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RESEARCH REVIEW

Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?

RICHARD G. PEARSON* and TERENCE P. DAWSON

Environmental Change Institute, School of Geography and the Environment, University of Oxford, 1 A Mansfield Road, Oxford OX1 3SZ, U.K. E-mail: richard.pearson@eci.ox.ac.uk

ABSTRACT

Modelling strategies for predicting the potential impacts of climate change on the natural distribution of species have often focused on the characterization of a species' bioclimate envelope. A number of recent critiques have questioned the validity of this approach by pointing to the many factors other than climate that play an important part in determining species distributions and the dynamics of distribution changes. Such factors include biotic interactions, evolutionary change and dispersal ability. This paper reviews and evaluates criticisms of bioclimate envelope models and discusses the implications of these criticisms for the different modelling strategies employed. It is proposed that, although the complexity of the natural system presents fundamental limits to predictive modelling, the bioclimate envelope approach can provide a useful first approximation as to the potentially dramatic impact of climate change on biodiversity. However, it is stressed that the spatial scale at which these models are applied is of fundamental importance, and that model results should not be interpreted without due consideration of the limitations involved. A hierarchical modelling framework is proposed through which some of these limitations can be addressed within a broader, scale-dependent context.

Key words bioclimate envelope, climate change, climate space, ecological modelling, ecological niche, hierarchy, scale.

INTRODUCTION

It is a central premise of biogeography that climate exerts a dominant control over the natural distribution of species. Evidence from the fossil record (Woodward, 1987; Huntley, 1999; Davis & Shaw, 2001) and from recently observed trends (for reviews see Hughes, 2000; McCarty, 2001; Walther *et al*., 2002) shows that changing climate has a profound influence on species' range expansion and contraction. It is therefore expected that predicted future climate change (IPCC, 2001) will have a significant impact on the distribution of species.

A number of modelling strategies for predicting the potential impacts of climate change on biodiversity have been developed. These have often focused on the identification of a species' 'bioclimate envelope' (alternatively termed 'climate space', Box, 1981; Huntley *et al*., 1995; Carey, 1996; Bakkenes *et al*., 2002; Berry *et al*., 2002; Pearson *et al*., 2002) either through techniques that correlate current species distributions with climate variables or through an understanding of species' physiological responses to climate change (Franklin, 1995; Mack, 1996; Guisan & Zimmermann, 2000). Having identified a species' climate envelope, the application of scenarios of future climate change enables the potential redistribution of the species' climate space to be estimated.

Recent studies have questioned the validity of the bioclimate envelope approach by pointing to the many factors other than climate that play an important part in determining species distributions and their dynamics over time. Notably, Davis *et al.* (1998a,b) in their paper entitled 'Making mistakes when predicting shifts in species range in response to global warming' identify the importance of biotic interactions between species, arguing that bioclimate envelope-based models are flawed. Similarly, Lawton (2000) notes a number of factors, including the importance of species dispersal, which may lead to erroneous results from bioclimatic models, whilst Woodward & Beerling (1997) suggest that such models should be disregarded and replaced by dynamic vegetation models.

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* Corresponding author.

It is the aim of this paper to review, clarify and evaluate criticisms of bioclimate envelope models and to discuss their implications for the different predictive modelling approaches used. The paper presents concepts that may be familiar to many ecologists, but which we think it may be useful to collate and re-evaluate in the light of recent critiques. The bioclimate envelopes approach is first explained and placed within the context of ecological niche theory. The main criticisms of the approach are then discussed in turn, using selected examples from the literature. It is demonstrated that the complexity of the natural system presents fundamental limits to modelling strategies, making predictive errors inevitable. However, it is also demonstrated that for certain species and at certain scales, the bioclimate envelopes approach can provide useful results, giving a first approximation as to the potentially dramatic impact of climate change on distributions. The implications of this critique for different predictive modelling techniques employed (correlative vs. physiologically based methodologies) are discussed and the advantages and disadvantages of each method clarified. The importance of spatial scale is stressed and a modelling framework is proposed whereby a hierarchy of factors is considered to influence the distribution of species across a range of spatial scales. This framework places bioclimatic models within a broader, scale-dependent context. It is concluded that, in light of the great complexity of natural systems, the bioclimate envelopes approach can provide a valuable means of exploring key characteristics of complex species-environment relationships. However, such models should only be applied, and their results interpreted, with a thorough understanding of the limitations involved.

BIOCLIMATIC MODELLING

The bioclimate envelope modelling approach has its foundations in ecological niche theory. Hutchinson (1957) defined the fundamental ecological niche as comprising those environmental conditions within which a species can survive and grow. Hutchinson proposed that the fundamental niche would completely define the ecological properties of a species: a conceptual space whose axes include all of the environmental variables affecting that species (Austin *et al*., 1990; Leibold, 1995). Bioclimate envelopes can be defined as constituting the climatic component of the fundamental ecological niche, or the 'climatic niche'. Thus, bioclimatic models in their purest form consider only climatic variables and do not include in their processing other environmental factors that influence the distribution of species, such as soil type and land-cover type. The definition of a bioclimate envelope, as with Hutchinson's definition of the fundamental ecological niche, also does not include the influence of biotic effects such as competition for resources.

The distinction between biotic and abiotic limitations on a species' distribution can be formalized in the distinction between *fundamental* and *realized* niches (Hutchinson, 1957). The term *realized* niche describes the case whereby a species is excluded from parts of its *fundamental* niche because of competition and other biotic interactions (Austin *et al*., 1990; Guisan & Zimmermann, 2000). This distinction between fundamental and realized niches is important in the context of bioclimatic modelling, particularly with regard to the methodologies used to characterize bioclimate envelopes. Some bioclimatic models are based on empirical relationships between observed species distributions and environmental variables (e.g. Huntley *et al*., 1995; Peterson *et al*., 2001; Bakkenes *et al*., 2002; Pearson *et al*., 2002). These models correlate climate variables with observed distributions, adopting the general thesis that the best indicator of a species' climatic requirements is its current distribution. Such correlative models thus characterize biocimatic envelopes based on the *realized* niche, since observed species' distributions are, in reality, constrained by nonclimatic factors, including biotic interactions. Other bioclimatic models look for a more physiologically based mechanistic relationship between climate parameters and species response (e.g. Woodward, 1987; Prentice *et al*., 1992; Haxeltine & Prentice, 1996; Sykes *et al*., 1996). These models aim to identify the *fundamental* niche by modelling physiological limiting mechanisms in a species' climatic requirements.

Early examples of modelling strategies using correlations between climate and observed species distributions include the work of Johnston (1924, cited in Mack, 1996), who predicted the invasive spread of prickly pear cactus in Australia based on the climatic characteristics of the species' home range in North America, Hintikka (1963; cited in Hengeveld, 1990), who discriminated between the climates of locations inside and outside the ranges of some European species based on the variables minimum and maximum temperature. More recently, Huntley *et al*. (1995) fitted climate response surfaces for eight species of European higher plants by locally weighted regression based on three climatic variables. The fitted response surfaces were used to simulate potential future distributions based on scenarios of climate warming.

A further example of the correlative approach is the SPECIES model (Pearson *et al*., 2002). SPECIES (Spatial Evaluator of Climate Impacts on the Envelope of Species) employs an artificial neural network (ANN) to characterize bioclimate envelopes based on observed species distributions and five environmental inputs (derived primarily from climatic data, but including a measure of soil-type). Application of the model to a number of European higher plant species has enabled predictions of the future redistribution of suitable climate space under scenarios of climate change to be made (Fig. 1). The environmental inputs used are thought to have direct physiological roles in limiting the ability of plants to survive and are derived from primary climate and soils data in a climate-hydrological process model. Thus, though fundamentally

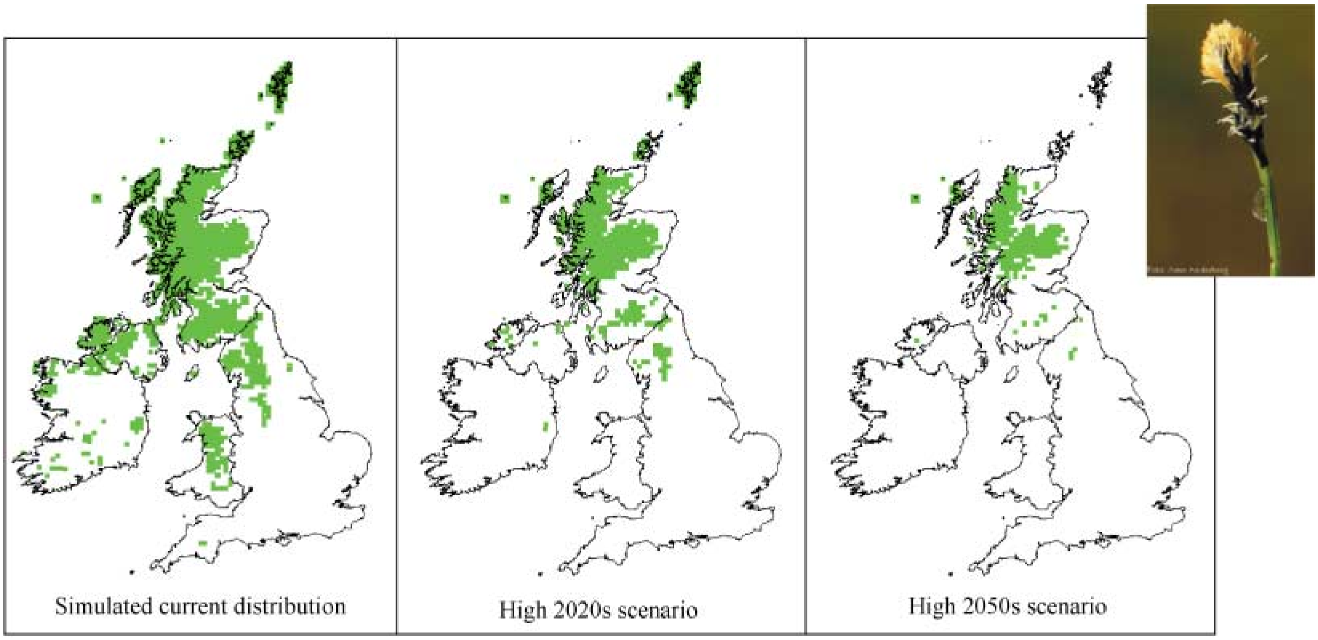

Fig. 1 Simulated redistribution of suitable climate space for stiff sedge (*Carex bigelowii*) under future climate scenarios in Great Britain and Ireland as predicted by the SPECIES model (Pearson *et al*., 2002). Climate change scenarios are those of Hulme & Jenkins (1998). Suitable climate space is expected to be lost, with a general migration northwards as the climate changes.

correlative, the SPECIES model incorporates physiologically based understanding of species' ecology. An important element of the SPECIES methodology is that training of the ANN is carried out at the European scale so as to include the full bioclimate envelope of the species being studied. The trained network is then downscaled in its application to Great Britain, ensuring that when applied to future climate scenarios the model is not used to extrapolate outside its training data range.

In contrast to models of an essentially correlative nature, models derived from physiological considerations provide a mechanistic basis for determining climatic limits on species distributions (Woodward, 1987). It is the thesis of this approach that models based on mechanistic considerations will be more robust under changed climatic conditions than those based on correlations between observed distributions and current climate variables. The weakness identified in the latter approach is that such correlations may not apply in the future as conditions, especially for interspecies relationships, change (Prentice & Solomon, 1991; Woodward & Rochefort, 1991; Prentice *et al*., 1992). Physiologically based models have often focused on patterns of global biomes (Prentice *et al*., 1992; Haxeltine & Prentice, 1996). For example, Prentice *et al*. (1992) present a predictive global biome model where the environmental limits of each plant type are assigned based on independent physiological data and physiological reasoning. The resulting predictions of global vegetation patterns were found to be in good agreement with the observed distributions, except where intensive agriculture has masked the natural patterns.

There are fundamental limitations to the predictive capacity of bioclimatic models, regardless of the methodology used to characterize the bioclimate envelope. Three of the main criticisms of the bioclimatic approach (biotic interactions, evolutionary change and species dispersal) are briefly reviewed in the next section, prior to a more detailed assessment of the strengths and weaknesses of the correlative and physiologically based modelling strategies.

CRITICISMS OF BIOCLIMATIC MODELLING

Biotic interactions

An important distinction exists between how a species would function on its own and how it actually does in the presence of other plants and natural 'enemies' (Leibold, 1995; Crawley, 1997). Davis *et al.* (1998a) identified inter–species interactions as the 'flaw' in bioclimate envelope modelling approaches. They used simple microcosm experiments on assemblages of three fruitfly species (*Drosophilia melanogaster*, *D. simulans*, *D. subobscura*) and a parasitoid wasp (*Leptopiliana boulardi*) to demonstrate the impact of competitive interactions on species distributions. It was shown that inter–species interactions in experimental clines markedly altered the distributions of all three fruitfly species from those found in single-species clines. The importance of such interactions for predictive modelling is that if species respond individually to climate change, as is suggested by the fossil record (Woodward, 1987; Huntley, 1999; Davis & Shaw, 2001), the current system of species interactions will change in future, making predictions from bioclimate envelope models erroneous.

The fact that competition, predation and symbiosis with other species influence a species' distribution was recognized long before the experiments of Davis *et al.* (1998a, 1998b). For example, Connell (1961) studied the factors that limit the range of a species of barnacle (*Chthamalus stellatus*) in the intertidal zone and showed that the lower edge of the range was set by interactions with other intertidal species, notably competition with another barnacle (*Balanus balanoides*) and predation by a snail (*Thais lapillus*). Similarly, Silander & Antonovics (1982) found complex responses when experimentally removing one species at a time from a salt-marsh community and observing the reactions of the others. Results showed that removal of one grass species (*Muhlenbergia capillaris*) led to equal range expansions by five other plants, whereas removing a sedge (*Fimbristylis spadicea*) resulted in the expansion of only one other plant (the grass *Spartina patens*).

Biotic interactions are thus shown to have important impacts on species distributions. We are left with a view of the natural system as a complex web of interactions and feedbacks between species, whereby changes to the distribution of a single species could have significant knock-on impacts on the distributions of many other species. It is thus apparent that modelling strategies based on bioclimate envelopes alone may in some cases lead to predicted distributions that are, in fact, wildly incorrect. However, it is argued that applying bioclimatic models at macro-scales, where climatic influences on species distributions are shown to be dominant, can minimize the impact of biotic interactions. Indeed, the fact that a number of bioclimatic models have been highly successful at simulating current species distributions at certain scales is in fundamental disagreement with the proposition that species distributions cannot be adequately defined by climatic factors alone.

For example, Pearson *et al.* (2002) found good agreement between observed and simulated European-scale distributions for 32 plant species based on correlations between observed distributions and 5 climatic inputs (Fig. 2). Similarly, Beerling *et al.* (1995) tested the predictive capacity of climate response surfaces for the distribution of Japanese knotweed (*Fallopia japonica*) and concluded that the close fit between observed and simulated distributions suggests that the species' European distribution is climatically determined. It is thus suggested that bioclimatic models applied at the macro-scale are suitable for making broad predictions as to the likely impacts of climate change on the distribution of species. The experimental scale studied by Davis *et al.* (1998a, 1998b), which led to their conclusion that bioclimate envelope studies are of limited use, is far from that proposed for bioclimatic studies.

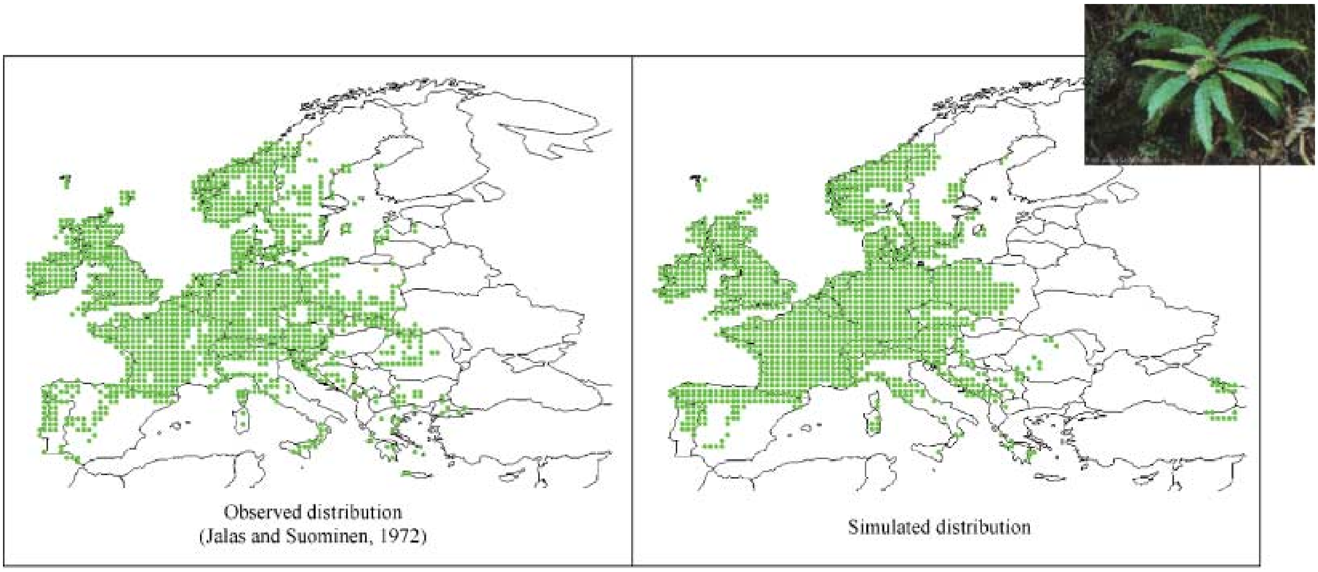

Fig. 2 Observed European distribution of hard-fern (*Blechnum spicant*) alongside the distribution as simulated by the SPECIES model (Pearson *et al.*, 2002). Presented as an example of the good agreement achievable between observed and simulated European-scale distributions using a bioclimatic model.

Evolutionary change

Genetic adaptation of species is rarely considered in the literature on the biotic effects of past and potential future climate change, with range shifts frequently seen as the expected response. It is usually expected that evolutionary change occurs only on long time scales and that the tolerance range of a species remains the same as it shifts its geographical range. However, studies have shown that climate-induced range shifts can involve not only migration into newly suitable areas, but also selection against phenotypes that are poor dispersers or are poorly adapted to local conditions (Davis & Shaw, 2001).

The potential importance of rapid evolutionary change has been demonstrated by Thomas *et al.* (2001) who examined insect species that have expanded their geographical ranges in Britain over the past 20 years. Two species of bush cricket (*Conocephalus discolor* and *Metrioptera roeselii*) were shown to have increased fractions of longer-winged (more dispersive) individuals in recently founded populations, whilst two butterfly species (*Hesperia comma* and *Aricia agestis*) have increased the variety of habitat types that they can colonize. Furthermore, it has been shown that rapid evolutionary change is not confined to the range margins of highly dispersive species. Woodward (1990) has shown the potential for rapid *in-situ* adaptation in plants during a long-term experiment whereby populations of navelwort (*Umbilicus rupestris*) were transplanted beyond the natural geographical limit of the species. The species was found to evolve rapidly new low-temperature responses of seed germination and winter survival, with temperatures that were observed to kill the species in 1979 endured by about 50% of the transplanted population in 1987.

The implications of rapid evolutionary change for bioclimate envelope modelling are important since the assumption of niche conservatism, whereby rates of adaptation are slower than extinction rates, will be wrong for species experiencing sufficiently rapid adaptation. However, it should not be interpreted from this evidence that all species will show adaptive responses to climatic change. Indeed, in an experimental study on a native legume of the American Great Plains (*Chamaecrista fasciculata*), Etterson & Shaw (2001) concluded that predicted rates of evolutionary response for plants of this kind are much slower than the predicted rate of climate change (due to antagonistic genetic correlations among traits within populations).

Bioclimatic studies of past climate-species distribution relationships also provide evidence that adaptation to future climates will not occur for some species. Huntley *et al.* (1989) fitted climate response surfaces to beech (*Fagus* spp.) distributions in Europe and eastern North America. They were able to simulate distribution patterns in Europe during the Holocene using the response surface derived for North America, and vice versa. This suggests that the North American and European beech populations have retained similar climatic tolerances since their separation between 25 and 10 My ago, supporting the hypothesis that, for this species, fundamental physiological limitations have been unaffected by evolutionary processes over this long timescale.

Predicting adaptive changes to species in response to climate change presents a huge challenge to vegetation modellers and has not, to date, been accounted for within the current bioclimatic modelling framework. It is thus apparent that applications of bioclimate envelope models for predicting distribution changes over the next century are most appropriate for species not expected to be able to undergo rapid evolutionary change over this timescale. This is most likely to be the case for long-lived species and poor dispersers, since intergenerational selection and/or selection at expanding range margins is required for evolutionary processes to take effect.

Species dispersal

Sufficiently mobile species can be expected to track the geographical position of their bioclimate envelope through dispersal (Graham & Grimm, 1990; Collingham *et al.*, 1996). However, the ability of a species to migrate at a sufficient rate to keep up with the changing climate will be dependent on the dispersal characteristics of individual species, with future migration rates required to be at least equal to those of the early postglacial period (Collingham & Huntley, 2000). Bioclimate envelope models do not account for species dispersal, but instead aim to predict the *potential* range of organisms under changed climate. Though there is great potential to couple bioclimate envelope models and dispersal simulations (Carey, 1996; Peterson *et al.*, 2001), it is apparent that current predictions of potential distributions may differ greatly from actual future distributions due to migration limitations.

The ability to migrate is a function not only of individual species' characteristics, but also the structure of the landscape over which dispersal is occurring, including the presence of natural barriers (such as mountain ranges) or the artificial fragmentation of habitats (through, for example, the growth of urban areas or deforestation). It can thus be expected that in many areas of the world, where artificial landscape fragmentation prevails and land-uses are changing rapidly, species will be unable to migrate at a sufficient rate to keep pace with the changing climate. In such cases predictions of future distributions derived from bioclimatic models will be erroneous. It is apparent then that accurate predictions of the future distribution of species will require detailed knowledge of the ability of species to migrate through dynamic heterogeneous landscapes within the constraint of changing bioclimate envelopes. This will be the case for all but the most disperse or sedentary species: it may be assumed that highly dispersive species will be able to fill all potential future climate space, whilst extremely poor dispersers will occupy only those current distributional areas that remain suitable under future climates (Peterson *et al*., 2001).

Restrictions to species' dispersal thus present an important limitation to the bioclimatic modelling approach. However, there is evidence from the palaeoecological record that climate change is, in fact, sufficient to explain continental-scale patterns of plant migrations. Indeed, the success of global bioclimate reconstruction models in simulating Holocene changes in distribution for some species (Huntley *et al*., 1989; Prentice & Solomon, 1991) refutes the hypothesis that organisms were unable to migrate fast enough to allow their range limits to track climatic changes. It is expected that the ability of species to migrate rapidly across large distances is driven primarily by rare long-distance dispersal events (Clark *et al*., 1998). Indeed, recent studies have highlighted the extreme importance of long-distance dispersal events, with illustrative examples drawn not only from palaeoecology but also from contemporary observations of island colonization and alien plant spread (Higgins & Richardson, 1999; Cain *et al*., 2000). In such cases, the assumption that species are able to migrate to occupy their suitable climate space may not be so unrealistic.

Evidence in disagreement with the migrational lag hypothesis is also provided by Johnson & Webb (1989) who examined factors determining the rates of migration of Fagaceous trees in eastern North America. It was concluded that since each species has the same potential dispersal rate, observed differences in their rates of migration during the Holocene are best accounted for by individual responses to climatic forcings during this period. It is thus again apparent that when applied at an appropriate scale bioclimate envelopes have the potential to describe changes in species' distributions. However, we should note that although simulations of past climate-biota relationships provide an important test of the performance of bioclimatic models, such studies have coarse resolutions in both space (300–400 km) and time (3000 years) (Davis & Shaw, 2001). These resolutions do not match the detail required to study subcontinental changes over the next 50–100 years.

CORRELATIVE VERSUS PHYSIOLOGICALLY-BASED MODELS

An important criticism of the correlative approach to bioclimatic modelling is that species distributions as we observe them today may not be in equilibrium with the current climate, nor indeed are they necessarily determined primarily by climate. Notably, the effects on species distributions of biotic interactions, physical barriers to dispersal and human management demonstrate that the realized niches used in correlative bioclimate envelope methodologies may not represent absolute limits to species ranges and that therefore future distributions may show very different realized niches.

Woodward (1990) presents an example of where the present-day distribution of a species is not in equilibrium with present-day climate. Careful study of small leaved lime (*Tilia cordata*), including extensive palaeo-reconstruction by pollen analysis (Pigott & Huntley, 1981; Huntley & Birks, 1983), has shown that the species reached its northern limit in the British Isles in the period between 7000 and 5000 BP. The present-day distribution extends to this same northern limit. However, estimations by Woodward (1990) suggest that the present-day reproductive limit of the species is about 200 km south of the northern limit. It is concluded then that the northern limit of this species is a relic from past climates, made possible largely by the longevity of the species.

A further example of nonequilibrium between species' distributions and current climate is provided by Peterson *et al.* (1999) who demonstrated the impact of dispersal barriers on the distribution of species in Central America. In their study of the conservation of ecological niches over evolutionary time scales, a correlative ecological niche model (incorporating inputs of mean annual temperature and precipitation) was successfully used to predict species' distributions based on the ecological characteristics of sister taxa (pairs of birds, mammals and butterflies). It was thus demonstrated that the ecological niches of related species, which are geographically differentiated (by the Isthmus of Tehuantepec in southern Mexico), have been conserved in evolutionary time and are therefore similar. Although this supports the basic assumption of bioclimatic modelling that niches are conservative over time, it is evident that the presence of a physical barrier to dispersal means that species are unable to occupy their full climatic niche. Correlating current climate with the observed species distribution will therefore not identify the full *potential* climatic range of the species. Results from correlative niche models that project future distributions under climate change scenarios in such situations (e.g. Peterson *et al*., 2002) should therefore be interpreted with caution.

It has, however, already been shown that a number of correlative bioclimate envelope models have been successfully used to simulate the distributions of higher plants in Europe (Beerling *et al*., 1995; Huntley *et al*., 1995; Pearson *et al*., 2002). These modelling results support the hypothesis that continental-scale distributions are principally determined by climate. It is thus suggested that many species distributions can in fact be considered to be in equilibrium with the current climate at the macro-scale. However, this is not the case for all species. For example, attempts to model the European-scale distribution of yew (*Taxus baccata*) using the SPECIES model (Pearson *et al*., 2002) yielded relatively low agreement between actual and simulated distributions (Fig. 3). It is apparent that although the model identified the broad distribution trends, the finer details of the distribution were not

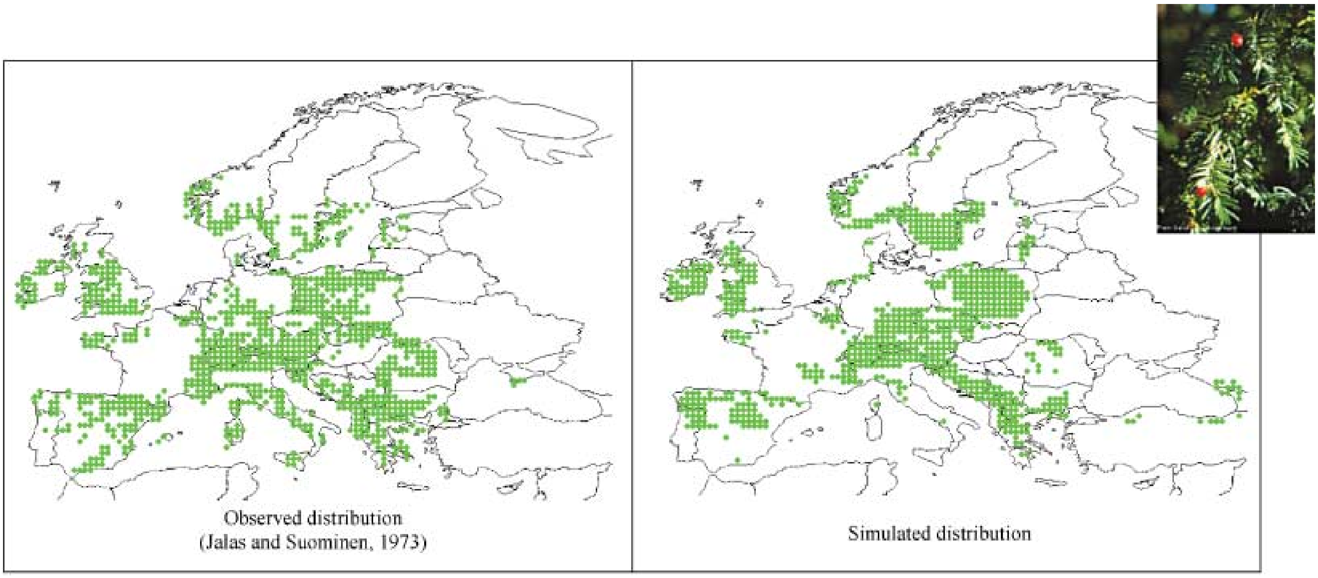

Fig. 3 Observed European distribution of yew (*Taxus baccata*) alongside the distribution as simulated by the SPECIES model (Pearson *et al.*, 2002). Although the broad distribution trends are identified in the simulated distribution, the finer details of the distribution are not captured.

identified. Such inaccuracies can be expected for species' distributions that show extensive fragmentation (for nonclimatic reasons) within a species' climate space. In the case of yew, it is expected that human exploitation has been sufficient to disrupt the large-scale equilibrium between distribution and climate (Plaisance, 1979).

Physiologically based bioclimatic models do not make the assumption of equilibrium and are not dependent upon identifying a relationship between the current distribution and climate for characterizing the bioclimate envelope of a species. It may thus be argued that in basing the model on physiological limits to a species' climatic tolerance, the bioclimate envelope identified will better represent a species' absolute climatic limits than that identified through the correlative approach. However, such models are equally limited in their inability to account for nonclimatic influences and have a number of important limitations that may lead to model inaccuracies.

For example, in simulating the European distribution of yew using a bioclimatic model based on physiological constraints to growth and regeneration, Sykes *et al.* (1996) were unable to simulate the fine structure of the distribution. As with the correlative approach (Fig. 3), they were only able to simulate the broad envelope of the species' range (the *potential* species range, or *fundamental* niche). Furthermore, the results of Sykes *et al.* (1996) suggest that there are areas, such as central France, which fall within the climatic range of yew but where the species is not found for what are presumed to be nonclimatic reasons. In contrast, the results obtained through the correlative approach suggest that there are in fact climatic reasons why the species does not occur in some of these regions (notably, central France).

Limitations applying to the physiologically based approach can be summarized as follows. Firstly, it is an obvious point of definition that fundamental niches are not realized, and nor will they be realized in the future. Thus, predicted future species distributions based on the physiologically determined fundamental niche are unlikely to be as accurate as those based on correlations between the observed distribution and the current realized niche. Secondly, there is increasing evidence that the concept of undifferentiated species comprising individuals with broad tolerances is not correct (Davis & Shaw, 2001). Intra-species variation makes it impossible to define precise limits to a species' climatic tolerance since there is no guarantee that the limits for one subpopulation at one range margin will be exactly the same as those for another subpopulation at another margin many miles away. Furthermore, the potential importance of rapid evolutionary change as climatic conditions change (Woodward, 1990; Thomas *et al.*, 2001) means that some species' climatic tolerances may alter in the future, making the fundamental niche unstable over time.

It is apparent that there are limitations to both correlative and physiologically based bioclimatic modelling methodologies. Though it has been proposed that physiologically based approaches are superior (Woodward, 1987; Prentice *et al.*, 1992; Sykes *et al.*, 1996), it is argued here that such models also have important limitations and that when applied at appropriate scales and to appropriate species correlative techniques can give equally informative results. Since correlative techniques do not require detailed physiological data about individual species, they also have the advantage that they can easily be applied to a large number of species. This enables conclusions regarding the potential impacts of climate change on a wide range of species, and thus habitat assemblages, to be made (e.g. Berry *et al.*, 2002).

A HIERARCHICAL MODELLING FRAMEWORK

It is proposed that identifying a species' suitable climate space through the use of bioclimate envelope models should form an important first step in a broader modelling framework. A useful framework for addressing the environment-biota relationship is that of a hierarchy of factors operating at different scales. Thus, at the continental scale, climate can be considered the dominant factor, whilst at more local scales factors including topography and land-cover type become increasingly important. Further down the hierarchy, if conditions at higher levels are satisfied, factors including biotic interactions and microclimate may become significant. Thus, the distribution of a species in Europe may be primarily defined by climatic tolerances if the data resolution is 50 km^2, whereas as the resolution is downscaled, to perhaps 5 km^2, land-cover type may become the dominant control over species presence. Similarly, as the resolution is downscaled to less than 1 km^2, biotic interactions may become important (Fig. 4).

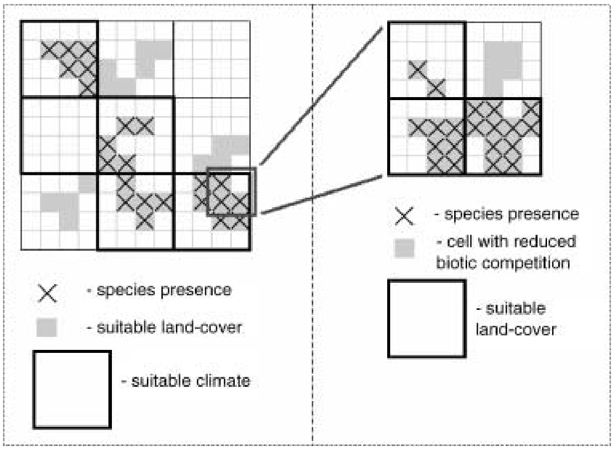

Fig. 4 Diagram illustrating a hierarchical modelling framework. Different factors affecting the distribution of species are considered to act at different scales. For example, the left-hand section shows species occurring in cells where both large-scale climatic and smaller-scale land-cover requirements are met. The right-hand section shows a downscaled portion from the larger diagram, demonstrating that at a still finer resolution biotic competition becomes significant.

Theories relating to hierarchical structure in ecological systems have been discussed by, amongst others, Kotliar & Wiens (1990), Wu & Loucks (1995), Collingham *et al.* (2000), Whittaker *et al.* (2001) and Willis & Whittaker (2002). Turner *et al.* (2001) define a hierarchy as being a system of interconnections wherein the higher levels constrain the lower levels to various degrees. These levels operate across different spatial and temporal scales, with different processes being more important at different scales (Fig. 5). Theoretically therefore analyses should be focused at scales at which the phenomena of interest are dominant (Turner *et al.*, 2001). Bioclimate envelope modelling fits well into this hierarchical framework, in identifying large-scale distribution limitations at the highest, most dominant level.

The application of hierarchy theory in the present context is supported by the tendency for biotic factors to be more limiting when physical limiting factors are less severe. This is characterized at the global scale by physical factors being more restrictive at higher latitude range margins (where conditions are harsher) and biotic interactions more limiting at lower latitude range margins (MacArthur, 1972; Brown *et al.*, 1996; Brown & Lomolino, 1998). Thus, physical (abiotic) factors such as climate may be considered to act at a higher level in the hierarchy than biotic factors.

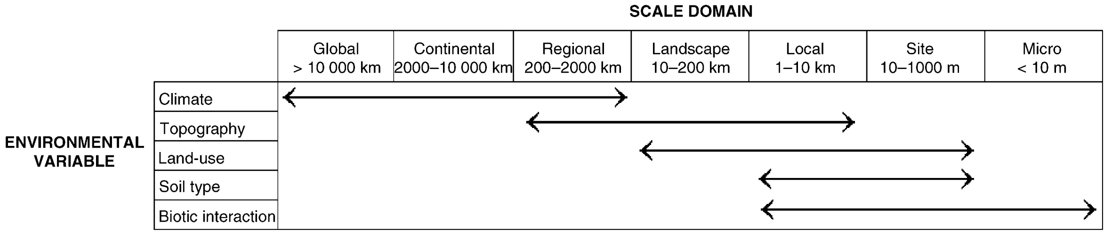

Fig. 5 Schematic example of how different factors may affect the distribution of species across varying spatial scales. Characteristic 'scale domains' are proposed within which certain variables can be identified as having a dominant control over species distributions. Approximate spatial extents have been assigned to categories of scale based in part on Willis & Whittaker (2002). It is assumed that large spatial extents are associated with coarse data resolutions, and small extents with fine data resolutions.

The hierarchical theory also goes some way to explaining the differing performance of bioclimate envelope models at different scales. For example, Pearson *et al.* (2002) were able to simulate principal trends in observed plant distributions at the European scale, but accuracy was reduced when the model was tested for Great Britain. This reduced accuracy is likely to be the result of the increasing influence of factors other than climate, including local land-cover type and inter–species interactions, which lead to a more fragmented species distribution at the finer scale.

The proposed hierarchical framework may be imperfect and over-simplified, yet provides a useful starting point for approaching the extreme complexity of the natural system. Identifying appropriate scales of analysis for different environmental drivers, thus validating the scale dependencies outlined in Fig. 5, should be the focus of further research. However, it is already apparent that the scale at which current bioclimatic studies are addressed is of fundamental importance, with climatic impacts on the distribution of species being most influential at regional to global scales.

CONCLUSION

A number of criticisms of the bioclimate envelopes approach have been discussed and inherent limitations of bioclimatic models based on both correlative and physiologically based mechanistic methodologies have been demonstrated. The discussion has also shown the great complexity of natural systems, suggesting that there are fundamental limits to the accurate prediction of future species distributions. Combining the complexities arising from issues of biotic interactions, evolutionary change and species' dispersal with the uncertainties all too evident in predictions of future climate and land-use change, it is apparent that accurate predictions of biogeographical responses to future climate change are not currently possible.

The development of dynamic global vegetation models (DGVMs), which include mechanistic representations of physiological, biophysical and biogeochemical processes, has demonstrated significant progress in the modelling of vegetation–climate interactions at the global scale (Woodward & Beerling, 1997; Cramer *et al.*, 2001). Recent development of these techniques for application at regional scales, including the breaking down of ecosystem processes into key components with characteristic spatial and temporal scales in a hierarchical system analogous to that advocated in this paper, shows much promise (Sykes *et al.*, 2001). However, the complexity of DGVMs makes their parameterization and validation problematic, and does not currently allow their widespread application to specific species and regions. It has been argued in this paper that relatively simple bioclimate envelope models can provide a useful starting point when applied to suitable species and at appropriate spatial scales. In many cases, bioclimate envelope models provide perhaps the best available guide for policy making at the current time (Hannah *et al.*, 2002). They have been usefully employed to identify possible magnitudes of future changes to distributions, and to suggest which species, habitats and regions are most at risk from climate change (Prentice *et al.*, 1992; Beerling *et al.*, 1995; Huntley *et al.*, 1995; Sykes *et al.*, 1996; Berry *et al.*, 2001, 2002; Hannah *et al.*, 2002; Midgley *et al.*, 2002). The importance of bioclimatic model predictions should thus not be underestimated, though model predictions should be interpreted with due caution and should be viewed as first approximations indicating the potential magnitude and broad pattern of future impacts, rather than as accurate simulations of future species distributions.

More realistic simulations of the impact of climate change on species distributions will require a better understanding of the complex interactions between the many factors affecting distributions. For example, it will be necessary to use dynamic models to simulate the relationship between changing climate space and the potential for species to disperse through fragmented landscapes, and to further our understanding of the complex dynamics of model systems consisting of multiple interacting species. A hierarchical modelling framework has been proposed through which it will be possible to integrate such factors, acting at different spatial scales.

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REFERENCES

Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs*, **60**, 161–177.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390–407.

Beerling, D.J., Huntley, B. & Bailey, J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science*, **6**, 269–282.

Berry, P.M., Dawson, T.P., Harrison, P.A. & Pearson, R.G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453–462.

Berry, P.M., Vanhinsberg, D., Viles, H.A., Harrison, P.A., Pearson, R.G., Fuller, R., Butt, N. & Miller, F. (2001) Impacts on terrestrial environments. *Climate change and nature conservation in Britain and Ireland: modelling natural resourse responses to climate change (the MONARCH Project)* (ed. by P.A. Harrison, P.M. Berry and T.P. Dawson), pp. 43–149. UKCIP technical report, Oxford. http://www.ukcip.org.uk/model_nat_res/model_nat_res.html

Box, E.O. (1981) *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography*. Junk, The Hague.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, MA.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review Ecological Systematics*, **27**, 597–623.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.

Carey, P.D. (1996) DISPERSE: a cellular automaton for predicting the distribution of species in a changed climate. *Global Ecology and Biogeography Letter*, **5**, 217–226.

Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, I.C., Schupp, E.W., Webb, T. III & Wyckoff, P. (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *Bioscience*, **48**, 13–24.

Collingham, Y.C., Hill, M.O. & Huntley, B. (1996) The migration of sessile organisms: a simulation model with measurable parameters. *Journal of Vegetation Science*, **7**, 831–846.

Collingham, Y.C. & Huntley, B. (2000) Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications*, **10**, 131–144.

Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. *Journal of Applied Ecology*, **37**, 13–27.

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710–723.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.

Crawley, M.J. (1997) The structure of plant communities. *Plant ecology* (ed. by M.J. Crawley), pp. 475–531. Blackwell Science, Oxford.

Davis, A.J., Jenkinson, L.S., Lawton, J.L., Shorrocks, B. & Wood, S. (1998a) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

Davis, A.J., Lawton, J.L., Shorrocks, B. & Jenkinson, L.S. (1998b) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600–612.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

Etterson, J.R. & Shaw, R.G. (2001) Constraint to adaptive evolution in response to global warming. *Science*, **294**, 151–154.

Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.

Graham, R.W. & Grimm, E.C. (1990) Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology Evolution*, **5**, 289–292.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeograpgy*, **11**, 485–495.

Haxeltine, A. & Prentice, I.C. (1996) BIOME3: An equilibrium terrestrial biosphere model based on ecophysical constraints, resourse availability, and competition among plant functional types. *Global Biogeochemical Cycles*, **10**, 693–709.

Hengeveld, R. (1990) *Dynamic biogeography*. Cambridge University Press, Cambridge.

Higgins, K. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.

Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.

Hulme, M. & Jenkins, G.J. (1998) *Climate change scenarios for the United Kingdom: scientific report*. UK Climate Impacts Programme Technical Report no. 1, Climatic Research Unit, Norwich.

Huntley, B. (1999) Species distribution and environmental change: considerations from the site to the landscape scale. *Ecosystem management: questions for science and society* (ed. by E. Maltby, M. Holdgate, M. Acreman and A. Weir), pp. 115–130. Royal Holloway Institute for Environmental Research, Virginia Water, UK.

Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989) Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. *Journal of Biogeography*, **16**, 551–560.

Huntley, B., Berry, P.M., Cramer, W. & Mcdonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, **22**, 967–1001.

Huntley, B. & Birks, H.J.B. (1983) *An atlas of past and present pollen maps for Europe: 0–13 000 B.P.* Cambridge University Press, Cambridge.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–457.

IPCC (2001) *Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell and C.A. Johnson). Cambridge University Press, Cambridge, UK.

Jalas, J. & Suominen, J. (1972) *Atlas Flora Europapaeae: distribution of vascular plants in Europe*, 1. The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki.

Jalas, J. & Suominen, J. (1973) *Atlas Flora Europapaeae: distribution* *of vascular plants in Europe*, 2. The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo, Helsinki.

Johnson, W.C. & Webb, T. III (1989) The role of blue jays (*Cyanocitta cristata*) in the postglacial dispersal of fagaceous trees in eastern North America. *Journal of Biogeography*, **16**, 561–571.

Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.

Lawton, J.L. (2000) Concluding remarks: a review of some open questions. *Ecological consequences of heterogeneity* (ed. by M.J. Hutchings, E. John and A.J.A. Stewart), pp. 401–424. Cambridge University Press, Cambridge.

Leibold, M.A. (1995) The niche concept revisited: mechanistic models and community context. *Ecology*, **76**, 1371–1382.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.

Mack, R.N. (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation*, **78**, 107–121.

McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320–331.

Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powerie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.

Pearson, R.G., Dawson, T.P., Berry, P.M. & Harrison, P.A. (2002) SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, **154**, 289–300.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J. & Buddemeier, R.W. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.

Peterson, A.T., Sanchez-Cordero, V., Soberon, J., Bartley, J., Buddemeier, R.W. & Navarro-Singuenza, A.G. (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling*, **144**, 21–30.

Peterson, A.T., Soberon, J. & Sanchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Pigott, C.D. & Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist*, **87**, 817–839.

Plaisance, G. (1979) L'if. *La foret privée — revue forèire Européenne*, **126**, 34–47.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.

Prentice, I.C. & Solomon, A.M. (1991) Vegetation models and global change. *Global changes of the past* (ed. by R.S. Bradley), pp. 365–383. UCAR/Office for Interdisciplinary Earth Studies, Boulder, CO.

Silander, J.A. & Antonovics, J. (1982) Analysis of interspecific interactions in a coastal plant community — a perturbation approach. *Nature*, **298**, 557–560.

Sykes, M.T., Prentice, I.C. & Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, **23**, 203–233.

Sykes, M.T., Prentice, I.C., Smith, B., Cramer, W. & Venevsky, S. (2001) An introduction to the European Terrestrial Ecosystem Modelling Activity. *Global Ecology and Biogeography*, **10**, 581–593.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Turner, M.G., Gardner, R.H. & O'Neill, R.V. (2001) *Landscape Ecology: in Theory and Practice*. Springer-Verlag, New York.

Walther, G.R., Post, E., Convey, P., Menze, 1, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity — scale matters. *Science*, **295**, 1245–1248.

Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.

Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London B*, **326**, 585–593.

Woodward, F.I. & Beerling, D.J. (1997) The dynamics of vegetation change: health warnings for equilibrium 'dodo' models. *Global Ecology Biogeography Letters*, **6**, 413–418.

Woodward, F.I. & Rochefort, I. (1991) Sensitivity analysis of vegetation diversity to environmental change. *Global Ecology Biogeography Letters*, **1**, 7–23.

Wu, J. & Loucks, O.L. (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review Biology*, **70**, 439–466.

BIOSKETCHES

Richard Pearson is a doctoral student with research interests in biogeography and spatial ecology. Particular interests include modelling species–climate interactions, the simulation of dispersal processes in heterogeneous landscapes, and the role of scale in ecology.

Terence Dawson is a University Research Lecturer and programme leader of the Terrestrial Ecology and Biodiversity research group of the Environmental Change Institute, University of Oxford. His research interests include the understanding of ecosystem form and functioning at varying spatial and temporal scales, and the study of complex human–climate–ecosystem interactions.