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Modelling floristic species richness on a regional scale: a case study in Switzerland

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In this paper a multivariate linear regression model is proposed for predicting and mapping regional species richness in areas below the timberline according to environmental variables. The data used in setting up the model were derived from a floristic inventory. Using a stepwise regression technique, five environmental variables were found to explain 48.9% of the variability in the total number of plant species: namely temperature range, proximity to a big river or lake, threshold of minimum annual precipitation, amount of calcareous rock outcrops and number of soil types. A considerable part of the unexplained variability is thought to have been influenced by variations in the quality of the botanical inventory. These results show the importance of systematic floristic sampling in addition to conventional inventories when using floristic data as a basis in nature conservation. Nevertheless it is still possible to interpret the resulting diversity patterns ecologically. Regional species richness in Switzerland appears to be a function of: (i) environmental heterogeneity; (ii) threshold values of minimum precipitation; and (iii) presence of calcareous rock outcrops. According to similar studies, environmental heterogeneity was the strongest determinant of total species richness. In contrast to some studies, high productivity decreased the number of species. Furthermore, the implications of this work for climate change scenarios are discussed.

Keywords: environmental heterogeneity; floristics; regional scale; regression model; species richness; precipitation threshold.

Introduction

Which region in Switzerland has the highest number of vascular plant species? Is it possible to create a map showing floristically poor and rich regions? Which are the most important environmental determinants of regional species richness? These questions sprang to mind when a large set of floristic distribution data became available, based on the distribution atlas of phanerogams and pteridophytes of Switzerland (Welten and Sutter, 1982; Wohlgemuth, 1993). The easiest way to answer the first and second questions is to count the number of species per mapping area and to display the results graphically. There is, however, a problem: how reliable are these data? During the mapping of the distribution of the Swiss flora from 1967 to 1979, about 170 botanists were involved in collecting data. Having such a high number of collaborators usually implies differences in collecting quality resulting in mapping inadequacy. For this reason, either precise instructions were given for carrying out the field work or standards for botanical systematics were used. However, several authors pointed out that the collecting quality is still a weak point (Rich and Woodruff, 1992; Palmer, 1995). Taking this into account, the aim was to model total species richness according to several readily available environmental variables (Richerson and Lum, 1980; Hnatiuk and Maslin, 1988; Heikkinen, 1996; Mourelle and

Ezcurra, 1996). The research is based on the hypothesis of 'environmental heterogeneity' (Thienemann, 1956) which is also comparable with Whittaker's (1977) notion of 'delta diversity' or Shmida and Wilson's (1985) 'large-scale habitat diversity'. Thienemann's hypothesis suggests that an increasing diversity of environmental factors coincides with an increasing number of species. Since, despite its small size, Switzerland has an enormous variety of environmental sites, it provides a good testing ground for this hypothesis (Malyshev, 1991). The purpose of this study is to map predicted species richness within Switzerland, to evaluate environmental correlates of species richness, and to compare the results with previous studies. Furthermore, the results are discussed with respect to climate change scenarios.

Material and methods

Floristic data: dependent floristic variables

The data set is drawn from the distribution atlas of pteridophytes and phanerogams of Switzerland (see above) and two additional supplements (Welten and Sutter, 1984; Wagner, 1995). The study area (41.285 km^2; Fig. 1) was divided into 593 mapping polygons: 350 areas below the timberline (see Fig. 2; the timberline in Switzerland varies between 1700 and 2300 m a.s.l.), 215 alpine areas (above the timberline) and 28 lake areas. In the present study, only areas below the timberline are considered.

In contrast to almost all similar inventories in other European countries, the mapping areas in the Swiss inventory were defined by topography. In order to simplify classification and avoid misidentification of plants in the field, subspecies which are difficult to distinguish were mostly grouped to species or species groups. Altogether, 2573 species were mapped, whereas in most descriptions of Swiss flora about 3000 species are distinguished (Hess *et al.*, 1976–80; Aeschimann and Burdet, 1994). In the distribution maps, the species are featured in two frequency classes: rare and frequent. Because the definitions of these

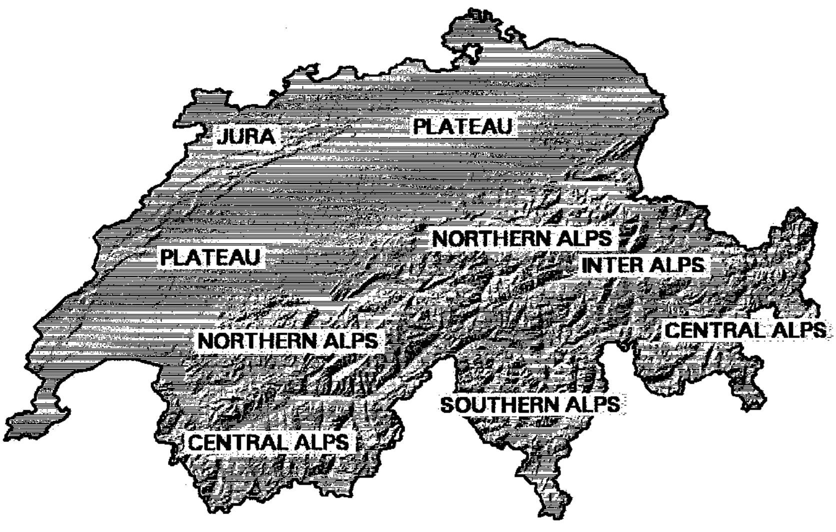

Figure 1. Location of the study area showing the major regions.

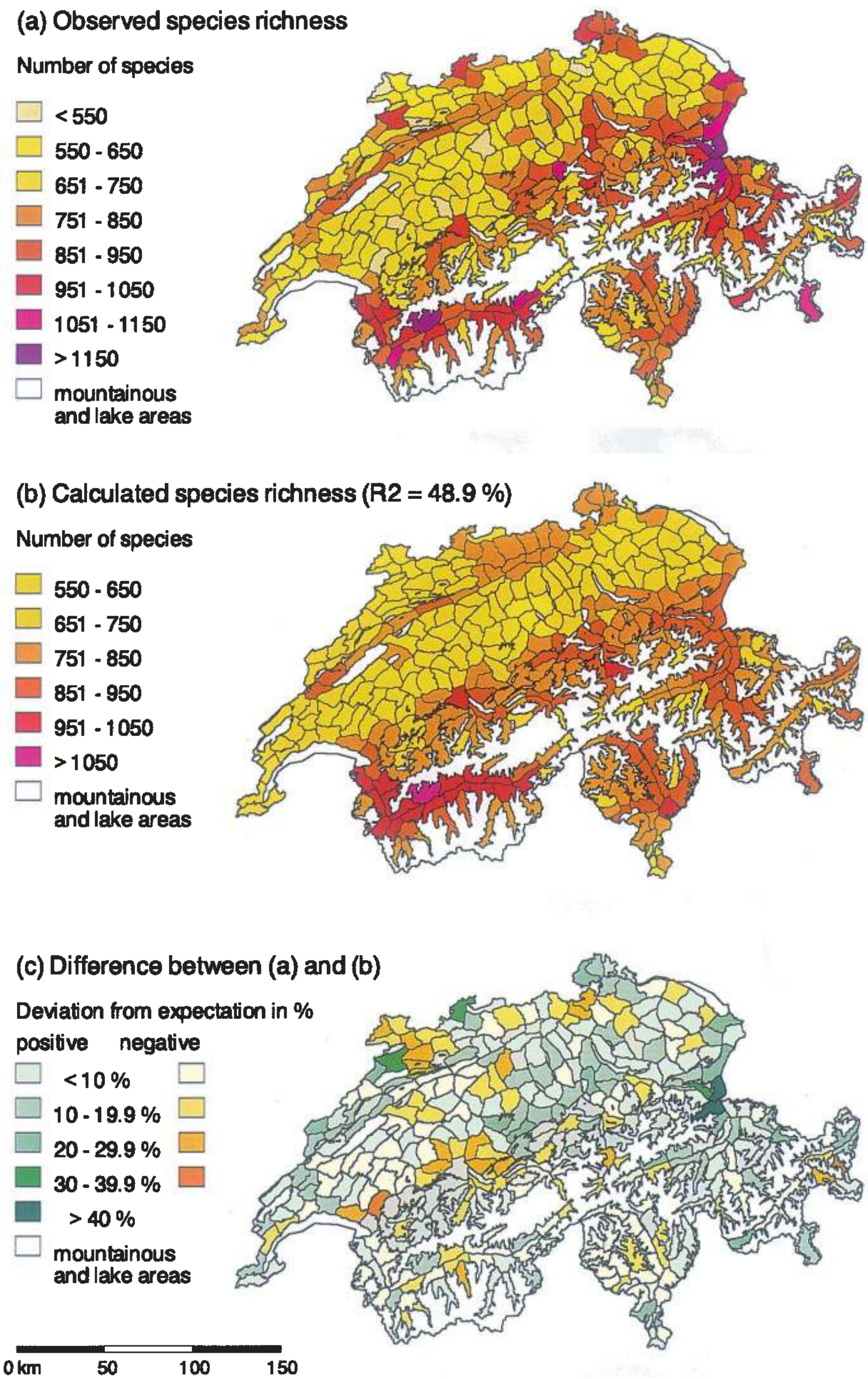

Figure 2a–c. (a) Observed species richness in Switzerland according to the mapping (1967–1979) and two additional supplements. (b) Calculated species richness according to the regression model with five independent variables. (c) Residuals of the regression model.

two classes are not consistent for all species, presence or absence values are used instead in all the following analyses.

Landscape data: independent environmental variables

The landscape data include a number of different factors which are mostly available in a digitized form (e.g. digitized maps). Each of the existing environmental maps was overlaid with the polygons of all mapping areas and its contents attached to these areas using GIS techniques (ARC/INFO). Thus, each mapping area is characterized with a multitude of environmental factors finally used as variables in the analysis (Table 1).

Area. Usually the size of an area (ARE) is the most important single variable for explaining species richness (e.g. Williams, 1964; Shmida and Wilson, 1985; Rosenzweig, 1995). Independent of the scale of the inventory, this variable is generally eliminated by choosing mapping areas of equal size. Due to the fact that Switzerland is environmentally very heterogeneous, square mapping units will often include very different climatic and geological areas. In the Swiss inventory, the mapping areas were therefore chosen topographically in order to minimize meaningless distribution patterns (Welten, 1971). At the same time, an attempt was made to choose more or less equally large areas to avoid the complicating variable of area. The average size of lowland areas was $86.2\,km^2$ (± 28.3), with a range of 11 to $172\,km^2$.

Temperature. Metric temperature data (TMAX1-12, TMIN1-12, T1-12, TY, TR1-12, TRY) were interpolated from meteorological stations using a digital elevation model (DEM) which provides information about elevation, aspect and slope for each 250 m point of the grid covering the whole of Switzerland (Brzeziecki *et al*., 1993). Monthly evapotranspiration (EV1-12) was calculated according to Turc's (1954) formula where mean annual temperature, mean cloudiness and solar radiation were interpolated from meteorological stations using DEM and spatial interpolation techniques (spline interpolation).

Additionally, a map featuring temperature levels based on phenological observations (Schreiber *et al*., 1977) was used to obtain categorical temperature variables (RTL). These data correlate highly with mean annual temperature. Because they are based on field work (mapping) and expert knowledge, they are considered more realistic. Using a similar approach with phenological observations, a map of the distribution of the warm wind, termed the Foehn effect (FOE), was tested.

Precipitation. Different precipitation measures were considered, such as annual and monthly sums (PM1-12, PMY), minimum precipitation within a mapping area (PMIN1-12, PMINY), and range of sums of precipitation within a mapping area (PR1-12, PRY). Different threshold values of the minimum annual precipitation (PTY80-120, PT1-12) occurring within a mapping area were also tested. The monthly water balance was calculated as well (WB1-12; monthly evapotranspiration minus monthly precipitation).

Geology. The number of geotechnical units (NGU) was counted in each mapping area according to the geotechnical map of Switzerland (1:200 000; De Quervain *et al*., 1963–1967). This includes information about soil mechanics, rock mechanics and the engineering aspects of applied geology. Rock outcrops are habitats containing many specialized species. The presence of rocky outcrops should, therefore, increase regional species diversity. In estimating this, two different sources were consulted: (i) information about

Table 1. List of variables initially used in the analysis

Variable	Description	Units	Derivation
Area			
ARE	Size of area per mapping areas	km^2	Map of mapping areas 1:100 000
Temperature			
TMAX1-12	Monthly absolute maximum temperature	°C	Interpolated from meteorological stations using digital elevation model (DEM: resolution 1 km^2)
TMIN1-12	Monthly absolute minimum temperature	°C	
T1-12, TY	Mean monthly and annual temperature	°C	
TR1-12, TRY	Range of monthly and annual mean temperature	°C	
EV1-12	Mean monthly evapotranspiration after Turc (1954)	cm	Mean temperature, cloudiness and radiation simulation with DEM (resolution 0.5 km^2; Zimmermann and Kienast, 1995)
RTL (categorical)	Range of temperature	3–18	Temperature levels map 1:200 000 based on
FOE (categorical)	Foehn effect (warm wind)	0–5	(Schreiber *et al*., 1977)
Precipitation			
PMIN1-12, PMINY	Monthly and annual minimum precipitation	cm	Precipitation map 1:400 000
PM1-12, PMY	Mean monthly and annual precipitation	cm	
PR1-12, PRY	Range of monthly and annual precipitation	cm	
PTY80-120 (categorical)	Threshold of minimum annual prec.: < 80, 90, 95, 100, 110, 120 cm	0–5	
PT1-12 (categorical)	Threshold of minimum monthly prec.: different values (cm)	0–5	
WB1-12	Mean monthly water balance	cm	Monthly evapotranspiration minus monthly precipitation
Geology (categorical data)			
NGU	Number of geotechnical units	3–15	Geotechnical map (De Quervain *et al*., 1963–1967)
RT	Range of rock outcrops	0–4	Geological map
RC	Range of calcareous rock outcropping	0–3	Aerial photography
RCC	Weighted range of rock outcrops	0–9	2RT + RC
Soil (categorical data)			
NST	Number of soil types	5–28	Soil quality map for
SG	Quantity of gravel and stones	1–5	production 1:200 000
ST	Thickness of soil	1–5	(Häberli, 1980)

Table 1. *Continued.*

Variable	Description	Units	Derivation
Diverse variables (categorical data)			
PRL	Proximity to big river or lake (< 700 m a.s.l.)	1–3	Mapping areas
AMA	Adjacent mountainous areas	1 or 2	Mapping areas
SAE	Slope, aspect and elevation diversity	15–288	DEM (resolution 0.5 km^2)
SAE-S	South exposed slope diversity	km^2	DEM (resolution 0.5 km^2)
Quality of sampling (categorical data)			
NBA	Number of botanists per mapping area	1–3	Original collecting protocol
CQ	Collecting quality	1 or 2	According to the highest species numbers per mapping area

outcrops rock provided in Welten and Sutter (1982) based on their interpretation of the geological map; and (ii) the absolute area containing calcareous rock based on aerial photography (Hegg *et al.*, 1993). These two sources were used separately and then combined according to the following equations:

$$RT = (C + S)$$

where C is calcareous rock outcrops ranging from 0 (none) to 2 (frequent); S is non-calcareous rock outcrops ranging from 0 to 2; and RC is area covered with calcareous rock ($0 = 0\,km^2$; $1 = 0.1–5\,km^2$; $2 = 5–20\,km^2$; $3 = >20\,km^2$)

$$RCC = 2RT + RC$$

Soil. Based on the Swiss soil quality map (1:200 000; Häberli, 1980), the number of soil types (NST) was counted in each mapping area. A soil type was defined with regard to its quality for agricultural production relying also on information from the topographic maps. There are zonal and azonal soil types. Derived quality variables such as the quantity of gravel and stones (SG) and the thickness of the soil horizons (ST) were also analysed.

Slope and aspect. It was assumed that topographic diversity, and in particular the number of south-facing slopes, are important variables influencing species diversity. Based on a DEM: (i) a diversity variable (SAE) was created using the number of different classes of altitude (< 300, 500, 800, 1100, 1400, 1800, 2200, >2200 m a.s.l.), slope (<10, 20, 30, 40, 50, 60, 70, 80, > 80°) and aspect (0–45, 90, 135, 180, 225, 270, 315, 360°) within a mapping area; and (ii) a slope variable (SAE-S) was calculated containing the summarized area of polygons with aspects from 90 to 270 degrees and slopes from 10 to 80 degrees.

Proximity to a big river or lake. A simple but rather effective variable (PRL) was obtained by measuring, within a mapping area, the distance of the nearest point below an altitude of 700 m a.s.l. to the next big river or lake: 1 = adjacent; 2 = <5 km distance; 3 = >5 km distance to next big river or lake. This variable subsumes various patterns of environmental diversity.

Adjacent mountainous areas. Mountainous species are mostly distributed in areas above the timberline, whereas many species are found only in lowlands. In the transition area between lowland and mountainous areas both species types may be present. Thus, in transition areas more mountainous species can be expected than in lowland areas not adjacent to mountains. This effect is represented with a dummy variable (AMA): 2 = adjacent to a mountainous area; 1 = not adjacent to a mountainous area.

Collection quality variables

Botanist per mapping area. Because the number of botanists who participated in the mapping of one area varied considerably, the variable 'botanist per mapping area' (NBA) was broken down as follows: 1 = one botanist; 2 = two botanists; 3 = three and more botanists.

Collecting quality. Many botanists mapped more than one area. To indicate the quality of the mapping, a dummy variable (CQ) was calculated by marking the botanists of areas with obviously high numbers of species (in correlation with RTL) and by weighting mapping areas with a 2 if one of these botanists was involved in the mapping. If they were not, the mapping area was weighted with a 1. This variable is derived from the dependent variable and thus violates the fundamental principles of the regression model. However, it provided an objective way to estimate quality (see Discussion).

Species richness model: multivariate linear regression

In order to model species richness as a function of environmental parameters, a multivariate linear regression was used (Hamilton *et al*., 1963; Johnson *et al*., 1968; Buckley, 1985). The dependent variable Y was defined as the number of species per mapping area. After reducing the variables according to their correlation with each other, 123 variables were analysed using stepwise regression and covariance analysis. All analyses were calculated with subsets and combinations of variables. The amount of variability about the mean was calculated with both R^2 and adjusted R^2. Adjusted R^2 takes into consideration the number of degrees of freedom and the number of observations. The stability of the model was tested by cross-validation at the level of 95, 90, 80, 66.6 and 50% using Monte-Carlo testing (500 repetitions). In addition, stepwise regression was calculated with only 50% of the data (10 repetitions), and covariance analysis with both 50% and 30% of the data.

Results

Mapped species richness

The number of species was counted in each mapping area. The mean number of species in all areas below the timberline was 776 and ranged from 484 to 1434 species. In Fig. 2a, the observed species richness in all areas below the timberline is indicated in different colours. Areas rich in species (reddish and purple colours) are located in various parts of the country, particularly in the Central Alps, the Inter Alps and the Northern Alps and in some parts of the Jura Mountains (Fig. 2a and Fig. 1).

Modelled species richness

Because many of the variables listed in Table 1 are either highly correlated or meaningless indicators of diversity, the variables were reduced to a set of meaningful or independent variables (Table 2). Collecting quality variables were partly included in the analysis. The proposed model excluding quality variables is shown in Table 3. It consists of the five independent environmental variables RTL (range of temperature), PRL (proximity to a big river or lake), RCC (weighted range of rock outcrops), PTY100 (threshold of minimum annual precipitation: < 100 cm) and NST (number of soil types) that together explain 48.9% (or with adjusted R^2 statistic 48.2%) of the variability in the dependent variable. The contribution of the independent variables is shown in Fig. 3, where R^2 appears to be dependent on a number of additional variables. In Table 4, the correlations between the variables finally chosen are presented. Most of these variables have the highest correlations with the number of species.

A considerable part of the variability in regional species richness is defined by RTL. The second and the third most important variables are PRL and RCC, which each increase R^2

Table 2. List of variables finally used in the multivariate regression analysis

Area	Temperature	Precipitation	Geology	Soil	Diverse variables	Collecting quality
ARE	TRY	PRY	NGU	NST	PRL	NBA
	TR7	PTY95	RT	ST	AMA	CQ
	TMIN7	PTY100	RC		SAE	
	TMAX1	PT5	RCC		SAE-S	
	EV9					
	RTL					
	FOE					

Table 3. Final regression model using a stepwise regression procedure, with a variability of species richness of 48.9% (adjusted 48.2%)

$R^2 = 48.9\%$; R^2(adjusted) = 48.2%
s = 99.39 with 350 − 6 = 344 degrees of freedom

Source	Sum of squares	*df*	Mean square	F-ratio
Regression	3253803	5	7e + 5	65.9
Residual	3398179	344	9878.43	

Variable	Coeff.	SE of coeff.	t-ratio	p-value (t)	Standardized estimate of coeff.
Constant	582.543	23.45	24.8	0.0001	0.00
RTL	13.8677	1.574	8.81	0.0001	0.39
PRL	−42.6519	6.045	−7.06	0.0001	−0.29
RCC	12.4411	2.736	4.55	0.0001	0.21
PTY100	19.1183	4.557	4.20	0.0001	0.17
NST	5.12634	1.444	3.55	0.0004	0.15

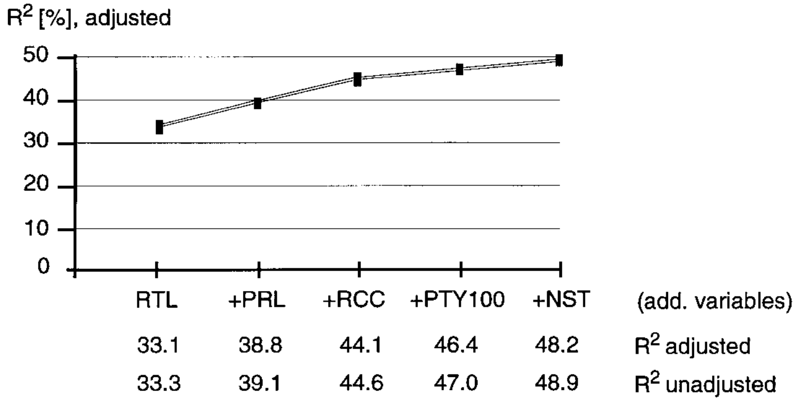

Figure 3. Change in variability of species richness in the regression model (adjusted and unadjusted R^2).

Table 4. Correlations between the five variables finally used in the regression model

	No. of species	RTL	PRL	RCC	PTY100	NST
No. of species	1.00					
RTL	0.58	1.00				
PRL	−0.30	−0.11	1.00			
RCC	0.37	0.39	0.21	1.00		
PTY100	0.30	0.16	−0.19	0.07	1.00	
NST	0.33	0.32	0.11	0.40	0.00	1.00

by more than 5%. The last two variables (PTM100 and NST) enhance R^2 by about 2% each. Figure 4a–e shows the maps for the five independent variables.

The following variables were removed during the selection procedure (significance level of 15% for partial F-value) since they do not contribute much to model quality: ARE (size of area), EV9 (mean evapotranspiration in September), SAE-S (south-exposed slope diversity), PTM95 (threshold of minimum annual precipitation: < 95 cm; selected instead of PTM100), TMAX1 (absolute maximum temperature in January), and PT5 (precipitation in May; selected instead of SAE-S). There was no correlation between the size of the mapping area (ARE) and the number of species per mapping area (Fig. 5; $r = -0.02$) despite the wide range of values (11 to 172 km^2).

The predicted number of species is illustrated in Fig. 2b. The diversity pattern is smoother but the fundamental pattern of species richness actually observed is preserved by the model. In Fig. 2c, the residuals of the numbers of species per area are shown in percentages.

The robustness of the model

Cross-validation with different levels of percentages showed a range of excess error of 5.3 to 7.1%. The results of the stepwise regressions of the variables with only 50% of the data corresponded highly with the results of the starting model. The found variables and their positions counted most frequently are listed below (variables of the starting model are shown in bold):

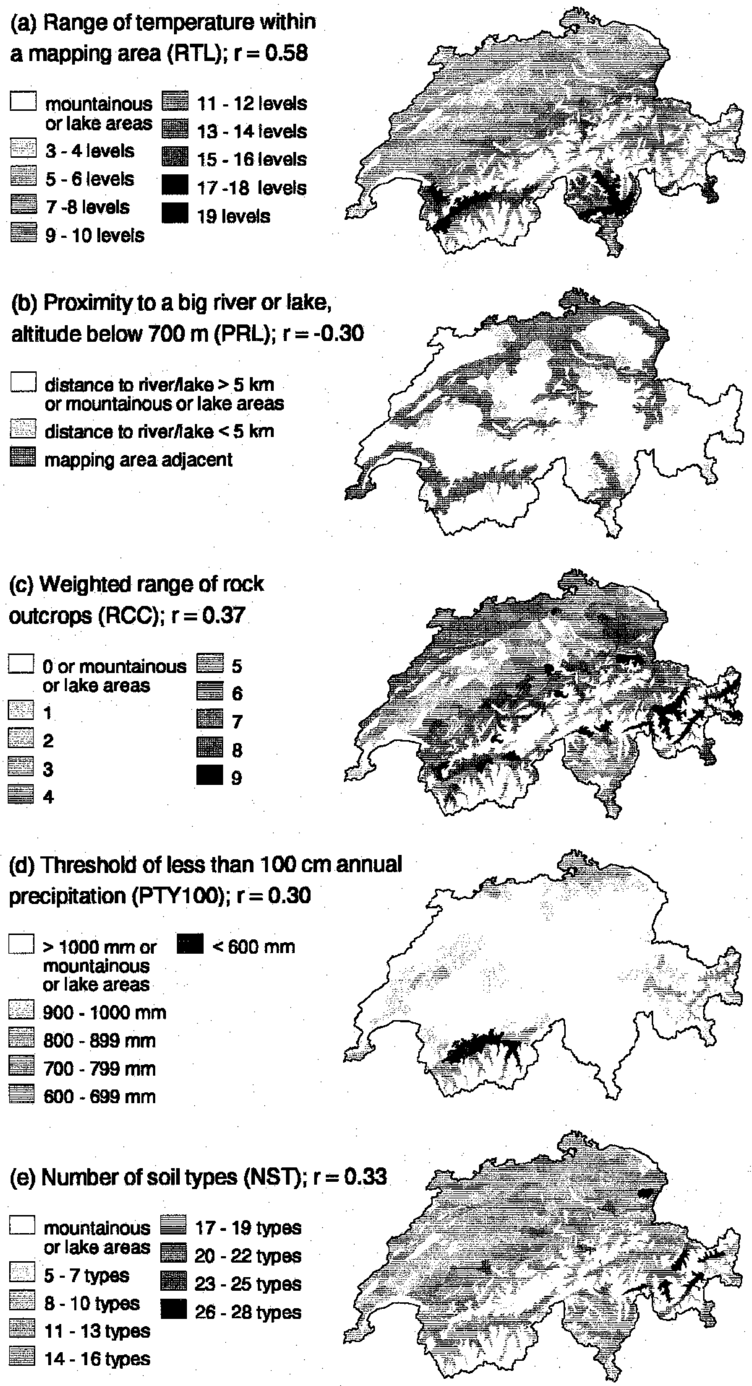

Figure 4a–e. Patterns of the five ecological variables finally used in the regression model.

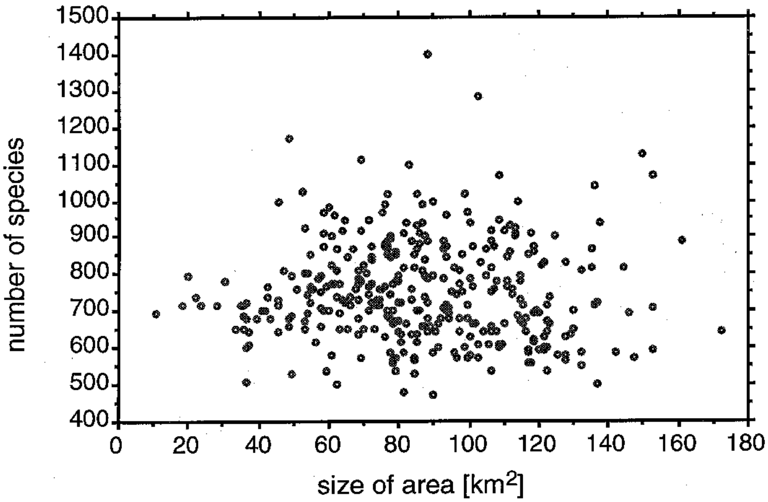

Figure 5. Distribution of size of area and number of species per mapping area in areas below the timberline.

(i) **RTL**, PRL, FOE (Foehn effect),
(ii) **PRL**, FOE, AMA (adjacent mountainous area),
(iii) PTY95, PRL, **PTY100**,
(iv) **RCC, PTY100**, TMAX1,
(v) **NST**, NGU (number of geotechnical units), ARE (size of area).

Discussion

Ecological interpretation of the model variables

1. Range of temperature (RTL). The most important environmental variable explaining regional variation in total species richness in Switzerland is RTL within one mapping area. Nearly as much variation can be explained by the variables: (i) mean annual temperature; (ii) altitudinal range; or (iii) degree-days. However, the map based on phenological observations has several advantages over the temperature, degree-day or altitude map for the following reasons:

(i) it is based on field work and expert knowledge,
(ii) it includes small-scale observations,
(iii) it is independent of the existing network of climate stations.

According to other investigations (Johnson *et al.*, 1968; Bowers and McLaughlin, 1982; Heikkinen, 1996), the altitudinal range, or in more ecological terms, the range of temperature levels is the most important determinant of environmental diversity.

2. Proximity to a big river or lake (PRL). This variable turned out to be one of the five variables to best explain total species richness. This is due to the fact that many rare species, and therefore a large part of the diversity, are concentrated in river and lake landscapes. There are different explanations for the increased species richness of these landscapes: (i) the climate of some large valleys in Switzerland are dramatically affected by warm Foehn-winds (Foehn effect, FOE); and (ii) proximity to a lake or big river results locally in milder climates. (i) and (ii) lead to a prolongation of the growing period and therefore enable a wider spectrum of plant species to grow. (iii) In these landscapes site conditions vary greatly including, possibly, wetlands, old and abandoned river courses, places eroded through mechanical disturbance (Gregory *et al.*, 1991; Ward, 1988); (iv) there are no immigration barriers within these landscapes.

3. Threshold of less than 100 cm annual precipitation (PTY100). The threshold of less than 100 cm annual precipitation occurring in parts of a mapping area turned out to be a suitable measure for explaining part of the species richness. A possible ecological explanation is that, in areas with low precipitation, the presence of dry site conditions is more frequent than in areas with overall high precipitation. Species with a low demand for water and nutrients are able to grow at these sites whereas in less dry conditions they would be competitively excluded by plants with higher water and nutrient requirements. The effect within a region is an increased number of species because these species are an addition to the number of species of mostly mesic plants.

The parameter of annual precipitation used without any threshold has not been found to correlate with total species richness according to other studies (Woodward, 1987; Leathwick, 1995).

4. Weighted range of rock outcrops (RCC). The presence of rock outcrops is a well-known but rarely discussed variable that increases regional species richness. In general, on rock outcrops and on neighbouring shallow soil deposits, many specialized species which can stand the extreme site conditions do occur. There is, in addition, a difference between calcareous and non-calcareous rock and their related soil conditions. Considering the indicator values of individual plants for Switzerland (Landolt, 1977), the number of species occurring primarily or exclusively on alkaline substrate is twice (about 950 species) that of those occurring primarily or exclusively on acid substrate (about 490 species). The distributions of many chalk-indicating species are restricted to the Alps whereas acidity-indicating species tend to be distributed more widely, generally circumpolar. The species pool for alkaline substrate is larger than for acid substrate.

Calcareous soil should be considered as providing an extreme habitat that is widely distributed (Gigon, 1971), at least in Central Europe. This habitat favours: (i) competitively weak species with specific chemical limitations (Walter, 1951); and (ii) species that are qualified to withstand drought (Braun-Blanquet, 1964). The influence of rock outcrops increases with increasing elevation due to the fact that mountainous regions naturally contain more rock outcrops.

In regions with calcareous rock outcrops present, both alkaline soils and acid soils can be found with the latter originating from superficial washing-out. In contrast, regions with exclusively acid substrate lack any alkaline soils and the corresponding species are, therefore, missing too.

5. Number of soil types (NST). To find a suitable variable which would take into account landscape variation as part of environmental diversity was not a trivial problem. Dividing the landscape into classes (variable SAE) was not successful. One solution was to take into consideration soil types combining information about geology, topography and soil structure, and including not only zonal soil types but also azonal ones, e.g. bogs or fertile plains. In contrast to RCC, soils with O_2-limitations are included in this variable.

6. The remaining variables. Interpreting a statistical model with only a few linear variables is useful for detecting some fundamental principles. However, there are usually still many remaining variables and more than 50% of variability remains unexplained.

For variables other than the five used in the final regression analysis (Table 2), threshold variables were found to be particularly suitable. A mean September evapotranspiration (EV9) could be interpreted as a threshold for the production of fruits in the summertime. A maximum mean temperature in January (T5) may be evidence of a prolonged growth period or may have led to reduced danger of frost allowing the presence of plants without frost-resistance and evergreen plants (e.g. in the warm south of Switzerland). A threshold of minimum precipitation in May (PT5) could again be related to a limitation on growth conditions. All these variables are correlated positively to species richness, i.e. they slightly increase species richness.

It might be possible that the inclusion of several interaction or polynomial terms improves the regression model. However, in order to establish a model with emphasis on its ecological interpretation, such variables must be explored. Yet, the variable RCC used in the model is a meaningful interaction term.

7. Species–area relationship. In contrast to numerous investigations about the species–area relationship (Connor and McCoy, 1979; Shmida and Wilson, 1985; Rosenzweig, 1995), in this study the area size appeared to have no special importance. There are various possible explanations: (i) the mapping areas were designed very skilfully; most of the mapping areas are parts of homogeneous regions (e.g. a small valley was treated as one area, a big valley as five adjacent areas); (ii) this result indicates a large amount of noise and low statistical power; (iii) there is a large number of confounding variables; or (iv) the distribution indicates a level of indifference within this range of area to the species–area curve.

After having visited numerous mapping areas, I tend to favour explanations (i) and (iii). A homogeneous landscape seems to be a suitable unit for comparing species richness because the species pool within such landscapes is more or less constant as the species share the same geofloristic history (McLaughlin, 1992).

Influence of non-environmental variables

Effects of collecting quality. It is very difficult to measure collecting quality objectively. Thus, it is a very delicate problem trying to assess the influence of the collecting quality of 170 botanists. This may be one of the reasons why there are so few such evaluation studies (Nilsson and Nilsson, 1985; Prendergast *et al*., 1993; McCune *et al*., 1997). By including collecting quality variables as described above in the regression (section Material and methods), the variability of regional species richness could be improved to a level of 53%. Although the regional patterns of species richness can be explained more accurately by including collecting quality variables, at the same time these variables obscure the ecological explanation. The patchy pattern of the residuals in Fig. 2c shows that although positive and negative differences between observed and calculated species are spread all over the country, some aggregations of positive residuals can be seen. In some cases, these aggregations originate from mapping areas which have been investigated by the same collector (Wohlgemuth, 1993). During the digitization of the distribution data and during my studies, I asked numerous botanists about the working methods they used while drawing up the inventory. This survey shows considerable diversity in methods, motivation and time expenditure, as well as variation in systematic and local knowledge. A rather special case was where the four areas with the highest numbers of species found throughout the country were mapped by just one botanist (Fig. 2c, dark green mapping areas in the eastern part of the country). In one of these areas he collected 1400 plants, about 300 more plants than any other botanist in other areas.

Since only the normal and high collecting quality has been assessed (variable CQ), the aggregation of high negative residuals is harder to explain. The study indicates that there is much unexplained variability, largely as a result of differences in the collecting quality. As a remedy to this problem I propose combining floristic inventories with systematic sampling, for instance providing a grid of sampling points where the data are collected using a specific method. The fact that recent inventories of mosses and lichens in Switzerland are performed in this way shows the feasibility of this approach (Urmi *et al.*, 1990).

Phytogeographical effects. A weak tendency from more positive residuals in eastern parts of the country to more negative residuals in western parts can be recognized, suggesting a phytogeographical gradient. In this study, no phytogeographical hypotheses have been considered. Lang (1994) hypothesizes, for example, that the main directions of immigration in Europe from south-east to north-west following the last period of glaciation result in a decreasing number of species (Lang, 1994). Accordingly, McGlone (1996) emphasizes the importance of historical factors for the understanding of present species richness. Furthermore, McGlone criticizes the use of strictly ecological factors in explanatory models of species richness at regional and large scales. It may be that a part of the variability observed in this study can be accounted for by such factors.

Hypotheses about species richness

Results from this study have shown that much of the variability of species richness can be explained by environmental variables such as RTL, PRL, NST and, to a lesser extent, RCC (together more than 42%). At the regional level, the hypothesis of Thienemann (1956) relating species richness to environmental heterogeneity could be confirmed.

The remaining variables, TMP and, less significantly, RCC are considered threshold parameters. The effects of thresholds are defined best with the Competitive Exclusion Principle in the reformulated sense given by Palmer (1994). Calcareous rock outcrops, as well as generally low precipitation, enable species that would be competitively excluded under mesic site conditions, to grow. According to Shmida and Wilson (1985), the regional coexistence of species needs to be explained by more than one hypothesis.

Comparison with similar studies

The results presented here are based on a contiguous inventory of plant species. In Europe, this kind of inventory has been performed in several countries (e.g. Perring and Walters, 1962; Haeupler and Schönfelder, 1989) and similar projects are still running. Surprisingly, only a few of these inventories are analysed with respect to total species richness (Hengeveld, 1990, p. 2). A comparison of the presented model with studies similar in scale and statistical approach, including a few selected island analyses, is possible (Table 5). The explained variability of the reviewed analyses reaches from 0.21 to 0.94. High R^2 resulted either from studies of large spatial extent and small number of mapping areas or from analyses of island groups. In half of the mentioned studies, topography (area, elevation, altitudinal range, number of peaks) is the most important variable, statistically, explaining species richness. Topography in these studies reflects, in part, environmental heteroge-

Table 5. Studies of floristic diversity and the statistical influence of environmental factors on the regional scale

Authors	Region	Extent [km^2]	n	Species number	Significance	R^2
Dzwonko and Kornas, 1994	Rwanda	26 300	146	173 fern sp.	max. precipitation	0.21
Heikkinen, 1996	Northern Finland	362	362	227 plant sp.	mean elevation	0.40
Myklestad and Birks, 1993	Europe	9 840 000	510	65 willow sp.	area	0.46
Connor and Simberloff, 1978	Galapagos Islands	7900	29	604 plant sp.	elevation	0.71
Linder, 1991	Cape region, South Africa	89 000	55	ca 1000 plant sp.	max. precipitation	0.72
Bowers and McLaughlin, 1982	Floras in Arizona	18 155	20	ca 3000 plant sp.	elevational range	0.77
Birks, 1996	Norway	386 000	75	109 plant sp.	July temperature	0.79
Richerson and Lum, 1980	California	400 000	94	5902 plant sp.	mean precipitation	0.81
Currie and Paquin, 1987	North America	19 500 000	336	620 tree sp.	climate variables	0.86
Mourelle and Ezcurra, 1996	Argentina	2 780 000	318	223 cactus sp.	p summer precipitation	0.86
White and Miller, 1988	Mountain peaks in Appalachian mountains	121	10	342 plant sp.	No. of peaks	0.89
Johnson *et al.*, 1968	Islands of California	152 000	10	3096 plant sp.	area	0.94

neity. In the other half of the studies, climatic variables such as mean precipitation, maximum precipitation, portion of summer precipitation or July temperature particularly influence total or partial species richness. These last variables can be summarized as productivity variables and were mostly found in analyses of partial species diversity (willow species, cactus species, tree species, alpine species, ferns). The result of the Swiss model corresponds to the first group of the reviewed studies, i.e. environmental heterogeneity, for which a large part is accounted by topography, seems to be a reasonable determinant of species richness at the regional scale. Productivity, expressed by precipitation variables, does not increase species richness in Switzerland. In contrast, in Switzerland, where annual precipitation is more than 540 mm y^{-1}, high productivity has a negative influence on total species richness. The regional climatic differences observed in Switzerland are supposed to be similar in most of the regions of the Alpine arc despite some local exceptions. It is therefore hypothesized that in the whole Alpine arc, floristic species diversity will be influenced particularly by spatial heterogeneity.

Applications

Most of the environmental variables used in the model are climatic variables. It is therefore possible to use the model for predicting responses of diversity to climate change. A long-term or middle-term increase of mean annual temperature (Hulme, 1996) tells us nothing about the connected changes in annual precipitation. For example, if the amount of precipitation stays constant while temperature increases, evapotranspiration is likely to increase. This would result in a local extension of dry areas. Plants with low water demand are likely to expand under such conditions. On the other hand, if annual precipitation decreases, then dry areas will obviously expand. According to the competition argument (variable TMP, RCC), a long term increase in species diversity will take place in many regions of Switzerland. The actual extension of species of the Mediterranean or continental area-type into big cities and along railway tracks in Switzerland, which have a locally milder or dryer climate, point to this tendency (Huber, 1992). Considering dry sites and rock outcrops as localities from where species can emerge, species enrichment is likely to be possible. Independent of the effect of less precipitation, the long-term increase of mean temperature would lead to an increase in the number of thermal levels (RTL). Because the borderline between lowland and mountainous areas in the Swiss inventory is defined climatically (timberline), thermal levels (variable RTL) would be moved to higher altitudes, resulting in a higher elevated timberline. The coldest thermal level would not be lost but a warmer thermal level would be gained. In all areas which are adjacent to mountainous areas, therefore, total species richness potentially would increase according to the increased number of thermal levels.

Conclusion

The floristic species richness at the regional scale is statistically correlated with spatial heterogeneity of the mapping areas. This is likely to exist in all regions in the Alpine arc. Variables related to precipitation influence the model in an unusual way, i.e. low annual precipitation statistically increases regional species richness.

The quality of the Swiss inventory varies according to the high number of collaborators involved. A considerable part of the unexplained variability is attributed to such variation in the quality of the data. As a remedial response to this problem, a combination of future inventories with representative sampling is suggested.

The resulting variables of the presented model can be used for calculating future scenarios with changed climatic factors. Theoretical considerations shows that under increased annual mean temperature and unchanged or decreased annual precipitation, a regional increase of species richness seems to be probable.

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