

RESEARCH
PAPER



Niche properties and geographical extent as predictors of species sensitivity to climate change

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ABSTRACT

Aim Bioclimatic envelope models are often used to make projections of species' potential responses to climate change. It can be hypothesized that species with different kinds of distributions in environmental niche and geographical space may respond differently to changes in climate. Here, we compare projections of shifts in species ranges with simple descriptors of species niche (position and breadth) and geographical (range size) distributions.

Location Europe.

Methods The future distribution for 1200 European plant species were predicted by niche-based models using seven climate variables known to have an important role in limiting plant species distributions. Ecological niche properties were estimated using a multivariate analysis. Species range changes were then related to species niche properties using generalized linear models.

Results Generally, percentage of remaining suitable habitat in the future increased linearly with niche position and breadth. Increases in potential suitable habitat were associated with greater range size, and had a hump-shaped relationship with niche position on temperature gradient. By relating species chorotypes to percentage of remaining or gained habitat, we highlighted biogeographical patterns of species sensitivity to climate change. These were clearly related to the degree of exposure according to regional patterns of projected climate change.

Main conclusion This study highlights general patterns about the relationships between sensitivity of species to climate change and their ecological properties. There is a strong convergence between simple inferences based on ecological characteristics of species and projections by bioclimatic 'envelope' models, confirming macroecological assumptions about species sensitivity based on niche properties. These patterns appear to be most strongly driven by the exposure of species to climate change, with additional effects of species niche characteristics. We conclude that simple species niche properties are powerful indicators of species' sensitivity to climate change.

Keywords

Bioclimatic 'envelope' modelling, climate change, future potential habitats, niche breadth, niche position, range size.

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INTRODUCTION

Recent anthropogenic climate change is already affecting biodiversity at various scales, for instance, by increasing extinction rates and by inducing displacements of species distributions (Hughes *et al.*, 2000; Parmesan & Yohe, 2003). It is therefore

urgent to evaluate the potential effects of future climate change on biodiversity. Such a task is best achieved using modelling tools to complement expert assessments (Sala *et al.*, 2000). For the last decade, several studies have attempted to project species distributions into the future using a range of future climate change scenarios (e.g. Huntley *et al.*, 1995; Sykes *et al.*, 1996; Peterson

et al., 2002; Thomas *et al.*, 2004; Thuiller, 2004). These studies attempted to assess the sensitivity of species to climate change, defined as the degree to which their distributions were affected by climate change.

These niche-based models are currently being used to relate present day species distributions with a set of climatic variables and to project future potential distributions under climate change scenarios. However, while these models have produced estimates of species turnover, range expansion and contraction under climate change scenarios (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002), no study has systematically explored the relationship between ecological and distributional properties of species (niche position and breadth, range size and chorotype) and their projected sensitivity to climate changes (but see Guisan & Theurillat, 2000; Peterson, 2003).

Nevertheless, a number of hypotheses about which species should be more or less sensitive to climate change have been suggested based on common ecological understanding. These include expectations that: (1) species with requirements near the mean climate conditions of the studied area should be less sensitive than species with outlying niches (marginal species) (Swihart *et al.*, 2003); (2) species encountering a broader array of climate conditions across their range (generalist species) are expected to have broader tolerances to climate change than climatically restricted species (specialist species) (Brown, 1995); (3) species with restricted ranges are more likely to be sensitive to climate change than widespread species (Johnson, 1998); and (4) species from phytogeographical groups strongly exposed to climate change should be more sensitive.

If these hypotheses are correct, then we should expect a convergence between simple inferences based on ecological characteristics of species and projections by bioclimatic 'envelope' models.

In this paper, we used projections from bioclimatic models to examine relationships between species sensitivity and niche properties. We used the BIOMOD application (Thuiller, 2003) to project future potential distributions of 1200 European higher plants in response to one severe climate change scenario in 2050. Projected stable, disappearing and potentially gained climatically suitable areas of each species were related to their niche and spatial characteristics, as well as to their exposure to climate change. We addressed the following questions: (1) are environmentally marginal species more sensitive to climate change? (2) are specialist species more sensitive than generalist species to climate change? (3) are species with restricted ranges more sensitive to climate change than widespread ones? and (4) are species from different chorotypes equally sensitive?

DATA AND MODELS

Species data

We used a subset (20%) of the *Atlas Florae Europaeae* (AFE) (Lahti & Lampinen, 1999), which contains digitized maps for more than 2600 species across Europe. Species with less than 20 records in the data set were excluded from the analysis to reduce

errors associated with excessively small sample sizes (Stockwell & Peterson, 2002). Species retained (1205 species) included all European pteridophytes, a sample of spermatophytes comprising representatives of all gymnosperm families (Coniferales, Taxales and Gnetales) and a fraction of angiosperm dicotyledons (Salicales, Myricales, Juglandales, Fagales, Urticales, Proteales, Santales, Aristolochiales, Balanophorales, Polygonales, Centrospermae and Ranales), but no monocotyledons as these have not yet been digitized. Species data were originally located in 4419 UTM (universal transverse Mercator) 50 × 50 km grid cells, but we used only 2089 grid cells excluding most of the eastern European countries (except for the Baltic states) because of low recording efforts in these areas (Williams *et al.*, 2000).

We defined 10 classes of chorology based on the phytogeographical and biogeographical properties of species: Alpine, Atlantic, Boreo-alpine (Boreo-subalpine and Artico-alpine), Euro-Siberian (Medio-European), Introduced, strict Mediterranean, Mediterraneo-Atlantic (Mediterranean species having a wide part of their distribution in the Atlantic region), Late Mediterranean (Mediterranean species distributed significantly beyond the Mediterranean region), Coastal (species occurring exclusively on the European seaboard) and Pluri-regional (species occurring in several biogeographical regions). The chorology of each species was determined according to the literature (Bolòs *et al.*, 1990; Tutin *et al.*, 1964–1993) and completed and corrected by experts.

Environmental data

Climate included seven variables interpolated for Europe in the context of the EC-funded advanced terrestrial ecosystem analysis and modelling (ATEAM) project <<http://www.pik-potsdam.de/ateam>>. All data were developed at a spatial resolution of 10' × 10' (c. 16 × 16 km) for European grid cells based on the ATEAM geographical window and then aggregated to the *Atlas Florae Europaeae* 50 × 50 km grid. Climate data were averaged for 1961–1990 and included the mean annual temperature, the mean temperature of the coldest month of the year, mean annual precipitation sum, the mean winter precipitation sum, mean summer precipitation sum, the mean annual growing degree days, and the mean ratio of annual actual over annual potential evapotranspiration.

Future projections for the 2050 time slice (averages for years 2036–2065) were derived using one general circulation model experiment (GCM) made available in the context of the EC-funded ATEAM project and was conducted at the UK Hadley Centre for Climate Prediction and Research (HadCM3, Mitchell *et al.*, 2004). This GCM projected the mean climate under one rather extreme scenario: the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (IPCC SRES) A1F1 storyline (Nakicenovic & Swart, 2000), which describes a future world of very rapid economic growth, a global population that peaks by mid-century and then declines, and the rapid introduction of new and more efficient technologies. Under this scenario, atmospheric CO₂ rises from 380 p.p.m. in 2000 to 580 p.p.m. in 2050. Mean annual temperature over Europe,

which equals 8.3 °C for 1961–1990, is predicted to reach 10.4 °C in 2050.

Future potential habitats

Future potential habitats were projected using the BIOMOD application in SPLUS (Thuiller, 2003). For each species, a generalized linear model (GLM), a generalized additive model (GAM), a classification tree analysis (CTA) and an artificial neural network (ANN) were calibrated on a random sample of the initial data (70%). Then for every species, the accuracy of each model was assessed and compared using the Area Under the Receiver operating characteristic (ROC) curve (AUC index) on the remaining 30% of the initial data (Pearce & Ferrier, 2000). The best model for each species according to the ROC curve criterion was utilised to project future potential climatically suitable habitats. A rough guide for classifying the accuracy of the models is: AUC 0.90–1 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; and 0.50–0.60 = fail (Swets, 1988).

For each species, we calculated the percentage of stable climatically suitable habitat defined as the grid cells suitable for the species both at present and under the scenario of change (Fig. 1). Of the currently suitable envelope, the remaining grid cells, predicted to become unsuitable, made the percentage of lost habitat. Finally, the percentage of new climatically suitable habitat, defined as

habitat unsuitable at present but predicted to become suitable, was calculated as the ratio between the number of new climatically suitable grid cells and the present day habitat size.

Species niche and spatial properties, and exposure to climate change

The ecological niche of a species can be described by its mean position and breadth along various environmental axes (Schoener, 1989). Here, niche position and niche breadth along climatic axes were described using the multivariate coinertia analysis, Outlying Mean Index (OMI: Doledec *et al.*, 2000). Unlike the more commonly used canonical correspondence (ter Braak, 1986) and redundancy analyses (Rao, 1964), OMI makes no assumption about the shape of species response curves to the environment, and it gives equal weights to species-rich and species-poor sites. The result of this analysis is a description of the mean niche position on each selected gradient (niche position) for each species, which represents a measure of the distance between the mean conditions used by the species and the mean conditions of the study area for that gradient. A species was then considered ‘marginal’ when its environmental requirements were far from the mean European conditions. For every selected gradient, it is then possible to estimate the variability of habitat conditions used by each species by calculating the variance of the

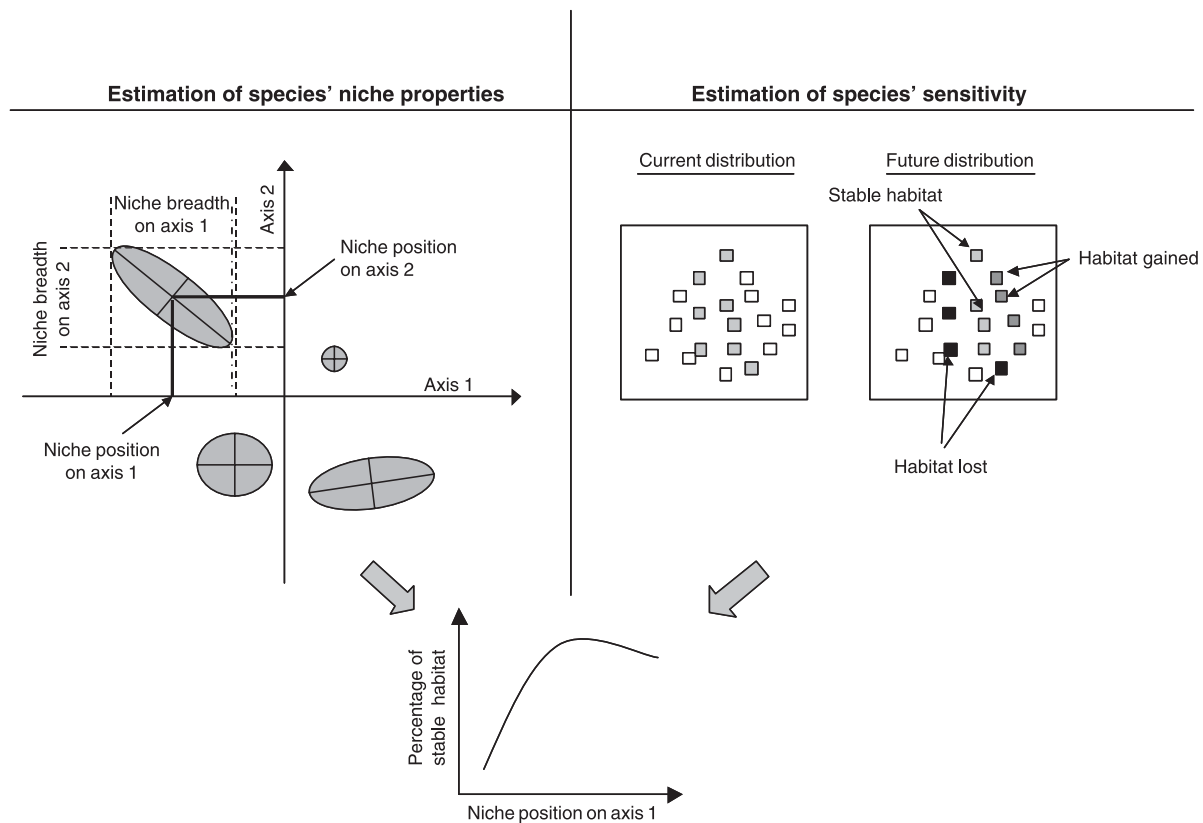


Figure 1 Conceptual scheme representing the approach used to relate species' niche properties on environmental gradients and species' sensitivity to climate change. Axes 1 and 2 are virtual environmental gradients. Ellipses represent species niches within the environmental space. Clear, grey and black squares represent stable habitat, new potential habitat, and habitat lost, respectively.

positions of each occurrence on the selected gradient (named niche breadth) (Thuiller *et al.*, 2004c) (Fig. 1). A single spatial measure describing the spatial distribution of species was used (i.e. range size). Finally, the exposure to climate change of each grid cell of the European map was estimated for each climatic variable using the coefficient of variation, calculated as:

$$100 * (var_{future} - var_{current}) / \text{mean}(var_{future}, var_{current}).$$

The conceptual framework used in this analysis is summarized in Fig. 1.

To relate patterns of change across species with their ecological niche and spatial properties, we ran stepwise generalized linear models using percentage of stable habitats and new potential habitats as response variables, and niche or spatial properties as explanatory variables (Fig. 1). This procedure selected the most relevant variables among the niche and spatial properties that could explain the overall sensitivity of a species to climate change according to the Akaike information criterion (Akaike, 1974).

RESULTS

Bioclimatic gradients in European plant distributions

OMI extracted two main gradients explaining over 93% of species niche separation (Table 1). The first axis, explaining 80% of the total variation in species distributions, captured a temperature gradient running from the northeast to the southwest, parallel to the Atlantic coast. The second gradient, explaining 13% of the variation, represented changes in seasonal and annual precipitation. For example, the Mediterranean region had a high score for the first OMI axis (high temperature) and generally low scores for the second axis (low precipitation). Score variation along the second axis highlighted regional differences in moisture availability from dry (e.g. eastern coast of Spain) to wet (e.g. northwest of the Iberian Peninsula) regions.

Future potential habitats

Models of current distributions exhibited a high predictive accuracy for almost all species because the AUC for the first quartile was higher than 0.9 and the mean AUC was 0.95. These models were used to generate projections of future climatically suitable habitat.

Table 1 Canonical correlation between climatic variables and the two first axes from the outlying mean index (OMI)

Climatic variable	OMI axis 1	OMI axis 2
Growing degree day	0.97	0.02
Annual temperature	0.94	-0.16
Mean temperature of the coldest month	0.87	-0.37
Humidity index	-0.86	-0.23
Summer precipitation	-0.74	-0.60
Annual precipitation	-0.21	-0.97
Winter precipitation	0.15	-0.92

Table 2 Summary of BIOMOD projections for 1200 higher European plants in year 2050 under the A1FI HadCM3 future scenario

	Percentage of stable suitable habitat	Percentage of potentially new suitable habitat
Minimum	0%	0%
First quartile	53.3%	13.1%
Median	70.7%	29.5%
Third quartile	86.6%	59.4%
Maximum	100%	414.1%

Consequences of climate change on the selected European plant species were predicted to be fairly severe (Table 2). On average, plants in this study would retain only 70% of their current suitable habitat (30% habitat loss). Extremes for stable habitats ranged from 0 (e.g. *Quercus fructicosa*) to 100% loss (e.g. *Dianthus fruticosus*), showing highly idiosyncratic responses across species. Some species could extend their current distributions by up to 400% (e.g. *Silene exaltata*), whereas others were predicted to gain no new suitable habitat (e.g. *Betula pubescens*).

Relationships between ecological niche and spatial properties and future projections

Stepwise GLM selected niche position on the temperature gradient (axis 1), range size and niche breadth on the temperature gradient (axis 1) as the most powerful variables to explain the percentage of stable climatically suitable habitat (Table 3; Fig. 2a). The relationship between niche position on the temperature gradient and percentage of stable climatically suitable habitat was almost linear, showing that species occurring in colder regions (negative side) are expected to lose larger proportions of habitat than species from warmer regions (positive side). The bell-shaped relationship between range size and percentage of stable suitable habitat showed that species with very low numbers of occurrences were projected to lose large proportions of suitable habitat (45–60%), but more abundant species were also expected to lose substantial amount of habitat (40–50%). Finally, the positive linear relationship between niche breadth on the temperature gradient and the remaining suitable habitat showed that species with narrow tolerance to temperature were expected to lose large proportions of habitats (40–60%), whereas the species tolerant to aridity were predicted to be the most stable under future conditions.

Stepwise GLM selected range size, niche position on the temperature gradient (axis 1) and niche breadth on the precipitation gradient (axis 2) to explain variation in the percentage of potential habitats gained by species (Table 3; Fig. 2b). Species with low numbers of occurrences were expected to gain the largest proportion of potentially suitable habitat. The bell-shaped relationship between percentage of potentially gained habitat and niche position on the temperature gradient showed that marginal species (i.e. species from warmest or coldest habitats) were expected to gain the lowest proportion of new habitats. The negative relationship between niche breadth and the precipitation gradient

Table 3 Summary of stepwise generalized linear model (GLM) carried out on percentage of stable and gained habitats

Step	d.f.	Deviance resid.	d.f. resid.	Deviance	AIC
<i>Percentage of stable habitats</i>					
Poly (mean position on T° gradient, 2)	2	38.5	1185	250	256
Poly (range size, 2)	2	25.9	1183	224	234
Niche breadth on T° gradient	1	2.5	1182	222	234
<i>Percentage of gaining habitats</i>					
Poly (range size, 2)	2	15238	1185	36642	36648
Poly (mean position on T° gradient, 2)	2	8703	1183	27938	27948
Poly (niche breadth on predicted gradient, 2)	2	3428	1181	24511	24525

d.f., degree of freedom; resid, residual; AIC, Akaike Information Criteria (Akaike, 1974), and Poly (x, 2), polynomial function with 2 degrees.

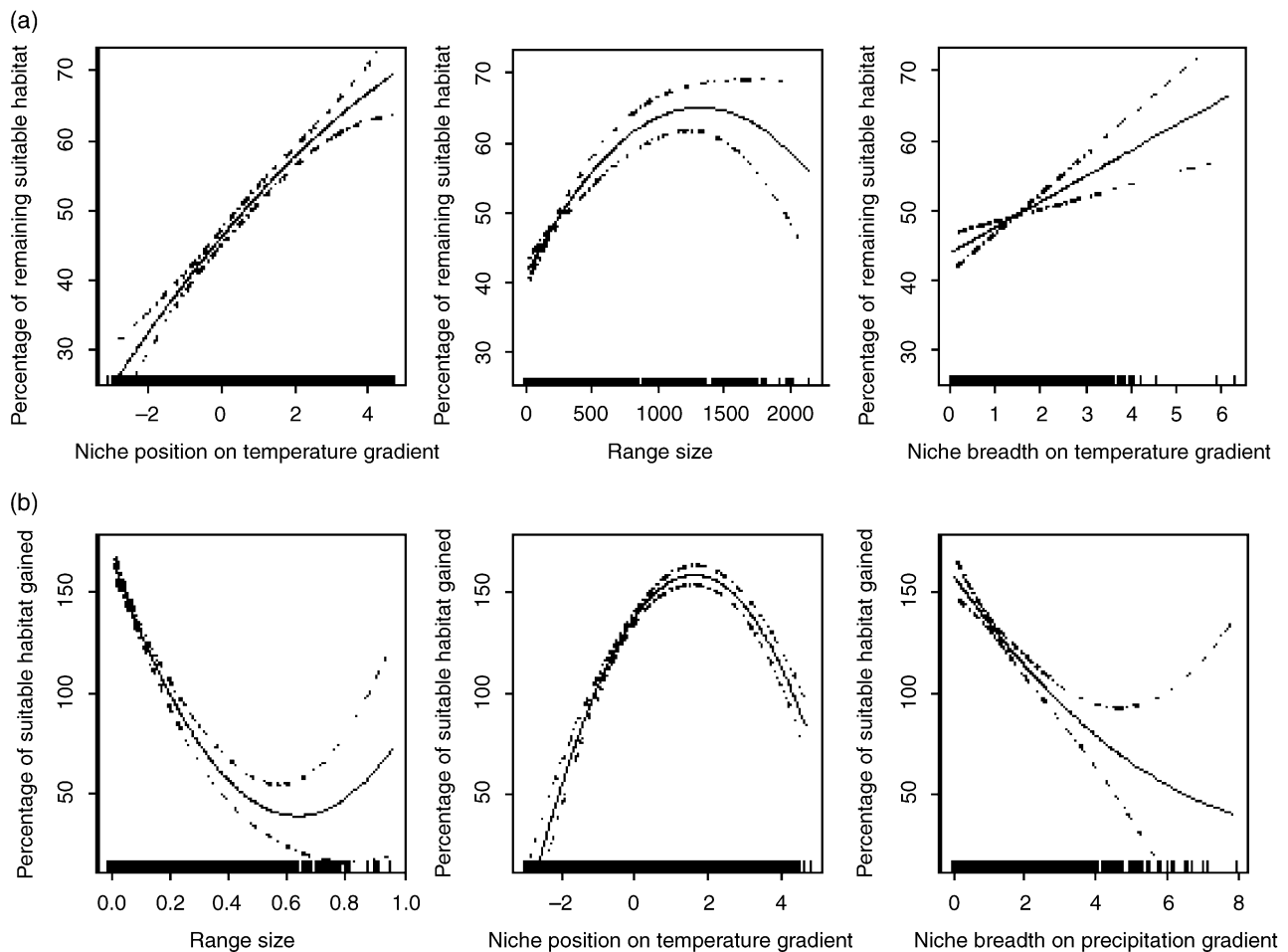


Figure 2 Response curves from stepwise GLM relating percentage of stable (a) and potentially new suitable (b) habitat to significant species ecological niche properties, plotted in order of decreasing explained deviance. Upper and lower pointwise twice-standard-error curves are included for each plot (dashed line). A univariate histogram is displayed along the base of each plot, showing the occurrence of each species.

showed that to gain potential suitable habitat, species should have a narrow niche breadth on this axis (i.e. species with a narrow tolerance to precipitation were predicted to gain the largest amount of new habitats). This relationship could result from the fact that Boreo-alpine species have a wide precipitation tolerance but are predicted to gain no potential habitats owing to their marginal position on the temperature gradient.

Relationships between exposure, species chorology and future projections

We observed a strong heterogeneity in exposure to climate change (Fig. 3). Mean annual temperature, mean temperature of the coldest month and growing degree days (major component of the first OMI axis) were predicted to vary most strongly, especially

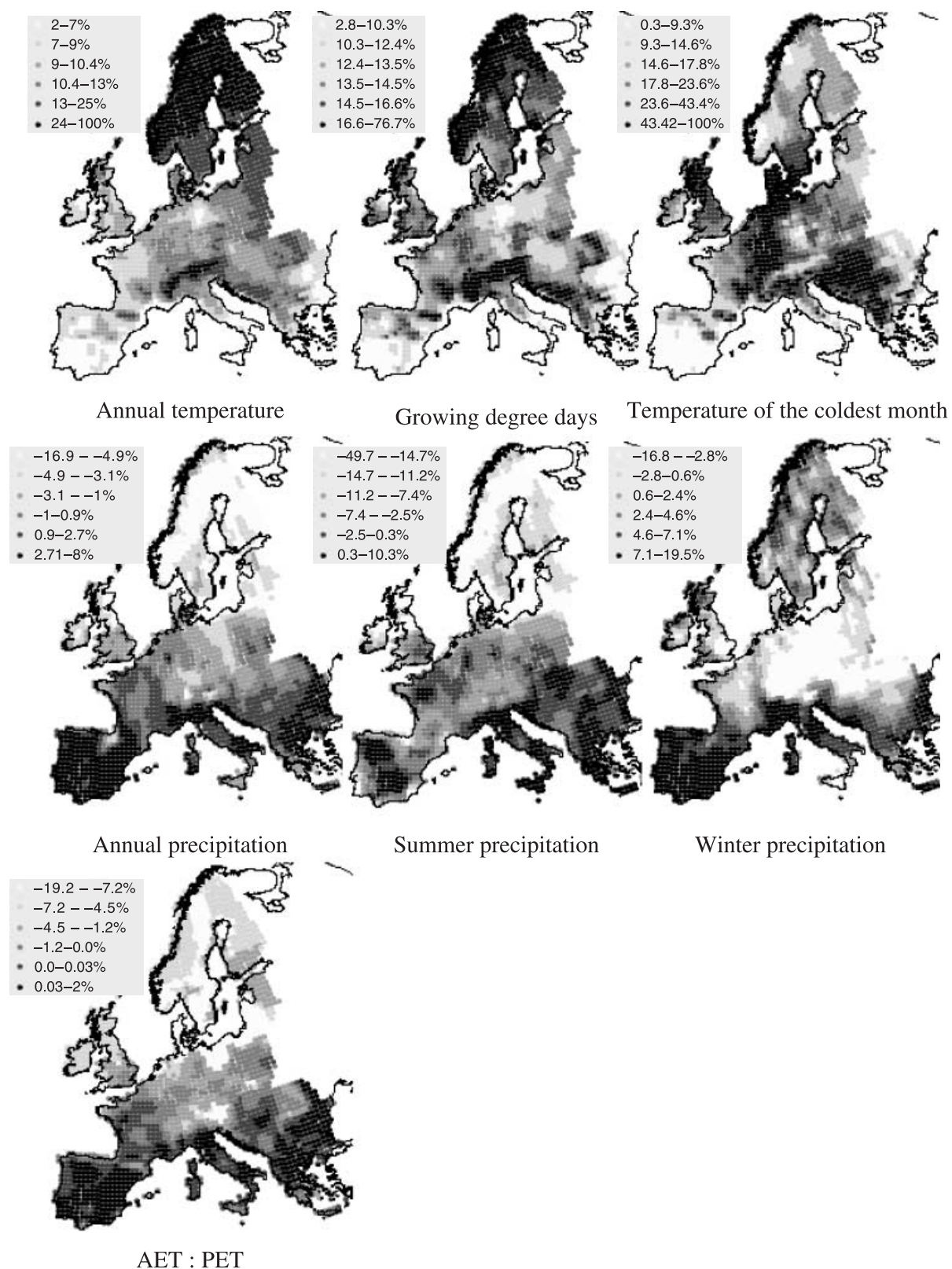


Figure 3 Exposure of regions to climate change for every climatic variable. Values in the legend represent the coefficient of variation between future and current variables. AET : PET is the ratio of actual to potential evapotranspiration.

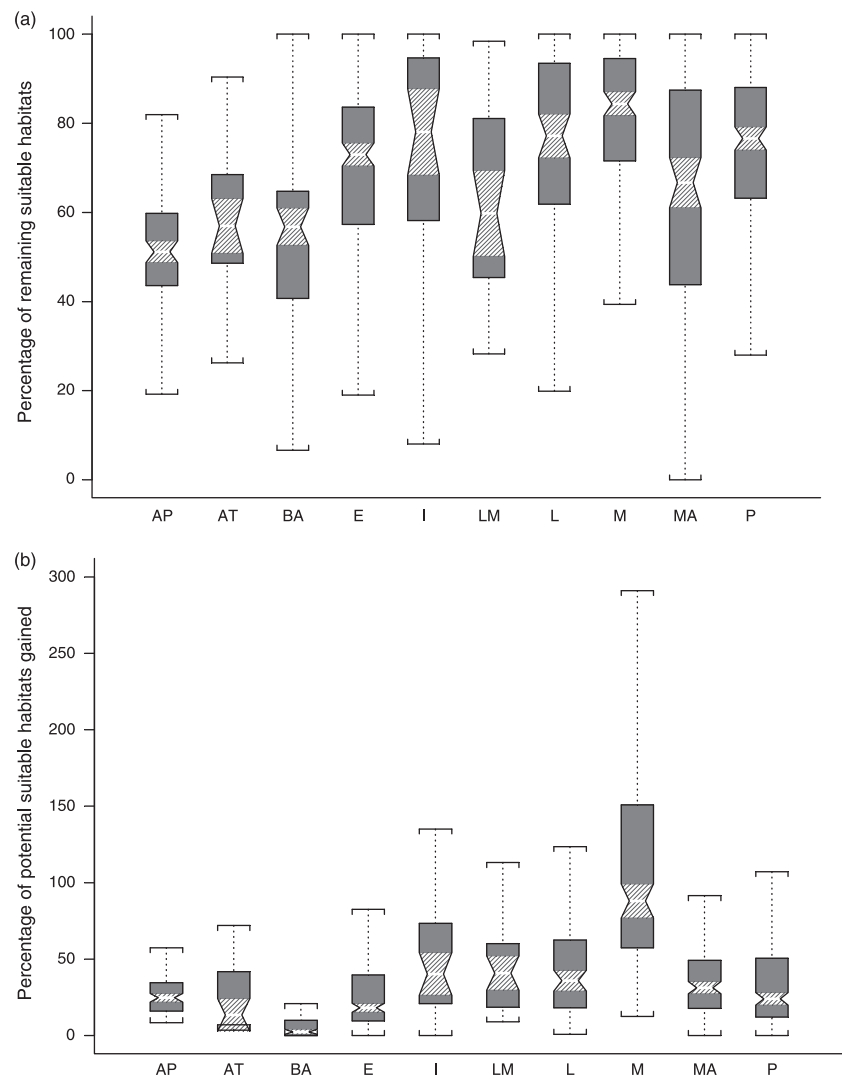


Figure 4 Relationship between species chorotypes and (a) percentage of stable suitable habitats and (b) percentage of new potential suitable habitats gained by species. AP, Alpine; AT, Atlantic; BA, Boreo-alpine; E, Euro-Siberian; I, Introduced; LM, Late Mediterranean; L, Coastal; M, Mediterranean; MA, Mediterraneo-Atlantic; and P, Pluri-regional species. Hatched shapes correspond to confidence intervals at 95%.

in European mountain ranges and the Boreo-arctic region. The Mediterranean region was predicted to become drier, whereas precipitation in the Boreo-arctic region should remain stable.

Examining sensitivity among chorological groups suggested that, despite the large interspecific variability within types, chorotypes susceptible to lose the largest amount of habitat were Atlantic, Alpine and Boreo-alpine species (median loss = 55%), whereas Mediterranean species were projected to lose the lowest amount of habitat (Fig. 4). Conversely, Mediterranean species were projected to gain potentially the highest proportion of habitat (median = 80%), whereas Boreo-alpine species should gain the least (median = 8%).

This analysis of exposure and species chorology helped us clarify the observed relationships between niche properties and species sensitivity. For instance, marginal species in cold regions should be more sensitive to climate change, whereas marginal species in warm regions would be less sensitive to temperature warming because of differing levels of exposure (Fig. 2a). This adds complexity to the original expectation that marginal species overall should be more sensitive than those having mean habitat conditions in Europe. As expected, analysing the effect of exposure and

chorology suggested that sensitivity depends strongly on the position of species niches on the climatic gradient undergoing change and the expected direction of the change. These two factors would, for example, explain why species tolerating warm temperatures were predicted to expand despite being marginal. These conclusions also apply to rare species, and to those with narrow niche breadth.

DISCUSSION

Methodological limitations

The analyses performed here depend critically on the modelled ecological niche as a stable constraint on the species' geographical distributional potential. The main assumption for modelling ecological niches is the equilibrium concept, which assumes that modelled species are at equilibrium with their environment (Prentice, 1986; Guisan & Zimmermann, 2000). Here, we assumed that species were near equilibrium at the spatial extent and resolution of our data set. In particular, at the scale considered, land use/cover had no detectable effect on species presence/absence,

which could be explained solely on the basis of climate distribution (Pearson *et al.*, 2004; Thuiller *et al.*, 2004a).

Another limitation concerns the full description of the dimensions of species' ecological niches. First, the analysis did not capture the full environmental range of some species to describe accurately their ecological niches (Pearson *et al.*, 2002). This was especially the case for species at the edge of their climatic range, such as many eastern and southern Mediterranean species. Second, projections into the future with climatic conditions outside the current range that were used to calibrate models will necessarily involve uncertainties in the form of both over and underestimations (Thuiller *et al.*, 2004b). Third, the degree to which biotic interactions may limit current species distributions across large spatial scales can lead to under or overestimating the potential distributions under current climate, and hence disturb projections of future suitable habitats (Leathwick & Austin, 2001).

Projections of potential suitable habitats are also strongly dependent on the resolution of the bioclimatic analysis. This might apply to Alpine species, as 50 × 50 km cells cannot reliably account for the heterogeneity and spatial structure of mountains, such that any conclusions with regard to these species should be interpreted with care (Guisan & Theurillat, 2000).

Exposure of European plant species to climate change

Global climate change was projected to influence strongly the future potential suitable distributions of the selected higher European plants. Even if our analysis concerns only a portion of total European plant diversity, we have shown that the response of species to climate change could be informed by geographical and ecological considerations.

At the continental scale, exposure to climate change is geographically variable. Our analysis illustrates the basic idea that the sensitivity of a given species would depend on its geographical distribution and ecological properties relative to the regional patterns of exposure to climate change. A species with a niche position within regions most exposed to climate change is bound to be more sensitive than a species in a less exposed region. European climate was described by a dominant temperature gradient and a secondary precipitation gradient. Knowing the niche position of species on these gradients makes it possible to estimate the potential pressures of climate change, especially for species with aggregated distributions or for those occurring in a single biogeographical region. In a warming context, species occurring preferentially in warm and dry areas should benefit from climate change, conserving their initial habitats and/or expanding to new suitable habitats. Conversely, species occurring in cold regions should either disappear because of a loss of suitable habitat, or migrate northwards or up slope towards new potential habitat, if this is geographically available.

Predicting species sensitivity from niche properties

Are marginal species sensitive to global climate change?

Our analysis suggests that marginal species are not always the most sensitive to global climate change as sensitivity is strongly

related to exposure, niche breadth and range size. Marginal species, like several Mediterranean species, were projected to lose little current suitable habitat and gain potential new suitable habitats. However, range expansions (especially for southern species) should be accepted with caution owing to several limitations of niche-based models. For instance, projected range expansion for the southernmost species of our study area may be exaggerated by extrapolating species distributions into non-analogue warm future climates. Indeed, our models do not take into account their upper temperature limits as these are currently out of our study range, which could lead to modelling using truncated temperature response curves. Finally, species migration may drastically limit expansion as it depends on successful fecundity, dispersal, recruitment, and growth, all of which are dependent on climate, land use and biotic interactions. Generally, our results concur with analyses for South Africa, in which the most vulnerable species to climate change were either marginal species with disjointed ranges, or those occurring predominantly in western arid areas, likely to be the most exposed part of South Africa (Erasmus *et al.*, 2002).

Marginality should always be related to the gradient considered, because species occupying specialized habitats are by definition more susceptible to changes in their habitats. For instance, Boreo-alpine species are projected to lose an important proportion of their current distributions and gain little new potential habitats. These species are highly marginal on the temperature gradient, which is the most susceptible to change, and have small niche breadths and low range size. They could therefore be considered as particularly sensitive to climate change. Likewise, for very marginal alpine species with a small niche breadth on the temperature gradient, BIOMOD projected a substantial loss of suitable habitat. The analysis, however, was not able to take into account spatial heterogeneity, aspect or slope, and hence should be interpreted with caution, as there are many potential topographic refugia and the possibility for some species to migrate upslope (Gottfried *et al.*, 1995).

Are specialist species more sensitive than generalists?

It was expected that species that encounter a broader array of climatic conditions across their range would have broader tolerances to climate change than restricted species (Brown, 1995). Our analysis corroborated this expectation on the temperature gradient. The linear relationship observed between the percentage of stable habitat and niche breadth indicates that species occupying a large range of climatic conditions should be the most tolerant to climate change. However, these species were not predicted to gain large amounts of potential habitat because they could only expand their range within the limit of available habitats. As expected, species with narrow niche breadth were predicted to lose a high proportion of their current habitat if they occurred preferentially in cold and exposed parts of Europe (Swihart *et al.*, 2003). This is mainly the case for Boreo-alpine and some Euro-Siberian species.

Are species with restricted ranges more sensitive to climate change?

Rare species occupy a central place in biodiversity concerns because they are the most prone to extinction (Pimm *et al.*, 1988; Gaston, 1994). We did not address the risk of extinction of very narrowly distributed species as we removed from our analyses the rarest species with fewer than 20 occurrences. However, for species with very restricted ranges, our projections provided evidence that climate change should contribute to increased extinction risk, as a result of a steep decrease in suitable habitat, especially for those most exposed to climate change. Nevertheless, species with restricted ranges are expected to potentially gain disproportionately large amounts of habitat if they occur in temperate regions. This curvilinear relationship between restricted ranges and the percentage of new potential suitable habitat does not take into account geographical distances, dispersal ability and the expected problems due to non-analogue situations, especially for southern species. Species with restricted ranges are often considered to have a low dispersal ability, be weak competitors and have small local populations (Gaston, 1994). All of these attributes would compromise the ability of species with restricted ranges to increase their range by colonizing new geographically disjunct habitats.

CONCLUSION

This study highlights general patterns about the relationships between sensitivity of species to climate change and their ecological properties. We showed a strong convergence between simple inferences based on ecological characteristics of species and projections by bioclimatic 'envelope' models, confirming macro-ecological assumptions on species sensitivity based on niche properties. These patterns appear most strongly driven by the exposure of species to climate change, with additional effects of species niche characteristics. We can therefore suggest the following generalizations:

- (1) Niche characteristics are powerful indicators of species' sensitivity to climate change.
- (2) Boreo-alpine species, being marginal at the cold end of the temperature gradient, with a narrow niche breadth are predicted to be highly sensitive as they occur in the most exposed regions to climate warming.
- (3) Alpine species, which are also marginal at the cold end of the temperature gradient, but have larger niche breadth than Boreo-alpine species, are under pressure by climate change but could also gain large amounts of suitable habitat by upslope migration, a feature that was not captured by the resolution of our models.
- (4) Mediterranean species, which are at the warm end of the temperature gradient, with medium niche breadth and medium range size, were predicted to lose proportionally less suitable habitat and gain substantial amount of new habitats. Even if these species do not have wide niches, they are not in regions very exposed to climate warming. Further analyses are, however, required for these species because non-analogue situations could disturb the modelled potential responses.

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REFERENCES

- Akaike, H. (1974) A new look at statistical model identification. *IEEE Transactions on Automatic Control*, **AU-19**, 716–722.
- Bakkenes, M., Alkemade, 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.
- Bolòs, O.D., Vigo, J., Masalles, R.M. & Ninot, J.M. (1990) *Flora manual dels Països Catalans*. Pòrtic, Barcelona.
- ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.
- Brown, J.H. (1995) *Macroecology*. The University of Chicago Press, Chicago.
- Doledec, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.
- Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8**, 679–693.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Gottfried, M., Pauli, H., Reiter, K. & Grabherr, G. (1995) A fine-scaled model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions*, **5**, 241–251.
- Guisan, A. & Theurillat, J.P. (2000) Assessing alpine plant vulnerability to climate change: a modelling perspective. *Integrated Assessment*, **1**, 307–320.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (2000) Conservation of insect diversity: a habitat approach. *Conservation Biology*, **23**, 1788–1797.
- 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. *Journal of Biogeography*, **22**, 967–1001.

- Johnson, C.N. (1998) Species extinction and the relationship between distribution and abundance. *Nature*, **394**, 272–274.
- Lahti, T. & Lampinen, R. (1999) From dot maps to bitmaps — *Atlas Florae Europaeae* goes digital. *Acta Botanica Fennica*, **162**, 5–9.
- Leathwick, J.R. & Austin, M.P. (2001) Competitive interactions between tree species in New Zealand's old growth indigenous forests. *Ecology*, **82**, 2560–2573.
- Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. (2004) *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1990–2000) and 16 scenarios (2001–2100)*. Tyndall Centre Working Paper. Tyndal Centre for Climate Change Research, Norwich.
- Nakicenovic, N. & Swart, R. (2000) *Emissions scenarios*. A special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- 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.
- Pearson, R.G., Dawson, T.P. & Liu, C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography*, **27**, 285–298.
- Peterson, A.T. (2003) Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. *Global Change Biology*, **9**, 647–655.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988) On the risk of extinction. *American Naturalist*, **132**, 757–785.
- Prentice, I.C. (1986) Vegetation response to past climatic variation. *Vegetatio*, **67**, 131–141.
- Rao, C.R. (1964) The use and interpretation of principal correspondence analysis in applied research. *Sankhya*, **26**, 329–359.
- Sala, O.E., Chapin, S.F. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Hueneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Schoener, T.W. (1989) The ecological niche. *Ecological concepts: the contribution of ecology to an understanding of the natural world* (ed. by J. Cherret), pp. 790–813. Blackwell Scientific, Oxford.
- Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.
- Swets, K.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- Swihart, R.K., Gehring, T.M. & Kolozsvary, M.B. (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundary. *Diversity and Distribution*, **9**, 1–18.
- 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 climate. *Journal of Biogeography*, **23**, 203–233.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siquiera, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarseveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W. (2003) BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller, W. (2004) Patterns and uncertainties of species range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.
- Thuiller, W., Araújo, M.B. & Lavorel, S. (2004a) Do we need land cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353–361.
- Thuiller, W., Brotons, L., Araújo, M.B. & Lavorel, S. (2004b) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **27**, 165–172.
- Thuiller, W., Lavorel, S., Midgley, G.F., Lavergne, S. & Rebelo, T. (2004c) Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* species in the Cape Floristic Region. *Ecology*, **85**, 1688–1699.
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (1964–1993) *Flora Europaea*. Cambridge University Press, Cambridge.
- Williams, P.H., Humphries, C., Araújo, M.B., Lampinen, R., Hagemeyer, W., Gasc, J.P. & Mitchell-Jones, T. (2000) Endemism and important areas for representing European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology*, **2**, 21–46.

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