsequent recovery and range expansion when climatic change is halted or reversed.   In the same study, Huntley *et al*. (in press) report no overlap between present and potential future ranges for 3 – 10 % of species.   For a further 3 – 12 % of species the overlap was less than 10 % of their present range.   The latter can be considered in the context that reduction of a species' population by 90 %, albeit over a shorter period than is considered in this simulation study, qualifies a species to be placed in the IUCN 'Critically Endangered' category.   It must thus be considered very likely that those species with zero overlap would be committed to extinction, and likely that those species with < 10 % overlap also would be so committed.   Furthermore, given that the mean area of overlap amongst the 431 species examined in the study was just 38 – 53 %, it is very likely that a majority of species would experience some loss of adaptive genetic variance.   Climatic changes of the magnitude considered in this study (3·3 – 3·5°C global mean warming) thus clearly exceed the resilience of the biosphere and are likely to lead to significant irreversible biodiversity loss.   In turn such loss is likely to lead to reductions in the effectiveness of many ecosystem services.

The challenge is to assess how much climatic change must be reduced from the scenario used in these simulations in order not grossly to exceed the resilience of the biosphere.   One 'rule of thumb' approach is to consider that the maximum warming, relative to the recent past, that occurred during the last *ca*. 800,000 years??of??the??Quaternary??period??ought??to??be??within??the??resilience??threshold??of??the ??biosphere,??given??that??any??components??of??biodiversity??unable??to??survive??such??warming??can ??be??expected??already??to??have??been??lost.   Estimates of past global temperatures suggest they have not exceeded those of the recent past by more than 1 – 2°C during the past 800,000 years (Overpeck *et al*., 2005).   Even taking the upper limit of this estimate suggests that the limit to the resilience of the biosphere, beyond which irreversible biodiversity loss and other damage can be expected, is *ca*. 2°C.   For the average European species this translates into a range displacement of *ca*. 300 km.   Such a displacement still would lead to mean overlaps between present ranges and potential future ranges of only *ca*. 40 %, and would result in some species having no overlap.   In the short-term this inevitably would result in substantial range and population reductions, and concomitant loss of genetic diversity, for many species.   Furthermore, at typical past rates of range boundary displacement, such a range adjustment would be achieved only after 150 – 1500 years.   It thus seems likely that even such a modest warming, because of its rapidity, will severely challenge the resilience of the biosphere.   Any greater warming, however, seems certain to exceed that resilience, and thus to lead to irreversible damage and loss of function.

2.   Gene flow through a species' population is essential for adaptation to climatic change

As Box 6 illustrates, loss of genetic diversity within species is a likely consequence of their realised range failing fully to occupy their potential range because of the rapidity and magnitude of projected climatic change.   However, the example illustrated assumes 'universal dispersal' of adaptive alleles through the species' population.   As is noted in Box 6, if such 'universal dispersal' of alleles were not to be achieved, then the genotypes adapted to that part of the climatic range to which the species potentially is restricted, as a result of its dispersal limitations not enabling it fully to occupy its potential future range as quickly as that range becomes suitable, may be lost.   The implications of this are that the remaining species' population will be maladapted to the conditions in which it finds itself, enhancing the probability of the species' eventual extinction.   Thus for successful adaptation to climatic change, gene flow through the species' population must be much more rapid than the rate of dispersal of species' populations.   In the case of Europe the disproportionate concentration of intra-specific genetic diversity of many temperate species in their southern European populations exacerbates the potential biodiversity loss because in future these species' potential ranges generally shift northwards and areas they currently occupy in the south potentially become climatically unsuitable for their persistence.

Phylogeographic evidence, as well as understanding of the genetic consequences of the hypothesised dependence of past rapid range expansions upon repeated long-distance dispersal events, leads to two conclusions of relevance to this issue of gene flow.   Firstly, those species examined typically show considerable genetic differentiation across their European ranges (see e.g. Grivet & Petit, 2002; Hewitt, 1996, 1999; Magri *et al.*, 2006; Petit *et al.*, 2002b; Santucci *et al.*, 1998), albeit that this generally is examined using non-functional elements of their genome.   Furthermore, the genetic pattern examined in many of these phylogeographical studies is that associated with the maternally inherited genomes of organelles;   this may thus not provide an accurate reflection of patterns of gene flow of the nuclear genome that includes the majority of loci associated with adaptive traits.   Nonetheless, the patterns of differentiation observed, even in maternally inherited genome components, imply that gene flow certainly is not 'universal' in most species.   Secondly, in the same studies it generally is reported that species' populations near the extremities of the areas into which their ranges expanded during the post-glacial are those most impoverished in terms of the diversity of genotypes represented.   This observation is consistent with the expected impact of the repeated 'founder effects' associated with long-distance dispersal events.   It implies that a similar genetic impoverishment of species' populations is to be expected at their 'leading edge' as this advances rapidly in response to climatic change.

Despite these general patterns, there are substantial differences between species in the mechanisms of gene flow through their populations.   Thus whereas in many higher plants gene flow can be achieved through the dispersal of pollen, which for anemophilous species may enable gene flow between populations separated by considerable distances (Liepelt *et al.*, 2002), in the case of most higher animals gene flow requires that individuals move from their natal site before breeding. Such dispersal limited gene flow is likely to limit the rate at which adaptively favourable alleles are able to 'migrate' through populations of these species' to a rate similar to that observed for the species' range boundary adjustments.   The extent to which populations of such species are able to exhibit adaptive genetic responses to climatic change will, as a result, depend fundamentally on the geographical distribution of the alternative alleles that selection must act upon to bring about the adaptive response.   Although little currently is known about how such genetic variance is distributed geographically across species' ranges, the frequency with which species exhibit clinal variation that is adaptive with respect to the range of climatic and other environmental conditions spanned by their geographical distribution (e.g. Mooney & Billings, 1961), and the results from numerous 'provenance trials' and 'common garden' experiments carried out by foresters and others (see e.g. Bachmann, 2002; Benowicz *et al.*, 2000; Blumenrother *et al.*, 2001; Bower & Aitken, 2006; Keller *et al.*, 2004; Matyas, 1996; Paques, 1996; Repo *et al.*, 2000; vanNiejenhuis & Parker, 1996), lead to an expectation that such adaptive genetic variance generally will be geographically patterned within a species' range.

In recent years conservation of local genetic diversity within species has been identified as a target for conservation management.   This has led conservation managers to seek to use material of local provenance when augmenting species' populations or when undertaking 'creative' conservation practices, such as the seeding of roadside verges with 'wildflower mixes'.   Of course, such practices have not always been possible, some re-introduction schemes for raptorial birds in the United Kingdom (e.g. *Haliaeetus albicilla* – White-tailed Eagle;   *Milvus milvus* – Red Kite) have at least in part released offspring from populations in relatively remote areas of Europe.   An insistence upon the use only of genetic material of local provenance in habitat creation schemes and other such practices, however, may be counter-productive in the face of climatic change;   instead, steps that facilitate the spread of potentially favourable alleles, as well as of threatened components of a species' intra-specific genetic diversity, may be more desirable.   Indeed such a strategy may prove to be essential to the longer-term conservation of the species' overall genetic diversity, including the local genotypes upon which attention often is currently focused.

> **Recommendation 2:**   *Adaptation strategies must recognise the need to facilitate, rather than to hinder, gene flow through species' populations if they are to adapt to projected climatic changes.   In addition, such strategies must include mechanisms designed to ensure that intra-specific genetic diversity loss is minimised, especially that component of the genetic diversity of many European species that is concentrated near the 'trailing edge' of their distribution, and thus is most vulnerable to the negative impacts of climatic change upon these 'trailing edge' populations.*

3.   Communities and ecosystems are impermanent

Many individual protected areas and protected area networks are based upon a concept of protecting representative or high-quality examples of the communities and ecosystems found in a region (see e.g. Ratcliffe, 1977a, b; Scott & Lemieux, 2005).   The individualism of species' responses to climatic change, however, will result in changes in the composition of communities, and hence in the structure and functioning of ecosystems.   Such changes are readily apparent in the Quaternary palaeoecological record and are paralleled by the spatial gradients in community composition and ecosystem structure familiar to phytosociologists and others.   The present management of many protected areas, however, has amongst its declared aims that of maintaining the *status quo* in terms of community composition and ecosystem structure.   Even in the absence of climatic change, such a management goal often is contrary to the historical ecological and/or palaeoecological evidence of the longer-term dynamics of many ecosystems in which regular, albeit often infrequent, disturbance events are essential to the maintenance of the composition and structure of these ecosystems.   In the face of climatic change, or indeed any other natural or anthropogenic environmental change, such a management goal is both inappropriate and unachievable in the medium or longer term.   It is tempting here to remind readers of the story of Canute 'The Great', King of England between 1016 and 1035 AD, whose humility led him to demonstrate to his courtiers that even he could not turn back the waves of the rising tide!   All too many current conservation management plans for protected areas demonstrate a lack of such humility on the part of those who formulated these plans, apparently in ignorance of the inevitable and inherent dynamism and change of ecosystems, even when not facing the additional pressures now imposed as a result of anthropogenic climatic change.

> **Recommendation 3:**   *Adaptation strategies must have amongst their goals that of facilitating community and ecosystem changes resulting from climatic changes, as well as of permitting and in some cases facilitating the ecosystem dynamic processes upon which the realisation of such changes often depends.   These changes are an essential component of adaptation by the biosphere to climatic change.*

4. Protected areas are necessary but not sufficient to conserve biodiversity in a changing world

Protected areas have long been one of the cornerstones of conservation strategy, complemented by the legal protection for many species that perhaps is the second such cornerstone. Climatic change, despite its implications that some of the species, communities and ecosystems found today within a given protected area may be replaced by different species, communities and ecosystems in the future, does not render protected areas any less important. Indeed, the converse is almost certainly true, they are likely to become of greater importance for a variety of reasons.

One of the key attributes that determines the rate at which a species is able to expand its range into newly suitable areas appears to be what has sometimes been referred to as the 'propagule pressure' that it is able to exert. An alternative way to view this is in terms of the number of propagules or offspring the species produces each year; the greater this number the larger the number of dispersing units, and in turn the greater the likelihood of one or more of these dispersing units successfully dispersing over a long distance and establishing in the new location which it reaches. What this means in practice is that species with relatively large populations and/or those that are more fecund, producing larger numbers of offspring or propagules, are able to achieve more rapid range margin adjustments.

Herein lies one of the principal reasons why protected areas are of vital importance as part of a strategy for adaptation to climatic change. Such areas often harbour the best quality habitats, frequently those least altered by human activities, for many species; for many species they thus support higher population densities than lower quality habitats outside the protected area. In terms of the metapopulation paradigm (Hanski & Thomas, 1994), they support source populations that, by definition, produce an excess of dispersing offspring or propagules. Such source populations are the 'engine' of species' range shifts; only through maintaining and enhancing the network of protected areas are such populations likely to be sustained or enhanced, and hence are species likely to be able to achieve the range adjustments necessary in response to climatic change. Ironically, a particular protected area may often be of most critical importance in this respect for just those species for which conditions within the protected area are likely to become unsuitable in future. Unless those species are able successfully to disperse from the protected area and establish in other areas that will remain suitable after the protected area is no longer suitable, then any local component of their intra-specific genetic diversity is going to be lost.

Conservation biologists have in the past focussed a great deal of attention upon issues such as the 'best' size, shape and number of protected areas, or on developing reserve selection algorithms that will assist the conservation practitioner in determining what is, according to some criterion that the algorithm seeks to optimise, the 'best' set of protected areas to designate in a given region. Such efforts, however, have in general been predicated upon a view of the natural world that is to be conserved as static. As a result, the 'best' sets of protected areas have been assessed in terms of their ability to conserve the species and ecosystems of an area distributed as they were when the assessment was carried out. How effective such sets of protected areas may be in the new dynamic world of climatic change is now an area of considerable concern, stimulating conservation biologists to consider new criteria for the selection of sites as protected areas; these new criteria are designed to take into account the potential impacts of projected climatic changes (see e.g. Araujo *et al.*, 2004; Coulston & Riitters, 2005; Pyke & Fischer, 2005). In some cases this is achieved by explicitly considering how species may in future be distributed (e.g. Araujo *et al.*, 2004) and then applying criteria similar to those used in previous reserve selection procedures but incorporating the information about species' potential future as well as present distributions. In other cases what has been termed a 'coarse filter' approach (Hunter *et al.*, 1988) is adopted (Coulston & Riitters, 2005). The latter approach focuses on providing a network of protected areas that maximises the representation of the range of combinations of environmental conditions found in a region, rather than a network that explicitly maximises the representation of the range of species in one or more taxonomic groups found in the region. Such a coarse filter approach, however, will generally succeed in capturing a large part of the regional diversity in well-known taxonomic groups, and has the additional virtue that it is probably at least as likely, if not arguably more likely, to capture an

equivalent part of the regional diversity in lesser known or cryptic groups of organisms than are selection algorithms that focus upon maximising representation of one particular well recorded group.

Given the considerable uncertainties about exactly how climate will change in Europe during the present century, and the further uncertainties inherent in any attempt to predict species' future distributions, any evaluation of the potential effectiveness of the present protected area network in conserving biodiversity in the face of climatic change is probably best undertaken using a coarse filter approach. Similarly, the selection of additional areas to augment the existing protected area network ought to be based upon achieving an improved representation of the range of environmental conditions and physical habitats found across Europe, rather than targeted on the basis of the present distributions of species or ecosystems. Such a coarse filter approach should use topographic, hydrogeomorphic, geological and edaphic attributes, as well as a series of bioclimatic attributes. Further augmentation of the protected area network may also be necessary so as to ensure that there are no excessively large spatial gaps in the network. Although it will be difficult objectively to determine what may be considered an excessively large spatial gap, a useful 'rule of thumb' might be that the distance between protected areas ought not to exceed the average long-distance dispersal capacity of those species that depend upon the more extensive patches of habitat, free from direct human disturbance, that often are found only within such protected areas. Any greater separation of protected areas is likely to result in the failure of such species to adjust their distributions in response to climatic change.

Protected areas thus will play a vital role in any strategy designed to assist in the adaptation of species and ecosystems to climatic change. However, whilst necessary, they will to a much greater extent than previously, no longer be sufficient.

In order to respond to climatic change species will need to adjust their geographical distributions. In order for them to achieve this, offspring and propagules dispersing beyond the species' current range margin into areas where the climatic conditions are newly favourable must be able to survive, and ultimately to establish themselves and breed. For many species, the distances between neighbouring protected areas offering them suitable habitats will exceed their dispersal capabilities; at the very least these distances may be such that dispersing individuals will require 'safe' staging posts if they are to cross the intervening area. Thus, for species that generally are threatened within the wider landscape, or else whose habitat has been so reduced and fragmented in the wider landscape that they persist principally only in protected areas, successfully to cross the intervening landscape, the structure and management of that landscape will in many areas need to change. Even for species that persist in semi-natural habitat fragments in the wider landscape, successful dispersal and establishment will require a suitably structured landscape (see e.g. Hill *et al.*, 2001). What this may mean in practice is discussed below: The key point to be made here is that, for protected areas to be effective as a conservation tool in the face of climatic change, it will be essential that they are complemented by appropriate management and structure of the wider landscape. The protected areas can perhaps be seen as the key 'nodes' in the conservation site network, but that network must also extend to a much larger number of habitat patches in the landscape as a whole if species are to be able to achieve the responses to climatic change that will be necessary.

> *Recommendation 4: Adaptation strategies must aim to ensure the continued protection and appropriate management of existing protected areas. A coarse filter type approach should be implemented at a European scale to identify gaps in this network of existing protected areas, and the network then should be augmented in order to maximise the representation of the full range of environmental conditions and physical habitats. The network also should be augmented where necessary to ensure that there are no excessively large spatial gaps in the network of protected areas. Appropriate management of the wider landscape, and the development of a suitable landscape structure, will be essential to complement the protected area network; without such management of the wider landscape, many species will be unable to achieve the responses to climatic change that are essential to their long-term survival.*

5. Buffer zones – useful but not a panacea

The development of buffer zones around existing protected areas clearly is desirable for a variety of reasons, although these are related mainly to minimising the negative impacts upon the protected area arising from unfavourable management of adjacent land and to reducing the edge effects that decrease the effective extent of a protected area and that are most important in the case of protected areas of small extent and/or with large ratios of edge to area.   It has also sometimes been suggested, however, that buffer zones should form part of a conservation strategy aimed at assisting adaptation to climatic change, or that protected areas should be expanded "*towards the poles and/or towards higher altitudes*" (e.g. Li *et al.*, 2006, p. 257).   Whilst upslope buffer zones, or the expansion of protected areas to higher altitudes, may in some cases be a successful strategy, the extent of such upslope extensions must be considerable if they are to accommodate the expected upslope shifts of species' ranges and of ecotones.   Delcourt and Delcourt (1998), for example, estimate an upslope shift of *ca*. 480 – 1020 m for species and ecotones in the Appalachians, depending upon the magnitude of the climatic warming that takes place this century.   Thus even in areas of high relief, the extent of species' range shifts far exceeds what might be considered a plausible buffer zone.

In areas of lower relief the mismatch in scale between buffer zones, or even the extent of most European protected areas, and species' expected range adjustments is such that buffer zones are unlikely to be of any direct value in relation to strategies aimed at adaptation to climatic change. That does not mean that they are irrelevant, just that their value lies in enhancing the effectiveness of protected areas regardless of climatic change.

> *Recommendation 5:   Adaptation strategies ought to exploit buffer zones as a valuable tool for enhancing the effectiveness of protected areas, but should not consider them generally as contributing directly to adaptation to climatic change.*

6. Corridors – are they either necessary or viable?

Much has been written in the literature of conservation biology about the value of 'corridors' in increasing the 'connectivity' of landscapes.   A series of recent studies, however, offers conflicting conclusions as to the positive or negative effects of the establishment of corridors and the extent to which they may benefit some species but not others in an ecosystem (see e.g. Bailey, 2007; Carroll & Miquelle, 2006; Chetkiewicz *et al.*, 2006; Damschen *et al.*, 2006; Davies & Pullin, 2007; Diekotter *et al.*, 2007; Horskins *et al.*, 2006; Roy & de Blois, 2006; Shepherd & Whittington, 2006; Vogt *et al.*, 2007; Weldon, 2006).   A number of general conclusions emerge from such studies: Firstly, developing a corridor through a landscape for one group of species may inhibit movement by another group (Thomas, 1991);   secondly, developing a corridor through a landscape may alter predator behaviour in ways that are seen as beneficial to the predatory species (Shepherd & Whittington, 2006) but may also alter predation risk of prey in unintended and perhaps undesirable ways (Weldon, 2006); thirdly, developing a corridor through a landscape may have differential benefits for different species in the assemblage found in the habitat patches that the corridor is designed to connect (Horskins *et al.*, 2006; Roy & de Blois, 2006);   fourthly, using corridors to increase the connectivity of a landscape may decrease the likelihood of a species dispersing to isolated patched of suitable habitat (Diekotter *et al.*, 2007);   fifthly, corridors may be of lesser value in some landscapes, and for some species, than general improvements in the management of the landscape matrix to enhance its value for and use by wildlife species (Carroll & Miquelle, 2006);   and sixthly, and perhaps most importantly, the evidence as to the value of corridors generally is conflicting (Bailey, 2007; Damschen *et al.*, 2006; Davies & Pullin, 2007).

An alternative approach to considering the extent to which corridors may be necessary to achieve connectivity between habitat patches in a landscape is to examine the evidence available as to the nature of the pre-historic landscape across which species dynamically adjusted their ranges in response to past climatic changes.   When we do this then it quickly becomes apparent that patches of many habitat types were unlikely ever to have been connected by continuous corridors in the landscapes of the past.   Perhaps the most obvious examples are many types of wetland habitat, including reed

swamps, valley mires and saline lakes. In contrast to riverine habitats, that generally are characterised by their linear and strongly connected form, these wetland types either occupy isolated drainage basins (e.g. many saline lakes), or are limited either to particular topographic situations (e.g. valley mires) or to particular substrate and water conditions (e.g. reed swamps). The specialised species associated with such habitats must in the past have dispersed between the isolated patches of habitat available to them. There are many other less obvious examples of habitats, and of their associated specialised species, of which the same is true. Thus in Europe the many species found in the calcareous grasslands of chalk and limestone areas are unlikely all to have achieved their post-glacial expansion before the bulk of the landscape become forested. That at least some of the species found today in patches of such habitats can disperse between these patches is demonstrated by studies of the metapopulation dynamics of chalk grassland butterflies (Hill *et al.*, 1996), although these same studies also illustrate the critical importance of patch isolation in reducing or preventing successful dispersal (Gutierrez *et al.*, 1999). There are of course clear exceptions to this general pattern; many montane and Arctic–Alpine species have patchy distributions today that represent fragments of once more continuous distributions at the end of the last glacial stage. Such relict distribution patterns arise from a quite different mechanism from that which has operated for the species of the other patchily distributed habitat types discussed previously. It is perhaps tempting to suggest, when considering the pre-historic landscape of Europe, that the most continuous and connected habitat types were the forest habitats, principally because they occupied the bulk of the landscape, and that this may be of relevance in considering landscape connectivity in the context of conservation management. However, even forests vary in composition across the landscape as soil conditions, topography and other components of the physical habitat vary; forests also are interrupted by features such as riverine corridors, and are subject to periodic disturbance events that lead to canopy gaps of varying extent.

Given all of the evidence, it is difficult to conclude that corridors are a necessary part of a strategy for the management of the wider landscape to favour biodiversity conservation in the face of climatic change. Although it would generally be unwise to fragment corridors where they already exist, where they do not exist, it is probably unnecessary to regard their provision as necessary or as a management priority.

The viability of corridor provision as a tool to assist in the conservation of biodiversity in the face of climatic change is in any case open to question (Halpin, 1997). Although in some landscapes, such as parts of Fennoscandia, where human population densities are relatively low and land-use is relatively extensive, it may be viable to identify and take measures to conserve 'corridors' of semi-natural habitat, the scale at which such corridors would need to be developed probably precludes them as a viable option in most of the more densely populated regions of Europe with their intensive land-use. Where they are a viable option, effective corridors need to extend for as great a distance as possible, and minimally to link neighbouring extensive protected areas. They also need to be relatively broad so that their value is not overwhelmed by edge effects, and also in order that they can encompass the heterogeneity of the landscape that they traverse and sustain ecological processes along their course (cf. Rouget *et al.*, 2006).

> **Recommendation 6:** *Adaptation strategies should not focus upon the provision of corridors as a necessary part of achieving landscape structures that are favourable for the dynamic range adjustments of species in response to climatic change. Furthermore, in most of Europe corridors of the necessary scale to be truly valuable will not be a viable option. Nonetheless, where the provision of such large-scale conservation corridors (cf. Rouget et al., 2006) is a viable option, this option ought to be pursued as part of the overall adaptation strategy.*

7.   Permeable landscapes

Although, as argued above, protected areas will play a vital role in the conservation of biodiversity in the face of climatic change, and the network of such sites will need to be maintained and enhanced, species will be prevented from achieving the range boundary adjustments required to cope with climatic change if they are unable to disperse through the intervening landscape.   In order to facilitate species' range boundary adjustments, therefore, the landscape as a whole, especially in the many parts of Europe where human-altered landscapes and human land-use predominate, must be managed in ways that render it 'permeable' to species dispersing into newly climatically suitable areas.   Such landscape permeability will require management strategies that address two principal targets.   Firstly, development of a network of 'stepping stone' sites to provide connectivity between protected areas, especially for those species less able or unable to utilise the more human-altered landscape matrix, and requiring patches of a particular habitat type to support their dispersal. Secondly, management of the matrix of the landscape, including agricultural land, land used for commercial forestry, and other more heavily human-altered areas, in ways that enhance the value of this matrix for species able to utilise these habitats and also that render the matrix less inimical to more demanding species.

i.   *"Stepping stones" to facilitate dispersal*

The concept of 'stepping stones' can be traced back to the island biogeography theory of McArthur and Wilson (1967);   it also is inherent in metapopulation models (Hanski & Thomas, 1994).   Essentially, what is proposed is that small patches of a particular habitat located at intervals between two large patches will facilitate the dispersal between those large patches of organisms associated with that habitat type.   This facilitation is achieved because the probability of successful dispersal is greater over shorter distances.   Even where the distances between stepping stones are themselves great enough that they will be crossed only rarely, the product of the probabilities of making several such steps substantially exceeds the probability of dispersal directly between the two large patches.   Indeed, it is arguable that for many organisms there is a threshold distance beyond which the probability of dispersal effectively is zero.   This might be the case, for example, for actively dispersing animals if they are unable to obtain food resources except from their favoured habitat;   in such cases the maximum dispersal distance will be determined by the endurance of the individual.   Chance effects may of course allow individuals to exceed this endurance limit;   a butterfly, for example, may be assisted in dispersal by a favourable wind, but even then the species' endurance is still likely to be limited simply by the period for which it can stay aloft.   Similar threshold dispersal distances are likely for the propagules of many plants because they rely upon animals for their long-distance dispersal (Giannakos, 1997; Wilkinson, 1997).

Although conceptually relatively straightforward, the stepping stones model is much more complex in practice.   Thus, for some larger mobile species a stepping stone may need only to provide a habitat where it can forage successfully, and/or a safe place to rest.   For other species, a stepping stone may need to support a breeding population that is able to produce dispersing offspring or propagules in order for dispersal to be achieved to the next stepping stone in a series.   Similarly, a large mobile species may readily move up to 10 km between stepping stones, and may do so within a single night.   A smaller and less mobile species may only rarely achieve long-distance dispersal of more than a few hundred metres of its annually produced dispersing units, whether they be offspring or propagules.   As with so many of the challenges posed by global climatic change, for the great majority of species we lack the fundamental ecological knowledge required to determine the optimal landscape pattern of stepping stones that will ensure their success in traversing that landscape. Indeed, for most types of habitat we do not even have a comprehensive knowledge of what species and types of organism are present;   only for the more obvious and easily recognised taxonomic groups, including birds, mammals, butterflies and higher plants, do we have anything approaching complete lists for any habitat patches.   Even if we did have a comprehensive knowledge of what was where and of how each species uses the landscape, it would still be the case that stepping stones that are useful to one species or group of species will be irrelevant to others and *vice versa*.

This does not mean that we can or should do nothing, however.   We can propose a general hypothesis and design our landscapes accordingly.   Monitoring the effectiveness of the landscapes in

facilitating species' dispersal will then provide an evidential basis for future adaptive management (Hulme, 2005; Sutherland *et al.*, 2004; Sutherland, 2006).

The general hypothesis to be proposed is itself underpinned by a number of assumptions, many of which themselves form testable hypotheses.   Primary amongst these are the following:

- That species' range adjustments depend upon successful establishment of dispersing offspring or propagules in sites offering suitable habitat and other environmental conditions, but lying beyond the current margin of the species' realised range.

- That species' maximum rates of range adjustment are determined by their long-distance dispersal capability, and thus depend upon the successful establishment of at least some of the very small proportion of offspring or propagules that achieve such long-distance dispersal.

- That a species' long-distance dispersal capability is in general related to its 'size';   i.e. the distance beyond which a particular proportion (e.g. the 1% of most distantly dispersed) of offspring or propagules are dispersed is greater for larger-bodied animals and/or larger plants than for smaller-bodied animals and/or smaller plants.

- That a species' long-distance dispersal capability is in general related to its lifespan or, more specifically, to its age at maturity;   i.e. the distance beyond which a particular proportion (e.g. the 1% of most distantly dispersed) of offspring or propagules are dispersed is greater for species that take years or even decades to reach maturity than for species that are reproductively mature after a period of less than one year and perhaps even only a few weeks.

- That a species' long-distance dispersal capability is in general related to its fecundity;   i.e. the distance beyond which a particular proportion (e.g. the 1% of most distantly dispersed) of offspring or propagules are dispersed is greater for less fecund, i.e. more 'K-selected', species than for more fecund, i.e. more 'r-selected', species.

- That a species' long-distance dispersal capability is in general related to its degree of habitat specialisation;   i.e. the distance beyond which a particular proportion (e.g. the 1% of most distantly dispersed) of offspring or propagules are dispersed is greater for species that exhibit a greater degree of habitat specialisation than for more generalist species.

- That a species' long-distance dispersal capability is in general related to the 'rarity' of its habitat; i.e. the distance beyond which a particular proportion (e.g. the 1% of most distantly dispersed) of offspring or propagules are dispersed is greater for species that require rare and/or spatially-restricted habitats, e.g. wetlands, than for species that use common and/or spatially-extensive habitats.

- That the minimum extent of a patch of suitable habitat in which a species can establish, breed and produce offspring or propagules that may disperse to another habitat patch is in general related to the 'size' of the species;   i.e. the minimum viable patch extent is greater for larger-bodied animals and/or larger plants than for smaller-bodied animals and/or smaller plants.

- That the minimum extent of a patch of suitable habitat in which a species can establish, breed and produce offspring or propagules that may disperse to another habitat patch is in general related to the lifespan, or more specifically to the age at maturity, of the species;   i.e. the minimum viable patch extent is greater for species that take years or even decades to reach maturity than for species that are reproductively mature after a period of less than one year and perhaps even only a few weeks.

- That the minimum extent of a patch of suitable habitat in which a species can establish, breed and produce offspring or propagules that may disperse to another habitat patch is in general related to the fecundity of the species;   i.e. the minimum viable patch extent is greater for less fecund, i.e. more 'K-selected', species than for more fecund, i.e. more 'r-selected', species.

Although 'size', age at maturity and fecundity are correlated to a degree, they are dealt with here as three distinct factors because their general pattern of correlation is weak.   The basis of the latter three assumptions/hypotheses is that successful long-distance dispersal is related to the number of offspring or propagules produced by a species' population, sometimes referred to as the 'propagule
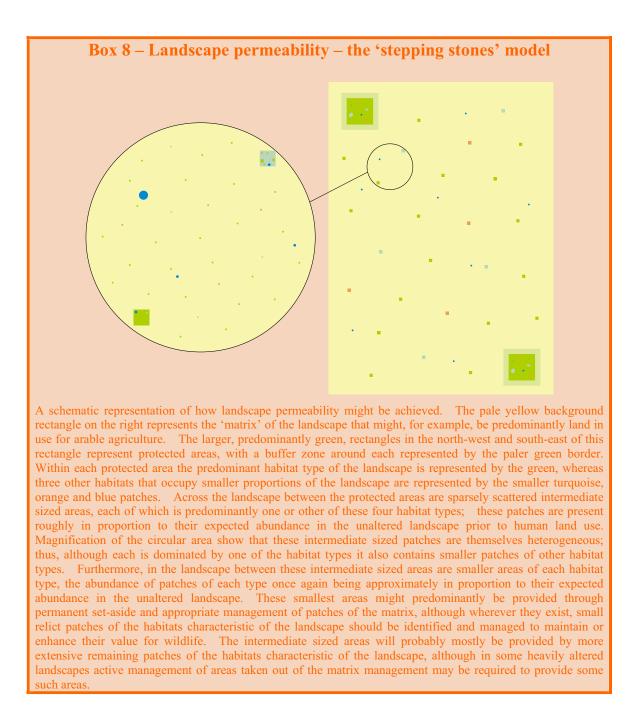
pressure' exerted by a species' population. More fecund species produce more offspring or propagules from a given population; a larger population of a smaller species than of a larger species typically can be supported by a given area of suitable habitat; and species that take longer to reach reproductive maturity generally either also are larger, in the case of plants, or else, in the case of animals, remain dependent upon their parents for longer and thus require a larger resource base.

The general hypothesis then is that a permeable landscape is one in which patches of all the physical habitats found in that landscape are present, those patches being of varying sizes, with smaller patches separated by shorter intervening distances across the background 'matrix' than larger patches and with smaller patches located between larger patches. Furthermore, the representation of the range of physical habitats amongst the patches should approximate, at least in terms of the rank order of their extents, their probable representation in the landscape, including the 'matrix', prior to human alteration of the landscape [Box 8].

As written, this general hypothesis is qualitative; in order to begin to plan strategies for the management of landscapes in ways that will render them permeable to species making range adjustments in response to climatic change, however, at least some attempt must be made to quantify some elements of the hypothesis. Some guidance in this can be derived from estimates of species' early Holocene migration rates. For example, trees that achieve reproductive maturity after perhaps 20 years, yet achieved long-term average range boundary adjustments at rates of $ca.$ 500 m yr^{-1}, must regularly have achieved successful long-distance dispersal over distances of at least $ca.$ 10 km (Huntley & Birks, 1983; Huntley, 1991). There is evidence suggesting that some tree species achieved even greater long-distance dispersal, their range boundary advancing by the initial establishment of distant outlier populations and later infilling of the landscape between these 'bridgeheads' (Woods & Davis, 1989) and/or their rate of range boundary adjustment being more rapid, perhaps at rates of as much as $ca.$ 2 km yr^{-1}. Taken at face value this would suggest that patches suitable for the growth to maturity of trees may be as much as 10 km apart. However, it is necessary to consider the mechanism by which trees achieve dispersal over such distances. Only exceptionally will wind-dispersal of propagules or their dispersal by birds result in dispersal over such distances, whereas larger mammals can readily disperse propagules over such distances (Giannakos, 1997). In most of Europe today, however, the large mammals responsible for such dispersal are no longer present. This implies that such dispersal distances are unlikely to be achieved and thus that patches of suitable habitat must be much closer together.

An alternative source of guidance are data recording recent range boundary expansions. For example, Hill et al. (2001) report range boundary adjustments of $0\cdot51 - 0\cdot93$ km yr^{-1} for the butterfly $Pararge$ $aegeria$ in two parts of Great Britain; they successfully simulate its range changes using the MIGRATE model (Collingham et $al.$, 1996) and dispersal characteristics that include a maximum dispersal distance of 20 km. However, they also demonstrate that its successful dispersal and establishment, and hence its effective rate of range boundary adjustment, is strongly influenced by habitat availability in the landscape, a 24% reduction in the extent of suitable habitat resulting in a simulated 42% and an observed 45% reduction in the rate of range boundary adjustment. By means of a sensitivity analysis, they also estimated that the minimum extent of suitable habitat that could support establishment and subsequent dispersal was $0\cdot8$ ha.

Such evidence suggests that the smallest patches could perhaps be only $ca.$ 1 ha in extent, and that such patches, of any given habitat type, should be no more than a few kilometres apart. A continuum of progressively larger patches at greater distances would then lead up to the most extensive protected areas, hundreds of square kilometres in extent but perhaps separated by distances of as much as $50 - 100$ km. Only by establishing and monitoring examples of such landscapes, however, will it be possible to collect the evidence required to assess their effectiveness and to adapt the landscape management as necessary to ensure that a sufficiently effective network of sites is available and maintained.

Box 8 – Landscape permeability – the 'stepping stones' model

A schematic representation of how landscape permeability might be achieved.   The pale yellow background rectangle on the right represents the 'matrix' of the landscape that might, for example, be predominantly land in use for arable agriculture.   The larger, predominantly green, rectangles in the north-west and south-east of this rectangle represent protected areas, with a buffer zone around each represented by the paler green border. Within each protected area the predominant habitat type of the landscape is represented by the green, whereas three other habitats that occupy smaller proportions of the landscape are represented by the smaller turquoise, orange and blue patches.   Across the landscape between the protected areas are sparsely scattered intermediate sized areas, each of which is predominantly one or other of these four habitat types;   these patches are present roughly in proportion to their expected abundance in the unaltered landscape prior to human land use. Magnification of the circular area show that these intermediate sized patches are themselves heterogeneous; thus, although each is dominated by one of the habitat types it also contains smaller patches of other habitat types.   Furthermore, in the landscape between these intermediate sized areas are smaller areas of each habitat type, the abundance of patches of each type once again being approximately in proportion to their expected abundance in the unaltered landscape.   These smallest areas might predominantly be provided through permanent set-aside and appropriate management of patches of the matrix, although wherever they exist, small relict patches of the habitats characteristic of the landscape should be identified and managed to maintain or enhance their value for wildlife.   The intermediate sized areas will probably mostly be provided by more extensive remaining patches of the habitats characteristic of the landscape, although in some heavily altered landscapes active management of areas taken out of the matrix management may be required to provide some such areas.

ii.   "Wildlife friendly" management of the matrix

Even if effective networks of sites are successfully established, dispersing individuals or propagules will need to cross the general landscape matrix in order to move between the components of such networks.   This will only be possible if that matrix also is managed in ways that are favourable for wildlife.   Furthermore, given appropriate management, the matrix also can provide additional habitat for many species that will further facilitate their range adjustments in response to climatic change and help sustain their populations, thus contributing directly as well as indirectly to biodiversity conservation.   Such favourable management can, of course, take many forms.

In the case of species that principally utilise the landscape matrix where that is managed, for example, for agricultural or forestry purposes, favourable management practices may be essential to

their conservation. Thus only through appropriate favourable management practices can many birds that breed in farmland, such as *Crex crex* (Corncrake), successfully be conserved (Berg & Gustafson, 2007; O'Brien *et al.*, 2006). More generally, populations of farmland birds typically require sympathetic management practices, often of a less intensive and/or more diverse character than modern agro-industrial management practices, if they are to be sustained (Gregory *et al.*, 2004; Wilson *et al.*, 2005). Such less intensive management and diversification of the agricultural matrix, furthermore, also is favourable for other species, including mammals such as *Lepus europaeus* (Brown Hare) (Reichlin *et al.*, 2006; Vaughan *et al.*, 2003) and arable weeds (Roschewitz *et al.*, 2005), and also has been shown to improve the resilience of populations of some species to extreme climatic events, e.g. *Rana temporaria* (Common Frog) (Piha *et al.*, 2007). Similarly, forest birds require appropriate sympathetic management if they are to use commercial forestry areas in the landscape. Thus, for example, if they are not to become restricted entirely to the small remaining fragments of old-growth forest, then those birds, such as *Picoides tridactylus* (Three-toed Woodpecker), that depend upon standing dead timber for feeding and/or for breeding sites require that commercial forestry areas are not subjected to the modern practice of 'sanitary felling' of diseased or dead trees (Imbeau & Desrochers, 2002; Pakkala *et al.*, 2002; Wesolowski *et al.*, 2005). Other forest species may require other forms of sympathetic management, such as that which maintains the lek sites used by *Tetrao urogallus* (Capercaillie) (Pakkala *et al.*, 2003). Interestingly, lower intensity management practices designed to be favourable to one target species once again also prove to be indirectly favourable to other species (Pakkala *et al.*, 2003).

Given the evidence that less intensive management practices and the maintenance of greater heterogeneity of the landscape generally are favourable to species that use the managed landscape matrix, it seems reasonable to hypothesise that similar management practices are likely also to be more favourable to species dispersing across the landscape matrix than are more intensive management practices and landscape management strategies that promote homogeneity of the matrix. This proposition is supported by modelling evidence that shows that 'fine-grained' heterogeneous landscapes sustain greater rates of species' range boundary adjustment than do 'coarse-grained' and/or more homogeneous landscapes (Collingham & Huntley, 2000). Thus, the responses of wildlife to climatic change are likely to be facilitated by the maintenance and enhancement of schemes that provide incentives, or requirements, for the managers of land used for agriculture or forestry to plan and manage their land holdings less intensively and in ways that promote heterogeneity.

Recommendation 7: Adaptation strategies should aim to develop permeable landscapes that provide functional networks of habitat 'stepping stones' of various sizes and separations linking protected areas that will form the principal nodes in these functional networks. In general, the smallest habitat stepping stones should be separated by the shortest distances and should provide the links between more widely separated but larger stepping stones along a continuum of sizes and separation distances extending up to those characteristic of the protected areas of the region. Size and separation, as well as the number of patches, also will relate to the size, separation and frequency typical of the habitat(s) represented within any particular stepping stone – thus habitat types that are naturally represented by patches that are relatively small in extent, widely separated and/or infrequent can be represented by fewer, smaller and more remote stepping stone patches than can habitats that naturally are extensive, continuous or near-continuous and dominant in the landscape.

Recommendation 8: Adaptation strategies also should aim to ensure that these 'stepping stones' are embedded in a landscape matrix that is managed less intensively than is typical of much modern commercial agriculture and forestry practice, as well as in ways that promote relatively fine-grained heterogeneity.

Recommendation 9: Adaptation strategies should exploit and, where possible, enhance, existing incentive schemes that aim to promote lower intensity land management and the development of greater landscape heterogeneity. Such schemes can help provide stepping

stone habitat patches where these do not already exist, as well as a more favourably managed landscape matrix.

VII. STRATEGIES FOR ADAPTATION

In the previous section, the implications of the evidence discussed in the earlier sections was considered in relation to strategies for biodiversity conservation in a world where climatic conditions are changing rapidly;   key conclusions in relation to strategies for adaptation were outlined.   These conclusions are reiterated below and some of the their further ramifications, and some of the practical aspects of the strategies that must be developed, considered.

The first group of conclusions presented above relates to the dynamic and individualistic responses of species' geographical ranges to climatic change:

Recommendation 1: Adaptation strategies must recognise the dynamism of species' geographical ranges. This will require a re-evaluation of the management goals of protected areas, as well as of the basis for maintaining the protection of areas that in future may no longer support one or more of the species whose local conservation was a primary reason for the initial recognition of the protected area.   A re-evaluation of the use of the concept of 'native' species in setting conservation priorities also will be required, both at the level of individual countries and at the European scale. In addition, strategies will be required that aim to facilitate the achievement by species of the potential future range changes required as they adjust to the projected climatic changes.

Recommendation 2:   Adaptation strategies must recognise the need to facilitate, rather than to hinder, gene flow through species' populations if they are to adapt to projected climatic changes. In addition, such strategies must include mechanisms designed to ensure that intra-specific genetic diversity loss is minimised, especially that component of the genetic diversity of many European species that is concentrated near the 'trailing edge' of their distribution, and thus is most vulnerable to the negative impacts of climatic change upon these 'trailing edge' populations.

Recommendation 3:   Adaptation strategies must have amongst their goals that of facilitating community and ecosystem changes resulting from climatic changes, as well as of permitting and in some cases facilitating the ecosystem dynamic processes upon which the realisation of such changes often depends. These changes are an essential component of adaptation by the biosphere to climatic change.

The principal further ramification here is the need to design conservation management strategies, both for protected areas and for the additional 'stepping stone' areas required in the wider landscape, that are compatible with, and designed to facilitate, species' dynamic responses to climatic change. These strategies also must be designed to facilitate, rather than to impede, the consequences of species' range changes with respect to community composition and ecosystem structure.

Practically, this may mean taking steps to accelerate community and ecosystem transformation, principally through management actions that increase the frequency of disturbance episodes, but also perhaps through translocations, either of species or of species' genotypes.   Such management will enhance the ability of species and ecosystems to maintain a dynamic equilibrium with the changing climate.   Care will be necessary, however, to ensure that the dynamic state of the ecosystem being managed, and its regeneration dynamics, are diagnosed correctly [Box 9].   It will also be necessary carefully to assess the implications of any management strategy for rare or threatened species present in the area.   Whilst, in the longer term, such species may be unlikely to persist in the particular area being managed because it no longer will have suitable climatic conditions, in the short term it will be imperative to maintain populations of these species that are as large as possible in order to maximise their 'propagule pressure' and hence their potential to disperse to newly suitable areas in the future. In this respect, it may seem that appropriate management strategies should differ according to where within the species' overall geographical range the area being managed is located, and also how this location relates to the projected likely future change in the species range.   However, given the likelihood that a species' success in responding to climatic change will depend upon maintaining within its population the genotypes that are found principally close to the 'traling edge' of its range, the maintenance of such pupulations will be at least as important as maintaining populations close to the 'leading edge' of its range.

Box 9 – Ecosystem dynamics

Ecosystem dynamics principally concerns the dynamics of the vegetation component of the ecosystem, although typically the other groups of organisms found in the ecosystem exhibit parallel dynamics,   One simple way to view ecosystem dynamics is in terms of three distinct processes that operate typically over progressively greater temporal scales:

- **Regeneration cycles:**   maintain the structure and composition of an ecosystem.

  Regeneration cycles operate at a range of spatial and temporal scales.   It often is convenient to contrast two classes of regeneration process.

  Firstly, many communities and ecosystems exhibit what is often referred to as 'gap-phase' regeneration; such regeneration is triggered by the death of an individual mature plant that results in a gap that then is re-colonised and in time once again is occupied by a mature individual plant, although not necessarily of the same species as that which initially died.   Such regeneration of calcareous grasslands may have a characteristic spatial scale of gaps of only a few square centimetres and new individuals may be established within months of the death of the previous individual.   In forests of broad-leaved trees, however, canopy gaps resulting from death of single trees may extend over $10^2 - 10^3$ m^2 and a new individual may only become established in a gap after decades to a century.   In this latter case the gap typically will be occupied by individuals of a series of different species at different stages of the cycle.   The recurrence time of regeneration at any point is determined by the typical lifespan of the species concerned.

  Secondly, other ecosystems and communities characteristically exhibit what may be referred to as episodic regeneration that is triggered by some form of disturbance.   The disturbance that triggers an episode of regeneration may take many forms, of which fire, extreme climatic events, disease epidemics and outbreaks of defoliating insects, are perhaps amongst the most frequently observed.   The principal characteristic of episodic regeneration is that the disturbance leads to the synchronous death of many individuals, often, but not always, of many different species.   As a result, there is then synchronous regeneration across the spatial extent of the disturbance.   That spatial extent may be between as little as a few hectares and as much as a few hundred square kilometres.   Replacement of the original vegetation cover typically takes between a decade and a century or two, with the area usually being occupied by communities of species of different life forms in sequence before vegetation similar to that present before the disturbance once again occupies the site.   The interval between disturbance episodes determines the frequency with which such episodic regeneration takes place on any area.

- **Autogenic succession:**   leads to sequential changes in the composition and/or structure of the ecosystem present at a given locality as a consequence of changes to the local environmental conditions brought about by the ecosystem.   Changes in the character of the soil are often involved, arising from the properties of the species present in early stages of the successional sequence.

  Although the sequence of communities seen in some examples of episodic regeneration may succeed one another at least in part as a result of autogenic processes, the most important examples of autogenic succession are primary successions on substrates such as newly exposed glacial deposits.   Such autogenic successions easily can be distinguished from regeneration cycles in which autogenic processes play a part because, whereas the end point of the latter is a return to a community similar to that present prior to disturbance, autogenic successions progress through a series of communities to an end point that is unlike any previous stage of the succession.   Such successions usually have durations of at least centuries and in many cases may require millennia for their completion.

- **Allogenic succession:**   is the mechanism that brings about changes in the composition and/or structure of the ecosystem present at a given locality in response to changes in the wider environment, including especially climatic changes.

  The changes that take place are determined by the environmental changes taking place.   Although their overall rate is determined by the rate of environmental change, there often is a lag between the onset of this change and the ecosystem response, the length of which typically is determined by the frequency of disturbance and/or by the lifespan of the dominant species.   Where the magnitude of the environmental change is such that species not present in the region potentially form part of the new community, a further lag may arise from the requirement for these species to extend their geographical range by dispersal of propagules or offspring and establishment in areas beyond their initial range.

Management strategies thus must combine and balance the need to facilitate species' responses to climatic change and the need to maximise populations of rare and threatened species. Achieving this balance will perhaps be one of the primary challenges facing managers of protected areas. Furthermore, success in achieving this balance in a given protected area will principally be reflected not just by successful transformation of the ecosystems of that area, but by the successful dispersal to other protected areas, and establishment therein, of rare or threatened species that may ultimately be unable to persist under the new climatic conditions of the given area.

> *Recommendation 10: Management strategies must combine and balance the need to facilitate species' responses to climatic change and the need to maximise populations of rare and threatened species. Achieving this balance will perhaps be one of the primary challenges facing managers of protected areas. Furthermore, success in achieving this balance in a given protected area will principally be reflected not just by successful transformation of the ecosystems of that area, but by the successful dispersal to other protected areas, and establishment therein, of rare or threatened species that may ultimately be unable to persist under the new climatic conditions of the given area.*

There also is a legislative implication of such eventual loss of rare or threatened species, as well as of the transformation of the ecosystems of the area.

> *Recommendation 11: The framework for the provision of legal protection for designated protected areas also must be rendered dynamic. Such protection for any individual area must no longer be dependent upon the successful conservation therein of particular target rare or threatened species, or the maintenance therein of a particular community or ecosystem viewed as characteristic of the region.*

One way to address this issue is to adopt a more holistic approach that considers not individual protected areas but the overall network of protected areas. This network should derive its legal status and protection from its ability, taken as a whole, to protect the biodiversity of an overall region, including its rare and threatened species, as well as examples of the full range of ecosystems. Furthermore, the network must be rendered functional by ensuring the necessary permeability of the wider landscape that will provide the required network 'connectivity', and the legal framework must recognise that success in facilitating change, including supporting species and ecosystems not found today in the region, will be an essential attribute of the network. Conversely, failure to maintain in the region species for which suitable climatic conditions are no longer present should not be viewed as a failure of the network. Given the spatial scale of species' responses to projected climatic change, such functional networks must be viewed at continental scales.

> *Recommendation 12: The concept of a 'native' species, especially where that is embedded in legislation relating to biodiversity conservation, requires re-evaluation.*

Many species that currently are not considered as natives of a given European country may in future potentially expand their geographical ranges into that country as part of their response to climatic change. In some cases such species may be rare or threatened at the European or even global scale; they must not be excluded from the necessary protection, nor should their requirements be ignored when determining conservation management strategies, in a given country simply because they have historically not been found in that country. At the very least, a 'continental' rather than a national view must be taken when considering the 'native' status of a species. Given that some species found today in north Africa or the Middle East, but not in Europe, may in future extend their ranges to Europe, however, the concept of a 'potential native' species may in future be more useful than that of a 'native'. One useful way to determine the 'potential native' status of a species might be in terms of the major biogeographical provinces. Thus 'potential native' species of Europe might be considered to include not only all of those species actually native to the continent, but also those found today in Africa north of the Sahara, in the Middle East north of the principal desert regions, and in northern Eurasia. Of course, any such categorisation is somewhat arbitrary because, for example,

given enough time and suitable conditions, a species of north-western North America might extend its range to Europe *via* Beringia and northern Eurasia, whereas an Australian species is much less likely to do so even over geological time scales because of the need to cross the equatorial zone, as well as to disperse successfully across the seaways of south-east Asia.

'Alien' species thus would be those that have experienced inter-continental translocations, or equivalent translocations between ocean basins, usually as a result of human actions, albeit often accidentally rather than deliberately. In contrast, species that reach Europe from connected or adjacent regions by natural dispersal, and especially species that simply shift their range within Europe, should be considered as having been successful in realising the dynamic adjustment of their distribution in response to climatic change; they should be given any necessary protection rather than persecuted. Although as now, the majority of the truly alien species will fail even to become naturalised, that small proportion that becomes invasive will require similar control measures to those already in place in many cases. Climatic change is likely to result in invasive behaviour by species that have not previously exhibited such a tendency in Europe, thus monitoring of the behaviour of alien species, and especially of those that become naturalised, should be undertaken in order to provide 'early warning' of those that may pose potential threats to the persistence of 'native' and/or 'potential native' species.

The second group of recommendations presented above relates to the importance of maintaining and augmenting the existing network of protected areas:

> **Recommendation 4:** *Adaptation strategies must aim to ensure the continued protection and appropriate management of existing protected areas. A coarse filter type approach should be implemented at a European scale to identify gaps in this network of existing protected areas, and the network then should be augmented in order to maximise the representation of the full range of environmental conditions and physical habitats. The network also should be augmented where necessary to ensure that there are no excessively large spatial gaps in the network of protected areas. Appropriate management of the wider landscape, and the development of a suitable landscape structure, will be essential to complement the protected area network; without such management of the wider landscape, many species will be unable to achieve the responses to climatic change that are essential to their long-term survival.*
>
> **Recommendation 5:** *Adaptation strategies ought to exploit buffer zones as a valuable tool for enhancing the effectiveness of protected areas, but should not consider them generally as contributing directly to adaptation to climatic change.*

Protected areas will continue to be of paramount importance for the conservation of biodiversity, especially in relation to rare and/or threatened species. They will represent vital nodes in the overall network of sites managed to facilitate the dynamic response of species to climatic change and thus to conserve biodiversity. Even those that in future no longer support the species or ecosystems that formed the basis for their initial designation are important and must in general be maintained. Such areas represent valuable areas of physical habitats free from, or with only limited impacts from, human land uses that are inimical to many species. They will provide 'safe havens' for species newly dispersing into an area and in some cases may even become of enhanced value if those species include some that are even more threatened than those for which the site was first designated. In order to ensure their continuity, however, it will often be necessary to amend the designation criteria, because in many cases these are based upon the species or ecosystems present now, and formulated with a 'static' view of the world. In considering such revision of the basis for designation and protection, a more flexible and 'dynamic' framework should be adopted, perhaps recognising the importance for biodiversity conservation of maintaining the protection of a network of sites representing the range of physical habitats in a region, rather than focusing upon the species or ecosystems present in a site today. The physical habitat – including topographic features, geology and the hydrological network – is much more permanent than are the species and ecosystems, especially in a world in which climate is changing rapidly as a consequence of human activities.

As outlined above, protected areas will be needed both to sustain for as long as possible, and in the maximum possible numbers, those species that they currently support, and also to provide the 'safe havens' for species newly arriving in the area as a result of their dynamic range adjustments in response to climatic change. In order to achieve both goals, however, contrasting management may be required: For example, minimal disturbance may favour the continued presence of species currently present, whereas enhanced disturbance may facilitate the arrival of species whose range is newly expanding into the region (Bradshaw & Zackrisson, 1990; Sykes & Prentice, 1996).

Recommendation 13: *Accommodating such contrasting management strategies will in general require that, wherever possible, the extent of protected areas be increased.*

Arguably, this need for enlargement is proportional to the extent by which the rapidity of the anthropogenic climatic change exceeds the capacity of species' dispersal, and consequently the rate at which species are able to make their dynamic range adjustments. Given that it is estimated that anthropogenic climatic change during the 21st century may be at least an order of magnitude faster than the most rapid changes of the recent geological past, the need for additional protected area is likely to be considerable, and also to persist for the several centuries that the biosphere may take to reach any new equilibrium, assuming that anthropogenic climatic change eventually is halted.

Recommendation 14: *Increases in the size of existing protected areas should be targeted to provide the greatest flexibility and ability to 'buffer' against the effects of climatic change.*

Thus, for example, in the case of protected areas in regions of high relief, additional areas should encompass the highest elevation parts of the region and/or as diverse a range of slopes and aspects, including especially steep poleward facing slopes, in order that they may offer refuge sites for species 'fleeing' from warmer situations at lower elevations or on equatorward facing slopes. Although it is sometimes proposed that the extent of protected areas should be increased preferentially also on their poleward margins, as has been argued above, the scale of species' responses to climatic change is orders of magnitude greater than any realistic scale upon which the vast majority of protected areas might be increased in extent. A more appropriate and valuable strategy when selecting areas that might be added to a protected area to increase its extent will be one that seeks to maximise the attainment of two goals: Firstly, to maximise the extent within the protected area of the dominant physical habitat type and ecosystem of the region in which the protected area is situated; and secondly, to maximise the range of physical habitats represented, especially by including areas with diverse combinations of the principal physical habitat qualities found in the region (e.g. combinations of geological substrate types with topographic situations). Increasing the effective extent of protected areas through the addition of buffer zones also will generally be even more desirable in a world of climatic change.

Recommendation 15: *In addition to increasing the size of existing protected areas wherever this is feasible, additional protected areas will be required in many regions to ensure that a functional network of sites is attained.*

In identifying such additional protected areas the optimal strategy will be similar to that for selecting areas to be added to existing protected areas, with the additional constraint that the spatial location, as well as the physical habitats, of the area selected should be chosen so as to fill any identified gap in the existing network of protected areas. Having satisfied these primary requirements, where they arise, then areas selected should preferably be heterogeneous in terms of their physical habitats, and especially in terms of topography, and will be favoured if they include physical habitats of limited extent or frequency in the landscape, in addition to the dominant physical habitat type of the region. Only exceptionally should the presence today of particular species or communities be a primary consideration in the selection of such additional areas; such exceptions will arise only where the existing network of protected areas does not already provide adequate protection for these species or communities.

The third group of recommendations presented above relates principally to the requirement to ensure 'connectivity' of the network of protected areas through management of the intervening landscape in ways that will render it 'permeable' to species responding to climatic change:

Recommendation 6: Adaptation strategies thus should not focus upon the provision of corridors as a necessary part of achieving landscape structures that are favourable for the dynamic range adjustments of species in response to climatic change. Furthermore, in most of Europe corridors of the necessary scale to be truly valuable will not be a viable option. Nonetheless, where the provision of such large-scale conservation corridors (cf. Rouget et al., 2006) is a viable option, this option ought to be pursued as part of the overall adaptation strategy.

Recommendation 7: Adaptation strategies should aim to develop permeable landscapes that provide functional networks of habitat 'stepping stones' of various sizes and separations linking protected areas that will form the principal nodes in these functional networks. In general, the smallest habitat stepping stones should be separated by the shortest distances and should provide the links between more widely separated but larger stepping stones along a continuum of sizes and separation distances extending up to those characteristic of the protected areas of the region. Size and separation, as well as the number of patches, also will relate to the size, separation and frequency typical of the habitat(s) represented within any particular stepping stone – thus habitat types that are naturally represented by patches that are relatively small in extent, widely separated and/or infrequent can be represented by fewer, smaller and more remote stepping stone patches than can habitats that naturally are extensive, continuous or near-continuous and dominant in the landscape.

Recommendation 8: Adaptation strategies also should aim to ensure that these 'stepping stones' are embedded in a landscape matrix that is managed less intensively than is typical of much modern commercial agriculture and forestry practice, as well as in ways that promote relatively fine-grained heterogeneity.

Recommendation 9: Adaptation strategies should exploit and, where possible, enhance, existing incentive schemes that aim to promote lower intensity land management and the development of greater landscape heterogeneity. Such schemes can help provide stepping stone habitat patches where these do not already exist, as well as a more favourably managed landscape matrix.

The overall goal of any strategy for the management of the wider landscape in ways that will contribute positively to the attainment of biospheric responses to climatic change must be the provision of a 'permeable' landscape through which components of biodiversity responding to climatic change are able to move. As discussed above, the provision of 'stepping stone' sites throughout the landscape is seen as key to attaining such permeability. Such stepping stones might be provided by a variety of mechanisms, according to the characteristics of any particular landscape or region and the opportunities that it may offer. In some parts of the world it will be possible to designate and protect relict patches of unaltered ecosystems where these occur in otherwise extensively altered landscapes; in most of Europe, however, the focus will need to be upon designating and protecting patches of semi-natural ecosystems, because few unaltered ecosystem patches remain.

Recommendation 16: Especially in the extensively and heavily altered landscapes of much of western Europe, an effort should be made to retain as many as possible of the remaining patches of semi-natural habitats because replacing them, if they are allowed to be destroyed, is much more difficult, as well as both more expensive and only possible on relatively long time scales in many cases.

Attaining this goal will probably require that the landowners are offered appropriate incentives to maintain these sites;   alternatively a large expenditure will be required if all such sites are to be taken into 'public' ownership.   In practice, some combination of the two approaches is likely to be required.

In many landscapes, however, the density and range of such relict natural or semi-natural sites will be insufficient to provide the required landscape permeability.   In these cases it will be necessary also to take steps to develop additional such patches.   Such habitat creation will often be a relatively long-term process and requires continuity of commitment and support if it is to be effective.   Once again, the most efficient strategy is likely to be one that deploys appropriate incentives to encourage, or even require, landowners to undertake such creative management;   the alternative of public land acquisition and management is likely to be prohibitively expensive in most cases, although should be considered as a possible 'last resort' where necessary.   There is likely to be considerable scope to amend and further develop existing incentive schemes, such as those that encourage the 'set aside' of areas of agricultural land or the development of 'farm woodlands', in order to target them more effectively to the provision of landscape permeability.   Key attributes of any such scheme will include a requirement for an indefinite commitment to the maintenance of such sites into the future, an obligation upon land-owners who own more than some minimum land holding to participate in the scheme (the alternative perhaps being the compulsory public acquisition of the necessary parts of their land holding) and some 'centralised' strategic planning so as to ensure that the overall provision includes the appropriate proportional representation of the diversity of physical habitats, as well as of ecosystems, necessary to provide landscape permeability in the region.   Thus, whilst the network as a whole may, for example, require a proportion of flood-plain areas occupied by woodlands, it will not be feasible or sensible to require every individual land-owner to provide a patch of this type, even amongst those whose land holding includes areas of flood plain.

The other vital attribute of a permeable landscape is that species moving across that landscape have the same level of legal protection they would enjoy within protected areas.

Recommendation 17: *Legal protection from persecution, hunting and other forms of destructive human activity must be extended to the majority of biodiversity components wherever they may be found.*

The 'default' position should be that an organism is protected from disturbance or destruction of itself or its habitat.   It then will be necessary to identify and justify exceptions to this 'blanket' protection;   such exceptions might include recognised 'pest' species that cause significant damage to some human activity and species whose numbers are artificially increased through human management in order to provide 'quarry' species for hunters.

Recommendation 18: *In addition to including these various components, any adaptation strategy for biodiversity conservation in a world of climatic change also must be international, and preferably sub-continental or continental, in scope if it is to be effective, because this is the spatial scale at which climatic change will impact upon the distributions of species and the composition and structure of communities and ecosystems.*

Recommendation 19: *Such adaptation strategies also must include provision for the translocation of genotypes, species or even such poorly understood parts of ecosystems as the soil invertebrate and microbe communities, and also for the use of captive breeding programs where this is feasible.*

Although both translocation and captive breeding should be considered as options of last resort, and are only likely to be used in the case of particularly vulnerable components of biodiversity, especially those whose habitat is most threatened, reduced in extent and/or fragmented, in such cases they may offer the only option other than acceptance of the extinction of this component of biodiversity.   Given the unfortunate history of deliberate introductions, however, including some of

those made as part of programs of 'biological control', translocations should be very carefully evaluated before they are carried out, especially where the proposed translocation is of a species to a region where the suite of species with which it will interact is very different from that in the area from which it is being translocated.

VIII. CONCLUSION

As has been discussed above, evidence from the recent geological past as well as from the past few decades, shows that species exhibit a hierarchy of responses to climatic change. Of these, however, a combination of an adaptive genetic response and a spatial response are of primary importance when responding to climatic changes of larger magnitude. Placed in the context of the climatic changes of the recent geological past, the changes in global climate projected for the 21st century are clearly of large magnitude. Furthermore, these projected changes also are likely to take place at least an order of magnitude faster than the most rapid of global climatic changes of the last million or so years, and as a result more quickly than species are able to respond. The projected changes also lead to a 'destination' that is without parallel in recent earth history, with global climatic conditions likely to be warmer than at any time for ten million years or more. It thus must be expected that species will exhibit range shifts and adaptive responses, but that the former at least are unlikely to keep pace with the changing climate. The magnitude of the potential range shifts will be large, many species' range boundaries potentially shifting by 500 – 1000 km, and thus often will result in species' ranges potentially extending into countries from which they are currently absent. Strategies for the conservation of biodiversity in this world of rapid climatic change thus must focus upon the requirement to view the biosphere, as well as important components of its environment, as dynamic.

Evidence from the past, as well as that of species' present geographical distributions, shows that species' respond to climatic conditions and to climatic change in an individualistic manner. As a result, species assemblages ('communities') and ecosystems do not respond to climatic change as coherent entities, but rather such features of the biosphere are temporary assemblages brought together by the conditions prevailing at any time. Evidence of species' individualistic responses to the climatic changes that already have taken place during the 20th century supports the expectation that individualistic spatial responses of species' will dominate the biospheric response to projected 21st century climatic change. Strategies for the conservation of biodiversity in this world of rapid climatic change thus must focus upon the conservation of species, and of their inherent genetic variance, rather than upon the conservation of the communities or ecosystems that they form in any given region under present climatic conditions.

Maintaining and, wherever possible, enlarging and augmenting, the existing network of protected areas will be a key part of any strategy for the conservation of biodiversity in a world of climatic change. Although many protected areas may experience substantial changes in the complement of species present, and in the communities and ecosystems that these species form, they nonetheless will provide vital nodes in an overall network that is necessary if species are to be able to attain their responses to climatic change. Key challenges will include that of ensuring that the designation of sites as protected areas can be maintained, even when the original legal basis upon which their current designation rests may no longer exist because of inevitable changes in species' distributions and in the character of the ecosystems present. It also may often be the case that the management of a protected area required, on the one hand, to maintain maximal populations of rare or threatened species present therein so as to maximise their potential to achieve dispersal and range adjustment in response to climatic change, and on the other hand, to facilitate colonisation by dispersing propagules or offspring of species for which the area has become newly suitable as a consequence of climatic change, may conflict. In itself this is a strong argument for the substantial enlargement of existing protected areas, where this is possible, or for the addition of complementary areas to the network where enlargement of existing areas is not possible. The extent to which such an increase in the overall area encompassed by protected areas is necessary is to a substantial degree a function of the rapidity of climatic change and, in particular, of the magnitude of the mismatch between the rate of climatic change and the rate at which species are able to attain the spatial response required to maintain their range in approximate dynamic equilibrium with the changing climate.

Protected areas, however, whilst necessary, are not in themselves sufficient. These areas must be embedded within landscapes that are managed, as part of the overall adaptation strategy, in ways that ensure their 'permeability' to species making spatial adjustments to their ranges in response to climatic change. Such permeability does not require the establishment of corridors or continuity of habitat availability, but rather that there is 'connectivity' between the protected areas. Such connectivity can be provided by 'stepping stones' of natural, semi-natural or newly created habitat. Stepping stones should be of various sizes and separation, with a general inverse relationship such that more distant patches generally will be larger in extent, and will have more closely spaced but smaller patches located in the intervening areas. Permeability of the landscape also requires that species remain protected throughout that landscape.

The challenge of developing and implementing such an adaptation strategy must be addressed internationally, because the scale of species' potential responses often transgresses national boundaries. Furthermore, the concept of species 'native' to a country or region must be re-assessed in order to accommodate the dynamic range changes that species' are expected to make in response to climatic change.

Although the future promises to be challenging both for the components of biodiversity and for those seeking to conserve this biodiversity, it also offers unprecedented opportunities to develop legal frameworks, incentive schemes and overall strategies that will improve the long-term outlook for biodiversity whatever the future may in due course bring. Society must rise to this challenge and must succeed; if it fails then our legacy to future generations will be a world immeasurably reduced in value and interest, as well as in its capacity to sustain the environmental services upon which we depend, whether these are clean air or water, or as yet undiscovered natural resources.

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