

LETTER

Prediction uncertainty of environmental change effects on temperate European biodiversity

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Abstract

Observed patterns of species richness at landscape scale (gamma diversity) cannot always be attributed to a specific set of explanatory variables, but rather different alternative explanatory statistical models of similar quality may exist. Therefore predictions of the effects of environmental change (such as in climate or land cover) on biodiversity may differ considerably, depending on the chosen set of explanatory variables. Here we use multimodel prediction to evaluate effects of climate, land-use intensity and landscape structure on species richness in each of seven groups of organisms (plants, birds, spiders, wild bees, ground beetles, true bugs and hoverflies) in temperate Europe. We contrast this approach with traditional best-model predictions, which we show, using cross-validation, to have inferior prediction accuracy. Multimodel inference changed the importance of some environmental variables in comparison with the best model, and accordingly gave deviating predictions for environmental change effects. Overall, prediction uncertainty for the multimodel approach was only slightly higher than that of the best model, and absolute changes in predicted species richness were also comparable. Richness predictions varied generally more for the impact of climate change than for land-use change at the coarse scale of our study. Overall, our study indicates that the uncertainty introduced to environmental change predictions through uncertainty in model selection both qualitatively and quantitatively affects species richness projections.

Keywords

Biodiversity, climate change, environmental change, multimodel inference, projection, species richness, uncertainty analysis.

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INTRODUCTION

Understanding the causes and drivers of species diversity is of immediate importance for land-use management policy (e.g. Atkinson *et al.* 2005). To preserve biodiversity, we need to be as certain as possible about which management practices are likely to affect it, and which will likely not. There are obvious answers at the local scale, in that for example draining swamps or heavily applying pesticides to crops will reduce species richness. At a larger spatial scale, i.e. at several square kilometres, local effects are aggregated (Eggleton *et al.* 2005). In which way, is unclear: Is a mosaic of land uses best for biodiversity? Do we need certain minimum area to maintain a desired level of species richness? Can corridors of semi-natural habitat ensure the viability of population in small patches in otherwise fragmented landscapes? Answers to these questions are of high relevance for conservation strategies and landscape planning. However, as data on species richness across large geographical transects for different species groups are rare, there may be a risk of over-interpreting the results.

The traditional approach to predicting the effects of environmental change on species diversity is to analyse the present situation and find the best statistical model, usually according to information theoretical criteria, as a basis for extrapolation to future change scenarios (Burnham & Anderson 2002). Several factors may, however, make the identification of a single best model impractical (Chatfield 1995): (i) collinearity amongst explanatory variables; (ii) sample size constraints on model complexity; (iii) ill-posed nature of the problem, i.e. lack of uniqueness of a solution (also known as 'equifinality'). These problems led to the recent re-embracement (Chatfield 1995; Hilborn & Mangel 1997) of the multiple working hypotheses-idea of Chamberlain (1897). Additionally, relying on one model to capture the ecological reality will almost certainly be inappropriate (Chatfield 1995; Burnham & Anderson 2002; Thuiller 2004; Araujo *et al.* 2005; Link & Barker 2006). In consequence, both inference (Link & Barker 2006) and prediction (Araújo & New 2007) should ideally be based on multiple models (Wintle *et al.* 2003). While on the positive side multimodel analysis leads to a better representation of the problem, its interpretation is more difficult and predictions will often show larger uncertainty. Furthermore, multimodel analyses are 'deep waters, mathematically, and no consensus has emerged in the substantial literature on a single approach' (Link & Barker 2006, p.2630).

Here, we analyse one of the best multigroup data sets on species richness across temperate Europe, assembled as part of the EU project GREENVEINS (Billetter *et al.* 2008), with particular emphasis on alternative explanations, uncertainty and management implications. To analyse a wide range of landscape structures and land-use intensities, species diver-

sity data were collected in seven different countries, also covering different soils and climate. In our analysis we assembled several alternative explanatory models for seven groups of organisms (plants, birds, spiders, wild bees, ground beetles, true bugs and hoverflies), models which cannot be differentiated on statistical grounds, but with potentially fundamentally different local management consequence. Our intention here is to contrast inference of biodiversity pattern based on 'the single-best model approach' and a multiple-model analysis (see also Wintle *et al.* 2003). Moreover, we use model averaging for predicting species diversity for future climate, land-use intensity and landscape structure scenarios, and quantify the uncertainty of predictions because of alternative explanations for species diversity pattern.

MATERIALS AND METHODS

Data

The basis of the present analysis is the species richness data from the EU project GREENVEINS (Bugter *et al.* 2001). These data are unique in several respects, most importantly because they comprise seven groups of organisms and because land-use intensity and landscape structure data are available for each site. The methods are described in detail in Schweiger *et al.* (2005) and Dormann *et al.* (2007). Along a pan-European transect from France through Belgium, the Netherlands, Germany, Switzerland, Czech Republic to Estonia, species richness within 25 sites of 16 km² each were assessed using a common protocol in 2001 and 2002. Vascular plants were recorded in 85–300 relevés in each site; birds were recorded in 20 points per site; arthropods (wild bees: Apoidea, true bugs: Heteroptera, spiders: Araneae, ground beetles: Carabidae, hoverflies: Syrphidae) were collected in 16 duplicated sets of flight and pitfall traps in each site in a stratified sampling design. Using individual-based species-accumulation curves (Coleman *et al.* 1982) we re-calculated species richness for each site to correct for the large differences in the number of trapped individuals per site (Gotelli & Colwell 2001).

Landscape structure metrics were computed for digital vector maps based on ortho-rectified aerial photographs and ground-validated habitat classification (Bailey *et al.* 2007). Land-use intensity (i.e. fertilizer and pesticide application frequency, stocking densities, numbers of crop in rotation) was assessed by questionnaire-based interviews with local farmers (Herzog *et al.* 2006). Soil variables were extracted from the FAO/UNESCO world soil map (FAO/UNESCO 2003). Climate data are based on Willmott *et al.* (2004). To reduce the number of explanatory variables, we combined different land-use types to arable, woody, herbaceous and other. Woody and herbaceous were again summed to

semi-natural habitat. To quantify landscape structure (McGarigal *et al.* 2002), we used a measure of habitat integrity (log-transformed proximity index). Temperature and precipitation data for the months December to February were aggregated as winter, March to May as spring and so on.

Statistical analysis

First, we reduced the number of explanatory variables from an initial 33 to a remaining 19 based on cluster analysis (Harrell 2001; based on Spearman's rank correlation cutoff of $\rho^2 = 0.4$), using expert consensus on which variables to retain. Within this reduced set of variables, inter-correlations were still apparent (Table S1).

Next, we decided on a minimum number of 18 residual degrees of freedom for our analysis, thereby restricting the model complexity to five terms plus intercept. We constructed all possible combinations of the 19 variables, including quadratic effects and first-order interactions, of fewer than six terms (see Whittingham *et al.* 2007 for a similar analysis). Because our response variables (SAC-corrected species richness for each group) had normally distributed residuals, we used multiple linear regression to estimate model parameters. We ranked models based on these combinations by their Bayesian Information Criterion (Burnham & Anderson 2002; Wintle *et al.* 2003). The best model represents the outcome of a traditional one-model analysis.

Finally, we calculated the Bayesian Information Criterion (BIC) weight w_i for each model i , defined as

$$w_i = \frac{\exp(-\text{BIC}_i/2)\pi_i}{\sum_j \exp(-\text{BIC}_j/2)\pi_j}$$

where the priors π are taken to be identical (Link & Barker 2006). The importance of an environmental variable in a

model (expressed as partial R^2) was multiplied by the BIC-weight and summed over the best 100 models (multimodel inference). This weighted mean importance follows the same logic as in the model averaging: the better the model (larger BIC-weight), the more reliable is its information on the importance of its variables.

The predicted mean species richness was calculated as $\mathbf{y}_b = \mathbf{X}_b \mathbf{b}$, where \mathbf{b} is the parameter vector from the multiple regression of \mathbf{y}_{obs} on \mathbf{X} , and \mathbf{X}_b are the environmental variable values for the validation data or scenarios, respectively. To quantify uncertainty in model forecasts, we used the following formula to calculate standard deviation of the forecast, s_b^2 (Neter *et al.* 1993, p. 235):

$$s_b^2 = \text{MSE} \left(\frac{1}{k} + \mathbf{x}_b^T (\mathbf{X}^T \mathbf{X})^{-1} \mathbf{x}_b \right)$$

where MSE is mean residual sum of squares for a model and k is the number of parameters in the model. Based on this formula the probability density function (PDF) of predicted species richness for the single-best and for each of the best 100 models are defined as normal distributions with mean y_b and standard deviation s_b . PDF from the 100 best models were combined using multimodel forecasting (Link & Barker 2006). Here, the multimodel PDF is the weighted sum of the 100 normal distributions, where the weights are the BIC-weights.

The above analysis yields PDF for species richness. We repeated the analysis twice, once as a sixfold cross-validation to assess prediction error (fitted on five-sixth of the data set, validated on one-sixth), and then on the full data set to derive the PDF to be used in the scenario predictions (defined below). In the cross-validation, PDF-derived probabilities of the observed hold-out sample p_i were converted into deviance ($= -2 \sum_{i=1}^n \log p_i$ where n is the number of hold-out cases) and averaged over the six cross-validations: the lower the deviance, the higher the prediction accuracy.

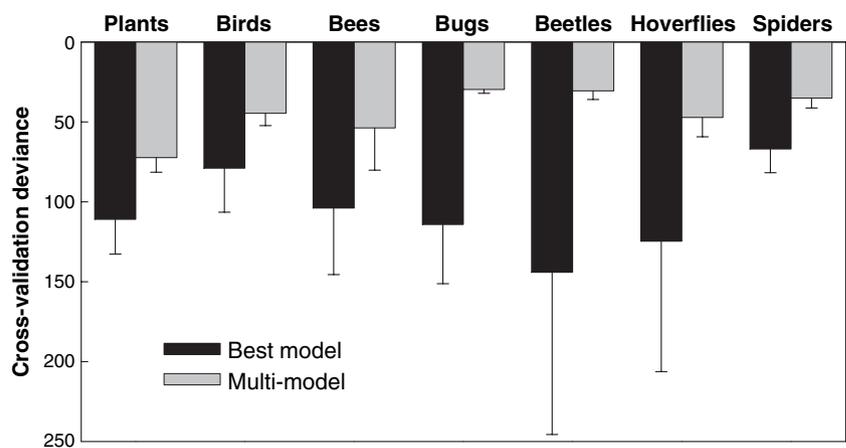


Figure 1 Prediction accuracy of the single-best and the multimodel approach based on sixfold cross-validation (mean \pm 1 SE). Lower deviance values indicate better agreement between model prediction and observation on hold-out samples.

For the scenario predictions, we fitted models on the full data set and calculated PDF for the respective scenario. All analyses were implemented in the software package R (R Development Core Team 2005), with the additional packages *gtools* and *vegan*.

Environmental change scenarios

To illustrate the consequences of differences between models, we subjected them to three example scenarios. In temperate Europe land use is likely to change severely in the decades to come, mainly because of Common Agricultural Policy of the EU (European Commission Directorate-General for Agriculture 2003). At the same time, climate change is predicted to affect precipitation and temperature pattern across Europe (IPCC 1998). While there may be interactions between land use and climate, we consider them as independent scenarios for illustration purposes.

Our present-day reference is the measured species richness for mean environmental conditions. For the climate change scenario, precipitation and temperatures in summer and autumn were increased by 10%, while they were decreased by the same amount in winter and spring. This is not to reflect a specific scenario for temperate Europe, but the tendency predicted by the IPCC (1998). In the land-use intensity change scenario, climate, soil properties and landscape structure were left constant, but nitrogen fertiliser input increased by 50% and pesticide load by 25% (following Busch 2006). To construct a landscape structure scenario, we followed the trend forecasted by Rounsevell *et al.* (2006), with the percentage of arable land decreasing by 6% and that of forested land and semi-natural habitats increasing by 3% until 2050. The proximity index of the different habitats was adjusted according to the correlation between percentage semi-natural habitat and proximity index in the data set. A 3% increase for example in woodland leads to a $3\% \times 0.6 = 2.4\%$ increase in proximity of woodland habitats (0.6 being the slope estimate between percentage and proximity of woodland). Increasing the amount of forest and semi-natural habitats while reducing farming area is a trend derived from the EU's Common Agricultural Policy (European Commission Directorate-General for Agriculture 2003), contrasting with true long-term trends (Strijker 2005).

RESULTS

Prediction accuracy and model weights

The single-best model-approach has consistently lower prediction accuracy than the multimodel approach (Fig. 1). Across all seven species groups, deviance in the single-best model was over twice that of the multimodel approach,

while cross-validation variability (in terms of standard errors) was over five times higher.

BIC-weights for the different models (Fig. 2) give evidence that in several groups the best two or three models have similar fits. This means that alternative explanations for the observed data exist, which are captured in the multimodel approach. While the single-best model may be either correct or misleading, the multimodel prediction encompasses many alternatives, outbalances wrong predictions, and yields lower cross-validation prediction errors.

Drivers of species richness across temperate Europe

Variance in species richness was explained by the different sets of environmental variables to differing degrees for the different taxa. Species richness analyses for wild bees and true bugs yielded excellent model fits (bees: mean adjusted $R^2 = 0.88$, multimodel range 0.80–0.89; bugs: mean = 0.75, range 0.69–0.81). All other groups had good to moderate R^2 -values (vascular plants: mean = 0.58, range 0.51–0.63; birds: mean = 0.60, range 0.52–0.63; spiders: mean = 0.61, range 0.49–0.70; ground beetles: mean 0.60, range 0.52–0.67; hoverflies: mean 0.52, range 0.44–0.67).

Climate, landscape structure, land use and soil properties were of very different importance for the seven groups of organisms, but general trends emerged (Table 1). Across all groups, climate was most important (accounting for 36%

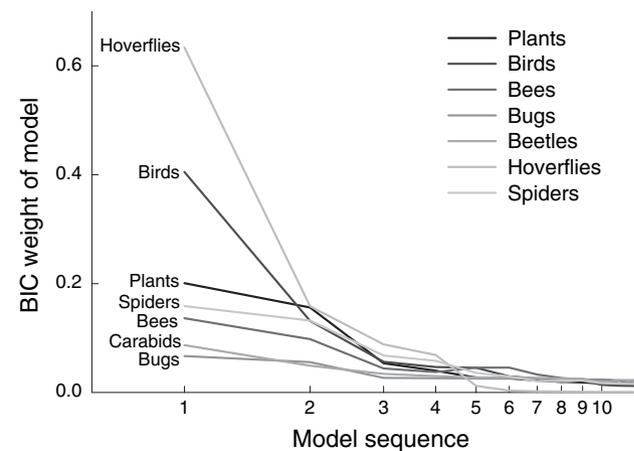


Figure 2 Weights given to the best models (based on Bayesian Information Criterion, BIC). Only the first 12 models of all 100 models used for the ensemble forecast are shown, because from model eight onwards the weights are lower than 0.01 (i.e. 1%). Plants, ground beetles and bugs spread the main weight over four to five models, while for spiders, birds, bees and hoverflies the first (and second) model carry most of the weight. Compare Fig. 4 for birds to see that models 2 to 100 can still overrule the dominant model 1.

Table 1 Relative statistical importance (partial R^2) of environmental variable sets for species richness by best model (GLM) and multimodel (MM) approach (total explained variance = 100%)

	Plants		Birds		Wild bees		True bugs		Ground beetles		Hoverflies		Spiders	
	GLM	MM	GLM	MM	GLM	MM	GLM	MM	GLM	MM	GLM	MM	GLM	MM
Climate	29.6	35.6	74.3	72.9	54.7	64.1	13.8	22.0	0.0	4.9	59.2	58.3	5.7	4.6
Soil	19.0	16.0	0.0	0.1	27.8	7.1	9.1	25.9	41.6	40.2	15.1	15.3	34.0	46.5
Landscape structure	21.2	15.2	25.7	26.8	17.6	27.7	77.1	49.3	58.4	53.7	0.0	0.0	0.0	6.4
Land-use intensity	30.2	33.1	0.0	0.2	0.0	1.2	0.0	2.9	0.0	1.2	25.8	26.4	60.4	42.6

Figures in bold highlight pronounced differences in relative importance of particular variable sets.

of variation in species richness), followed by landscape structure (27%), soil properties (21%) and land-use intensity (16%). The importance of environmental variables from each group of predictors inferred by the single-best model was generally similar to that inferred by the multimodel approach for most groups. Explained variance for wild bees, true bugs and spiders, however, differed notably (i.e. to over 10%) between the best and the multimodel approach (Table 1). Wild bees were far less sensitive to soil properties as the best model would have made believe, while the opposite was true for true bugs. While spider species richness was primarily driven by land-use intensity according to the best model, soil properties won over in multimodel inference.

More important than changes in the balance of importance is the fact that the best model often cannot incorporate variables from each group of variables, while the multimodel approach can. BIC weights were spread more evenly for bugs, carabids, bees, spiders and plants than for birds and hoverflies (Fig. 2). This implies that in the bird and hoverfly analysis the difference in inference between the best and the best 100 models should be smallest, as is indeed the case (Table 1). Because of multimodel projections, climate entered the predicting model for carabids, soil properties for birds, landscape structure for spiders and land-use intensity for bees, bugs and beetles (Table 1). Hence, predictions for single- and multimodel approaches can be expected to differ most for these combinations.

Multimodel projections of the effects of climate, land-use intensity and landscape structure change on species richness

Across all predictions and all groups, change in species richness was usually low to moderate (Fig. 3). For most groups, environmental change predicted increased species richness, although clearly the level of uncertainty was large. Wild bee species richness declines at warmer climates, and hoverflies and spiders at increased land-use intensity. The asymmetric probability density functions for bird species

richness under climate change illustrates one of the strengths of multimodel projections. Similar, but less pronounced, asymmetries in PDF can be observed for all groups. Asymmetric, and its extreme multimodal, PDF indicate that there are alternative statistical models explaining the data, which differ fundamentally in their predictions of environmental change. For future diversity pattern this means greater prediction uncertainty, because the data do not allow to sufficiently accurately pin-point the most likely drivers of today's species richness.

Surprisingly – and also reassuringly, as virtually all previous analyses of diversity used the best model approach – single-best model and multimodel projections were rather similar (Fig. 4). Prediction error was slightly larger for the multimodel predictions, and as expected from changes in importance (Table 1), sometimes only the multimodel approach predicted changes at all (e.g. increase of bee and bug species richness under intensified land use).

DISCUSSION

Drivers of species richness

Our analysis indicates that climate and land-use intensity, but also soil variables and landscape structure are determinants of species richness of vascular plants, birds and arthropods along a European transect. Importance of each of these four groups of environmental factors varies considerably between organism groups (Table 1). Incorporating not only climate variables but also soil, landscape structure and land-use intensity variables at this large spatial scale has not been attempted before. Our results lend support to previous studies (Franklin 1998; Seoane *et al.* 2003; Travis 2003; Buckley & Roughgarden 2004; Pearson *et al.* 2004; Stefanescu *et al.* 2004), which indicate that using climate models alone (Berry *et al.* 2002; Pearson & Dawson 2003; Huntley *et al.* 2004; Thomas *et al.* 2004; Thuiller *et al.* 2004; Araújo *et al.* 2005; Luoto *et al.* 2005) might overestimate effects of climate change because other important drivers were omitted.

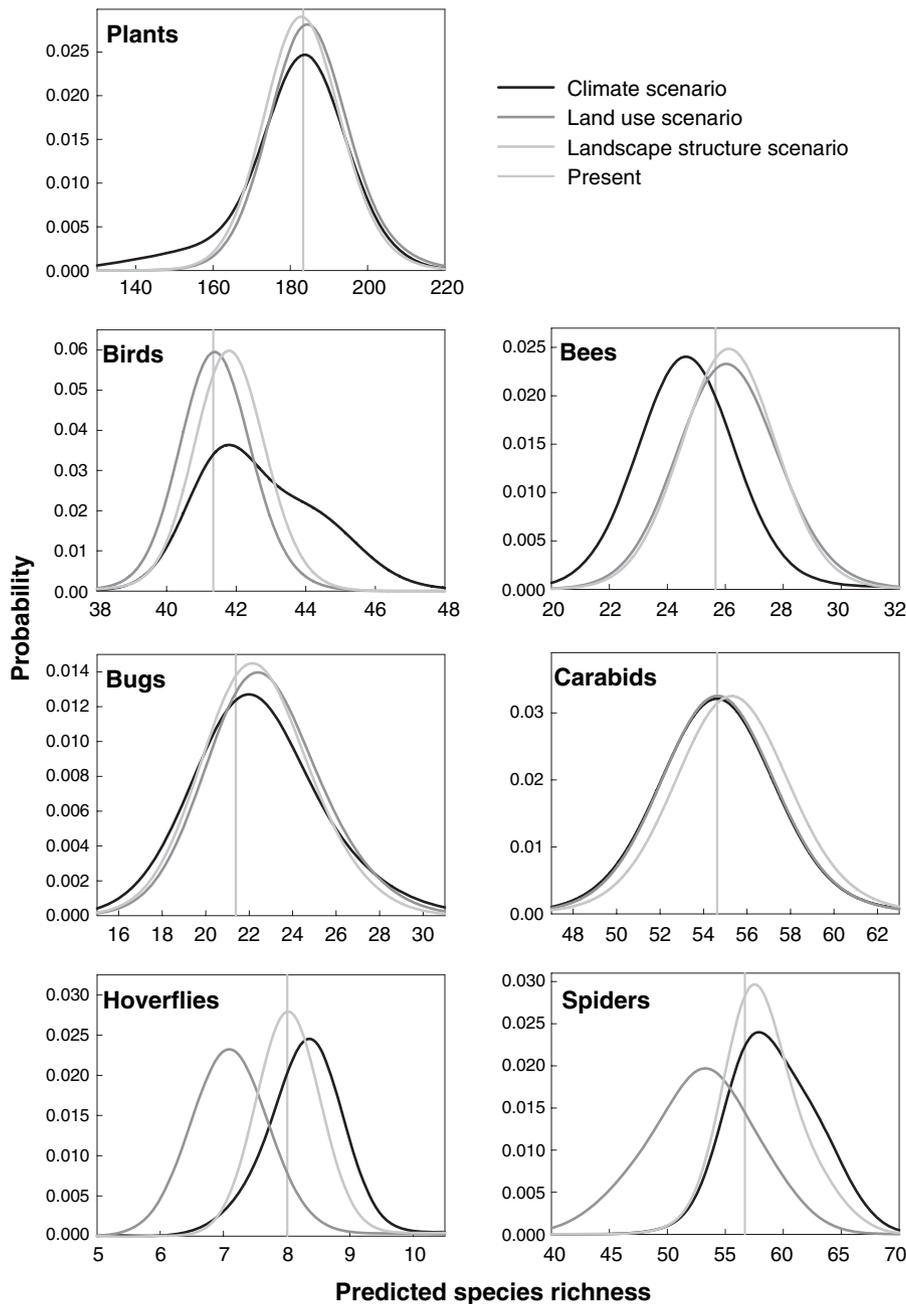


Figure 3 Probability density functions of species richness for scenario predictions based on multimodel predictions. For each organism group, scenarios for changes in climate, land-use intensity and landscape structure are presented. Note different scaling in all panels.

The important role of soil characteristics is not surprising for plants as their sessile and photo-autotrophic life style makes them extremely dependent on substrate structure and composition. A relatively large impact of soil properties might also be quite obvious for ground dwelling organisms such as carabid beetles or spiders, but would be less expected for flying insects such as bugs, bees and hoverflies. In most terrestrial arthropod species at least one develop-

mental stage is bound to the soil (Evans 1984). Larvae as well as imago of ground dwelling carabid beetles and spiders are largely affected by microclimatic conditions that are mediated by soil composition in interaction with climate (Thiele 1977), although there are also direct effects of soil properties on spiders (Schmidt *et al.* 2004) and indirect effects on herbivores through plant quality and defence (Hartley & Jones 1997). Most of the European bee species

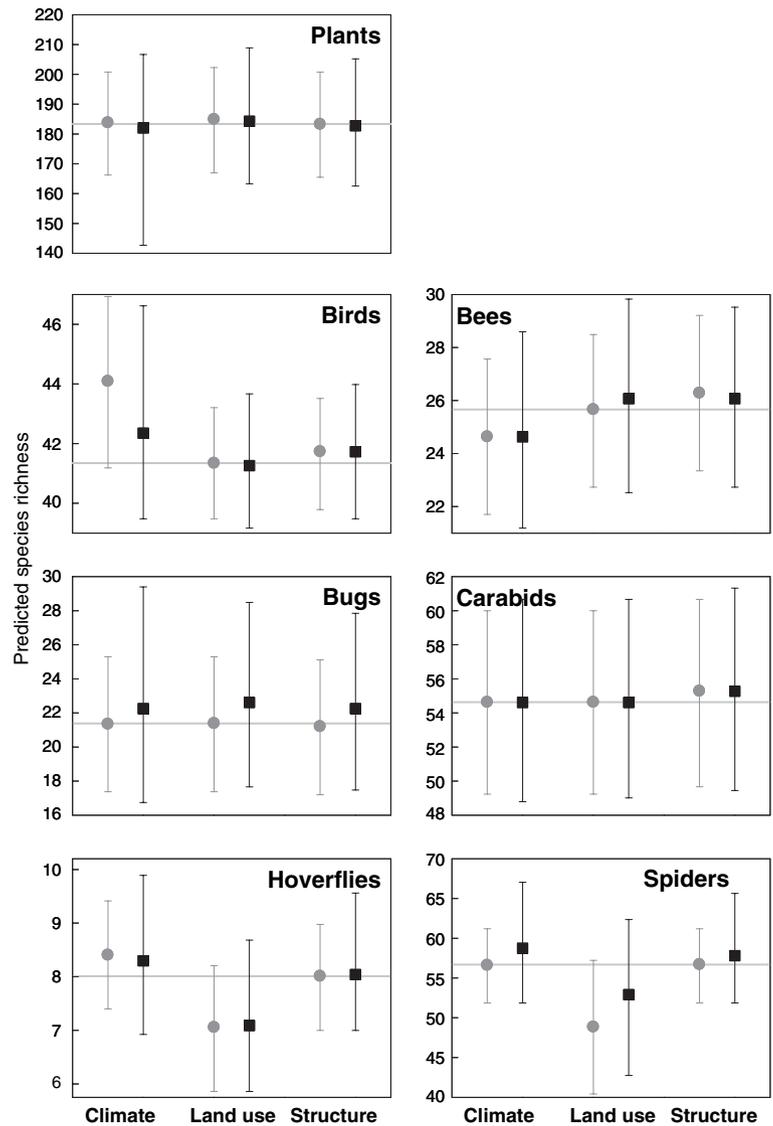


Figure 4 Comparison of species richness predictions based on the single-best model (grey dots) and the multimodel approach (black squares) for climate, land-use and landscape structure scenarios. Error bars are 95% confidence intervals for the three scenarios. The horizontal line indicates present species richness (corrected for sampling effort).

(c. 70%) are soil nesters (Cane 1991; Westrich 1996; Müller *et al.* 1997) and a large proportion of fairly mobile insects such as bugs or hoverflies hibernate in the soil (Evans 1984). Our results indicate that soil properties most likely affect arthropod species richness by acting on morphological (e.g. ease of nest digging affected by soil bulk density) and/or physiological demands (e.g. via pH or soil moisture as an interplay of clay content and precipitation). There was no correlation between plant species richness and richness of any other group, as might have been expected for pollinators (wild bees) or mainly phytophagous insects (such as true bugs). In contrast to plants and insects, diversity of birds was little affected by soil properties and instead was governed by climatic effects, and landscape structure (Kerr & Packer 1997; Hawkins *et al.* 2003).

Relative to climatic factors land-use intensity was important for species richness only in plants, hoverflies and spiders, while birds, bees, bugs and beetles were little affected by land use in European agricultural landscapes (consistent with van Diggelen *et al.* 2005; Kleijn *et al.* 2006). These findings seemingly contradict the common interpretation of the importance in anthropogenic land-use change (see Sala *et al.* 2000). This might be because of co-variation between anthropogenic and natural factors as the latter influence the suitability of landscapes for agricultural (and urban) development (Kühn *et al.* 2004) or to the long history of human agriculture having already exterminated species sensitive to land use. However, climate and soil are factors that are less amenable to planning and management at the local level (but see Bonan 2002; Webb *et al.* 2006, for

examples of how landscape structure effects local climate). Moreover, the significant contribution of landscape structure indicates the relevance of anthropogenic land-use change on species diversity. Thus, in a specific site, particularly one with very little semi-natural habitat, changes in land-use intensity and landscape structure can have a large impact on local species diversity (Schweiger *et al.* 2005). Policy recommendations (e.g. within the Common Agricultural Policy of the European Union Commission of the European Communities 1999) building on the scientific knowledge that set-aside fields, reduced pesticide application, widening of field margins and so forth will lead to higher *local* richness (Tschardt *et al.* 2002), are by no means refuted by our analysis at the much larger, landscape scale.

Prediction uncertainties

Embracing alternative models will often lead to increased prediction uncertainty, leaving conservationists and policy makers with the dilemma of either choosing a potentially misleading model or apparently large uncertainty when evaluating options for landscape-scale management. Nevertheless our analysis indicates that land-use management, and not only climate, affects species richness even at this large spatial scale. Landscape structure and land-use intensity are important correlates of species richness (Table 1). Thus there is potential for mitigating effects of climate change by adaptive management at the local scale.

Predictions of the effect of climate and land-use change on species richness of the investigated seven groups of organisms differ to varying degrees between models. Climate change often (but not always) showed the largest variability in predictions and strongest effects, but also changes in land-use intensity affected species richness (Fig. 3). All these projections are based on a correlative analysis, and hence assume stationarity (i.e. all environment-species richness relationships remain constant), which ignores consequences of species adaptations to changing climate and land use. The uncertainty attached to violations of these assumptions cannot, as yet, be estimated and is hence inevitably ignored (Dormann 2007).

The difference between the single-best and the multi-model approach lies in model selection, while sampling error remains constant: To derive the single best, all next-bests necessarily are discarded. As our comparison shows, this is to the detriment of prediction accuracy. Our conclusion is that selection of the single-best model introduces model selection error, which can be, to some extent, overcome by the multimodel approach. Weighted model averaging (e.g. Hoeting *et al.* 1999; Johnson & Omland 2004) is one option to combine the different predictions of qualitatively different models for species richness. As our results show,

model averaging attaches larger error to environmental change predictions. On the other hand, using multiple models also allows factors to influence predictions that have not been singled out by the best model.

Ideally, we would understand the causal mechanism driving species diversity, as that would allow us to construct a mechanistic model and use that for predictions. However, ecological processes are intrinsically complex (Turchin 2003) and a causal explanation for regional biodiversity pattern will certainly remain elusive for some time. This study shows that while at present our data for some groups are not sufficient to make robust predictions on the effect of environmental change, we can use the multimodel approach to account for model selection uncertainty of environmental change predictions.

In conclusion, our study shows that any prediction of the effects of climate or landscape-scale management on species richness is burdened with potentially high uncertainty. By focussing on the uncertainty arising from the difficulty of identifying one single best model, this study analyses an important aspect of prediction uncertainty. Using multiple alternative models is a promising approach to embrace model building uncertainty and to use it for quantifying prediction uncertainty.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Correlation matrix (Pearson's r) of the 19 environmental variables used in the analysis.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01142.x>.

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