



Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe

Wilfried Thuiller^{1,2,3,4,*}, Sandra Lavorel^{1,4}, Martin T. Sykes⁵ and Miguel B. Araújo^{1,3,6,7}

¹Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de Recherche Scientifique, 1919 route de Mende, 34293 Montpellier cedex 5, France; ²Climate Change Research Group, Kirstenbosch Research Center, South African National Biodiversity Institute, P/Bag × 7, Claremont 7735, Cape Town, South Africa; ³Macroecology and Conservation Unit, University of Évora, Estrada dos Leões, 7000–730 Évora, Portugal; ⁴Laboratoire d'Ecologie Alpine, CNRS, Université J. Fournier, BP 53X, 38041 Grenoble cedex 9, France; ⁵Geobiosphere Science Centre, Department of Physical Geography and Ecosystems Analysis, Lund University, Sölvegatan 12, 223 62 Lund, Sweden; ⁶Biodiversity Research Group, School of Geography and the Environment, Oxford University, Mansfield Road, Oxford, OX1 3TB, UK; and ⁷Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, C/Gutiérrez Abascal, 2, 28006, Madrid, Spain

*Corresponding author. Wilfried Thuiller, Laboratoire d'Ecologie Alpine, CNRS, Université J. Fournier, BP 53X, 38041 Grenoble cedex 9, France. E-mail: thuiller@sanbi.org

ABSTRACT

Rapid anthropogenic climate change is already affecting species distributions and ecosystem functioning worldwide. We applied niche-based models to analyse the impact of climate change on tree species and functional diversity in Europe. Present-day climate was used to predict the distributions of 122 tree species from different functional types (FT). We then explored projections of future distributions under one climate scenario for 2080, considering two alternative dispersal assumptions: no dispersal and unlimited dispersal. The species-rich broadleaved deciduous group appeared to play a key role in the future of different European regions. Temperate areas were projected to lose both species richness and functional diversity due to the loss of broadleaved deciduous trees. These were projected to migrate to boreal forests, thereby increasing their species richness and functional diversity. Atlantic areas provided an intermediate case, with a predicted reduction in the numbers of species and occasional predicted gains in functional diversity. This resulted from a loss in species within the broadleaved deciduous FT, but overall maintenance of the group. Our results illustrate the fact that both species-specific predictions and functional patterns should be examined separately in order to assess the impacts of climate change on biodiversity and gain insights into future ecosystem functioning.

Keywords

Climate change, functional diversity, niche-based models, species richness.

INTRODUCTION

Rapid anthropogenic global climate change has already affected a range of species, communities and ecosystems (Parmesan & Yohe, 2003). These impacts have taken the form of loss, expansion and relocation of habitats, changes in phenology and physiology (Hughes, 2000; Walther *et al.*, 2002), coupled with possible repercussions on biotic interactions (Hughes, 2000). Recent projections forecast that such a range of effects may be widespread in the future and affect both fauna and flora globally (Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). Furthermore, there is abundant evidence from the Quaternary that plant species responses to past climate change have predominantly been expressed as large-scale shifts in their geographical distributions (Huntley, 1990; Webb, 1992). This expectation has been also supported by recent analyses showing that plants have greater degree of equilibrium with current climate than vertebrates with generally poorer dispersal abilities (Araújo & Pearson, 2005). Nevertheless,

the analogies from past to future species distributions must be made with caution because there is a possibility that non-analogue situations might be created with current climate change. For example, levels of atmospheric CO₂ concentrations are greater now than in any period of the Pleistocene and these may cause changes in water use efficiency by plants, which may in turn influence competitive interactions (Cowling & Sykes, 1999; Berry & Roderick, 2004). However, as rapid climate change ranks high among drivers of expected changes in biodiversity (Sala *et al.*, 2000), it is useful to address this driver separately. Projections of the role of climate for future vegetation and habitat distributions are based on the idea of modelling stable current relationships between species distributions and environmental variables (predominantly climatic at large scales). These modelled relationships are then used to predict how species potential distributions may be altered in response to potential future climate change scenarios (Sykes *et al.*, 1996; Cramer *et al.*, 2001; Bachelet *et al.*, 2003; Woodward & Lomas, 2004; Thuiller *et al.*, 2005a).

Recent studies have highlighted the potential ecosystem impacts of changes in functional diversity due to climate change (Chapin III, 2003; Díaz & Cabido, 2001; Lavorel & Garnier, 2002). An important reason for concern about changes in species distributions and diversity is indeed that species can differ substantially in their effects on landscape structure and ecosystem processes (Loreau *et al.*, 2001). The replacement of a species in a selected community by an 'equivalent' species (Rosenfeld, 2002) belonging to the same functional group is likely to have a minimal impact on community and landscape structure or on ecosystem functioning as compared to the replacement by a species belonging to a different functional group (Walker, 1992; Rosenfeld, 2002). For example, the replacement of a grass species by a woody deciduous broadleaved species would considerably modify carbon and nitrogen dynamics in a temperate ecosystem. Moreover organisms seldom affect a single process in isolation. Instead, effects often cascade through a broad range of ecosystem processes due to the tight linkages among carbon, nutrient and water cycles of ecosystems (Tateno & Chapin III, 1997). Species also influence landscape structure and processes through their effects on the spread of materials, organisms or disturbance and on the response of landscapes to spatially heterogeneous perturbations.

Large-scale dynamic vegetation models have been developed in recent years to link dynamically changes in vegetation through time and space with the carbon and water cycles (e.g. Woodward *et al.*, 1998; Daly *et al.*, 2000; Sitch *et al.*, 2003). Given the number and variety of species at continental or global scales, appropriate levels of descriptions of plant function to simulate ecosystem dynamics and biogeochemistry have necessarily been coarse, using plant functional types rather than species (Nemani & Running, 1996). Such plant functional types (PFT) do provide some information about plant diversity at a coarse level, but cannot be applied when information on individual plant species responses is required. To achieve this, there remains a fundamental need to establish bridges between these ecosystem models and detailed projections of changes in distributions for single species. Despite this, to date, few studies have attempted to extrapolate the likely impacts of climate change on functional diversity from single-species projections. While various estimates of species-extinction risk or species turnover are often taken as a surrogate for the sensitivity of species diversity to climate change, they do not allow modellers to project impacts on functional diversity with any degree of accuracy. Analyses that examine modifications to the functional diversity of ecosystems rather than focusing solely on extinction risks for single species would be needed to start assessing the functional impacts of species range shifts associated with climate change (Peterson *et al.*, 2005).

Here we focus on tree diversity within Europe (EU + Switzerland). Forests, woodlands and even individual trees are major elements in the European landscape, whether natural or managed. Forests occupy one-third of the land area of Europe and have major functions for wood production, recreation, hunting and conservation (Broekmeyer & Vos, 1993). Thus, trees are a major element in the functioning and the services provided by many European ecosystems. Tree species differ in the role they play in ecosystems. For example, broadleaved summer-deciduous and needle-leaved

evergreen trees have very different effects on the structure and functioning of the whole ecosystem, including light and moisture regimes, or litter decomposition rates (Broekmeyer & Vos, 1993). Hence, changing tree species ranges can affect ecosystem function but also the composition and diversity of understorey vegetation and associated biota (Broekmeyer & Vos, 1993).

In this paper we assess the potential impacts of a particular climate change scenario for 2080 on 112 tree species in Europe, and address the following questions:

- What are the most susceptible functional types to climate change in Europe?
- How will changes in species richness affect the tree functional diversity?
- How will the spatial distribution of tree functional types in Europe be affected by climate warming as a result of changes in species distributions?

METHODS

Tree distributions and characteristics

A total of 112 tree and tall shrubs species were selected for this study, encompassing all Gymnospermae families (Coniferales and Taxales), and a major part of the Angiospermae families (Salicales, Myricales, Juglandales, Fagales and Urticales). We did not include Rosales and Liliales as they were not available to us in a digital format. Distributional data for these taxa were obtained from the *Atlas Florae Europaeae* (AFE, Jalas & Suominen, 1972–96). Species data were originally located in 4419 UTM (Universal Transverse Mercator) 50 × 50 km grid cells (Lahti & Lampinen, 1999), but we used only 2089 grid cells excluding most of the eastern European countries (except for the Baltic States) because of few records in these areas (Williams *et al.*, 2000).

Species were classified into broad functional types similar to those used by dynamic global vegetation models (Sitch *et al.*, 2003). We retained four classes: deciduous broadleaved, evergreen broadleaved, evergreen coniferous and deciduous coniferous (Tutin *et al.*, 1964–93; Bolòs *et al.*, 1990; Hodgson *et al.*, 1999; Peat & Fitter, 2002). Finally, because changes in functional diversity could be spatially structured, we also extracted the chorology (phytogeographical classes) of every species from Tutin (1964–93) and Bolòs *et al.* (1990, no. 1814). This allowed us to create subfunctional types based on the chorology of the species composing them (e.g. boreal evergreen coniferous vs. mediterranean evergreen coniferous).

Bioclimatic data

Seven bioclimatic variables interpolated for Europe in the context of the EU Framework 5 ATEAM project (Schröter *et al.* 2005) were used. All data were produced at a spatial resolution of 10' for European grid cells based on the ATEAM geographical window and then aggregated to the *Atlas Florae Europaeae* 50 × 50 km grid. Bioclimate data were averaged for the period of 1961–90 and included mean annual temperature, mean temperature of the coldest month per year, mean annual

precipitation sum, mean winter precipitation sum, mean summer precipitation sum, mean annual growing degree days and mean ratio of annual actual to potential evapotranspiration.

Future projections for 2080 (averages for years 2070–99) were derived using one general circulation model experiment (HadCM3, Mitchell *et al.*, 2004). This GCM projected mean climate under the A1Fi storyline (IPCC, 2001), which describes a future world of very rapid economic growth, and with global population peaking by mid-century and then declining, accompanied by the rapid introduction of new and more efficient technologies. This scenario is the one assuming greater intensity of energy use in the IPCC scenarios (IPCC, 2001), and we chose it to address the extreme effects of climate change on functional diversity. For this exercise we ignored the impacts of changing land use on species range, although we acknowledge it can compound the effects of climate change on species (Travis, 2003). However, at the spatial extent and resolution considered in this study, land use has been found to be largely overridden by climate (Thuiller *et al.*, 2004a) and should not affect the power of our analysis.

Ecological niche modelling

Models relating species distributions to the seven bioclimatic variables were fitted using the BIOMOD framework (see details in Thuiller, 2003, 2004) on a random sample of the initial data (70%). For each species, generalized linear models (GLM), generalized additive models (GAM), classification tree analysis (CTA) and artificial neural networks (ANN) were calibrated. Then each model for each species was evaluated on the remaining 30% of the initial data set using the values obtained either for Cohen's k (Cohen, 1960) and for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (1-specificity) (Swets, 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted (Fielding & Bell, 1997). We transformed the probability of occurrence from models into presence-absence using either a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000) or the probability threshold that maximized its performance as measured by Cohen's k (Manel *et al.*, 2001).

As we required only one projection per species for impact assessment into the future, we derived for each species eight projections (4 models \times 2 threshold methods) and then, carried out an assessment of consensus using principal component analysis to explore central tendencies in the projections and select the niche-based model representing the greatest commonality among projections (Thuiller, 2004).

There is an increasing evidence that model projections can be extremely variable and there remains a need to test the accuracy of models and to reduce uncertainties (Thuiller, 2004; Thuiller *et al.*, 2004b; Araújo *et al.*, 2005a). One recent analysis has, however, provided the first test of the predictive accuracy of such models using observed range shifts of bird species and climate change in two periods of the recent past (Araújo *et al.*, 2005b). This work provides the first validation of niche-based models

under climate change and demonstrated how uncertainty can be reduced by selecting the most consensual projections, as done in the study presented here. We are therefore confident that this strategy provides a robust and defensible approach to the projections of species ranges for the purposes of conservation planning and biodiversity management. For each species, we estimated the number of pixels lost, gained (assuming unlimited migration), and unchanged, which allowed us to assess the degree of range change for each species.

Current species richness (SR) and future SR assuming unlimited and no migration ability were estimated by summing the number of species present each pixel.

Functional diversity estimation

Concepts of functional diversity vary; according to Martinez (1997), functional diversity can be quantified by determining the nature and extent to which functional groups are represented in an ecological system. Functional diversity can also refer to the number of such groups in a community each of which contains one or more species (Huston, 1994). Whatever the nature of the functional groups, it is generally accepted they will be fewer than the species under study (Mooney, 1996). In this sense, functional 'diversity' is simply a measure of group richness rather than an estimate of evenness or dominance based on the abundance of individuals per group (Petchey & Gaston, 2002).

As with species diversity, it would seem reasonable to derive a parallel measure of functional diversity based on the abundance of individuals per functional type but without species-weighting. While logically viable, this is likely to be limiting in practice as to record all individuals in a 50 \times 50 km grid cell can be excessively time-consuming at the European scale. Unsurprisingly, this information was not available to us. For these reasons, we explore the possibility of using species instead of individuals to serve as a 'higher-order' measure of abundance by deriving a species-weighted, rather than a spatial or density-driven, measure of functional diversity based on abundances of individuals. A species-weighted form of functional diversity can therefore be defined as the diversity of functional types expressed as a function of the number of species per type. While the definition can be compared with that of Mooney (1996), this approach is more sensitive to evenness and dominance. We achieve this in the same way that species abundance is used to calculate species diversity but with the important difference that counts of species per functional type are used instead of counts of individuals per species. For this we apply the Simpson index of diversity as it takes into account both richness and evenness (Magurran, 1988; Wilsey *et al.*, 2005): Index of Simpson: $1 - \sum f_i^2$, where f_i is the proportion of the PFT i (number of species) in a pixel.

RESULTS

The niche-based models performed very well on average in the validation set ($0.81 < \text{AUC} < 1$, mean $\text{AUC} = 0.96$, $0.6 < k < 0.95$, $k = 0.74$). Although not being an indisputable measure of performance (Araújo *et al.*, 2005a), good accuracy on the validation

set increases our confidence that tree distributions might be governed by climatic factors at the European scale.

Changes in functional richness

The observed patterns of species range loss (assuming no dispersal ability) and range expansion (assuming unlimited migration) displayed distinct patterns according to the functional types and phytogeographical classes analysed (Fig. 1). With regard to species range loss, two groups could be discerned. The first group, which encompasses boreal (both broadleaved deciduous and coniferous), Iberian (both broadleaved deciduous and evergreen), mountain (both broadleaved deciduous and deciduous and evergreen coniferous) and temperate (both broadleaved evergreen and coniferous) species, was predicted to lose on average > 60% of the current species ranges. The second group consisting of Mediterranean and temperate broadleaved deciduous species did not show consistent patterns.

With regard to species expansions, two groups were identified. The first included only Mediterranean trees and showed greater range expansions (ranging from 40 to 140%) but with a large variation around the mean. The other group included all of the remaining species with small range expansions (< 50%) and low variability.

Current and future (no and unlimited dispersal) species richness maps by functional type highlighted the northwards shift of deciduous communities (Fig. 2). Assuming no dispersal, a remarkable decrease in the richness of deciduous species was shown in temperate regions and mountains. Evergreen species richness was also predicted to drop mainly to the south of Iberian Peninsula; however, this effect may not in fact be real as it could be due to the lack of information on the climatic preferences of the northern African ranges of these species (Thuiller *et al.*, 2004c). Finally, coniferous species showed contrasting patterns according to latitude. Mediterranean coniferous richness was predicted to strongly decrease in Central Spain, southern France and the Adriatic coast, supporting patterns revealed in Fig. 1. Conversely, boreal coniferous richness was predicted to remain stable even in the absence of migration. Under the assumption of unlimited migration, there was a strong shift of deciduous richness from central Europe towards Scandinavia, compensated by a northward expansion of broadleaved evergreen trees.

Changes in functional diversity

To assess the potential impact of climate change on functional diversity, we plotted the variation between future and current Simpson's diversity index (Fig. 3). The severity of the change is much greater without migration.

Assuming no migration, the loss of deciduous species (Figs 1 & 2) in mountain areas and on the Atlantic coast, in addition to the loss of richness among coniferous species in Scandinavia, made functional diversity higher in these two areas. This was realized by providing a greater evenness between deciduous and evergreen trees in southern Europe, and between deciduous and coniferous trees in northern Europe.

Table 1 Spearman rank correlation between variation in index of diversity (δD) and current species (SR) richness, and between variation in index of diversity (δD) and variation in species richness (δSR)

	δD vs. SR		δD vs. δSR	
	No migration	Unlimited migration	No migration	Unlimited migration
Alpine north	-0.01 (NS)	0.27	-0.55	0.49
Boreal	0.16	0.45	-0.44	0.36
Nemoral	-0.23	-0.14	0.59	0.57
Atlantic	-0.50	-0.66	0.37	0.39
Alpine south	0.22	0.19	0.32	0.28
Continental	-0.42	-0.29	0.32	0.05
Atlantic central	0.29	0.15	-0.26	-0.58
Pannnonian	-0.15	-0.33	0.30	0.26
Lusitanian	0.13	0.27	-0.29	-0.40
Med. mountain	-0.14	-0.21	0.13	0.13
Med. north	0.33	0.47	-0.15	-0.40
Med. south	0.31	0.35	-0.27	-0.45

Assuming unlimited migration, the expansion of evergreen species in central France compensated by a shift of deciduous species resulted in a net increase in functional diversity by providing an increase in the evenness of diversity in these areas currently dominated by deciduous broadleaved trees.

Central western Europe was predicted to have a decrease of functional diversity because of a decrease in species richness of both deciduous and coniferous functional types.

Relationships between variation in the index of diversity and variation in species richness, assuming unlimited dispersal, according to the biogeographical region showed that functional diversity was not systematically, nor always positively, related to species diversity (Fig. 4 and Table 1).

The Mediterranean, Central Atlantic coast and Lusitanian regions showed a negative correlation (increase in functional diversity but decrease in species richness). In the case of the Mediterranean and Lusitanian regions, the trend reflected a decrease in both broadleaved deciduous and Mediterranean coniferous. Their decrease was likely due to increasing drought, which should lead to more open vegetation and thereby more shrubs (Gritti *et al.*, 2005). The decrease was strongest for broadleaved deciduous, therefore, the evenness of the tree communities decreases, leading to decreased functional diversity.

For the central Atlantic region the main pattern was a loss in the strong dominance of broadleaved deciduous trees along with colonization by Mediterranean broadleaved evergreen trees.

DISCUSSION

Advantages and caveats of the approach

We will not discuss the pros and cons of the ecological niche modelling approach as several papers have already highlighted

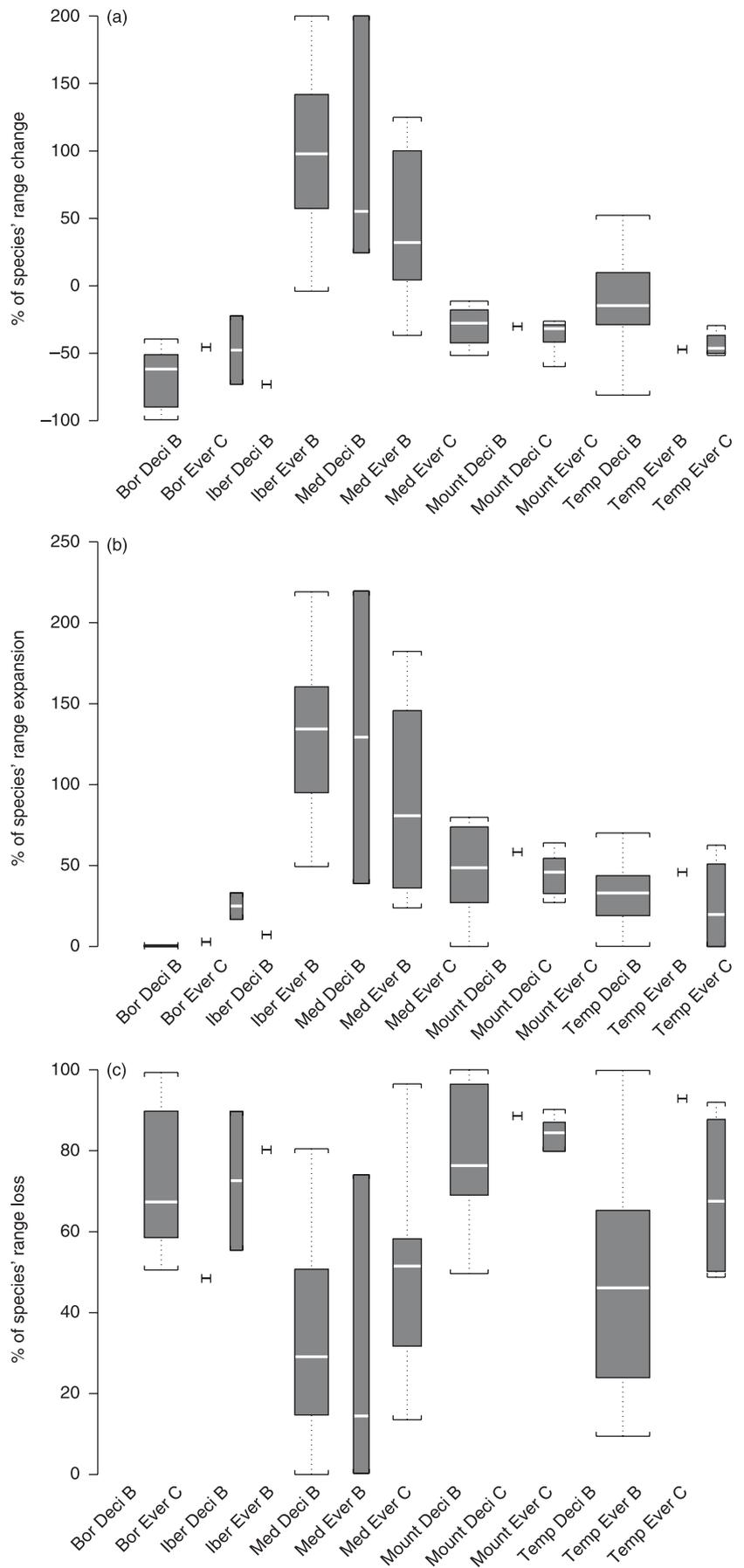


Figure 1 Predicted percentage of tree species' range change (a), expansion (b) and loss (c) by functional types and phytogeographical classes. Abbreviations: Bor, Boreal; Iber, Iberian (Spain and Portugal); Med, Mediterranean; Mount, Mountainous; Temp, temperate. Deci and Ever mean deciduous and evergreen, respectively. B and C mean broadleaved and coniferous, respectively.

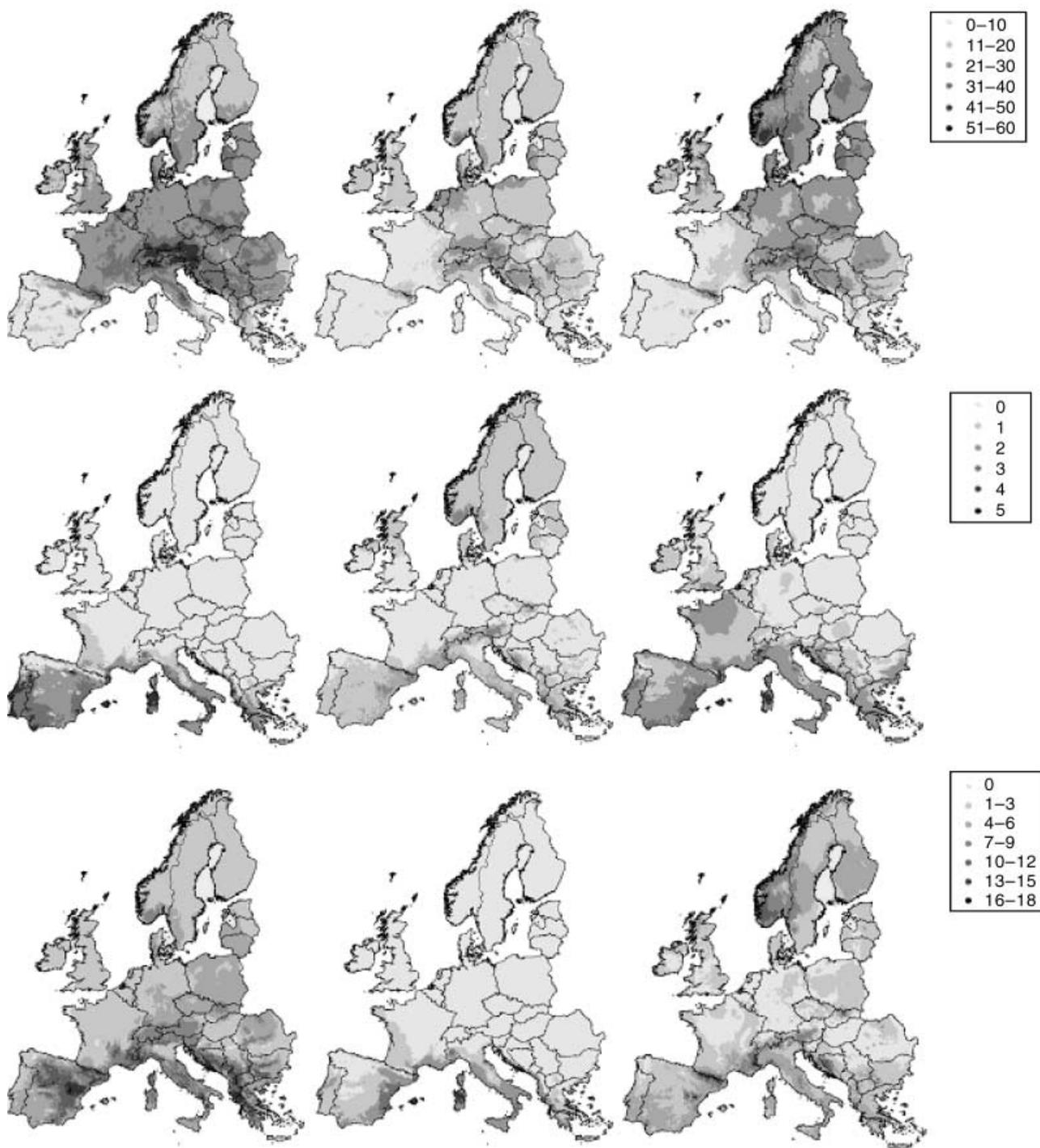


Figure 2 Spatial patterns of current species richness (a), future species richness assuming null migration (b), and future species richness assuming unlimited migration (c) for each functional type. Respectively, broadleaved deciduous (1), broadleaved evergreen (2) and coniferous evergreen (3) trees. The grey scale legend corresponds to the number of species per class.

their limitations (Woodward & Beerling, 1997; Davis *et al.*, 1998; Hampe, 2004; Svenning & Skov, 2004; Guisan & Thuiller, 2005) and the underlying methodological uncertainties (Thuiller, 2004; Araújo *et al.*, 2005b). Nevertheless, one of the major weaknesses of current niche-based models is that they cannot take into account the migration process of species as they track environ-

mental change. Although palaeological records and simulations for the Quaternary have suggested a range of migration rates up to 1000 m year⁻¹ (Cain *et al.*, 1998; Clark, 1998), it is difficult to estimate the migration process for each simulated species (Higgins *et al.*, 2003). Furthermore, without simulations of both the current highly fragmented landscape within Europe and the possible

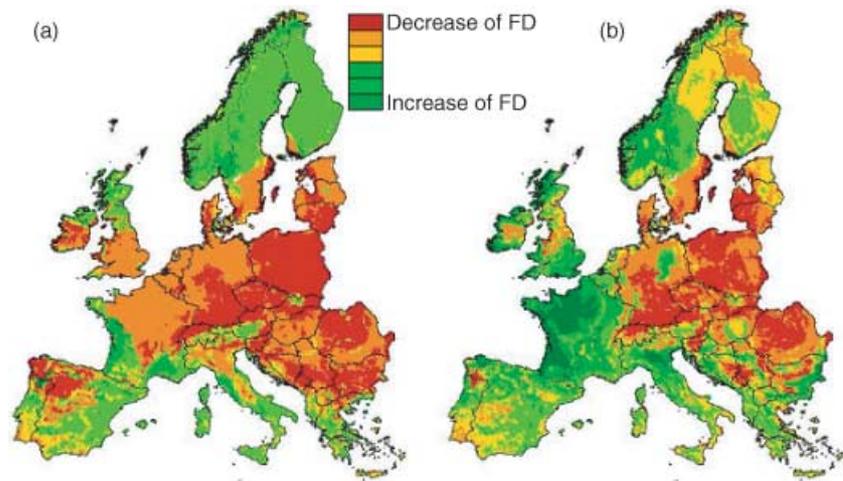


Figure 3 Variability in tree functional diversity under null (a) and unlimited (b) migration assumptions. FD means functional diversity.

future changes in land use, time lags are unknown. In this paper, therefore, we contrasted two simple assumptions, no dispersal beyond a species present site, as opposed to unlimited dispersal to all sites (Peterson *et al.*, 2002; Thuiller *et al.*, 2005b). Reality for species lies within these boundaries.

In this study, we deliberately focused only on functional and structural aspects of impacts of climate change using broadly defined tree functional types. Functional diversity, the extent of functional differences among the species in a community (Tilman, 2001), is an important determinant of ecosystem processes. There is an ongoing debate on how to estimate functional diversity. A common measure of functional diversity is the number of functional groups represented by the species in a community (Hooper, 1998; Tilman, 2001). Of the problems associated with assigning species to groups (Lavorel *et al.*, 1997), perhaps the least tractable is the arbitrary scale at which differences between species qualify as functionally significant (Simberloff & Dayan, 1991). There is no simple, satisfactory or standardized measure of functional diversity (Díaz & Cabido, 2001). Recently, some new measures of functional diversity have been proposed based on functional distances among taxa (Petchey & Gaston, 2002), similar to methods used to estimate phylogenetic diversity (Faith, 2004; but see Clarke & Warwick, 1999). Further analyses would thus be required for using such estimates. Instead, we used Simpson's diversity index, which combines a measure of the number of functional types in one pixel and a measure of evenness (Magurran, 1988).

Impact of climate change on functional diversity

Climate is one major driver of species, biomes and functional type distributions (Woodward, 1987). In this study, we apply this premise to assess the potential impact of climate change on tree functional diversity. The major objective of our analyses was then to assess how species range shifts and variation in species richness could produce changes in functional assemblages. Our results clearly show that is a likely outcome.

Based on phytogeographical classes, we showed that boreal broadleaved deciduous and coniferous species are likely to

undergo large range reductions (no migration hypothesis) and remain unlikely to find new suitable habitats (unlimited migration hypothesis). Potential replacements may be by temperate broadleaved deciduous and temperate coniferous species. Such changes are unlikely to produce strong functional changes if they largely represent a replacement by species belonging to different phytogeographical class but within the same functional types that are already present. We, however, predicted an increase of functional diversity in these areas, resulting from an increased evenness of the tree communities. These changes in functional richness and diversity could then have significant structural and functional effects on ecosystems (Cramer *et al.*, 1999). For example, the timing and frequency of phenological events such as leafing out or leaf fall influence the distribution of light both in the forest canopy and on the forest floor, thereby directly affecting ecosystem functioning (Martens *et al.*, 2000). Soil carbon content and thus soil biogeochemistry depend on litter type and different timings for litter fall (Gill & Burke, 1999). The observed increase in the share of deciduous species could also strongly modify ecosystems and especially their microclimate and surface properties (Chapin III *et al.*, 2000). For instance, the albedo of the vegetation soil surface determines the proportion of incoming radiation that is absorbed, which in turn influences the quantity of heat that reaches the ground and the energy available to drive water loss from the ecosystem through transpiration and soil evapotranspiration. Forests dominated by conifers have a lower albedo (i.e. reflecting less energy back to the atmosphere) than do deciduous-dominated forests because the low albedo of coniferous canopies and clumped distribution of leaves cause much of the reflected radiation in these forests to be absorbed by other leaves rather than being reflected directly back to space (Chapin III, 2003). Finally, fire regimes, forest productivity and thus carbon storage are often species-dependent and may be modified by changes in species and/or functional composition (Johnstone & Chapin III, 2003). Changes in the ratio between coniferous and deciduous trees could influence the probability or severity of fires. Boreal conifers are more flammable than deciduous trees because of their large leaf and twig surface area, low moisture content and high resin content

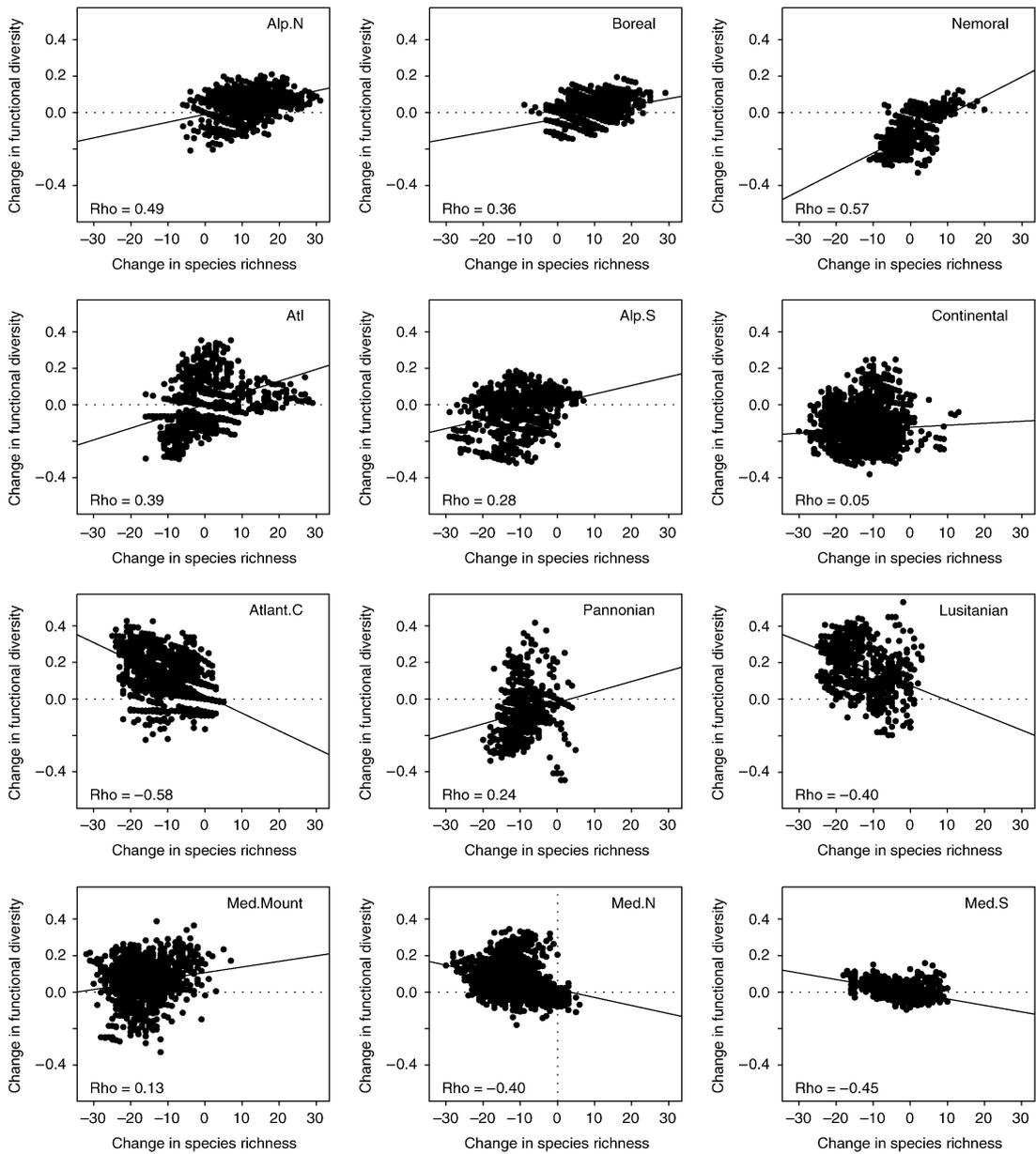


Figure 4 Relationship between potential future change in tree species ‘richness’ change in tree functional diversity (change in Simpson’s diversity index) for the different biogeographical regions analysed. Rho values represent Spearman rank correlations, which are all significant ($P < 0.05$).

(Johnson, 1992). Similar effects have been documented during the invasion of boreal forests in Alaska by black spruce in the middle Holocene, which caused an increase in fire frequency (Lynch *et al.*, 2003). Conversely, dynamic models predict an increase in deciduous species and concurrent changes in fire regimes for these regions under scenarios of climate change (Rupp *et al.*, 2000).

In the southern part of temperate Europe, we predicted a replacement of temperate deciduous broadleaved species by Mediterranean trees (all functional types). These resulted in an increase in functional diversity, producing communities more functionally mixed. Greater phenological diversity may lead to a longer period of annual functioning and therefore greater stocks

in carbon. The ranges of temperate tree species can often be related to the length of the growing season (GDD5) and especially to absolute minimum temperature (Woodward, 1987). In particular, the limit where broadleaved evergreen species are replaced by deciduous species is mostly climatically determined (Woodward, 1987). However, the northern limit of Mediterranean species in Europe appears to be controlled by a combination of growing season length (or cumulated heat) and minimum winter temperature (Woodward, 1987). Climate change is likely to be reflected in these with increasing growing season length and decreasing minimum temperatures. Such changes are likely to lead to the northwards expansion of Mediterranean species,

principally evergreen, but also deciduous, causing range reductions at least at the southern edge of temperate deciduous and coniferous species distributions. Our simulated patterns are confirmed by observations in Europe (Walther *et al.*, 2001). For example, *Ilex aquifolium* (holly) has been used as a classical example of a climate-limited distribution (Larcher, 2003). A synchronized shift in both its distribution and climate was observed in southern Scandinavia (Walther *et al.*, 2005), confirming the relevance of climatic envelopes to model and predict the distribution of temperate trees. Walther *et al.* (2001) also noted the capacity of other climate-sensitive transition zones to respond to changes in environmental conditions and observed that in Switzerland, Japan and Georgia, indigenous and exotic evergreen broadleaved species are already expanding their ranges into deciduous forests habitats. This replacement of deciduous by evergreen broadleaved trees could have significant functional impacts such as a reduction of cycling for biogeochemistry and especially of decomposition and nitrogen mineralization. Litter from species typical of productive environments (e.g. deciduous trees) typically decomposes more rapidly than that species from less productive environments (e.g. evergreen trees) (Cornelissen, 1996).

The possible increase of shrubs in Mediterranean and Lusitanian regions as a result of the regression by broadleaved deciduous trees could increase the evenness and have profound impacts on the landscape pattern and the disturbance regimes. For instance, shrub-dominated landscapes are more prone to invasion by grasses or herbs than forests, which could produce strong fire regime changes (Grigulis *et al.*, 2005).

Unfortunately, the static nature of our modelling, as well as the scale and resolution considered, does not allow us to derive more detailed conclusions about the effect of climate change on ecosystem processes. Even if the link between plant traits and ecosystems is now well recognized (Chapin III, 2003), the lack of information about abundance of each species in a pixel precludes the projection of community structure, and thereby the possibility to link trait values with ecosystem function (Garnier *et al.*, 2004).

ACKNOWLEDGEMENTS

This research was funded by the European Commission's FP5 ATEAM (Advanced Terrestrial Ecosystem Analysis and Modelling, EVK2-CT-2000-00075) and FP6 ALARM (Assessing LArge-scale environmental Risks with tested Methods, GOCE-CT-2003-506675) integrated projects. MBA thanks T. Lahti and R. Lampinen for providing a digital version of *Atlas Florae Europaeae*. We thank T.D. Mitchell of the Tyndall Centre for Climate Change Research for providing climate and scenario data, and S. Zaehle and M. Erhard at the Potsdam Institute for Climate Impact Research for aggregating climate data.

REFERENCES

- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005a) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Whittaker, R.J., Ladle, L. & Erhard, M. (2005b) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.
- Bachelet, D., Neilson, R.P., Hickler, T., Drapek, R.J., Lenihan, J.M., Sykes, M.T., Smith, B., Sitch, S. & Thonicke, K. (2003) Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemical Cycles*, **17**, 14.11–14.21.
- Berry, S.L. & Roderick, M.L. (2004) Gross primary productivity and transpiration flux of the Australian vegetation from 1788 to 1988 AD: effects of CO₂ and land use change. *Global Change Biology*, **10**, 1884–1898.
- Bolòs, O.D., Vigo, J., Masalles, R.M. & Ninot, J.M. (1990) *Flora manual dels Països Catalans*. Pòrtic, Barcelona.
- Broekmeyer, M.E.A. & Vos, W. (1993) European Forest Reserves. *Forest reserves in Europe: a review* (ed. by M.E.A. Broekmeyer, W. Vos and H. Koop), Pudoc Scientific Publishers, Wageningen, the Netherlands.
- Cain, M.L., Damman, H. & Muir, A. (1998) Seed dispersal and the Holocene migration of woodlands in southern Sweden. *Ecological Monographs*, **68**, 325–347.
- Chapin III, F.S. (2003) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany*, **91**, 455–463.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.
- Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, **152**, 204–224.
- Clarke, K.R. & Warwick, R.M. (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series*, **184**, 21–29.
- Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, **20**, 37–46.
- Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, **84**, 573–582.
- Cowling, S.A. & Sykes, M.T. (1999) Physiological significance of low atmospheric CO₂ for plant-climate interactions. *Quaternary Research*, **52**, 237–242.
- 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 CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Cramer, W., Shugart, H.H., Noble, I.R., Woodward, F.I., Bugmann, H., Bondeau, A., Foley, J.A., Gardner, R.H., Lauenroth, B., Pitelka, L.F., Sala, O.E. & Sutherst, R.W. (1999) The terrestrial biosphere and global change: implications for natural and managed ecosystems. *Ecosystem composition and structure* (ed.

- by B.H. Walker, W.L. Steffen, J. Canadell and J.S.I. Ingram), pp. 190–228. Cambridge University Press, Cambridge.
- Daly, C., Bachelet, D., Lenihan, J.M., Neilson, R.P., Parton, W. & Ojima, D. (2000) Dynamic simulation of tree–grass interactions for global change studies. *Ecological Applications*, **10**, 449–469.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.
- Faith, D.P. (2004) Quantifying biodiversity: a phylogenetic perspective. *Conservation Biology*, **16**, 248–252.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Gill, R.A. & Burke, I.C. (1999) Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia*, **121**, 551–563.
- Grigulis, K., Lavorel, S., Davies, I.D., Dossantos, A., Lloret, F. & Vila, M. (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands. *Global Change Biology*, **11**, 1042–1053.
- Gritti, E., Smith, B. & Sykes, M.T. (2005) Vulnerability of Mediterranean basin ecosystems to climate change and invasion by exotic plant species. *J. Biogeography*. In press.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hampe, A. (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–476.
- Higgins, S.I., Lavorel, S. & Tackenberg, O. (2003) Climate change and biodiversity: synergistic impacts. *Plant dispersal and habitat loss synergies* (ed. by L. Hannah and T.E. Lovejoy), Yale University Press, New Haven.
- Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, **85**, 282–294.
- Hooper, D.U. (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology*, **79**, 704–719.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Huntley, B. (1990) European post-glacial forests: compositional changes in response to climate change. *Journal of Vegetation Science*, **1**, 507–518.
- Huston, M.A. (1994) *Biological diversity*. Cambridge University Press, Cambridge.
- IPCC (2001) *Climate change 2001: Impacts, adaptation, and vulnerability. Contribution of working group II to the third assessment report of the IPCC*. Cambridge University Press, UK and New York.
- Jalas, J. & Suominen, J. (1972–96) *Atlas Florae Europaeae*, The Committee for Mapping the Flora of Europe Societas Biologica Fennica Vanamo, Helsinki, Finland.
- Johnson, E.A. (1992) *Fire and vegetation dynamics studies from the North American boreal forest*. Cambridge University Press, Cambridge.
- Johnstone, J.F. & Chapin III, F.S. (2003) Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology*, **9**, 1401–1409.
- Lahti, T. & Lampinen, R. (1999) From dot maps to bitmaps — Atlas Florae Europaeae goes digital. *Acta Botanica Fennica*, **162**, 5–9.
- Larcher, W. (2003) *Physiological plant ecology*, 4th. Springer, Berlin/Heidelberg.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant trait: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 471–478.
- Loreau, M., Naeem, S., Inchausti, P., Grime, J.P., Hector, A., Hooper, D.U., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.
- Lynch, J.A., Clark, J.S., Bigelow, N.H., Edwards, M.E. & Finney, B.P. (2003) Spatial and temporal variations in fire history in boreal ecosystems of Alaska. *Journal of Geophysical Research*, **10**, D24.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- Martens, S.N., Breshears, D.D. & Meyer, C.W. (2000) Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecological Modelling*, **126**, 79–93.
- Martinez, N.D. (1997) Biodiversity: a biology of numbers and difference. *Defining and measuring functional aspects of biodiversity* (ed. by K.J. Gaston), pp. 114–148. Blackwell Science, Oxford.
- 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. Tyndall Centre, Norwich, UK.
- Mooney, H.A. (1996) Plant functional types: their relevance to ecosystem properties and global change. *Ecosystem function of biodiversity*. (ed. by T.M. Smith, H.H. Shugart and F.I. Woodward), pp. 341–354. Cambridge University Press, Cambridge.

- Nemani, R. & Running, S.W. (1996) Implementation of a hierarchical global vegetation classification in ecosystem function models. *Journal of Vegetation Science*, **7**, 337–346.
- 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.
- Peat, H. & Fitter, A. (2002) *The ecological Flora of the British Isles*.
- Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.
- 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.
- Peterson, A.T., Tian, H.Q., Martínez-Meyer, E., Soberón, J. & Sánchez-Cordero, V. (2005) Biodiversity and climate change. *Modeling distributional shifts of individual species and biomes* (ed. by T.E. Lovejoy and L. Hannah), Yale University Press, New Haven.
- Rosenfeld, J.C. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- Rupp, T.S., Chapin III, S.F. & Starfield, A.M. (2000) Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Change Biology*, **6**, 541–555.
- Sala, O.E., Chapin III, S.F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, 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.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W. *et al.* (2005) Ecosystem service supply and human vulnerability to global change in Europe. *Science*, DOI: 10.1126/science.1115233. In press.
- Simberloff, D. & Dayan, T. (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*, **22**, 115–143.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Global Change Biology*, **9**, 161–185.
- Svenning, J.-C. & Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565–573.
- Swets, K.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- 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.
- Tateno, M. & Chapin III, F.S. (1997) The logic of carbon and nitrogen interactions in terrestrial ecosystems. *American Naturalist*, **149**, 723–744.
- 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., Araújo, M.B., Pearson, R.G., Whittaker, R.J., Brotons, L. & Lavorel, S. (2004b) Uncertainty in predictions of extinction risk. *Nature*, **430**, 34.
- Thuiller, W., Brotons, L., Araújo, M.B. & Lavorel, S. (2004c) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **27**, 165–172.
- Thuiller, W., Lavorel, S. & Araújo, M.B. (2005a) Niche properties and geographic extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005b) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences, USA*, **102**, 8245–8250.
- Tilman, D. (2001) Functional diversity. *Encyclopedia of Biodiversity* (ed. by S.A. Levin), pp. 109–120. Academic Press, San Diego, CA.
- Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 467–473.
- 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. (1964–93) *Flora Europaea*. Cambridge University Press, Cambridge.
- Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.
- Walther, G.-R., Berger, S. & Sykes, M.T. (2005) An ecological 'footprint' of climate change. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **272**, 1427–1432.
- Walther, G.-R., Carraro, G. & Klötzli, K. (2001) Fingerprints of climate change — adapted behaviour and shifting species ranges. *Evergreen broad-leaved species as indicators for climate change* (ed. by G.-R. Walther, C.A. Burga and P.J. Edwards). Kluwer Academic/Plenum Publishers, New York.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Gudberg, O. &

- Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Webb, T.I. (1992) Global warming and biological diversity. *Past changes in vegetation and climate: lessons for the future* (ed. by R.L. Peters and T.E. Lovejoy). Yale University, New Haven and London.
- 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.
- Wilsey, B.J., Chalcraft, D.R., Bowles, C.M. & Willig, M.R. (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology*, **86**, 1178–1184.
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.
- Woodward, F.I. & Beerling, D.J. (1997) The dynamics of vegetation change: health warnings for equilibrium ‘dodo’ models. *Global Ecology and Biogeography Letters*, **6**, 413–418.
- Woodward, F.I. & Lomas, M.R. (2004) Vegetation dynamics — simulating responses to climatic change. *Biological Reviews*, **79**, 643–670.
- Woodward, F.I., Lomas, M.R. & Betts, R.A. (1998) Vegetation–climate feedbacks in a greenhouse world. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **353**, 29–38.