REPORT

The performance of models relating species geographical distributions to climate is independent of trophic level

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Abstract

Species–climate 'envelope' models are widely used to evaluate potential climate change impacts upon species and biodiversity. Previous studies have used a variety of methods to fit models making it difficult to assess relative model performance for different taxonomic groups, life forms or trophic levels. Here we use the same climatic data and modelling approach for 306 European species representing three major taxa (higher plants, insects and birds), and including species of different life form and from four trophic levels. Goodness-of-fit measures showed that useful models were fitted for >96% of species, and that model performance was related neither to major taxonomic group nor to trophic level. These results confirm that such climate envelope models provide the best approach currently available for evaluating reliably the potential impacts of future climate change upon biodiversity.

INTRODUCTION

The last decade has seen a renewed interest in the factors determining species geographical distributions, and in the development of models to predict the likely response of species distributions to environmental change. There have been two principal reasons for this development. First, there has been a progressively widening acceptance among the scientific community of the evidence of an increasing anthropogenic influence upon global climate (Houghton *et al.* 1990, 1996), leading to the conclusion that: 'most of the observed warming over the last 50 years is likely to have been due to the increase in greenhouse gas concentrations'

(Houghton *et al.* 2001, p. 10). Secondly, the United Nations Conference on Environment and Development in 1992 resulted in adoption of the Convention on Biological Diversity that seeks to conserve the biological diversity of the planet by protecting species and ecosystems (Grubb *et al.* 1993). These two factors, together with the abundant evidence from the Quaternary that species responses to past climate changes have predominantly been expressed as large-scale shifts in their geographical distributions (Davis 1989; Huntley & Webb 1989; Graham & Grimm 1990; Huntley 1991; Davis & Zabinski 1992; Graham 1992; FAUNMAP Working Group 1996; Graham 1997; Preece 1997; Huntley 1999), have led researchers to model the

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relationships between species distributions and climate and to use these models to predict how species potential distributions may be altered in response to potential future climate scenarios (Huntley 1995; Huntley *et al.* 1995; Sykes *et al.* 1996; Sykes 1997; Thompson *et al.* 1998; Hill *et al.* 1999; Berry *et al.* 2002; Githaiga-Mwicigi *et al.* 2002; Midgley *et al.* 2002; Pearson *et al.* 2002; Hill *et al.* 2003; Thuiller 2003; Thomas *et al.* 2004).

These models relating species distributions to climate have been developed for species from a variety of major taxonomic groups, including plants, insects, mammals and birds. They thus potentially provide a basis for evaluating the extent to which differences exist between taxonomic groups, or between species from different trophic levels, with respect to the strength of the relationships between their geographical distributions and climatic variables. The possibility that such differences exist between species at different trophic levels was already being debated more than half a century ago (Andrewartha & Birch 1954; Nicholson 1954), although no generally accepted consensus was reached. The debate has re-opened in recent years as a result of the renewed interest in the factors determining species geographical distributions. The paradigm that biotic factors are of greater importance, and conversely that abiotic factors are of lesser importance, in determining distributions of species at higher trophic levels is still adhered to by some ecologists; for example, Austin (2002, p. 81) recently stated that 'The ecological theory that determines the success of predictive species modelling differs radically between plant and animal ecology…The physical environment in terms of climate and soils is clearly more important for plants'. Whether or not such differences exist is of importance from the perspective of current understanding of the 'assembly' (Weiher & Keddy 1999) and functioning of ecosystems; it is also of considerable relevance in relation to determining the appropriate measures that will maximize the conservation of biodiversity in the face of climate change (Peters & Lovejoy 1992; Mace *et al.* 1998).

If climate is indeed more influential in determining the distributions of plants than animals, then we would expect models relating the distributions of plant species to climate to perform systematically better than models relating the distributions of animal species to climate. However, whereas most plants are autotrophs, representing the first trophic level, animals occupy several higher trophic levels. Given that animals at higher trophic levels are increasingly remote along trophic pathways from plants, then if climate is more influential in determining the distributions of plants we can hypothesize that the strength of the relationship between species distributions and climate will further diminish at higher trophic levels.

The results from previously published studies cannot be used to test this hypothesis, however. Not only do these studies differ with respect to the climatic variables and modelling approaches used, but model performance has been evaluated using various different measures of goodness-of-fit, a majority of which show a systematic effect of species prevalence (the number of grid cells from which the species is recorded as present expressed as a proportion of the total number of grid cells from which data are available for the species) upon apparent goodness-of-fit (Manel *et al.* 2001). Any analysis of the differences in reported model performance among taxonomic or trophic groups in such studies is thus unlikely to be meaningful. In order to test the hypothesis, therefore, we have fitted models relating geographical distribution to climate for species drawn from three major taxonomic groups (higher plants, insects and birds) and representing four trophic levels, using the same fitting method and the same three climatic variables throughout. Model performance was assessed consistently using a measure of goodness-of-fit selected because it has been shown to be relatively insensitive to prevalence (Manel *et al.* 2001). Our results thus provide a basis, for the first time, for a systematic assessment of the extent to which differences exist between species from different trophic levels with respect to the strength of the relationships between their geographical distributions and climate.

MATERIALS AND METHODS

A total of 306 species was selected for this study; species were selected from three broad taxonomic groups, for two of which (higher plants and birds) published data were available to us recording their geographical distribution in Europe in terms of presence/absence for the cells of a *c.* 50 km UTM grid. Within the higher plants and birds subsidiary taxonomic groups were selected in order to gain representation of contrasting life forms (i.e. trees vs. herbs) and trophic levels; all species from each subsidiary group were included in the analysis. Our selection of species groups was not biased by any *a priori* knowledge of the performance of models for these groups; in no case had models been fitted previously for more than a small minority of species in any group selected. Table 1 lists the nine species groups selected, the number of species in each group and the trophic level to which each group is assigned. The 'trees' group comprises all of the species of the two genera *Pinus* and *Quercus* found native in Europe, while the 'herbs' group comprises all of the species in the genus *Silene* native to Europe. Distributional data for these taxa were obtained from Jalas & Suominen (1973, 1976, 1986). The insect group used comprises all of the non-migratory butterfly species that are native to Great Britain. In this case the gridded distribution data were prepared from published (Tolman 1998) and unpublished distribution maps for the species; because of the limited

Table 1 Species groups for which response surfaces were fitted

Species group	Trophic level	N	N′
Higher plants	1	153	146
Trees (*Pinus* spp. plus *Quercus* spp.)	1	31	31
Herbs (*Silene* spp.)	1	122	115
Insects – Herbivorous Lepidoptera (butterflies)	2	52	52
Birds	2–4	101	98
Granivorous passerines (*Emberiza* spp. plus *Carduelis* spp.)	2	21	19
Granivorous/insectivorous passerines (*Parus* spp.)	2.5	9	9
Insectivorous passerines (*Sylvia* spp. plus *Phylloscopus* spp.)	3	20	19
Insectivorous raptors (including owls)	3	6	6
Raptors (including owls) with predominantly herbivorous prey	3	38	38
Raptors (including owls) with predominantly carnivorous prey	4	7	7

N, number of species for which an attempt was made to fit a model; N′, number of species for which a useful model was fitted.

availability of reliable distribution information from eastern Europe the gridded data were truncated for these species at 30°E. Distribution data for birds were obtained from Hagemeijer & Blair (1997). Six groups of birds were used, three of which comprised all of the species from either one or two genera representing the same trophic level, and the other three of which comprised all of the raptors, including owls, subdivided according to their trophic level (for raptor species assigned to each trophic level see Appendix 1).

The bioclimatic variables used to fit the models were estimated for the geographical midpoint and mean elevation of each *c*. 50 km UTM grid cell using the procedure described by Huntley *et al*. (1995). Mean monthly temperature, precipitation and sunshine values were estimated using an elevation-sensitive interpolation technique (Hutchinson 1989) applied to an extensive compilation of meteorological station data for these variables (Leemans & Cramer 1991: data relate principally to the period 1931–1960). Values for bioclimatic variables were then calculated from these meteorological variables. Three bioclimatic variables were used in modelling, these being selected to reflect three primary qualities of the climate that, on the basis of prior knowledge, have known roles in imposing constraints upon species distributions as a result of widely shared physiological limitations. The variables used were the mean temperature of the coldest month (°C, representing winter cold), the annual temperature sum above 5 °C (degree days, representing accumulated warmth) and Priestley–Taylor α (an estimate of the annual ratio of actual to potential evapotranspiration – representing moisture availability) (Prentice *et al*. 1992). Following Prentice *et al*. (1992), data relating to soil water capacity and the calculated daily potential insolation, according to the latitude of each grid cell, were also used in the calculation of this last variable. Maps of these variables for the 50 km UTM grid used by Jalas & Suominen (1972, 1973, 1976, 1986) were published

in Huntley *et al*. (1995); these variables exhibit only relatively weak correlations in Europe, principally because of the strong longitudinal gradient in climatic continentality that characterizes the region.

Models relating species distributions to the three bioclimatic variables were fitted using the method of species–climate response surfaces (Huntley *et al*. 1995; Shafer *et al*. 2001), surfaces being fitted using locally weighted regression (Cleveland & Devlin 1988) and their value at any location in the space of the bioclimate variables being the probability of the species being present in a grid square at that location in bioclimatic space. This approach requires no prior assumptions to be made about the form of the relationship between a bioclimatic variable and the species probability of occurrence, nor about the possible nature of any interactions between variables. It is also able to model complex nonlinear and potentially multimodal responses to variables, including their potentially complex interactions. The method does, however, require an *a priori* decision as to the selection of bioclimatic variables to be included in the model. This might be viewed as a disadvantage, whereas it is in practice an advantage in that an appropriate selection of variables can be made upon the basis of their known relationships to physiological limits that constrain species geographical distributions.

As there were systematic differences in mean prevalence among the nine species groups, assessment of the intergroup differences in goodness-of-fit required a measure that was minimally influenced by prevalence. We assessed, for our dataset, the extent to which prevalence influenced the values obtained either for Cohen's κ (Cohen 1960) or for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (1 – specificity) (Metz 1978), sensitivity being defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. Both values are computed from the

four values in a confusion matrix, i.e. the numbers of: correctly predicted positives (a); falsely predicted positives (b); falsely predicted negatives (c); and correctly predicted negatives (d) (sensitivity = a/(a + c); specificity = d/(b + d)). Both Cohen's κ and AUC have previously been claimed to be independent of species prevalence (Manel *et al.* 2001). When calculating Cohen's κ we wished to avoid the use of the arbitrary probability threshold of 0.5 to distinguish simulated presence from simulated absence. We therefore selected for each model the probability threshold that maximized its performance as measured by Cohen's κ (Huntley *et al.* 1995); the appropriate threshold was in each case determined by evaluating κ at successive probability increments of 0.01 across the entire range from 0.00 to 1.00.

RESULTS

Of the 306 species for which we attempted to fit models, useful models were obtained for all except 10 species (3.3%) of very low prevalence (mean prevalence 1.69×10^{-3}; recorded present principally from scattered grid cells in poorly recorded regions). Figure 1 illustrates six representative and biogeographically contrasting examples of the models fitted and used for the intergroup comparison. A plot of κ vs. prevalence for the 296 useful models fitted revealed a strong dome-shaped relationship between the two for our dataset, κ being systematically higher for species of intermediate prevalence. This subsequently was revealed by simulation modelling (R. E. Green, unpublished data) to be largely an artefact of the way in which κ is calculated.
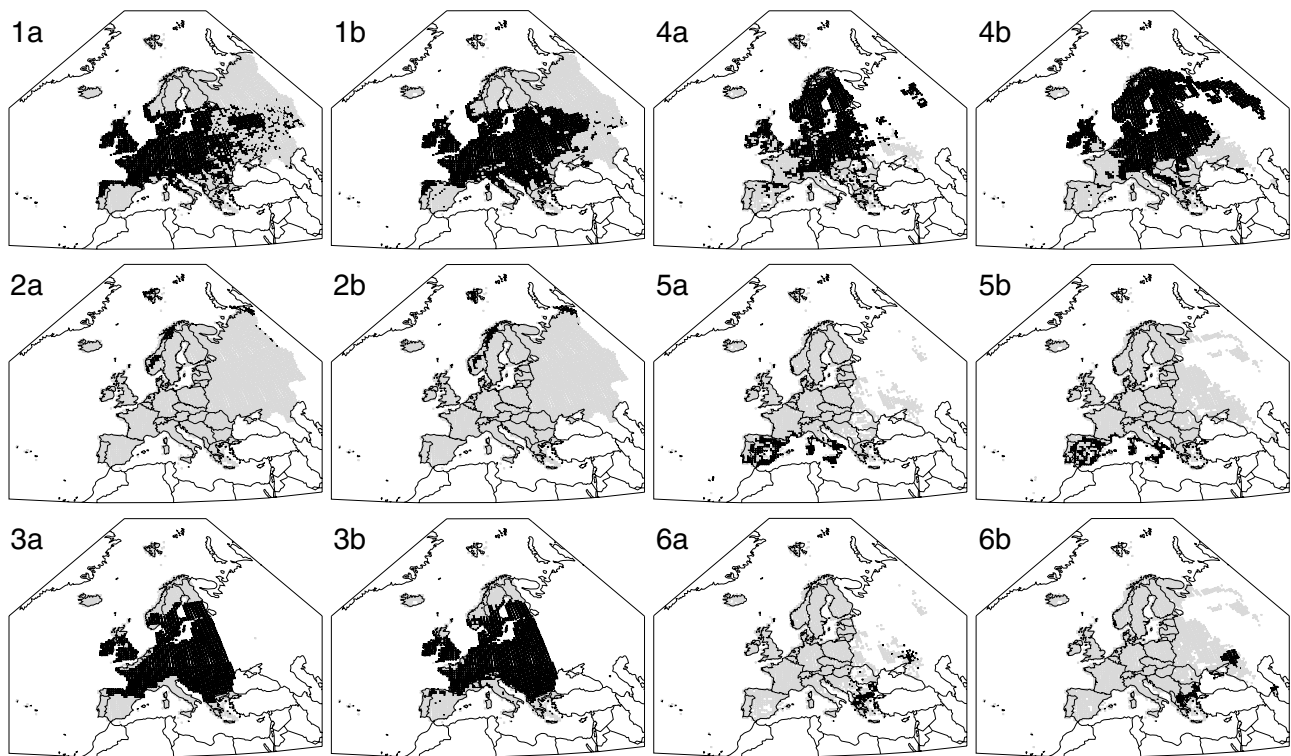

Figure 1 Recorded distributions (a) and distributions simulated by response surface models (b). 1, *Quercus robur* (Pedunculate Oak): primary producer, trophic level 1, $\kappa = 0.759$, AUC = 0.956 (recorded distribution after Jalas & Suominen 1976). 2, *Silene uralensis*: primary producer, trophic level 1, $\kappa = 0.613$, AUC = 0.976 (recorded distribution after Jalas & Suominen 1986). 3, *Aphantopus hyperantus* (Ringlet butterfly): herbivore, trophic level 2, $\kappa = 0.811$, AUC = 0.969 (recorded distribution west of 30 °E after Tolman (1998); more easterly records are unreliable). 4, *Carduelis spinus* (Siskin): granivore, trophic level 2, $\kappa = 0.774$, AUC = 0.951. 5, *Sylvia conspicillata* (Spectacled Warbler): insectivore, trophic level 3, $\kappa = 0.754$, AUC = 0.960. 6, *Accipiter brevipes* (Levant Sparrowhawk): raptor preying principally upon carnivores, trophic level 4, $\kappa = 0.690$, AUC = 0.930. (Recorded distributions of 4–6 after Hagemeijer & Blair 1997.) For 1–3 black dots on recorded distributions indicate presence and grey dots absence or cells lacking data; distributions are simulated for all cells of the respective grids. For 4–6 black dots on recorded distributions indicate presence, grey dots absence and white areas no data; distributions are simulated for all cells with recorded presence or absence and also for cells with no data that fall within the climatic envelope of the recorded data (principally in Russia and other parts of eastern Europe), black dots indicating simulated presence, grey dots simulated absence and white areas no simulation made.

AUC, however, showed only a slight, albeit statistically significant, increase with increasing prevalence in our dataset (linear least squares regression $F_{(1,294)} = 2.83$, $P < 0.001$). This effect was equivalent to a mean AUC of 0.928 when prevalence was zero, compared to 0.991 when prevalence was 1 ($0.5 \leq$ AUC ≤ 1.0). However, there was no indication of variation among the nine species groups in this slight effect of prevalence (ANCOVA groups × prevalence interaction term, $F_{(8,278)} = 1.05$, $P = 0.398$). AUC was therefore used as the basis for intergroup comparisons of model performance, excluding from these assessments the 10 species of very low prevalence for which useful models could not be fitted.

Following the general guidance for the interpretation of values of AUC proposed by Swets (1988), none of the 296 models fitted had AUC values that would lead to them being considered of 'low accuracy' ($0.5 <$ AUC ≤ 0.7) and only 38 (12.4%) had AUC values that might be considered only as 'useful for some purposes' ($0.7 <$ AUC ≤ 0.9); 84.3% of the fitted models had AUC values considered as representing 'high accuracy' (AUC >0.9) (Fig. 2). The AUC values for the nine species groups (Table 2) showed highly significant variation in AUC among species groups (ANOVA, $F_{(8,287)} = 9.22$, $P < 0.001$). This remained the case when the effect of prevalence was allowed for (ANCOVA with common AUC vs. prevalence slope within groups, $F_{(8,286)} = 2.51$, $P = 0.012$) (Table 2). However, there was no evidence of significant variation in AUC for species groups among trophic levels (ANOVA $F_{(4,4)} = 2.93$, $P = 0.161$). This remained the case when AUC values were adjusted for the effects of prevalence (ANOVA $F_{(4,4)} = 1.37$, $P = 0.384$). Neither was there any indication of a linear or curvilinear relationship between AUC and trophic level (Fig. 3). This was confirmed by a least squares linear regression of mean AUC on trophic level ($F_{(1,7)} = 0.185$, $P = 0.680$), by an Olmstead and Tukey corner test for association (Sokal & Rohlf 1969)
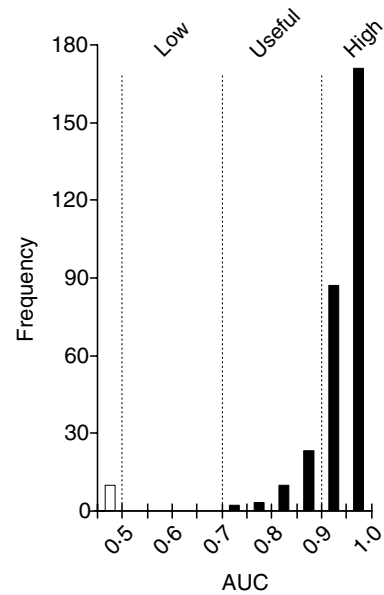

Figure 2 Frequency plot of values of AUC for the 306 response surface models fitted. The unshaded histogram bar indicates the 10 species for which no useful model could be fitted at 50 km resolution and for which AUC was hence 0.5. Categories of fit indicated follow Swets (1988).

(absolute quadrant sum $= 2.33$, n.s.) and by quadratic regression ($F_{(2,6)} = 2.72$, $P = 0.144$). Nor was there a significant linear or quadratic relationship between the species group means of AUC and trophic level when AUC values were adjusted to those expected at prevalence equal to 0.5 using the common within groups regression (linear regression: $F_{(1,7)} = 0.002$, $P = 0.966$; quadratic regression: $F_{(2,6)} = 1.79$, $P = 0.246$; Fig. 3). Inspection of Fig. 3 indicates the possibility of a negative trend of AUC with

Table 2 Mean AUC values and prevalence for three major taxonomic groups and nine species groups

| Major taxonomic/species group	Mean AUC	SE (mean)	Mean prevalence	Mean AUC adjusted to prevalence of 0.5	SE (adjusted mean)
Higher plants	0.9272	0.0035	0.0457	0.9468	0.0063
Pinus plus *Quercus*	0.9388	0.0074	0.0821	0.9547	0.0088
Silene	0.9240	0.0038	0.0364	0.9416	0.0066
Insects (Lepidoptera)	0.9744	0.0058	0.6521	0.9679	0.0059
Birds	0.9512	0.0042	0.3197	0.9586	0.0046
Emberiza plus *Carduelis*	0.9714	0.0094	0.3150	0.9772	0.0094
Parus	0.9574	0.0137	0.4914	0.9578	0.0135
Sylvia plus *Phylloscopus*	0.9659	0.0094	0.3467	0.9711	0.0094
Insectivorous raptors	0.9527	0.0168	0.3062	0.9601	0.0166
Raptors predominantly preying upon herbivores	0.9338	0.0067	0.2640	0.9428	0.0071
Raptors predominantly preying upon carnivores	0.9415	0.0155	0.3505	0.9472	0.0154
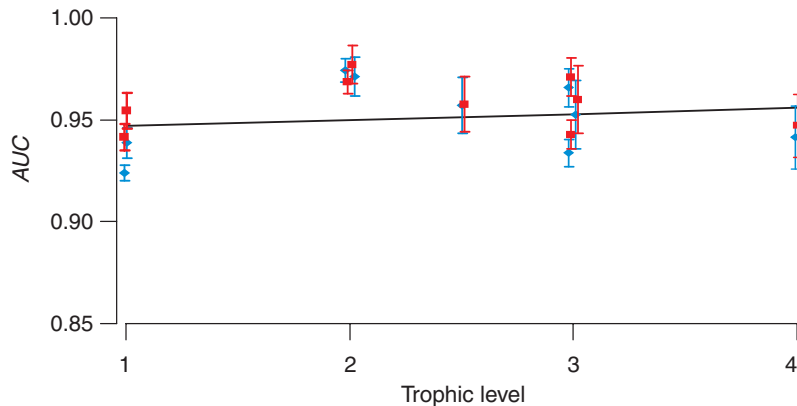
Figure 3 Mean goodness-of-fit (AUC for receiver operating characteristic (ROC) plots) for the nine species groups (Table 1) plotted against trophic level, with (red) and without (blue) adjustment for the effect of prevalence. 'Error' bars indicate ±standard error of the mean. Linear regression analysis (fitted line shown) of mean AUC values (without adjustment for the effect of prevalence) on trophic level reveals no significant relationship between mean goodness-of-fit and trophic level ($F_{(1,7)} = 0.185$, $P = 0.680$).

trophic level if higher plants are excluded. This tendency was almost significant for AUC (linear regression; $F_{(1,7)} = 6.51$, $P = 0.051$), but less so for AUC adjusted for the effects of prevalence (linear regression: $F_{(1,7)} = 4.38$, $P = 0.091$). Even if this weak evidence of a relationship between AUC and trophic level for heterotrophs is accepted, the effect is still very small; the mean AUC for herbivores estimated from the fitted regression was 0.9696 compared with 0.9369 for raptors that prey upon carnivores.

Similar analyses of mean AUC were performed aggregating the species into the three major taxonomic groups: higher plants, insects and birds (Table 2). There was no indication of variation among major taxonomic groups in the effect of prevalence (ANCOVA interaction term, $F_{(2,290)} = 2.06$, $P > 0.10$). Although the mean AUC values for the three major taxonomic groups showed highly significant variation among the groups (ANOVA, $F_{(2,293)} = 7.80$, $P < 0.001$), there was no significant difference in mean AUC when allowance was made for the effect of prevalence (ANCOVA, $F_{(2,292)} = 2.68$, $P > 0.10$).

DISCUSSION

The results presented above demonstrate that the distributions of species from diverse taxonomic groups, and representing different life forms and trophic levels, can be modelled very successfully using a limited number of bioclimatic variables. Furthermore, the majority of the resulting models (>84%) are of 'high accuracy' when assessed using an appropriate and stringent measure of goodness-of-fit with a low sensitivity to prevalence (Manel *et al.* 2001). The absence of any significant effect of trophic level upon model performance falsifies the hypothesis that we sought to test; we find no evidence that the strength of the relationship between species distributions and climate diminishes at higher trophic levels. If the effect of varying prevalence is taken into account, then there are also no

significant differences in model performance between the three major taxonomic groups. This contrasts with the views of some ecologists (e.g. Austin 2002) that the physical environment, especially climate, is more important in predicting the distributions of plants than of animals; even after taking into account the effect of their generally lower prevalence, mean model performance was worst, albeit not significantly so, for the higher plants.

In addition to their intrinsic interest, these results are relevant in the context of assessing the value of correlational models as a basis for investigating species potential responses to climatic change. The use of such models in this way is most often criticized either on the basis of the oft-repeated biological mantra that 'correlation does not demonstrate causation', or by arguing that, because the individualistic response of species will result in no-analogue assemblages in response to no-analogue climatic conditions, the boundaries of species realised niches will change as they interact with different species in these new conditions (Davis *et al.* 1998a,b).

The first of these bases for criticism is substantially weakened by the evidence that such correlations are found repeatedly and generally for species from different taxonomic groups, life forms and trophic levels. In addition, in the present case the models, although correlational, are fitted to just three variables selected *a priori* on the basis of their known roles in limiting species distributions through well understood and quite general physiological mechanisms. Shipley (2000), discussing cause and correlation in biology, refers to the 'correlational shadow' of a causative process. In the case of species distributions, it is certainly correct to say that for most species we cannot trace the, often complex and indirect, causative pathway between climate and the realised distribution of the species; nonetheless, as the results presented above show, these pathways cast a long correlational shadow that it would be perverse to ignore.

The criticism of the use of such models to explore species potential responses to climatic change on the basis that species interactions in no-analogue communities will result in changes to the boundaries of species realised niches may appear to be more substantive. However, it must be remembered that most species interactions are generalist as opposed to specialist (Huntley *et al.* 1997), and that most species are involved in such generalist interactions with large numbers of other species in any given ecosystem. In addition, and as a direct consequence of the individualistic behaviour of species, the effects of the interacting species at any one locality are substituted by the effects of other species as the assemblage changes across the focal species geographical range. Furthermore, published studies that have evaluated the performance of such models under changed climatic conditions, or in different regions where the focal species is interacting with quite different suites of other species, consistently provide evidence of the robustness of the model simulations. For example, a species–climate response surface fitted for a species introduced to Europe provided a good simulation of the extent of its native range in eastern Asia (Beerling *et al.* 1995), while Prentice *et al.* (1991), using pollen–climate response surfaces fitted to pollen abundance data for modern surface samples and the current climate, showed that the dynamics of the post-glacial distributions of several eastern North American tree taxa could be simulated successfully from an independent reconstruction of climate history made using other pollen taxa. Further evidence of the general robustness of such models was provided by Huntley *et al.* (1989); their results led to the conclusion that the relationships between the distribution and abundance of a tree taxon and climatic variables had been conserved over a long period of evolution in isolation, and despite selective extinction in different regions of other tree taxa with which it principally interacts.

Although there is a need for more such tests of the modelling approach, especially with the aim of discovering circumstances in which it may not be applicable – perhaps including species exhibiting rapid range changes apparently unrelated to climate, for example the 20th century expansion of the range of *Streptopelia decaocto* (Collared Dove) across Europe (although see Hengeveld 1988) – it is nonetheless likely that species realized niches as components of complex ecosystems generally are better represented by their observed natural distributions than by their behaviour in microcosm experiments examining the interactions between only small numbers of species (Davis *et al.* 1998a,b). As others also have noted (Hodkinson 1999; Voigt *et al.* 2003), such experiments are neither an adequate representation of the complexity of the environment nor of the ecosystems in which species interact in nature. It is important to emphasize in this context that our results do not lead us to conclude that biotic factors are unimportant.

They do, however, support the conclusion that, whereas the proximate factor determining any given part of a species range limit may be a biotic interaction, such biotic interactions are generally modulated by abiotic factors, including climate, that thus are the ultimate determinants of species range limits. That climate can modulate interspecific interactions in this way has been demonstrated by numerous field studies and, ironically, by the results of microcosm studies that have been used as a basis for criticisms of the modelling approach presented here (Lawton 2000).

Given our results, it is interesting that Voigt *et al.* (2003) have recently presented evidence showing that, in calcareous grasslands, species at higher trophic levels exhibit greater sensitivity to climatic perturbations. Although these authors offer a number of hypotheses to account for their results, it is inescapable that these results are contrary to what might be expected were abiotic factors of lesser importance to organisms at higher trophic levels. Furthermore, in the context of their results, the tendency observed in our results for the two major heterotrophic taxonomic groups to exhibit generally stronger relationships to climate than does the autotrophic group is striking and certainly worthy of further investigation.

While many more experimental studies, both in the field and in controlled environments, are needed to advance our understanding of the processes underlying the responses of species populations and of ecosystems to environmental change, the formulation of strategies for the long-term conservation of biodiversity in the face of inevitable and rapid climate change cannot await these results. As others too have argued (Pearson & Dawson 2003), species–climate models provide a basis for ecologists to make at least preliminary assessments of the likely nature and magnitude of the impacts of climate change (Berry *et al.* 2002; Midgley *et al.* 2002; Thomas *et al.* 2004). By showing that such models can be applied with equal validity to species from different trophic levels, and that they generally perform well for species from disparate taxonomic groups, the present study has provided additional evidence of the robustness and general applicability of such models. Nonetheless, it is vital that those using such models apply them critically, taking into account especially the extent to which the simulations of potential future ranges of species involve extrapolations being made into no-analogue regions of environmental space. Perhaps of greatest concern in this respect is the evidence from the Quaternary record of the interacting effects of changes in climate and in atmospheric concentrations of carbon dioxide (Cowling & Sykes 1999).

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Appendix 1 Trophic group assignments of raptors

Preying principally upon insects (6)

Pernis apivorus	Honey Buzzard	*Falco eleonorae*	Eleonora's Falcon
Falco naumanni	Lesser Kestrel	*Otus scops*	Scops Owl
Falco vespertinus	Red-footed Falcon	*Athene noctua*	Little Owl

Preying principally upon herbivores (38)

Milvus migrans	Black Kite	*Aquila chrysaetos*	Golden Eagle
Milvus milvus	Red Kite	*Hieraaetus pennatus*	Booted Eagle
Gypaetus barbatus	Lammergeier	*Hieraaetus fasciatus*	Bonelli's Eagle
Neophron percnopterus	Egyptian Vulture	*Falco tinnunculus*	Kestrel
Gyps fulvus	Griffon Vulture	*Falco biarmicus*	Lanner
Aegypius monachus	Black Vulture	*Falco cherrug*	Saker Falcon
Circus aeruginosus	Marsh Harrier	*Falco rusticolus*	Gyrfalcon
Circus cyaneus	Hen Harrier	*Falco peregrinus*	Peregrine Falcon
Circus pygargus	Montagu's Harrier	*Tyto alba*	Barn Owl
Circus macrourus	Pallid Harrier	*Bubo bubo*	Eagle Owl
Elanus caeruleus	Black-winged Kite	*Nyctea scandiaca*	Snowy Owl
Accipiter gentilis	Goshawk	*Surnia ulula*	Hawk Owl
Buteo rufinus	Long-legged Buzzard	*Glaucidium passerinum*	Pygmy Owl
Buteo buteo	Buzzard	*Strix aluco*	Tawny Owl
Buteo lagopus	Rough-legged Buzzard	*Strix uralensis*	Ural Owl
Aquila nipalensis	Steppe Eagle	*Strix nebulosa*	Great Grey Owl
Aquila pomarina	Lesser Spotted Eagle	*Asio otus*	Long-eared Owl
Aquila clanga	Spotted Eagle	*Asio flammeus*	Short-eared Owl
Aquila heliaca/adalbertii	Imperial Eagle	*Aegolius funereus*	Tengmalm's Owl

Preying principally upon carnivores (7)

Haliaeetus albicilla	White-tailed Eagle	*Pandion haliaetus*	Osprey
Circaetus gallicus	Short-toed Eagle	*Falco columbarius*	Merlin
Accipiter nisus	Sparrowhawk	*Falco subbuteo*	Hobby
Accipiter brevipes	Levant Sparrowhawk		