



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Impacts of climate change on Swiss biodiversity: An indicator taxa approach

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ARTICLE INFO

Article history:

Received 5 January 2010

Received in revised form 18 November 2010

Accepted 27 November 2010

Available online 22 December 2010

Keywords:

Boosted regression trees

Indicator

IPCC

Landscape

Species distribution models

Surrogate species

ABSTRACT

We present a new indicator taxa approach to the prediction of climate change effects on biodiversity at the national level in Switzerland. As indicators, we select a set of the most widely distributed species that account for 95% of geographical variation in sampled species richness of birds, butterflies, and vascular plants. Species data come from a national program designed to monitor spatial and temporal trends in species richness. We examine some opportunities and limitations in using these data. We develop ecological niche models for the species as functions of both climate and land cover variables. We project these models to the future using climate predictions that correspond to two IPCC 3rd assessment scenarios for the development of 'greenhouse' gas emissions. We find that models that are calibrated with Swiss national monitoring data perform well in 10-fold cross-validation, but can fail to capture the hot-dry end of environmental gradients that constrain some species distributions. Models for indicator species in all three higher taxa predict that climate change will result in turnover in species composition even where there is little net change in predicted species richness. Indicator species from high elevations lose most areas of suitable climate even under the relatively mild B2 scenario. We project some areas to increase in the number of species for which climate conditions are suitable early in the current century, but these areas become less suitable for a majority of species by the end of the century. Selection of indicator species based on rank prevalence results in a set of models that predict observed species richness better than a similar set of species selected based on high rank of model AUC values. An indicator species approach based on selected species that are relatively common may facilitate the use of national monitoring data for predicting climate change effects on the distribution of biodiversity.

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1. Introduction

Anthropogenic climate warming could result in an average global temperature increase of 4.0 °C by the end of the 21st century (Meehl et al., 2007). A recent global assessment of the impacts of climate change suggests that mountain ecosystems will experience unprecedented rates of warming during the 21st century, two to three times greater than observed during the 20th century (Nogués-Bravo et al., 2006). Mountain ecosystems are likely sensitive to global warming owing to the reduction of terrestrial area with increasing elevation (Guisan et al., 1995; Theurillat et al., 1998; Diaz et al., 2003; Beniston, 2006). Over the last two decades, continuing climate warming has been associated with increases in the northern latitudinal limits of birds in the northern hemisphere (Thomas and Lennon, 1999), changes in animal movement and habitat use (Walther et al., 2002) and advancing flowering phenology (Fitter and Fitter, 2002). Ongoing changes in temperature and other climate parameters at high elevations are expected to have

strong effects on plant communities and associated animal assemblages (Beniston et al., 1996; Walther, 2003). Impacts of global warming have appeared in the Alps and include the slow upward shift of tree line (Gehrig-Fasel et al., 2007) and the ranges of alpine and nival plants (Grabherr et al., 1994; Pauli et al., 1996, 2007; Walther et al., 2005; Vittoz et al., 2006). In this study, we address the continuing effects of climate change on patterns of species richness in Switzerland using ecological niche models and three groups of indicator species that represent geographic patterns of species richness in three divergent higher taxa.

The use of indicator species has seen considerable discussion. Some studies suggest that species at risk (protected by the Endangered Species Act in the United States or highly rated on the IUCN Red List) could be associated with patterns of total species richness (Mikusinski et al., 2001; Lawler et al., 2003; Warman et al., 2004) and have useful indicator properties (Pearman et al., 2006). However, rare species can have special habitat requirements that limit their coincidence with areas of high total species richness (Prendergast et al., 1999; Chase et al., 2000; Aubry et al., 2005; Orme et al., 2005). The geographical distribution of species richness is determined at both continental and regional extents by the spatial occurrence patterns of species that are widely

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distributed (Jetz and Rahbek, 2002; Vazquez and Aizen, 2003; Lennon et al., 2004; Pearman and Weber, 2007). This suggests that a subset of widely distributed (i.e., common) species can best indicate general patterns of species richness over geographic extents that are pertinent for habitat management, biodiversity monitoring and prediction of the impacts of climate change. Moreover, while national-level assessment of biodiversity trends is mandated by multinational agreements that promote biodiversity conservation (Weber et al., 2004), the use of multiple indicator taxa in an approach to national-level assessment and prediction of the impacts of climate change on biodiversity has not been developed previously. The prediction and assessment of climate change impacts using common indicator species could be advantageous. This is because the greater area of occurrence of these species likely provides better coverage within national boundaries, in comparison with the same number of narrowly distributed or uncommon species (Pearman and Weber, 2007). Further, focus on the potential response of species to climate change can provide estimates of changes in species composition that are not available when composite measures, such as species richness or diversity indices, are used without reference to species identity.

In this paper we report research using an indicator species approach and data from the Swiss Biodiversity Monitoring Program (BDM) Z7 field program (Plattner et al., 2004) to predict the impacts of climate change on the species richness of birds, butterflies, and vascular plants in Switzerland. The indicator species that we examine are widely distributed species that represent most (90%) of the geographic variation in the richness of all species in their respective higher taxa. We use ecological niche models (ENMs) and a variety of climate and land cover data to achieve a comprehensive understanding of the potential impact of climate warming on patterns of species richness in Switzerland. In this study we include land cover variables to investigate the relative importance of land cover and climate variability to current species distributions. We use predictions of future climate that are derived from general circulation models and the ENMs of the indicator species to predict future potential distributions of the species and of indicator species richness. We examine the efficacy of two groups of species as indicators of current patterns of species richness, species for which models exhibit superior performance (as measured by AUC) and the models of a group of the most-prevalent species. While change in species richness is part of the story of the predicted impacts of climate change, we also investigate turnover in assemblage composition and how it develops with time. Our findings suggest that turnover in assemblages of the indicator species we investigate will be a notable characteristic of ecological responses to climate change.

2. Methods

2.1. Species occurrence data

Data on species occurrences for this study come from an existing database of samples taken on Switzerland's landscape diversity ('Z7') sampling sites. This biodiversity monitoring program has been described in detail elsewhere (Plattner et al., 2004; Kéry and Schmid, 2006; Pearman and Weber, 2007). There are 380 regularly spaced, 1-km² square cells (quadrats) of the Z7 sample that are aligned within the approximately 41,295 1 km² units of the Swiss national coordinate system and are a sample thereof. An additional 140 quadrats are distributed in southern and western Switzerland and result in these areas having approximately twice the prevailing density of samples. These quadrats were excluded from the present analysis so as to maintain a single density of samples across the entire country. The establishment and sampling of

this set of 1 km² cells constitutes one of several steps taken to meet Switzerland's commitments resulting from the Rio de Janeiro Convention on Biological Diversity (www.biodiv.org). Unlike many atlas datasets, the data were collected with a documented sampling protocol that corresponds to the 1 km² cell size of the cells. This is particularly advantageous when modeling species distributions because predictions based on models that are calibrated with data from regularly spaced samples can far out-perform models based on data from ad hoc collections where a design is absent (Edwards et al., 2006). We used occurrence data to indicate species presence. Species were assumed to be absent at sites at which they were not observed. While this underestimates the number of species actually at a site and biases observed species prevalence downward (Kéry and Schmid, 2006), the structure of the data (i.e. no repeat visits conducted within a robust design) do not permit an estimate of probability of detection for species in all three groups and at all sites.

One fifth of the Z7 sites were sampled each year. These sites were a regularly spaced subsample of all sites and spanned the entire extent of the sampling area. A second selection of regularly spaced sites, not including the first sites and also constituting one-fifth of the total number of sites, was sampled in the second year, and so on until by the end of the 5th year all sites had been sampled. We used data from the first 5 years of sampling for each of the three taxonomic groups. At each site, the three taxa were sampled following standard protocols that were specific to each taxonomic group. The sampling efficiency for each taxon has been reported elsewhere (Plattner et al., 2004; Kéry and Schmid, 2006).

2.2. Selection of indicator species

Widely distributed species of birds, butterflies, and plants determine the geographic pattern of species richness in the Z7 BDM data and the richness of most prevalent 30% of species is highly correlated with overall species richness (Pearman and Weber, 2007). Our study focuses on these widely distributed species. Thus we avoid rare species that may be difficult to detect and contribute little to overall geographic patterns of species richness (Pearman and Weber, 2007). The relatively large number of occurrences of the chosen species in the Z7 dataset suggests that the models constructed for these species are unlikely to be influenced by the vagaries of field sampling to as great a degree as models of species that are uncommon or, equivalently, have very few observed occurrences. For the current analysis, we selected for modeling species that were present in at least 20 sites. We focus on the most prevalent ~30% of species that, in each taxon, present a pattern of species richness that is highly correlated ($r_p > 0.95$) with total species richness of the taxon. We report results for the modeling of each group of these indicator species, as well as each species (see [online supplementary materials](#)).

2.3. Environmental data

2.3.1. Land cover data

We created a habitat classification to capture variation in land cover that is likely relevant to the composition of natural communities and the resulting species richness. At the same time, we attempted to avoid a proliferation of categories, which would result in a large number of variables and challenge our ability to calibrate models meaningfully with a data set of only 380 or so samples. We reviewed land cover categories for the Swiss 'Arealstatistik 1992/1997' land cover summary, which are available within the GEO-STAT database (Bundesamt für Statistik, www.bfs.admin.ch), to form seven land cover types (Appendix 1). We then used a 100 m resolution rasterized version of the original lattice map in a geographic information system (GIS) to evaluate land cover in each

square kilometer grid cell of the Swiss national coordinate system. We converted these values into a proportion of each land cover type within each of the 41,295 square kilometers in the Swiss national grid system.

2.3.2. Climate data and variables

Construction of gridded environmental variables at our working resolution of 1 km required a number of steps. We assembled a vector of five climate variables (Table 1), at a resolution of 100 m, that were chosen to be closely related to physiological limits and requirements for metabolism in mountain plants (Körner, 2003), and are similar to variables that have functioned well in previous attempts to model distributions of mountain plants (Zimmermann and Kienast, 1999), the geographic distribution of birds (Tingley et al., 2009) and of butterflies (Lutolf et al., 2009). These variables were degree-days above 0 °C, yearly and winter mean potential evapotranspiration (PET), yearly average precipitation, and moisture index (yearly precipitation divided by yearly PET). Climate data represented five distinct periods. The current period was represented by average of monthly values for the period 1961–1990. We interpolated these climatological normals from weather station data collected from across Switzerland. For complete details on the derivation of bioclimatic variables see Zimmermann and Kienast (1999) and Guisan et al. (2007). For this study, these variables were averaged within 1 km² grid cells.

We used general circulation model output (below) to represent climate during the intervals 1991–2020, 2021–2050, 2051–2075 and 2076–2100. We used data that were derived from the Hadley Center Coupled Model (HadCM3), which was calibrated to project future climates under the A1FI and B2 scenarios of the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2001) as these were the most recent available at the time. The climate data were obtained directly from the CRU website representing the TYN SC 1.0 data set (Mitchell et al., 2004) and available in a 10' (ca. 18 km) resolution. These data were downscaled in three steps: First, we derived anomalies of future climate compared to the baseline (1961–1990) on a monthly basis using the same 10' spatial resolution originating from the CRU TS 1.2 data set (Mitchell et al., 2004). Second, the anomalies were re-projected from the Geographic to the Swiss National coordinate system and spatially interpolated to a resolution of 1 km using inverse distance weighted interpolation. In a third step, the spatial resolution was further refined to 100 m using bilinear interpola-

tions and the anomalies were added to the 100 m maps of climatological normals, above. For this study, these climate values were also averaged within 1 km² grid cells.

2.3.3. Topo-environmental variables

We also evaluated five topo-environmental variables (Table 1) that were chosen to represent relevant local variation at a resolution of 1 km², but which do not likely respond directly to climate change. These variables represent environmental variation that is determined primarily by topography and soils. They included solar radiation, average slope, topographic position, soil water holding capacity and soil coarse fragment content. Potential global solar radiation was calculated in ArcInfo using a method modified after Kumar et al. (1997). Average slope was determined by evaluating the mean inclination in degrees across the one kilometer grid cells. Topographic position expresses the degree of convexity or concavity around a center cell (Zimmermann et al., 2007), by evaluating a range of window sizes in a moving window algorithm. Soil water holding capacity (in mm) expresses the amount of water that soils can hold. Coarse fragment content expresses the fraction (in %) of coarse debris that reduces the capacity of soils to hold back water. Both these variables were taken from the Soil Suitability Map of the GEOSTAT database of Switzerland (www.bfs.admin.ch, BFS, 1992). These variables were assumed to remain at their original values during all time periods.

2.4. Ecological niche modeling

2.4.1. Modeling algorithm

We modeled species distributions using an iterative computer learning algorithm called the gradient boosting machine (Friedman, 2001). We used the algorithm as implemented in the R statistical package 'gbm: Generalized Boosted Regression Models', available on the R website (<http://cran.r-project.org>). Boosted regression trees are becoming increasingly popular in predictive modelling because of their often superior performance in prediction (Elith et al., 2006; Guisan et al., 2007). A full description of gbm and a users guide was recently published (Elith et al., 2008). We employed the 'area under the receiver operator characteristic curve' (AUC) as a criterion for evaluating the fit of gbm models to the calibration dataset and in evaluating predictive performance (Fielding and Bell, 1997). This measure of model fit is suited for comparing probabilistic predictions to observed presence-absences because it requires no arbitrarily defined threshold probability with which to establish prediction of species presence. In calibrating the model for each species, we generated an estimate of AUC by conducting 10-fold cross-validation on a calibration dataset that was selected randomly from the complete dataset and that conserved the overall proportion of presences/absences found in the full dataset (Efron and Tibshirani, 1998; Randin et al., 2006).

We retrieved directly from the gbm model (in fact, an R-object) the proportional contribution of each climate variable to the model. We also calculated the marginal influence of the three most important variables that were associated with the current species distribution as determined by the gbm algorithm (Ridgeway, 2007). Models built with gbm can 'overfit' the data when a large number (several thousands) of regression trees is combined into the final model. For this reason, we used the 'out of bag' criterion (Ridgeway, 2007) for determining a conservative estimate of the number of regression trees upon which the projections of species distributions should be based. Measures of model performance were also based on models using the number of regression trees suggested by application of this criterion.

One problem when predicting species distributions is that niche models provide projections of species distributions in the form of

Table 1
Variables, abbreviations, and four alternative model parameterizations. An 'x' indicates that the variable is included in the model under the corresponding numbered parameterization. The variables included in the model under a particular parameterization exhibited a correlation of $r_p < 0.7$.

Variable (abbrev.)	Parameterization			
	1	2	3	4
Forest, mature (pc.forest)		x	x	x
Other forest (pc.othfor)		x	x	x
Intensive agriculture (pc.intagr)		x	x	x
Extensive agriculture (pc.extagr)		x	x	x
Impervious surface (pc.imperv)		x	x	x
Other land cover (pc.others)		x	x	x
Degree-days 0 (dd00_av)	x			
PET, yearly average (etyy_av)			x	
PET, winter (etwi_av)			x	x
Precipitation, yearly average (pryy_av)	x		x	
Moisture index (miyy_av)				x
Solar rad., year, mean (sryy_av)	x	x	x	x
Slope, average (slop_av)	x	x	x	
Topography (topo_av)	x	x	x	x
Soil water holding cap. (swhc_av)	x	x	x	x
Soil quality (scfc)	x	x	x	x

probabilities that the species is found within map cells. The making of a distribution map entails deciding on a threshold probability value above which the species is predicted to be present. We used the criterion of the maximum coefficient of agreement (maximum Kappa, Cohen, 1960) to determine this threshold, based on an analysis of the performance of the models in correctly predicting the pattern of species occurrences and absences in the data with which the models were calibrated.

2.4.2. Model parameterization

The variables one selects to use as explanatory or predictor variables and whether they enter into the model as linear or higher-order terms determines the parameterization of the model. In many modeling exercises, the inclusion of many correlated variables can result in models that lack fit, predictive ability, and stability, meaning that the results are sensitive to the inclusion or omission of a small number of observations. To avoid this, we grouped variables into three categories: habitat variables, climate variables, and topo-environmental variables that are determined by physical, topographical and soil variation. In the current exercise, only variables derived from climate data are projected to change with ongoing climate change. Within each of these groups, we tested variables for correlation using 460 Z7 samples points. In composing sets of variables for model building, we chose only variables that had Pearson correlations of less than 0.70. While we eventually considered seven different model parameterizations, we settled on four of these to explore in detail (Table 1) in this paper.

The modeling results were analyzed graphically by mapping the sum total of species that were predicted to be present in each 1-km map cell. We also calculated two components of species turnover in order to identify both the time frame and geographic pattern of change in predicted species assemblage structure at the scale of 1-km². We calculated predicted percent gain of species as 100 times the proportion of the species predicted present at a future time point that were not predicted present during the original time period. We calculated the predicted percent loss of species as 100 times the proportion of species that were predicted present during the original time period that were no longer predicted present by the future time period in question. As in all models of this type, the validity of projection of the climate-distribution relationship to future climates assumes that climate-distribution relationships remain unchanging over the time period that is considered.

2.4.3. Indicator species evaluation

We ranked species by decreasing magnitude of model AUC and also by decreasing species prevalence. We then examined the correlation between observed species richness in the field data and the predicted species richness of groups of increasing numbers of species by including successive species in order of their rank. We determined modeled species richness that resulted from projecting the models of the species in each group to the current climate. We then determined the correlation between the predicted species richness values and the observed total species richness for each taxon across the sampled sites.

3. Results

3.1. Model performance

Models for species in each group are, on average, good (Tables A2–A4 in online supplementary materials; Swets, 1988). The models for bird species fit the original Z7 data somewhat better than the models for plants or butterflies, as shown by the average values of 10-fold cross-validated AUC. For all three groups, the average model AUC (\pm std. dev.) indicates that the models are useful (Araújo

Table 2

Most-influential variables, as percent of best models for most-prevalent species.^a

Influential variable	Species group		
	Birds	Butterflies	Plants
Percent mature forest	42.0	15.6	11.7
Percent intensive agriculture	13.4	3.1	5.8
Yearly evapotranspiration (PET)	5.6	4.8	7.9
Degree-days 0	19.4	48.0	40.4
Mean slope	5.6	4.7	1.1
Mean soil water holding capacity	2.8	1.6	4.5

^a These species were selected by ranking all species in order of prevalence, then selecting in order of prevalence until the species richness of the selected species at the sampled sites was correlated with overall species richness at a level of $r_p = 0.95$.

et al., 2005; birds: 0.84 ± 0.10 ; butterflies: 0.81 ± 0.10 ; vascular plants: 0.82 ± 0.09). Nonetheless, there is a wide range of AUC values, despite the tight distribution around the median value (Fig. 1).

Modeled species richness demonstrates a higher correlation with the species richness in the observed data when species are collected into groups in order of rank prevalence (Fig. 2) than when collected into groups in order of model performance (AUC). In the case of birds, the modeled richness of only very few of the most-prevalent species (10–20) closely approximates species richness of all avian species in the observed data (Fig. 2b). We observe similar but less striking patterns for modeled species of the most-prevalent butterflies and plants (Fig. 2).

3.2. Variable influence

For birds, the best models for most species are most-strongly influenced by habitat variables, which we did not modify as part of climate change scenarios. (Table 2, and Table A2 in supplementary online materials). Percent mature forest is the most influential variable in models for 15 bird species while percent intensive agriculture is the most influential variable in models of another five species. Among the variables that describe climate and express climate change, degree-days is the most influential variable in best models for seven bird species and yearly potential evapotranspiration is the most influential variable in best models for only two species.

Best models of butterfly distributions are primarily influenced by degree-days (31 models, Table 2, Table A3 in online supplementary materials). Yearly potential evapotranspiration acts as the primary influence on best models of an additional three species. The variables 'percent mature forest' and 'percent intensive agriculture' were most influential in models for fewer species, 10 and two of species best models, respectively. Similar to the case for butterflies, degree-days influences more best models for plant species (214 of

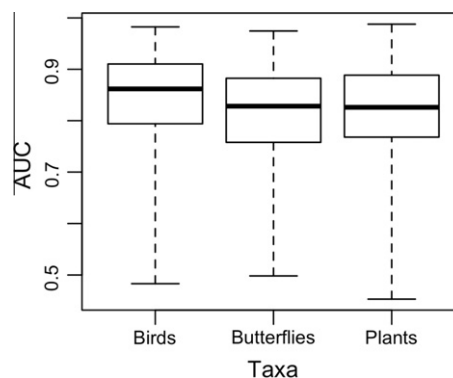


Fig. 1. Boxplot of 10-fold cross-validated AUC from projection of models onto the data used in their training. The median, first quartiles, and range are plotted for each of the three study taxa.

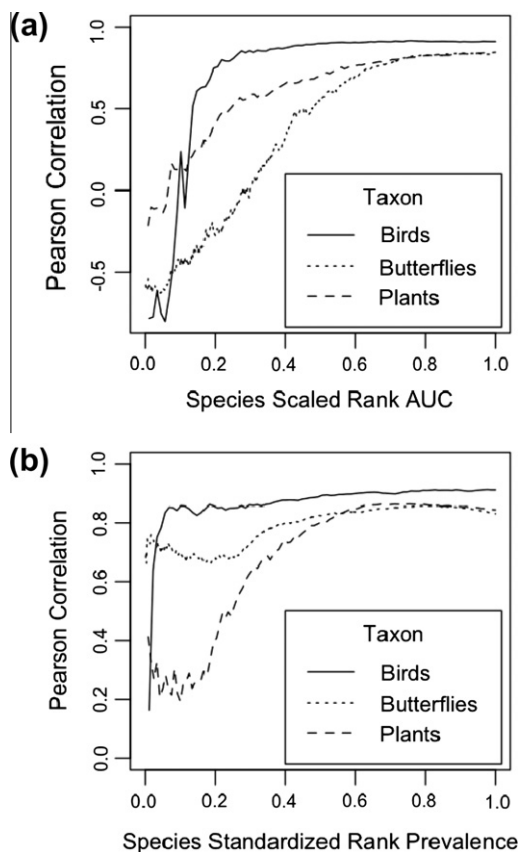


Fig. 2. Plots of the correlation between the species richness of modeled species at sampled Z7 sites (under current climatic conditions) and species richness of all recorded species. The modeled species are ranked in descending order of the magnitude of the variable on the abscissa, which has subsequently been scaled between 0 and 1 to account for small discrepancies among taxa in terms of the total number of sampled sites. (a) Species sorted in order of decreasing value of 10-fold cross-validation of AUC on the training data. (b) Species sorted in order of decreasing prevalence in the Z7 dataset.

530 models) than other variables. Percent mature forest acts as the strongest influence in models for an additional 62 species (Table 2, Table A4 in online supplementary materials). Thus, the variables mature forest and degree-days are the most influential variables for models in all three species groups, but the relative frequency with which these two variables are most influential is reversed for bird species in comparison with the other two groups (Table 2).

3.3. Current modeled species richness

The patterns of modeled species richness of the groups of indicator species vary among the higher taxa (Fig. A1 in online supplementary materials). The greatest modeled richness of bird and vascular plant indicators occurs at low elevations and decreases with increasing elevation. In contrast, species models predict the greatest richness of butterfly indicator species at middle elevations.

3.4. Future species richness and turnover

The models for each of the three indicator groups show the tendency for future species richness at relatively high elevations to be greater than current levels (see Figs. A2–A4 in online supplementary materials). There is a consistent gain in the modeled number of bird indicator species with suitable climatic conditions in the Alps (Figs. 3a and b; A2b and d, online supplementary materials). The models indicate loss of suitable climatic conditions for bird indicator species primarily in central southern Switzerland

(Fig. 3c and d). Species that are modeled to gain suitable climatic conditions at high elevation greatly outnumber those species for which models predict loss of suitable conditions under both the A1 and B2 scenarios (Fig. A2b and d).

In contrast to the results on bird indicators, the results for butterfly indicators show a trend towards increasing number of species with newly suitable climate conditions at relatively high elevations, and decreases in future predicted species richness in the middle elevations to the north and south of the Alps (Fig. A3, online supplementary materials). These middle elevations are modeled originally to have the highest richness of butterfly indicator species (Fig. A1b, online supplementary materials). The models predict that many areas that currently present suitable conditions for butterflies at middle and high elevations become unsuitable over the next 100 years (Fig. 4c and d). Further, the number of butterfly indicator species that we model to lose suitable climate conditions at middle elevations just north and south of the Alps exceeds the number modeled to gain area with suitable climate (Fig. A3b and d). The modeling results predict net decrease in richness of butterfly indicator species in currently occupied areas over the next 100 years under both the A1 and (relatively mild) B2 scenarios (Fig. A3b and d, online supplementary materials). Areas that we predict to increase in species richness (Fig. A3b, d) actually show almost complete turnover in the species that find suitable climatic conditions by the end of the century (Figs. 4b, d).

Predicted trends for the group of plant indicator species under the A1 scenario are intermediate to those predicted for birds and butterflies. We predict species richness of plant indicators to increase at relatively high elevations throughout the Swiss Alps (Fig. A4 in online supplementary materials). The Engadine valley in the extreme western part of Switzerland appears to acquire a climate that may support the influx of a substantial number of newly arriving plant species by the year 2100, under both the A1FI (Fig. 5b), and milder B2 (not shown) scenarios. The results predict substantial loss of suitable conditions for plant indicators in the middle and high elevations in the Swiss Alps (Fig. 5d). Similar to the case of butterflies, some high elevation areas that are predicted to experience increased suitability for additional species early in the century (Fig. A4a, online supplementary materials) end up being suitable for fewer species of plants as the century closes (Fig. A4b). Even where there is a net increase in the number of species that may find suitable climate (Fig. A4b), there is a large turnover in the species that are predicted to find suitable conditions (Fig. 5d).

4. Discussion

4.1. General patterns

By studying indicator species that are closely related to geographic patterns of species richness at a resolution of 1 km (Pearman and Weber, 2007), the predictions provided here reflect on species richness, turnover in community composition, and the amount of area with both suitable climate and habitat available for each of the species under consideration. However, compared to an earlier study where plant species richness was modeled directly as a dependent variable (Wohlgemuth et al., 2008), we also find that the numbers of plants and butterflies for which suitable conditions currently exist are highest at middle elevations. Conditions may be suitable for comparatively many species in middle elevation. However, this pattern may alternatively signify a mid-domain effect (Colwell and Lees, 2000) in which shared constraints on species range limits leads to higher species richness in the middle of a study area. In contrast, the diversity of birds shows no such pattern (Fig. A1a, online supplementary materials). This difference

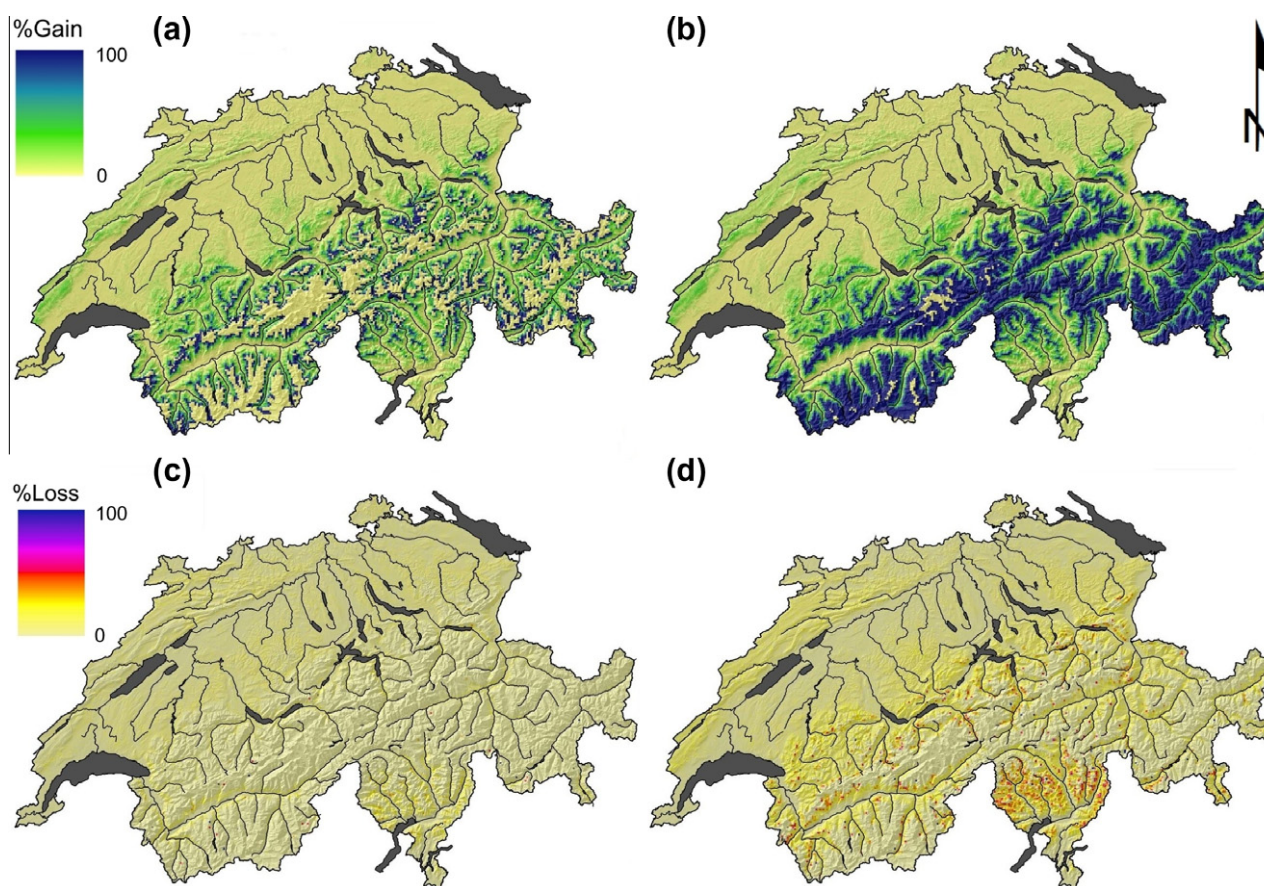


Fig. 3. Modeled turnover in indicator species of birds in Switzerland, under the A1FI scenario of the IPCC. The change in species richness corresponds to the average predicted climate during the years 2021–2050 (a and c) and 2076–2100 (b and d). The upper panels, 'Gain' (a and b), present the number of species predicted to be present under future conditions that were not predicted to be present under the initial average climate conditions for the period 1961–1990, as a percent of all species predicted present under future climate conditions. The lower panels, 'Loss' (c and d), present the number of species that are predicted to be present during initial climatic conditions, but are no longer modeled present in the future, as a percent of the number of species modeled present under the initial conditions.

between the distribution of birds compared to plants and butterflies is not due to differences between the taxa in model performance (Fig. 1). In each taxon, the distribution of observed species richness was well-represented by the modeled distribution of suitable environmental conditions.

The results of our analysis suggest that climate change will have broad impacts on species richness, across Switzerland. Climate forecasts project particularly strong impacts in mountain areas, where temperature change will exceed mean change globally (Diaz et al., 2003; Beniston, 2006; Nogués-Bravo et al., 2006). An increase in species richness at high elevations as these areas become warmer and suitable for additional species has already been observed (Braun-Blanquet, 1957; Hofer, 1992; Walther et al., 2005; Vittoz et al., 2006). As climate warms, it comes as no surprise that species are predicted to extend their distribution to higher elevations, or be faced with decreasing area with suitable climatic conditions if they are unable to migrate to follow the geographical displacement of areas with suitable climate. However, coarse-grained data likely do not contain information on microclimatic variation that may be important to plants.

4.2. Extinction and microclimate variation

Predictions of extinction due to climate change in mountainous regions may overlook the existence of microhabitats and therefore over-estimate the loss of area with suitable climatic conditions for species (Randin et al., 2009). Nevertheless, the prediction of disap-

pearance of areas with suitable climate, as measured at a scale of 1 km², suggests that availability of suitable conditions for many high-elevation species is greatly diminished. The climate and land cover data that were used in this study to characterize 1 km² grid cells were taken from rasters with a resolution of 100 m. Thus, the presence of small areas of suitable conditions may be captured to some degree in our 1 km climate and habitat layers. The results we obtained largely corroborate results from studies with larger grid cell size that suggest the loss of suitable conditions for many species at high elevations (e.g. Thuiller et al., 2005). Our study further predicts that many areas of middle elevation in the alpine region will show substantial change in community composition, as indicated by turnover of plant and butterfly indicator species that are predicted originally to have suitable habitat at intermediate elevation (Figs. 4 and 5).

4.3. Turnover in species composition

One potentially important phenomenon is that changes in species richness in these groups only tell part of the story of the impacts of climate change. Both butterflies and vascular plants will likely show increases in species richness in eastern Switzerland by the year 2050 under the A1FI scenario (Figs. A3 and A4, online supplementary materials). By the year 2100, communities at both middle and low elevations have predicted losses of approximately 50–80% of the original number of species that found suitable climate. The magnitude of species losses in the eastern Swiss Alps

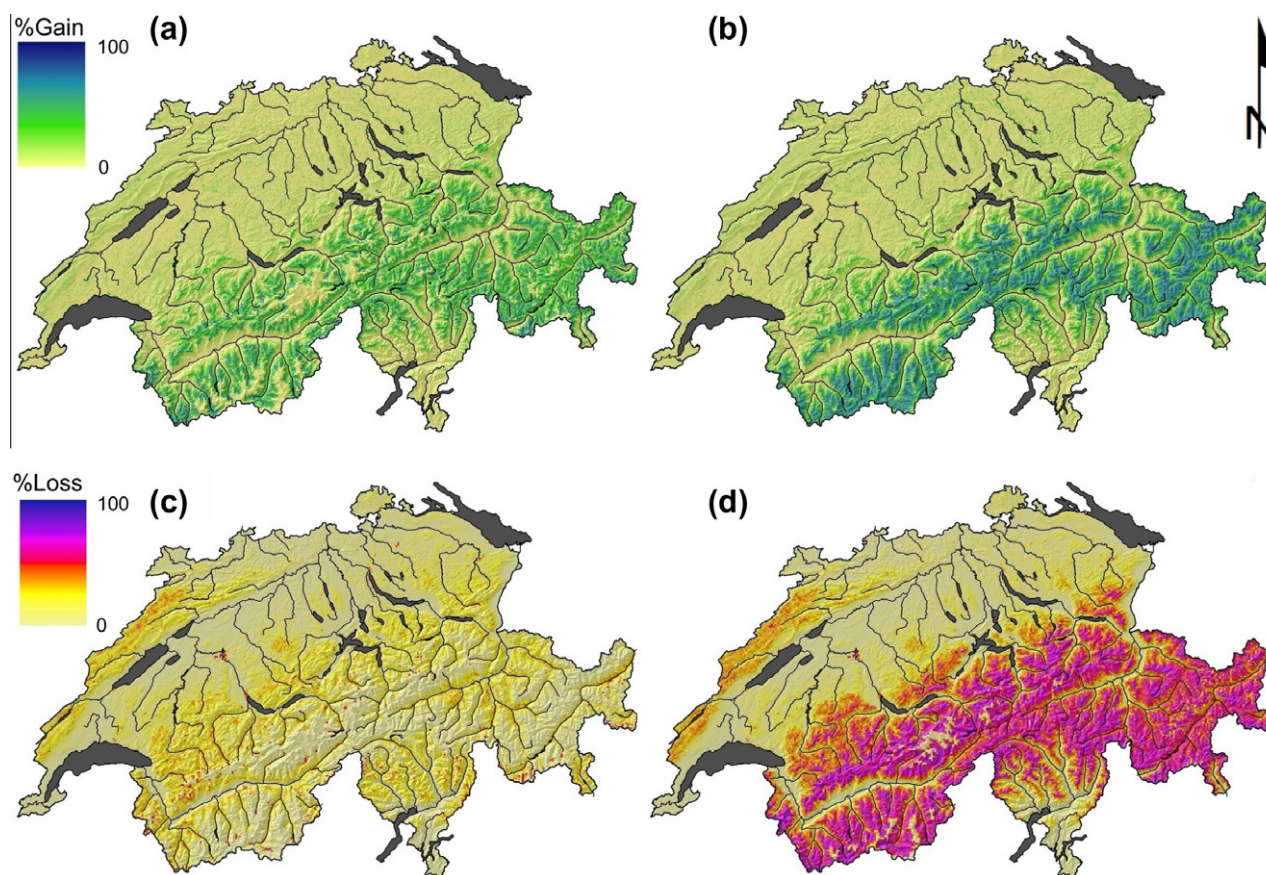


Fig. 4. Modeled turnover in indicator species of butterflies in Switzerland, under the A1FI scenario of the IPCC. Otherwise as in Fig. 2.

is markedly greater later in the period (Figs. A3d and A4d, online supplementary materials). Thus, the loss of species later in the period reduces the early trend toward increases in species richness of butterflies and plants in the eastern Swiss Alps.

4.4. Effects of climate change and habitat conversion

Groups of species (i.e., in higher taxa) may differ in their relationships to variables that change both spatially and temporally (Debinski et al., 2006). In our study, the distribution of suitable conditions for bird species appears to be more closely related to habitat variables than to climate variables. Variables reflecting forest cover and agriculture are assumed in this study not to respond to climate change. However, both climate change and cultural factors will likely bring changes in the distribution of mountain forests and meadows (Gehrig-Fasel et al., 2007). Other studies have found that land cover change alone will likely drive substantial changes in butterfly assemblages in the Alps (Lutolf et al., 2009), and that both predicted climate change and land use change (specifically, urban sprawl) combine to affect predictions of future neophyte species richness (Nobis et al., 2009). Future work should include estimates of the impact of interactions between climate change and social factors on the distribution of forest, intensive and extensive agriculture, and urban and other developed areas. Incorporation of temporal changes on the scale of the next 100 years may improve the accuracy of predictions for species for which patterns of suitable environmental conditions are primarily related to land cover variables. Nonetheless, we predict substantial impacts of climate change on species in these three higher taxa, apart from changing habitat and land cover patterns. Finally, climate change affects patterns of extreme climate in addition to

mean values. Inclusion of measures of climate variability and their projected development over the next century might lead to substantial (10–20%) improvement in the models and forecasted changes in species distribution (Zimmermann et al., 2009).

4.5. Indicator properties

We have tested the indicator properties of collections of the niche models of species in three higher taxa. Our analysis demonstrates that the models of approximately 10–40% of species with the highest prevalence in the BDM Z7 dataset can be used to predict site species richness within their higher taxon (Fig. 2). Models of these prevalent species perform better as indicators than do the models of the species with the highest rank values of model AUC. This suggests that the often-observed relationship between the distribution of common species and patterns of overall species richness (Lennox et al., 2004; Pearman and Weber, 2007) is sufficiently robust to render variation in AUC among species unimportant to establishing the correlation with observed species richness. Whether these indicator relationships hold up under continued climate change is an open question. Our data suggest that predicted patterns in the future distribution of common species may also be indicative of species richness. Nonetheless, the most effective indicator species could be the ones that are currently common, or they might be species that have predicted high prevalence in the future.

4.6. Modeling with monitoring data and limitations

Modeling the effects of climate change may be facilitated and improved through use of data from designed monitoring programs. The BDM Z7 samples do not present exhaustive censuses of the

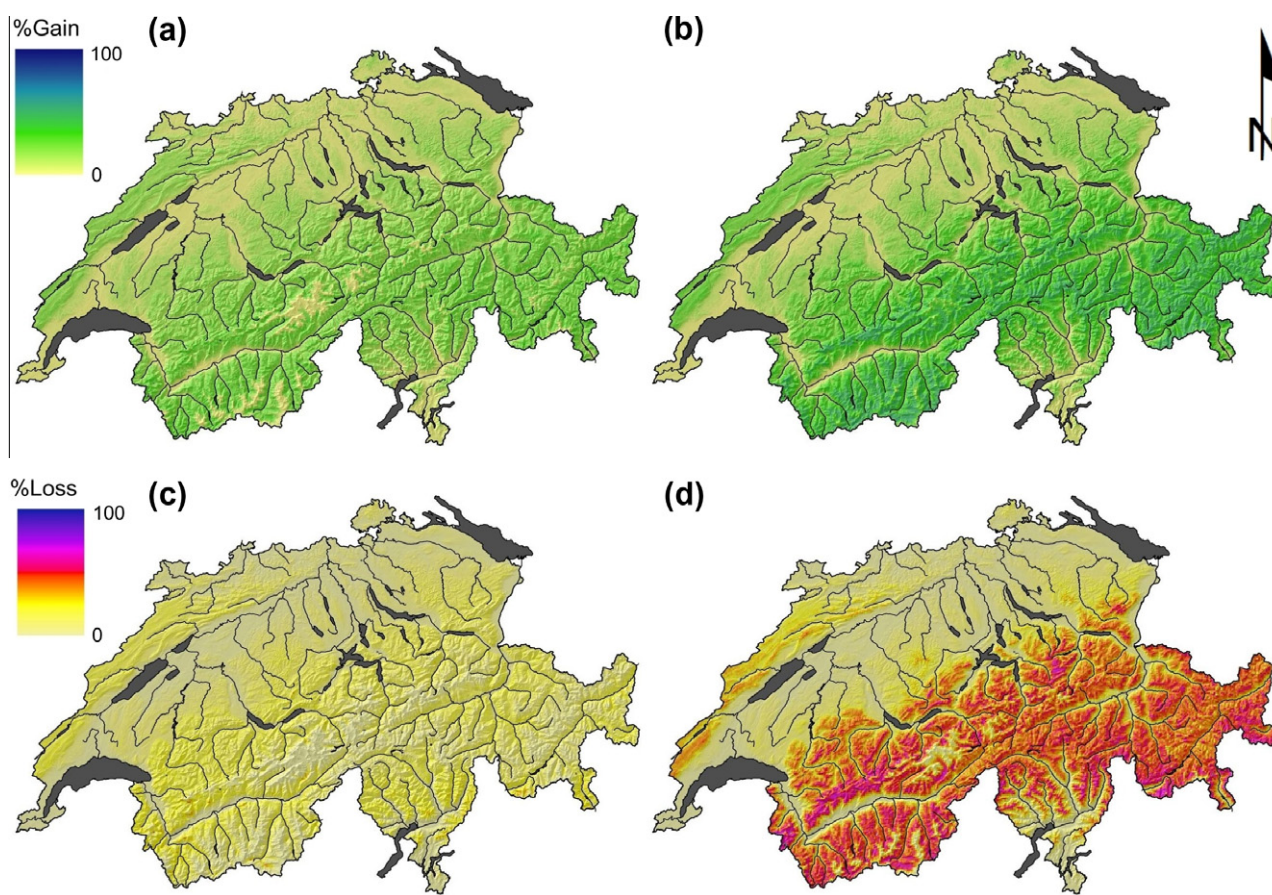


Fig. 5. Modeled turnover in indicator species of plants in Switzerland, under the A1FI scenario of the IPCC. Otherwise as in Fig. 2.

species that are present in the sampled 1 km² cells and it is clear that species go unobserved during sampling (Plattner et al., 2004; Kéry and Schmid, 2006). Nonetheless, clear advantages in the predictive performance of ENMs result from model calibration with data from a designed sampling program (Edwards et al., 2006). Further, the availability of species absences that are based on a designed sampling program removes the influence on modeling results that arbitrary decisions during the selection of pseudo-absence data can have (Chefaoui and Lobo, 2008; VanDerWal et al., 2009). The use of the BDM Z7 data in calibrating niche models provides advantages that are consistent with these considerations. Nonetheless, these models are subject to the assumption of an equilibrium between species distribution and environmental conditions, which may not be justified due to human impacts on land cover (e.g. Gehrig-Fasel et al., 2007). Here, we have presented the modeled potential distribution of future suitable conditions. The results on species richness and turnover with climate change assume that species are able to disperse to track the geographic distribution of suitable conditions. This is more likely the case for birds and butterflies than it is for plants.

A further consideration when using monitoring data, such as those we used here, is that many species have ranges that are substantially larger than the extent of the monitoring data. The BDM Z7 data do not include information on the environmental conditions that are coincident with the lower elevation limit of the distribution of some species. This deficit can limit the ability of niche models to describe the falloff in probability of species occurrence toward the 'hot-dry' end of environmental gradients. In the present study, this likely leads to underestimation of the loss of areas with suitable climate for species at low elevations, specifically in

northern Switzerland and in the canton Ticino in the south of the country. Loss of suitable conditions for mountain species and estimates of turnover in mountainous areas are likely less affected in analyses of the current data because climatic suitability is lost primarily for species that only find suitable conditions at higher elevations currently. The extent of this effect is impossible to assess more precisely without conducting expanded analysis that uses species occurrence data and environmental data that capture the entire environmental gradients over which the species are distributed. Such an exercise would help assess the accuracy of predictions of loss of area with suitable climate for species that are typical of low elevations in Switzerland. However, such data are not available at 1 km² over most of Europe and would likely come from lower resolution atlas data, illustrating a real trade-off between data resolution and geographic extent. New methods should be developed to address this issue and concomitantly to understand the implications that accompany the simultaneous use of data of various resolutions in ENMs.

5. Conclusions

Species occurrence data that come from designed sampling programs for monitoring species distributions and biodiversity provide a rich source of information for addressing questions in biogeography, effects of climate change, and conservation. This study demonstrates that ecological niche models of the most-prevalent species can perform better in predicting current levels of species richness than do an equal number of the best performing models, as measured by AUC. This implies that predictions of

future species richness may be more reliable when made with species distribution models of the currently most-prevalent species. This constitutes an empirically-based hypothesis that should be tested (1) as species distributions in the study region respond to ongoing climate change and (2) in additional mountainous regions where the same pattern might be detected. Similarly, our study suggests that species turnover in communities in the Swiss Alps could be substantial, although species richness may not be greatly affected in some areas. This suggests a second empirical hypothesis that will be testable over time locally and also constitutes a testable pattern that might hold for other mountain ranges in Europe and elsewhere.

Acknowledgements

The comments of T.C. Edwards, C.F. Randin and two anonymous reviewers led to improvements in earlier versions of the manuscript. We thank the consulting firm Hintermann and Weber AG, and Matthias Plattner for making the Z7 data from Biodiversity Monitoring Switzerland available for analysis. P.B.P. was supported during analysis and writing by the EU FP6 ECOCHANGE Project and by Hintermann and Weber AG. P.B.P. and N.E.Z. acknowledge the support of the Sinergia Project CRSII3-125240 'SPEED' and P.B.P. acknowledges the support of Project 3100A0-122433 'ENNIS', both funded by the Swiss National Science Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.11.020.

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