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ORIGINAL ARTICLE

Modelling vascular plant diversity at the landscape scale using systematic samples

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ABSTRACT

Aim We predict fine-scale species richness patterns at large spatial extents by linking a systematic sample of vascular plants with a multitude of independent environmental descriptors.

Location Switzerland, covering 41,244 km^2 in central Europe.

Methods Vascular plant species data were collected along transects of 2500-m length within 1-km^2 quadrats on a systematic national grid (n = 354), using a standardized assessment method. Generalized linear models (GLM) were used to correlate species richness of vascular plants per transect (SR_t) with three sets of variables: topography, environment and land cover. Regression models were constructed by the following process: reduction of collinearity among variables, model selection based on Akaike's information criterion (AIC), and the percentage of deviance explained (D^2). A synthetic model was then built using the best variables from all three sets of variables. Finally, the best models were used in a predictive mode to generate maps of species richness (SR_t) at the landscape scale using the moving window approach based on 1-km^2 moving windows with a resolution of 1 ha.

Results The best explanatory model consisted of seven variables including 14 linear and quadratic parameters, and explained 74% of the deviance (D^2 = 0.742). Used in a predictive mode, the model generated maps with distinctive horizontal belts of highest species richness at intermediate altitudes along valley slopes. Belts of higher richness were also present along rivers and around large forest patches and larger villages, as well as on mountains.

Main conclusions The approach involved using consistent samples of species linked to information on the environment at a fine scale enabled landscapes to be compared in terms of predicted species richness. The results can therefore be applied to support the development of national nature conservation strategies. At the landscape scale, belts of high species richness correspond to steep environmental gradients and associated increases in local habitat diversity. In the mountains, the belts of increased species richness are at intermediate altitudes. These general belt-like patterns at mid-elevation are found in all model parameterizations. Other patterns, such as belts along rivers, are visible in specific parameterizations only. Thus we recommend using several sets of parameters in such modelling studies in order to capture the underlying spatial complexity of biodiversity.

Keywords

Biodiversity, conservation biogeography, generalized linear models, hotspots, land cover, landscape scale, model prediction, spatial patterns, Switzerland, topography.

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INTRODUCTION

Species inventories and samples of species provide baseline information for the analysis of biodiversity. The value of the outputs depends largely on the quality of the original data (Kier *et al.*, 2005), the availability of environmental data, and the analytical methods used to combine them. Because vascular plants are an important component of terrestrial habitats, maps of species composition (vegetation maps) and of species richness (biodiversity maps) are valuable indicators for the derivation of spatially explicit conservation strategies.

Model predictions have proven valuable in the detection of biodiversity patterns (Engler *et al.*, 2004; Pimm & Brown, 2004). However, when the prediction of species richness is considered at the landscape scale, it is rare to have fine-grained information for large areas for both environmental factors and the corresponding species richness. For this reason, biodiversity maps that use a high extent/grain ratio are also rare (Zimmermann & Kienast, 1999; Araújo *et al.*, 2005). However, such fine-grained maps for large regions not only may provide an appropriate basis for local and regional conservation planning (Poiani *et al.*, 2000; Ferrier, 2002), but also may add insight to global diversity patterns (Currie *et al.*, 2004).

The ongoing refinement of spatial resolution of environmental factors (Pimm & Brown, 2004) will lead to an increase in the resolution of model predictions of variations in species abundances (Guisan *et al.*, 2002; Dullinger *et al.*, 2003; Lütolf *et al.*, 2006) as well as richness (Ferrier *et al.*, 2004). Refinement of the spatial resolution of species richness (response variable) follows two strands: one way to assess detailed species information at the landscape scale is to record species richness at a relatively fine grain, e.g. quadrats of 1 km^2 that are arranged contiguously (Heikkinen, 1996; Wyler, 2004). Another way – specifically suited to larger areas – is to use presence/absence data on single species rather than species richness. The latter are input into static models linking species occurrence with fine-grained environmental predictors. The models can be used to mimic potential fine-grain distributions of many species, leading to cumulative species richness assessment. Explanatory models of both approaches can then be used in a predictive mode to show fine-scale patterns of species richness, relevant to local planners.

Both the quality and the interpretability of models and the derived richness maps depend strongly on variable selection. In small regions with a limited altitudinal range, land use usually accounts for a high percentage of the variation in species richness (Heikkinen *et al.*, 2004; Kerr & Cihlar, 2004; Ortega *et al.*, 2004; Waldhardt *et al.*, 2004). In contrast, in mountainous regions, variations in energy or other climate parameters (Grytnes *et al.*, 1999; Vetaas & Grytnes, 2002; Bhattarai *et al.*, 2004; Hawkins & Pausas, 2004; Moser *et al.*, 2005), substrate (Wohlgemuth, 2002b; Bruun *et al.*, 2003) and topography (Heikkinen & Birks, 1996) are the main factors correlated with species richness. Patterns in the species composition and diversity of Switzerland reflect a wide range of the aforementioned ecological factors mainly influenced by topography as a proxy.

Environmental baseline information on Switzerland is available at a high level of resolution. Since 2001, presence–absence data on multiple taxa, including vascular plants, become available at various scales within the framework of the Swiss federal Biodiversity Monitoring programme (BDM, Plattner *et al.*, 2004; Weber *et al.*, 2004). Within this framework, vascular plant species richness has been collected on a systematic national grid of 1-km^2 plots (total n = 520). By the end of 2004, 68% (n = 354) of the sample quadrats were available for statistical analyses.

Here a predictive procedure is described that spatially quantifies the richness of plant species at the landscape scale, based on a systematic national sample and several sets of environmental variables at a fine grain. The procedure involves modelling species richness by regression techniques and predicting species richness by applying model predictors to a region using a moving window approach. In order to cope with the spatially unevenly distributed predictor variables, the study was based on three different sets of variables: topography, environmental factors (climate/substrate/water body) and land cover, and on a combination of the best fitting variables. The richness models and the subsequently derived maps are compared and used to discuss national landscape patterns of plant species richness. The suggested implications for biodiversity conservation are presented.

METHODS

Study area

The study area is Switzerland, which covers 41,244 km^2 in central Europe and ranges in altitude from 193 to 4634 m a.s.l. (45°49′–47°48′ N latitude, 5°57′–10°30′ E longitude; Fig. 1). Approximately 60% of the country is in the Alps and 10% in the Jura Mountains. The average elevation is 1300 m a.s.l. Almost 7% of the country is considered to consist of urban environments (indicated by land-cover types 16–24 in Table 1), including buildings, associated green areas, and road and rail networks (BFS, 1992/1997). The mean annual temperature ranges from −10.5 to 12.5°C, and annual precipitation from 438 to 2950 mm (Zimmermann & Kienast, 1999).

Plant species data

In the framework of the Swiss BDM, three types of indicators are monitored under the headings pressure, state and response. In total, 11 state indicators (Z, for German *Zustand*) are regularly assessed. The Z7 indicator monitors the diversity of vascular plants on a landscape scale using a systematic sample of 520 1-km^2 quadrats and minimum spacing ranging from 14.3 to 19.1 km (Hintermann *et al.*, 2000; Fig. 1). The grid is denser in the regions of the Jura Mountains and the Ticino. The BDM aims, among other objectives, to survey landscape

Figure 1 Swiss sample of vascular plant species richness on a landscape scale (1 km^2) within the framework of Switzerland's federal Biodiversity Monitoring programme.

biodiversity – from lowland to alpine zones – over a long period. By the end of 2004, 80% of the sample quadrats had been visited for a first assessment. Quality checks were made to exclude quadrats with incomplete species lists, and lists of quadrats adjacent to Switzerland's borders and < 1 km^2 in area. The resulting test data set for analysis was made up of species lists for 354 quadrats, 68% of the total sample (Fig. 1).

Data collection in the quadrats followed a strict procedure: for every sample quadrat, transect routes 2500 m long were defined by maintaining a close proximity to the quadrat diagonals. Wherever possible, transects followed existing paths or roads. Sample quadrats were each visited by one of 29 botanists. All vascular plant species growing in buffers of 2.5 m on both sides of the transect were registered electronically (Plattner *et al.*, 2004) and served as the measure of transect species richness of vascular plants (SR_t) in the following analyses. Quadrats will be reassessed every 5 years (Weber *et al.*, 2004), with 20% of the quadrats visited per year.

Environmental data

All the environmental predictors used in the study are available in digital form as 1-ha grids. They are derived from maps of various origins (Table 2). In order to predict species richness nationwide on a fine scale and with a 1-km^2 focal window, predictor maps were created with grain sizes of 1 ha by applying the focal functions mean, standard deviation, range, maximum and minimum on a 1-km^2 moving window with a 100-m increment. Three variable sets were included derived from the predictor maps: (1) topography, (2) environment consisting of climatic data, substrate and water bodies, and (3) land cover derived from an aerial assessment.

Topography set

Topography reflects the structure of the land surface. In mountainous regions, topography, as reflected by elevation, slope and aspect, greatly affects plant growth (Körner, 1999). Directly derived topographical variables often serve for modelling vegetation or plant species richness (Gottfried *et al.*, 1998; Guisan & Zimmermann, 2000). Elevation has served in many studies as a proxy for information on habitat diversity and species richness (Wohlgemuth, 1993; Pyšek *et al.*, 2002). Topographic heterogeneity also plays a role in the prediction of species richness at meso-scales (Fleishman & Mac Nally, 2002; Vormisto *et al.*, 2004; Sarr *et al.*, 2005). Because of the great variability in relief in Switzerland, topography was used as the first set of variables. Using a 100-m grid derived from the digital elevation model of 25-m resolution (DHM-25, Bundesamt für Landestopographie), the mean, minimum, maximum, range and standard deviation were derived (E.avg, E.min, E.max, E.ran, E.std) for each 1 km^2 (Table 2). In addition, variables were produced for the proportions of south- and north-facing slopes (N, S) and the relative amounts of different slope classes (FLAT, SLOPE, STEEP).

Environmental set

The definitions of the variables (Table 2) are based on earlier studies of the predictive power of both bioclimatic and habitat heterogeneity variables for total species richness of vascular plants in Switzerland (Wohlgemuth, 1998; Zimmermann & Kienast, 1999; Moser *et al.*, 2005).

The environmental variables temperature and precipitation refer to interpolations of measurements for the period 1961–1990 using DHM-25, 365 stations for precipitation sums, and 158 for average temperatures (Zimmermann & Kienast, 1999). Additional national data were acquired from the same source for the variables: potential direct solar radiation and monthly potential evapotranspiration (PET), using the formula of Turc (1961), which integrates cloudiness with corrected direct solar radiation. Water balance was calculated for July as the sum of precipitation minus PET.

The proportions of calcareous and siliceous substrate within quadrats were derived from the geotechnical map of

Table 1 Land-cover variables according to land-cover types in Switzerland 1992–1997 with 1-ha resolution (Bundesamt für Statistik, GEOSTAT, CH-2010 Neuchâtel).

Variables			Area of Switzerland		Sample plots (n = 353)		
Aggregation	Standard class	Cover type	km^2	%	Affected plots	Average area (ha)	Range used for simulation (ha)
Wooded areas							
L.forest[1]	1	Closed forest	10252.23	24.83	286	29.97	0–99
	2	Open forest	769.33	1.86	138	2.43	0–32
	3	Brush forest	605.14	1.47	72	2.08	0–63
	4	Woods	1089.75	2.64	256	3.12	0–20
L.tree[2]	2–4	Open woody formations	2464.22	5.97	275	7.64	0–67
Agricultural areas							
	5	Vineyards	154.36	0.37	15	0.27	0–54
	6	Orchards, fruit tree plantations	414.80	1.00	94	1.03	0–20
	7	Horticulture	40.36	0.10	16	0.10	0–70
	8	Arable land and grassland, lowlands	8373.55	20.28	201	19.66	0–97
	9	Farm pastures, lowlands	890.11	2.16	141	2.04	0–30
L.agrilow[3]	5–9	Agricultural lowlands	9873.18	23.91	208	23.11	0–97
	10	Mountain meadows	323.16	0.78	46	1.24	0–44
	11	Alpine pastures	5054.85	12.24	173	12.02	0–92
L.agrialp[4]	10–11	Agricultural alps	5378.01	13.02	181	13.26	0–92
Unproductive areas							
L.lake[5]	12	Lakes	1422.35	3.44	24	2.16	0–98
L.river[6]	13	Rivers and river shores	317.32	0.77	94	0.61	0–11
L.unprod[7]	14	Unproductive vegetation	2630.51	6.37	183	6.87	0–68
L.bare[8]	15	Bare areas: glaciers, rocks, sand, screes	6155.99	14.91	147	10.92	0–100
Urban areas							
	16	Buildings	385.08	0.93	107	0.77	0–10
	17	Surroundings of buildings	990.50	2.4	128	1.93	0–28
	18	Industrial buildings	72.92	0.18	21	0.10	0–50
	19	Industrial grounds	129.41	0.31	32	0.18	0–70
	20	Special urban areas	161.13	0.39	55	0.35	0–12
	21	Recreation areas and cemeteries	158.60	0.38	44	0.28	0–12
	22	Road areas	792.97	1.92	187	1.69	0–13
	23	Railway areas	84.49	0.2	27	0.14	0–60
	24	Airports and airfields	15.85	0.04	2	0.02	0–30
L.urban[9]	16–24	Urban areas	2790.95	6.75	221	5.46	0–50

Twenty-four standard classes and nine aggregated land-cover variables were used as a final set for modelling transect species richness (SR_t) per 1 km^2 (superscript numbers 1–9 refer to the legend of Fig. 2b).

Switzerland (De Quervain *et al.*, 1963–1967). Only two substrate types were distinguished because earlier studies have found these to be sufficient (Wohlgemuth, 1998, 2002a; Schmidtlein & Ewald, 2003; Wohlgemuth & Gigon, 2003). Lake and glacier surfaces in the geotechnical map were considered as additional substrate types. Water bodies that are indicated on the 1 : 25,000 topographic maps of Switzerland are available digitally (BFS GEOSTAT/Bundesamt für Landestopographie), with linear information on lakeshore length, river length and creek length.

Land-cover set

It was possible to distinguish between the environmental variables and a set of land-cover variables by concentrating on differences between ecological factors and those that are strongly influenced by human land use. Land-cover information was derived from aerial data and is available on a grid with a 100-m resolution in the land-use/land-cover data package GEOSTAT from the Swiss Federal Office of Statistics (Bundesamt für Statistik, 2001). The standard classification of 24 classes was used, as defined in Table 1. Each variable is indicated as a proportion with respect to a 1-km^2 quadrat. Using FRAGSTATS ver. 3.3 (http://www.umass.edu/landeco/research/fragstats/fragstats.html), landscape metrics were calculated, including Shannon's diversity index, Simpson's diversity index and the largest patch size index.

Numerical analyses

Alternative models were fitted using generalized linear models (GLM, McCullagh & Nelder, 1989) to analyse the relationship

Table 2 Variables used for regression models of transect species richness (SR_t) per 1 km^2

Variable root (1 ha)	Description	Derivation	Model variables (1-km^2 quadrats)
Topography set			
E	Elevation (m)	DEM-25 (Bundesamt für Landestopographie)	E. + avg, max, min, ran, std
Slope	0–3° = flat; 3–30° = slope; 30–100° = steep (%)		FLAT, SLOPE, STEEP
Aspect	340–50° = north; 160–230° = south (%)		N, S
Environmental set			
TY	Temperature, annual average (°C)	Zimmermann & Kienast (1999)	TY. + avg, max, min, ran, std
T1	Temperature, January (°C)		T1. + avg, max, min, ran, std
T7	Temperature, July (°C)		T7. + avg, max, min, ran, std
TR	Temperature, variation: T7–T1 (°C)		TR. + avg, max, min, ran, std
PY	Precipitation, year (mm)		Py. + avg, max, min, ran, std
P7	Precipitation, July (mm)		P7. + avg, max, min, ran, std
R3	Potential direct solar radiation, March		R3. + avg, max, min, ran, std
R7	Potential direct solar radiation, July		R7. + avg, max, min, ran, std
WB7	P7–PET7		WB7. + avg, max, min, ran, std
GEO	GLAC = glaciers, LAKE = lakes, CALC = calcareous substrate, SILI = siliceous substrate	De Quervain *et al.* (1963–1967)	GLAC, LAKE, CALC, SILI
LAK	Lake shores (m)	BFS GEOSTAT (Bundesamt für Landestopographie)	LAK. + avg, max, ran, std
RIV	River length (m)		RIV. + avg, max, ran, std
CRE	Creek length (m)		CRE. + avg, max, ran, std

avg, mean; max, maximum; min, minimum; ran, range; std, standard deviation.

between vascular plant species richness and sets of variables. For all models, the response variable was the transect species richness of vascular plants (SR_t) per 1-km^2 quadrat. Because count data such as species richness can never be less than zero, the assumption of ordinary least-squares regression is likely to be broken (Nicholls, 1989; Crawley, 1993; Mittelbach *et al.*, 2001). We assumed SR_t to be a Poisson-distributed random variable and used a logarithmic link function in GLM (Crawley, 1993). All variables enter the models with linear and quadratic terms. In order to compare the influence of different factor types, the analysis focused on four models using variables from the topography set (topography model), the environmental set (environmental model), the land-cover set (land-cover model), and the synthetic model. All GLM analyses were performed using R ver. 2.1.1 (R Development Core Team, 2005).

For the land-cover set, the 24 standard land-cover classes were aggregated into four categories: wooded areas, agricultural areas, unproductive areas and urban areas (Table 1). An ecologically oriented variable selection was carried out (Luoto *et al.*, 2002), resulting in an aggregation of nine variables with realistic composition. Landscape metric variables were compared with aggregated land-cover classes using univariate correlation coefficients with SR_t, but they were not considered in the models because combinations of selected land-cover variables are easier to interpret.

In order to reduce the large number of initial variables in the environmental model ($n = 61$), the collinearity among the variables was first analysed. Groups of highly correlated variables were defined using a cut level of $R^2 = 0.9$ (corresponding to a variance inflation factor of 10). From each resulting group, only the one with the best GLM performance based on Akaike's information criterion (AIC, Venables & Ripley, 1999) was selected for further analysis, resulting in 30 remaining variables.

In a second step, GLM were built using the refined variable groups. Starting with the best performing single variable model based on AIC, the number of variables was increased until the change in explained deviance D^2 was less than 1% [D^2 = (null deviance − residual deviance)/null deviance, Schwarz & Zimmermann, 2005]. Each of the best *n*-variable models was determined by comparing all possible *n*-variable combinations. If the D^2 stop criterion had not been used, the final models would have included a large number of additional variables that would have accounted for a very small percentage of D^2.

Highly influential plots and outliers were detected in a third analytical step by examining regression diagnostics (residuals vs. fitted values, normal *Q–Q* plots, and Cook's distance plots). Reduced samples were reanalysed (step 2) until no influential plot or outlier remained. One outlier was detected and removed (final $n = 353$): the city of Geneva, of which 96% is urban.

For the final models, linear and quadratic terms were tested separately by backward elimination based on AIC, and nonsignificant parameters were excluded (*z*-statistic, R Development Core Team, 2005).

In order to characterize the models, we calculated the importance of the variables for the model performance. Accordingly, linear and quadratic terms were removed separately or together from the GLM models. Resulting changes in the explained deviance D^2 indicated the importance of the parameters and variables. Model robustness was evaluated with 10-fold cross-validations. For robust results, the mean of 100 internal cross-validations was used. The non-spatially explicit GLMs were tested for spatial autocorrelation using Moran's I correlograms on model residuals (R package ncf by O.N. Bjornstad, ver. 1.0–8). The significances of the autocorrelations ($P < 0.01$) were tested by resampling ($n = 1000$) based on adjusted P-values (Holm, 1979).

Species-richness maps were generated by applying the final models to the pixel values of the corresponding fine-grained factor maps. No predictions were calculated for quadrats with predictor values that exceeded the range of values in the model calibrations. For example, in the land-cover model, areas where > 50% is urban (Table 1) were out of the model range. Thus, cities were excluded from predictions and large lakes were also excluded from the simulations.

According to earlier studies on regional species richness in Switzerland, elevation is the best proxy variable for environmental variability when applied to the regions with areas ranging between 10 and 100 km^2 (Wohlgemuth, 1993). In preliminary analyses of richness at a 1-km^2 scale, average elevation rather than the relative range was found to be more highly correlated with the variability of plants throughout the altitudinal range of Switzerland (193 to 4634 m a.s.l.). Therefore, the predictive power of the four final models was evaluated by applying the models to a varying number of plots using average plot elevation as an upper threshold criterion.

RESULTS

The variable selection for the different models is listed in Table 3. For the topography model, a combination of elevation (average and range), slope (SLOPE) and aspect (N) showed a D^2 of 0.61. Using environmental variables, the best model with a D^2 of 0.69 combined temperature (annual average, range of annual variation), radiation (average in March), substrate (glaciers, calcareous substrate) and water bodies (standard deviation of creek length, maximum length lake shores). The land-cover model, using ecologically oriented aggregations in nine classes, had a D^2 of 0.70. The correlation coefficients between landscape metrics (e.g. patch richness) and SR_t were consistently high, often higher than correlation coefficients between SR_t and single or aggregated land-cover classes (Table 4). Nevertheless, for ease of interpretation of the model results and species richness maps, these landscape metrics were not included as variables in the models. The statistically most meaningful synthetic model had a D^2 of 0.74, and combined elevation (average), land-cover classes (bare areas, lowland agriculture, open woody formations), substrate (calcareous substrate), temperature (range of annual variation) and water body (standard deviation of creek length). If all the variables from the previous models were used, the full synthetic model yielded a D^2 of 0.78.

The relative importance of the parameters used in the models is shown in Table 5. For instance, if both the linear and the quadratic terms of the average elevation (E.avg) in the topography model were removed, the remaining model deviance D^2 would be decreased by 95.4%. The most important variables found were average elevation (topography model, synthetic model), average of mean annual temperature (environmental model) and bare areas (land-cover model). All models were quite robust after a 10-fold cross-validation (Table 6). The cross-validated mean absolute error (MAE) in species richness ranged between 28.5 (synthetic model) and 33.3 (topography model) species. The mean SR_t of the Swiss sample was 224 species (range two to 364 species).

The simulated richness map based on the synthetic model is presented in Fig. 2a. A clipped area is compared with selected environmental factors (Fig. 2b) and with the model predictions derived from the three single variable sets (Fig. 2c). In all maps, the coarse patterns of species-poor high-altitude land in the Alps, in comparison with the more species-rich valleys and lowlands, are readily apparent. At finer scales, patterns differ with respect to the model parameters used. The highest values for SR_t were simulated along steep altitudinal gradients in the mountains (topography and environmental model) and along rivers (land-cover model). In the lowlands of the Central Plateau, the features 'villages' and 'forest edges' corresponded best to locally increased SR_t (land-cover set). The prediction, generated by the synthetic model shows spatial features similar to the previous model predictions. In all maps predicted by the models, the patterns of increased species richness were often arranged distinctively along linear features: straight along mountain valleys, curved along rivers, and in belts around villages, large forests and isolated large mountains.

Mid-elevation peaks for the Swiss sample and for the predictive synthetic model are shown in Fig. 3. Peaks range from 1200 to 1300 m a.s.l. Model performance measured as the correlation (R^2) between modelled and sampled species richness (SR_t) declined (Fig. 4b) when high-elevation plots were successively excluded (Fig. 4a). For the topography, environmental and synthetic models, exclusion of plots below 2000 m does not result in a further loss of predictive power. In contrast, the performance of the land-cover model increased when only plots with an average elevation of < 1900 m a.s.l. were entered, and exceeded the synthetic model below 1400 m a.s.l. Average modelled richness (SR_t) as a function of systematically reduced high-elevation plots shows a clear bell-shaped curve (Fig. 4c). A maximum value is reached with a sample consisting of all plots ranging from 200 to 1800 m a.s.l.

The transect species richness SR_t of the Swiss sample and the residuals of the synthetic model were only moderately autocorrelated in space (absolute values of Moran's $I \leq 0.11$). Significant autocorrelations were found only at a lag distance of 40 km for both the response variable SR_t and residuals of the topography and land-cover models.

Table 3 Selection of model variables.

Variable					
n	Names or selection procedure	AIC	Residual deviance	D^2	Percentage change in D^2
Topography model					
1	E.avg	6082.0	3540.8	0.548	–
2	E.avg + E.ran	5755.3	3210.1	0.590	7.7
3	E.avg + E.ran + N	5677.0	3127.8	0.601	1.8
4	E.avg + E.ran + N + SLOPE	5613.8	3060.6	0.609	1.4
5	E.avg + E.ran + N + SLOPE + S	5586.2	3029.0	0.613	0.7
9	Stepwise regression (AIC; backward elimination & forward selection)	5541.9	2978.7	0.620	
10	All variables	5550.0	2976.8	0.620	–
Environmental model					
1	TY.avg	6615.9	4074.7	0.480	–
2	TY.avg + TR.ran	6051.7	3506.5	0.552	15.1
3	TY.max + R3.ran + GLAC	5561.7	3012.5	0.615	11.4
4	TY.avg + TR.ran + GLAC + CALC	5316.3	2763.1	0.647	5.2
5	TY.avg + TR.ran + GLAC + CALC + CRE.sd	5159.5	2602.3	0.668	3.2
6	TY.avg + TR.ran + GLAC + CALC + CRE.sd + R3.avg	5071.9	2510.7	0.679	1.8
7	TY.avg + TR.ran + GLAC + CALC + CRE.sd + R3.avg + RIV.max	5014.0	2448.8	0.687	1.2
8	TY.avg + TR.ran + CALC + CRE.sd + R3.avg + RIV.max + LAKE + SILI	4965.5	2396.3	0.694	0.97
29	Stepwise regression after reduction of collinearity (VIF>10)	4581.7	1952.6	0.751	–
30	All variables after reduction of collinearity (VIF>10)	4599.9	1948.7	0.751	–
61	All variables	4288.1	1540.9	0.803	–
Land-cover model					
9	L.forest + L.tree + L.agrilow + L.agrialp + L.lake + L.river + L.unprod + L.bare + L.urban	4953.3	2382.2	0.696	–
24	All variables (non-aggregated land-cover classes)	4760.7	2131.5	0.728	–
Synthetic model					
1	E.avg	6082.0	3540.8	0.548	
2	E.avg + L.bare	5618.7	3073.6	0.607	10.9
3	E.avg + L.bare + L.agrilow	5235.4	2686.2	0.657	8.1
4	E.avg + L.bare + L.agrilow + E.ran	5009.8	2456.6	0.686	4.5
5	E.avg + L.agrilow + E.ran + GLAC + L.agrialp	4827.1	2269.9	0.710	3.5
6	E.avg + L.agrilow + E.ran + GLAC + L.agrialp + L.tree	4703.0	2141.8	0.726	2.3
7	E.avg + L.bare + L.agrilow + L.tree + CALC + TR.ran + CRE.sd	4585.0	2019.8	0.742	2.1
8	E.avg + L.bare + L.agrilow + GLAC + L.tree + CALC + TR.ran + CRE.sd	4532.3	1963.1	0.749	0.98
17	Stepwise regression (AIC; backward elimination and forward selection)	4291.4	1694.2	0.784	–
20	All variables	4299.4	1692.3	0.784	–

A change in deviance $D^2 < 1\%$ was used as a stopping criterion. Null deviance = 7830.3; d.f. = 352.

DISCUSSION

A comparison of models and maps

The differences between the four final models (elevation, environment, land use, synthetic) are conspicuous, although some have low explained deviance. A surprisingly high amount of the variability in species richness is associated with topography; this is explained by the wide altitudinal range in Switzerland as well as the high degree of environmental heterogeneity in the quadrats, with flat areas in the lowlands, steep slopes in the mountains and exclusively alpine zones above the timberline. On the landscape scale (grain 1 km^2, extent Switzerland), average elevation was the best proxy variable to explain transect plant species richness nationwide. Elevation range and the corresponding temperature range were the second best variables in the topography set and the environmental models, respectively. This finding contrasts with earlier studies of floristic richness in landscape studies in Switzerland by Wohlgemuth (1993), where range was most important. In the latter study, however, the mapping units corresponded to topographically defined landscape entities such as valleys, and the average areas of the mapping units amounted to 84 and 49 km^2 below and above the timberline, respectively.

Areas with a high proportion of land with a northern aspect showed decreased SR_t in the topography model. The influence of aspect on species distribution and vegetation along mountain ranges is well established (Moor, 1952; Landolt, 1983; Forman, 1995). Nevertheless, only a few specific studies have confirmed an explicit influence of slope orientation on species richness (Harner & Harper, 1976; Nichols *et al.*, 1998; Searcy *et al.*, 2003). The results from the topography model suggest

Table 4 Pearson's correlation coefficients of land-cover and elevation variables (left) and landscape metrics variables (right) with transect species richness (SR_t).

Variables used for models	*r*	Landscape metrics	*r*
*L.bare	−0.627	Mean perimeter–area ratio	0.611
E.min (minimum elevation)	−0.469	Mean patch area	−0.609
*L.forest	0.442	Shannon diversity, 24 classes	0.595
*E.avg (average elevation)	−0.420	Patch richness	0.594
Woods (4)	0.414	Shannon diversity, 9 classes	0.592
E.max (maximum elevation)	−0.362	Simpson diversity	0.583
*L.lake	−0.284	Edge diversity	0.552
*L.tree	0.205	Number of patches	0.542
Mountain meadows (10)	0.205	Interspersion/juxtaposition index	0.514
		Largest patch index	−0.510
		Contagion	−0.429
		Mean Euclidian nearest distance	0.264

Only coefficients >0.2 are displayed. For definitions of land-cover variables see Table 1. Landscape metrics variables were not considered for modelling. *, Variables included in the final land-cover model or in the synthetic model.

that south-facing slopes are more species-rich than those on northern slopes. This result is consistent with the species–energy hypothesis (Currie, 1991; Moser *et al.*, 2005) and can be explained by radiation differences between the two aspects causing contrasting temperature regimes.

Compared with the topography model, the fit of the environmental model is only marginally improved. In this model, both the average and range of annual temperature replace elevation variables. Nevertheless, these temperature variables do not take into consideration local variations due to differences in slope and aspect because the relevant climate stations used for interpolation are always located on flat ground (international standard). Instead, slope and aspect are replaced by average radiation in the environmental model.

The addition of water bodies and calcareous substrate improves model performance. Calcareous substrate plays a significant role in geologically diverse regions and at the landscape scale (Wohlgemuth, 1998, 2002b; Ewald, 2003; Wohlgemuth & Gigon, 2003). If present, a calcareous substrate increases landscape species richness because of increased habitat diversity (Wohlgemuth & Gigon, 2003). Correspondingly, calcareous substrates in temperate zones support a richer flora than acid substrates (Pärtel, 2002; Ewald, 2003). The inclusion of glaciated areas further improved the model performance. This is due to the species–area effect because quadrats fully or partly covered by glaciers support only a few or no vascular plant species. Glaciers in Switzerland cover 2.7% of the surface. In a similar way, high-elevation zones with low species richness greatly improve the model performance. If these zones are excluded from prediction, the performance is significantly lower (Fig. 4b).

The fit of the land-cover model using the full sample was superior to those of both the topography and environmental models, having bare area as the best model predictor. With respect to the sample quadrats, the proportion of bare area is greater at high levels and reflects the steep gradient between the mountains and lowlands linked to plant species richness. In general, in Switzerland, landscape species richness below the timberline is twice as high as that above the trees (Wohlgemuth, 1993). The remaining variables in the land-cover model tended to be equally important for model performance. This supports both the habitat-diversity hypothesis that predicts higher species richness as a result of increased habitat diversity (Shmida & Wilson, 1985) and the species–area effect with decreasing vegetation area at higher elevations. The results were confirmed by the generally high correlation coefficients of landscape metric variables listed in Table 4. When using the land-cover model predictors for extrapolating species richness spatially, the belts along steep altitudinal gradients, such as along valley slopes, are less pronounced than in maps based on environmental model predictors. This is because there are only a few possible land-cover categories along valley slopes – such as forests, mountain meadows and unproductive vegetation – that correspond to the general unimodal response of species richness along the altitudinal gradient. In comparison, the diversity of land cover categories present in lowland landscapes results in a better correspondence to fine-scale differences in species richness.

A further increase in model fit resulted from the synthesis of all predictors from the previous models. Although clearly visible in the mountainous regions, the influence of the altitudinal gradient is less pronounced than in the models of topography and environment. By analogy to the land-cover model, the synthetic model results in more interpretable patterns of species richness in culturally rich landscapes such as the Central Plateau than those that result from models using topography or environmental variables.

The comparison of the four model-predicted maps revealed the importance of including different variables to improve the predictability of species richness over larger and variously structured regions. As many studies have shown (e.g. Francis & Currie, 2003; Currie & Francis, 2004), topographic variables or derived climate variables explain the majority of richness variation at coarse scales across a large geographical extent. If the climatic variation of a region is small, however, land-cover diversity correlates better with species richness, following the habitat-diversity hypothesis.

Table 5 Calibrated linear (*l*) and quadratic (*q*) parameters of variables for selected models and effects of parameter removals on model performance.

	Linear parameter (*l*)			Quadratic parameter (*q*)			Percentage change in D^2		
Variable	Estimate	SE	*P*-value	Estimate	SE	*P*-value	$-l$	$-q$	$-(l+q)$
Topography model									
(Intercept)	5.00E+00	2.00E-02	***	–	–		–	–	–
E.avg	6.42E-04	3.27E-05	***	−3.49E-07	1.05E-08	***	8.2	24.2	95.4
E.ran	8.58E-04	6.35E-05	***	−6.08E-07	6.85E-08	***	3.9	1.7	16.9
SLOPE	4.94E-03	6.17E-04	***	−3.79E-05	5.04E-06	***	1.4	1.2	12.5
N	−1.49E-03	1.61E-04	***	n.a.	n.a.	n.s.	1.8	n.a.	n.a.
Environmental model									
(Intercept)	4.33E+00	3.08E-02	***	–	–		–	–	–
TY.avg	1.27E-03	4.10E-05	***	−6.87E-07	4.10E-08	***	19.1	5.4	29.5
TR.ran	7.61E-03	3.65E-04	***	−3.34E-05	2.35E-06	***	8.2	3.9	12.6
GLAC	−3.47E-02	2.77E-03	***	2.82E-04	3.60E-05	***	3.1	1.1	6.6
CALC	3.85E-03	6.23E-04	***	−1.45E-05	5.40E-06	**	0.7	0.1	5.3
CRE.sd	4.42E-03	5.83E-04	***	−3.98E-05	9.33E-06	***	1.1	0.3	2.5
R3.avg	3.09E-05	3.45E-06	***	n.a.	n.a.	n.s.	1.5	n.a.	n.a.
RIV.max	n.a.	n.a.	n.s.	5.28E-06	6.69E-07	***	n.a.	1.1	n.a.
Land-cover model									
(Intercept)	6.29E+00	7.85E-02	***	–	–		–	–	–
L.bare	−3.60E-03	1.19E-03	**	−1.87E-04	1.09E-05	***	0.2	5.4	15.9
L.unprod	−8.01E-03	1.53E-03	***	−1.55E-04	2.33E-05	***	0.5	0.8	5.9
L.agrilow	−5.12E-03	9.86E-04	***	−7.45E-05	7.13E-06	***	0.5	2.0	4.8
L.lake	−9.41E-03	1.71E-03	***	−5.84E-05	1.91E-05	**	0.6	0.2	4.6
L.forest	−5.12E-03	1.10E-03	***	−4.60E-05	6.34E-06	***	0.4	1.0	4.4
L.tree	n.a.	n.a.	n.s.	−2.48E-04	1.71E-05	***	n.a.	4.1	n.a.
L.agrialp	−5.90E-03	1.09E-03	***	−6.69E-05	9.26E-06	***	0.5	1.0	4.3
L.urban	n.a.	n.a.	n.s.	−2.36E-04	2.21E-05	***	n.a.	2.1	n.a.
L.river	2.09E-02	5.69E-03	***	−2.69E-03	6.87E-04	***	0.2	0.3	0.3
Synthetic model									
(Intercept)	4.94E+00	2.50E-02	***	–	–		–	–	–
E.avg	2.21E-04	4.09E-05	***	−1.60E-07	1.47E-08	***	0.5	2.0	7.49
L.bare	6.52E-03	8.82E-04	***	−1.32E-04	8.98E-06	***	0.9	3.7	7.11
L.agrilow	5.80E-03	5.63E-04	***	−8.29E-05	6.54E-06	***	1.8	2.8	3.26
TR.ran	5.07E-03	4.12E-04	***	−2.36E-05	2.54E-06	***	2.6	1.5	3.17
CALC	4.02E-03	6.28E-04	***	−1.98E-05	5.38E-06	***	0.7	0.2	3.06
L.tree	1.13E-02	1.04E-03	***	−2.28E-04	2.03E-05	***	2.1	2.3	2.31
CRE.sd	5.39E-03	6.08E-04	***	−6.09E-05	9.68E-06	***	1.4	0.7	2.11

***$P < 0.001$; **$P < 0.01$.

For every variable, removal effects of linear and/or quadratic parameters [$-l$, $-q$, $-(l+q)$] are indicated by changes in explained deviance D^2. SE, standard error.

Patterns of modelled species richness

Two conspicuous patterns emerged from model predictions: (1) low species diversity on high mountains is visible in all maps, and (2) there is a high frequency of linear arrangements of increased species richness at the landscape level. The low species number in high mountain environments is widely reported in the literature (e.g. Grabherr *et al.*, 1995; Körner, 1999). About 24% of Switzerland's surface area lies in the alpine zone above the timberline. Here, the species pool of vascular plants is smaller (Wohlgemuth, 2002b) because plant life in high mountains is generally limited by physical components of the environment (Körner, 1999). As a result, species richness on landscape scales is also markedly reduced.

As a result of the peak of species richness at intermediate altitudes (Rahbek, 1995) in the Swiss sample, model-predicted richness maps show belt-like features of maximum species richness along steep hill slopes and around isolated mountains. In the synthetic model, the corresponding steep environmental gradients at the landscape scale are large or steep mountain slopes in the Alps, ridges with smaller ranges in the Jura Mountains, and the edges of large agricultural areas in the lowlands of the species-poorer Central Plateau. The moving window approach amplifies steep factor gradients and landscape structures because of the finer resolution involved (Araújo *et al.*, 2005). Equally, by expanding the real underlying richness features, the process can be considered a soft-focus effect.

Table 6 Model robustness tested by cross-validation: model fits D^2 and mean absolute errors (MAE) in number of species for the four proposed models.

Model	Number of Variables	Number of Parameters	D^2	D^2 10-fold CV*	MAE	MAE 10-fold CV*
Topography	4	7	0.609	0.589	32.5	33.3
Environmental	7	12	0.686	0.653	29.7	31.1
Land cover	9	16	0.696	0.652	29.0	30.9
Synthetic	7	14	0.742	0.706	27.0	28.5

CV*, mean of 100 internal cross-validations (10-fold).

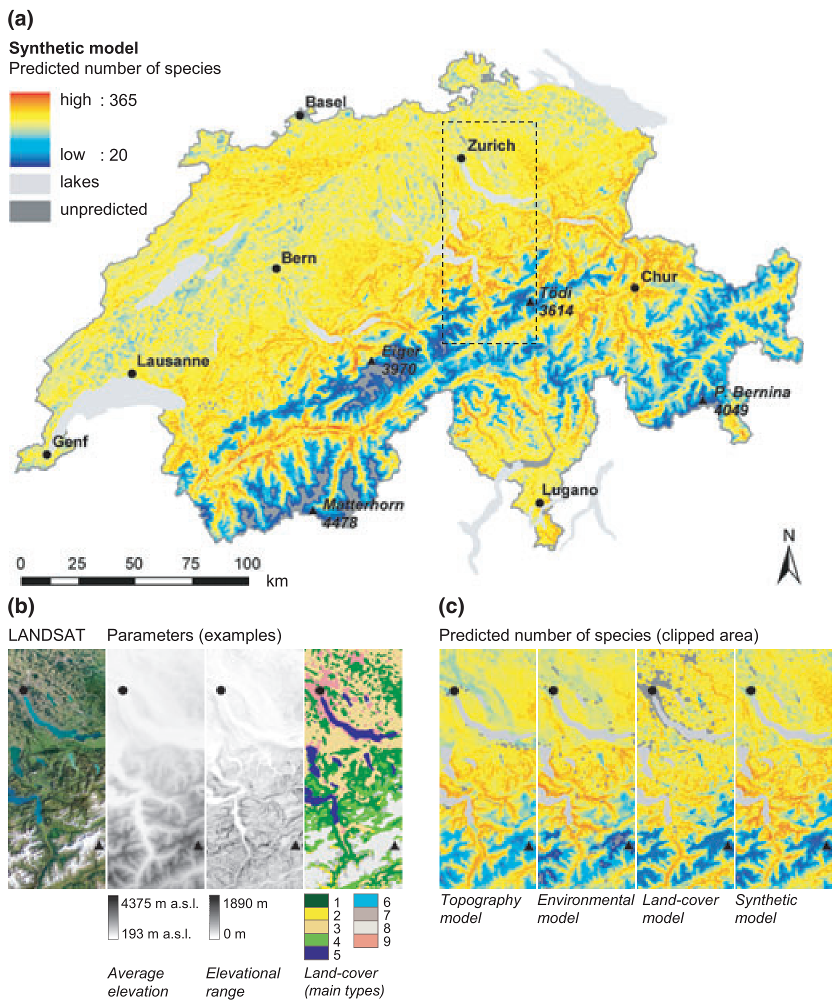

Figure 2 Extrapolation of vascular plant species richness in Switzerland using parameters of different generalized linear models: (a) synthetic model; (b) clipped area: composed satellite image ESA/Eurimage/swisstopo, NPOC 2006 swisstopo (DV033492), mean and range of elevation, dominant land-cover types; (c) topography model, environmental model, land-cover model, synthetic model. Variables are defined in Table 1.

Richness belts as spatial extensions of mid-elevational peaks

In the richness map derived from the synthetic model shown in Fig. 2, hotspots in the form of more-or-less isolated areas or localities are hardly visible. Rather, linearly shaped features or belts are frequent. Currently, it seems there is no review available of the occurrence of such belt-like, linear or curvilinear richness patterns within landscapes. However, many studies have highlighted the importance of linear structures such as riverine landscapes (Ward, 1998; Stohlgren *et al.*, 2005), green lanes (Croxton *et al.*, 2005), roads (Saarinen *et al.*, 2005) and field edges (Croxton *et al.*, 2002; Meek *et al.*, 2002). Many of the belt-like richness features found in the present study correspond to the edges of different land-covers (Nagy, 1997; Cullen *et al.*, 2001). In contrast, the belt-like features related to steep topographic gradients, for example along the valleys in the Alps, need a different explanation. In the literature, mid-elevational peaks of species richness or, more generally, mid-domain effects have been the subject of lively discussion (Rahbek, 1997; Zapata *et al.*, 2003; Colwell *et al.*, 2004; McCain, 2005). Many single factors have

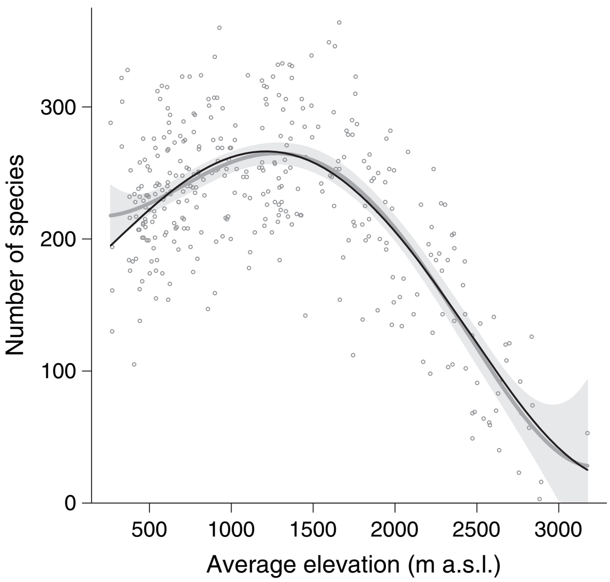

Figure 3 Mid-elevation peaks of vascular plant species richness on landscape scales (1 km^2) in Switzerland: grey line, fourth-order polynomial regression curve for the Swiss sample (dots: n = 353; $SR_t = 224.3–590.2 \times E.avg - 666.9 \times E.avg^2 + 20.5 \times E.avg^3 + 118.9 \times E.avg^4$; $R^2 = 0.54$; $P < 0.0001$); hatching, corresponding 95% confidence interval of the prediction; black line, fourth-order polynomial regression curve for samples of the simulated map (synthetic model: 1-km step for sampling; $SR_t = 215.9–7225.4 \times E.avg - 7420.0 \times E.avg^2 + 1081.2 \times E.avg^3 + 715.8 \times E.avg^4$; $R^2 = 0.77$; $P < 0.0001$).

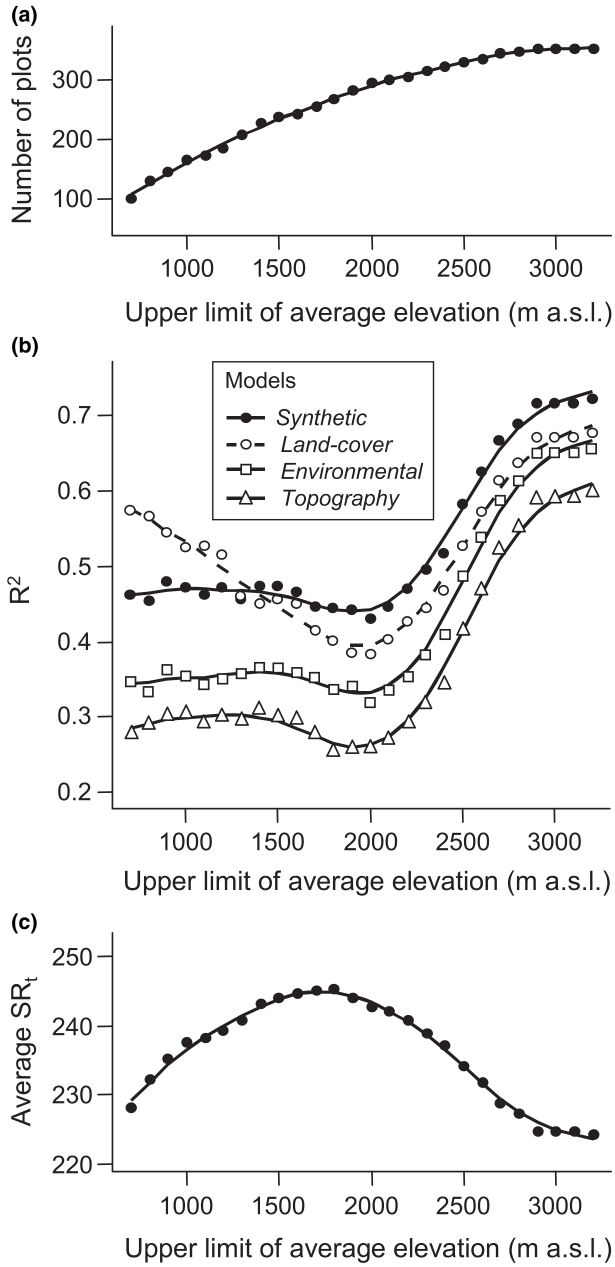

Figure 4 Effects of reducing sample size on model performance. (a) Cumulative number of sample plots sorted by mean elevation of each quadrat. (b) Change of model fits as a result of reduced sample size according to (a). Each model fit is expressed as the correlation (R^2) between model prediction and sampled transect species richness SR_t. (c) Average SR_t of plots with the same sample restrictions as applied in (a) and (b). All data series have been smoothed with cubic smoothing spline functions.

been cited to explain these mid-elevational peaks, and complex interrelationships among climatic factors are presumed to influence these diversity trends (Brown, 2001; Lomolino, 2001). In the present study, peaks of increased species richness were found at average elevations of 1200–1300 m a.s.l. both in the real data and in maps produced by the spatially applied model predictors (Fig. 3). In the richness maps, the unimodal peak appeared as linear or curvilinear features along the valley slopes in the Alps.

Implications for monitoring strategies

The rapid progress made recently in modelling both species distribution and species richness (Guisan *et al.*, 2002; Deutschewitz *et al.*, 2003; Engler *et al.*, 2004) has led to pressure to implement model results in the development of nature-conservation strategies (Ferrier, 2002; Noss, 2004). Systematic field samples, such as those presented here, help to improve the comprehensiveness of spatial biodiversity data across a planning region and may reduce sampling and expert bias (Noss, 2004). Model predictions of species richness based on fine-grained information in the environment have proved to be a cost-efficient approach for conservation. As a surrogate for factor maps over larger regions, fine-grained, remotely sensed information has great potential for use at landscape scales (Gould, 2000; Ortega *et al.*, 2004; Rocchini *et al.*, 2005).

In the Swiss sample, there is inadequate information on urban environments, which cover up to 7% of Switzerland. The impact of urban areas on biodiversity is important, and recent studies have reported high species richness in the city areas of Basel, Zurich and Geneva (Brodtbeck *et al.*, 1998; Landolt, 2001; Wyler, 2004). Either such areas were excluded from the model predictions (land-cover model), or the species richness at these locations was underestimated (synthetic model). A careful analysis of the features in the Central Plateau revealed that a locally high species richness often coincided with the presence of smaller villages and forests in the vicinity where the land-cover diversity increases. Corresponding quadrats for cities and urban centres are lacking in the Swiss sample (Table 2). The largest portion of urban land encountered in a sample quadrat was 50%. The only sample quadrat assessed in a city with 96% of urban area was eliminated as an outlier. For denser urban landscapes, no data on transect species richness were available. However, not only are cities species-rich because of the occurrence of many non-native species (Landolt, 2001; Tait *et al.*, 2005), but when present in comparable landscapes, they have also been found to be naturally rich in vascular plant species (Kühn *et al.*, 2004). To conduct better surveys of biodiversity in regions experiencing rapid change (Antrop, 2004; Wania *et al.*, 2006), the survey grid should be extended or stratified to include urban land.

The model-predicted richness maps presented here can be used to detect zones of low and high species richness, and to derive strategies for either upgrading or protecting landscape biodiversity as part of national conservation plans. This analysis is a first step that should be extended, for dependent variables, by including analyses of additional taxa (Bonn & Gaston, 2005) and specific species lists such as rare and common species (Vázquez & Gaston, 2004), Red-Listed species and functional groups. For explanatory variables, the inclusion of more detailed and ecologically relevant land-cover categories will improve model performance.

CONCLUSIONS

The approach presented here has proved useful for the detection of species-rich and species-poor areas at a fine grain over large areas. It allows for a comparison of landscape species richness with respect to environmental variables, and provides a potentially valuable basis for deriving national nature conservation strategies. Our analyses lead us to propose that more emphasis should be placed on the implementation of 'hot belts' in conservation planning. The present study demonstrates the complexity of linear arrangements of increased species richness at the landscape scale, which in turn are the result of the different spatial effects of ecologically relevant variables such as steep environmental gradients in the mountains, or high land-use diversity along corridors. However, agricultural and urban land that can undergo rapid temporal and spatial environmental change still needs further study.

The approach of using a large extent/grain ratio for predicting richness may be applied to any landscape as long as the required basic data for species and environmental variables are available. It is axiomatic that, as the size of the region concerned expands, the diversity of landscape features is likely to increase, although in homogeneous landscapes, such as the prairies in the USA, the extension will have to be very large. It follows that the number of factors that influence species richness at landscape scale are also likely to increase. In order to deal with this increasing factor complexity, it is proposed that species richness should be modelled using sets of appropriate variables that reflect the underlying spatial characteristics of the region concerned.

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