Plant Biosystems, Vol. 142, No. 3, November 2008, pp. 604–613

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BIODIVERSITY IN FOREST ECOSYSTEMS

Diversity of forest plant species at the community and landscape scales in Switzerland

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Abstract
Conservation strategies increasingly refer to indicators derived from large biological data. However, such data are often unique with respect to scale and species groups considered. To compare richness patterns emerging from different inventories, we analysed forest species richness at both the landscape and the community scales in Switzerland. Numbers of forest species were displayed using nationwide distributional species data and referring to three different definitions of forest species. The best regression models on a level of four predictor variables ranged between adj. $R^2 = 0.50$ and 0.66 and revealed environmental heterogeneity/energy, substrate (rocky outcrops) and precipitation as best explanatory variables of forest species richness at the landscape scale. A systematic sample of community data ($n = 729$; 30 m^2, 200 m^2, 500 m^2) was examined with respect to nationwide community diversity and plot species richness. More than 50% of all plots were assigned to beech forests (*Eu-Fagion*, *Cephalanthero-Fagion*, *Luzulo-Fagion* and *Abieti-Fagion*), 14% to Norway spruce forests (*Vaccinio-Piceion*) and 13% to silver fir forests (*Piceo-Abietion*). Explanatory variables were derived from averaged indicator values per plot, and from biophysical and disturbance factors. The best models for plot species richness using four predictor variables ranged between adj. $R^2 = 0.31$ and 0.34. Light (averaged L-indicator, tree canopy) and substrate (averaged R-indicator and pH) had the highest explanatory power at all community scales. By contrast, the influence of disturbance variables was very small, as only a small portion of plots were affected by this factor. The effects of disturbances caused by extreme events or by management would reduce the tree canopies and lead to an increase in plant species richness at the community scale. Nevertheless, such community scale processes will not change the species richness at the landscape scale. Instead, the variety of different results derived from different biological data confirms the diversity of aspects to consider. Therefore, conservation strategies should refer to value systems.

Keywords: *Species distribution, environmental correlates, plant species richness, regression models*
Flora: Aeschimann and Heitz (1996)

Introduction

Biodiversity deals with the variety of organisms in space and time, and species richness and rarity are among the most important diversity indicators. The availability of large biological data sets is fundamental to defining such indicators. Increasingly, decisions about priorities in nature conservation are therefore based on data sets, which are often inventories of species, vegetation or habitats, and models derived from these data (Poiani et al. 2000; Araújo et al. 2004; Cabeza et al. 2004; Tear et al. 2005). However, inventories of species or of vegetation are always limited with respect to the scale and the species groups considered. Patterns of alpha and beta diversity derived from any comprehensive inventory are fascinating, though usually unique and thus difficult to evaluate. The question arises whether differently assessed baseline data result in different diversity patterns and how such differences affect conservation strategies. It is difficult to answer this question because biodiversity assessments of large regions are time-consuming and costly and thus rarely done twice. Nevertheless, inventories from different time periods are available for many regions in Europe, and the outcomes of such inventories are, to some extent, comparable (Holderegger 1994; Klecak et al. 1997).

In Switzerland, nationwide distributional data on plant species were published by Welten and Sutter (1982), who compiled data from an inventory on plant

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ISSN 1126-3504 print/ISSN 1724-5575 online
DOI: 10.1080/11263500802410975

species distribution (1967–1979) in Switzerland using 593 contiguous, topographically defined mapping areas. In a seminal study on the analysis of large biological data, Ellenberg and Klötzli (1972) classified 71 forest associations using 2533 phytosociological relevés from all parts of Switzerland. The system has been applied by most cantons for decision support in forest planning and nature conservation (Keller et al. 1998). Recently, attention has been directed to representatively assessing the diversity of plant communities and landscapes in general (Hintermann et al. 2000) and of forest communities in particular (Kull et al. unpubl.). For the latter studies, national grids have been used.

In this article, we compare diversity patterns of forest species richness at both the landscape and the community scale. At the landscape scale, we concentrate on the richness of forest species, i.e. the number of species per mapping area. By analysing nationwide species distribution data in combination with three differently defined lists of forest species, we compare the resulting forest diversity patterns across Switzerland. Furthermore, we assess the relationship between forest species richness and different environmental parameters such as substrate, topography, temperature or precipitation. At the community scale, we describe forest community diversity nationwide and forest species richness at plot sizes of 30, 200 and 500 m^2, using the systematic forest vegetation sample of Kull et al. (unpubl.). In addition, we analyse plot species richness in relation to environmental parameters. Emerging patterns of forest species richness on both landscape and community scales are discussed to evaluate the implications for conservation strategies.

Data and analyses

Study region

Switzerland covers 41,244 km^2 in Central Europe (45°49′–47°48′ N latitude, 5°57′–10°30′ E longitude; Figure 1). About 60% of the country is part of the Alps and 10% lies in the Jura Mountains. Altitudes range from 193 to 4634 m a.s.l., with an average elevation of 1300 m a.s.l. The mean annual temperature ranges from –10.5 to 12.5°C, and annual precipitation from 438 to 2950 mm (Wohlgemuth et al. 2008). Almost 7% of the country is considered urban environment (buildings, urban green areas, road and railway networks; BFS 1992/1997), whereas 35% is agricultural (fields and pastures), 31% is woodland (forests and bush vegetation) and 25% is unproductive (water, glaciers, rock, unproductive vegetation).

Species richness at the landscape scale

Roughly 3000 vascular plant species grow in Switzerland (Aeschimann & Heitz 1996). For more than 2600 species, distribution maps referring to a system of 593 topographically defined, contiguous mapping areas are available (Welten & Sutter 1982; Wohlgemuth 1998; www.webflora.ch). The species richness of forests was calculated by counting the number of forest species present in each of the 350 mapping areas below the timberline (Figure 2). The mapping areas were originally designed to detect distribution patterns of vascular plants. Despite ranging from 9 to 175 km^2, area size does not correlate with total species richness (Wohlgemuth 1993, 1998). Forest species were defined according to the following species lists:

1. *Expert approach*: In the first Red List of vascular plants, Landolt (1991) listed 461 species growing mainly in forest communities. These species are all more or less shade tolerant and are associated with forests, forest edges and shrubs. We considered 388 of these species, excluding species present in less than 10 of the 350 mapping areas below the timberline.

Figure 1. Topography of the study area Switzerland. Light grey: lakes.

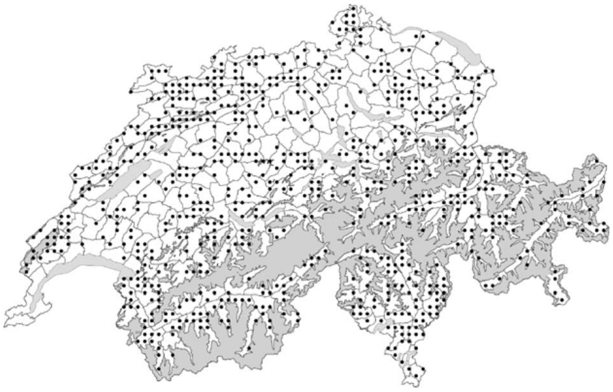

Figure 2. Location of circle plots of the systematic forest sample (dots; Kull et al., unpubl.) and system of mapping units below the timberline of the distribution atlas of Switzerland (Welten & Sutter 1982).

2. *Phytosociological approach*: The system of Swiss forest associations is based on 2533 relevés (Ellenberg & Klötzli 1972), which represent a collection of relevés from different authors mainly selected to describe typical forest vegetation from all parts of the country (Keller et al. 1998). Consequently, the relevés are distributed neither systematically nor randomly in Switzerland, and rare communities may thus be over-represented. In summary, the collection represents the contemporary state-of-the-art of the 1960s. For our analysis, we used the 350 most frequent species (present in 10 or more mapping areas).
3. *Systematic approach*: From 1995 to 1998, forest vegetation was assessed by systematic sampling on a grid of 4 × 4 km^2 throughout Switzerland (Kull & Rösler 1999; Kull et al. unpubl.). Forest vegetation in tree, shrub and herb layers was assessed in a total of 729 nested circle plots of 30, 200 and 500 m^2 area using the relevé-method by Braun-Blanquet (1964). The assessment was originally intended to study the impact of area size on the quality of community classification. In contrast to arbitrarily selecting relevés characteristic to the phytosociological approach, the systematically assessed vegetation represents the most frequent forest communities in Switzerland. Rare forest communities may be under-represented, though. We used the 466 species present in 10 or more mapping areas.

Species richness at the community scale

The systematic sample of Kull et al. (unpubl.) served to relate forest species richness (number of species) to environmental parameters at different community scales: 30, 200 and 500 m^2. In 21 of the 729 plots, trees were absent in the 200 m^2-circle. These plots were excluded, resulting in a final data set of 708 plots used in the analyses.

Explanatory variables

For the comparison of landscape species richness with environmental variables, a variable set used in an earlier study on species richness (Wohlgemuth 1998) was adopted (Table I). To analyse community forest species richness, three types of variables were used: averaged indicator values for Swiss vascular plants (Landolt 1977), biophysical variables and disturbance variables (Table II). Landolt's system of indicator values with ordinal values from 1 to 5 is fully comparable with the well-known system of Ellenberg et al. (1991), which refers to ordinal values from 1 to 9. Despite the obvious danger of circularity when using species-derived variables in ecological studies (Diekmann 2003), we decided to integrate them for comparison purposes. Costly measurements of environmental variables were usually omitted in large vegetation assessments of the past and vegetation itself was used as a site indicator.

Analyses

Landscape species richness was displayed by GIS techniques (ArcInfo ver. 9.2; Environmental Systems Research Institute, Inc., 380 New York Street, Redlands, CA 92373-8100, USA); for each of the three species lists, the number of forest species in each mapping area below the timberline (s. above)

Table I. Biophysical variables used in landscape richness models.

Variable	Description	Range	Units	Source
Topography				
FOR	Forest area, logarithmic	8–99	km^2	BFS (1992/1997)
PRL	Proximity to a large river or lake (<700 m a.s.l.)	1–3	cat	Mapping units
AMA	Adjacent mountain area	1–2	cat	
Temperature				
RTL	Range of temperature	3–18	cat	Schreiber et al. (1977)
FOE	Foehn (warm wind)	0–5	cat	
TMAX1	Max. temperature January	−9 to 2	°C	Zimmermann and Kienast (1999)
TMIN7	Min. temperature July	0–20	°C	
EV7	Evapotranspiration July	27–63	cm	
Precipitation				
PTY100	Threshold < 100 cm yr^{-1}	0–5	cat	Zimmermann and Kienast (1999)
PRY	Range yr^{-1}	2–242	cm	
Substrate				
NST	No. soil types	5–28	#	Häberli (1980)
NGU	No. geotechnical units	3–15	#	De Quervain et al. (1963–1967)
RCC	Rocky outcrop, silicatic (normal weight) and calcareous substrate (double weight)	0–9	cat	Wohlgemuth (1998)

Most variables are described in more detail in Wohlgemuth (1998). Cat, categorical variable.

Table II. Variables used in community richness models.

Variable	Description	Range	Units	Source
Averaged indicator values				
M	Moisture	1.56–3.76	cat	
N	Nutrients	1.89–4.00	cat	
R	Reaction	1.94–3.80	cat	Landolt (1977); calculated for all plot sizes, i.e. 30, 200 and 500 m^2
T	Temperature	2.18–4.00	cat	
L	Light	1.33–3.81	cat	
C	Continentality	2.00–3.78	cat	
Biophysical variables				
pH	pH at a depth of 10 cm	2.4–7.6		EAFV (1988)
SL	Slope	0–60	°	Zimmermann and Kienast (1999)
NN	Northness: cos (aspect)	−1 to 1		
EN	Eastness: sin (aspect)	−1 to 1		
CT5	Canopy of trees, 500 m^2	2–100	%	Field observation
SK	Soil skeleton	1–5	cat	Häberli (1980)
DD3	Degreedays > 3°C	64–357	#	Zimmermann and Kienast (1999)
DD5	Degreedays > 5.56°C	28–236	#	
FR	Frost days	0–106	#	
P1	Precipitation, January	38–170	mm	
P7	Precipitation, July	38–250	mm	
CO	Continentality-index Gams	8–70		
Disturbance				
PA	Pasture intensity	0–4	cat	EAFV (1988)
AM	Absence of management	0–109	y	
AGE	Stand age	5–400	y	
EF	Forest edge	1–2	cat	Field observation

Cat, categorical variable.

was displayed. Community sample plots were assigned an association using the nomenclature of Ellenberg and Klötzli (1972) and the method of Keller (1979). Linear regression was used to investigate the relationship between forest species richness, i.e. the number of vascular plant species, and various environmental parameters. To get parsimonious models, the best fitting models with 4, 3, 2 and 1 parameter(s) were calculated using the linear model procedure of *R* (ver. 2.4.1; R Development Core Team, 2006). At the community scale, models were fitted for each group of parameters separately. No transformation was necessary, because the data met assumptions of normality and homogeneity of variances.

Results

At the landscape scale, the average number of forest species amounts to 204, 239 and 336 species per mapping area for the species list of Landolt (1991), Ellenberg and Klötzli (1972) and Kull et al. (unpubl.), respectively (Table III). The patterns of forest species richness derived from the three species lists differ distinctly (Figure 3). The lists of Landolt (1991) and Ellenberg and Klötzli (1972) both result in the Jura Mountains being identified as species rich. According to Landolt's (1991) list, forest species richness is generally higher in eastern parts of the Central Plateau and generally low in higher elevated Alpine valleys. The list of Ellenberg and Klötzli (1972) results in moderate species richness throughout the whole Central Plateau and high species richness in the Northern Pre-Alps. High elevated valleys such as the Engadine are poor in forest species. The list of Kull et al. (unpubl.) shows lowest species numbers in landscapes of the Central Plateau and quite low richness in the Ticino. In contrast, the mapping areas in the Northern Pre-Alps are generally rich in forest species. According to all three lists, mapping areas of both the Chablais and the Rhine valley are very rich in species.

The best fitting linear models for the relationship between landscape species richness and environmental variables are listed in Table III. For the lists of Landolt (1991) and Ellenberg and Klötzli (1972), the most powerful models (adj. $R^2 = 0.51$ and 0.50 with four variables, respectively) to predict richness of forest species included TMAX1, RCC and PTY100: the number of species increased with increasing winter temperature, calcareous substrate and precipitation. Models based on the list of Kull et al. (unpubl.) returned even better fits (adj. $R^2 = 0.66$ with 4 variables), with RTL, the range of temperature

Table III. Regression models for richness of plant species in forests on the landscape scale, calculated on the basis of different species lists.

List	Landolt (1991)			Ellenberg and Klötzli (1972)			Kull et al. (unpublished)		
	203.7 ± 37.8			239.0 ± 33.0			335.7 ± 45.0		
No. of species	Variables	*F*-ratio	adj. R^2	Variables	*F*-ratio	adj. R^2	Variables	*F*-ratio	adj. R^2
1 var.	TMAX1	171.7	**0.328**	RTL	52.6	**0.129**	RTL	286.8	**0.450**
	PRL	70.8	0.167	FOE	51.0	0.125	AMA	218.4	0.384
	TMIN7	35.1	0.089	TMAX1	50.6	0.124	TMIN7	196.7	0.359
2 vars.	TMAX1, RCC	110.6	**0.386**	TMAX1, RCC	92.8	**0.345**	RTL, RCC	223.1	**0.560**
	TMAX1, FOE	106.7	0.377	TMAX1, FOE	56.5	0.241	RTL, PMINY	182.2	0.509
	TMAX1, PMINY	104.4	0.372	FOE, FOR	53.5	0.231	RTL, FOE	170.9	0.493
3 vars.	TMAX1, RCC, EV7	93.7	**0.443**	TMAX1, RCC, PMINY	87.2	**0.425**	RTL, RCC, PMINY	191.7	**0.621**
	TMAX1, RCC, PMINY	91.6	0.438	TMAX1, RCC, FOE	81.9	0.410	RTL, RCC, FOE	172.3	0.596
	TMAX1, RCC, TMIN7	89.5	0.432	TMAX1, RCC, FOR	69.6	0.371	RTL, RCC, EV7	154.6	0.569
4 vars.	TMAX1, RCC, PMINY, PRL	92.3	**0.511**	TMAX1, RCC, PMINY, FOE	89.5	**0.503**	RTL, RCC, PMINY, FOE	170.9	**0.661**
	TMAX1, RCC, TMIN7, FOE	84.8	0.490	TMAX1, RCC, PMINY, PRL	80.5	0.477	RTL, RCC, PMINY, PRY	149.8	0.630
	TMAX1, RCC, PMINY, EV7	82.0	0.481	TMAX1, RCC, PMINY, FOR	74.6	0.457	RTL, RCC, PMINY, TMIN7	148.3	0.628

The best models with one, two, three and four variables are displayed. Species richness: mean ± SD.

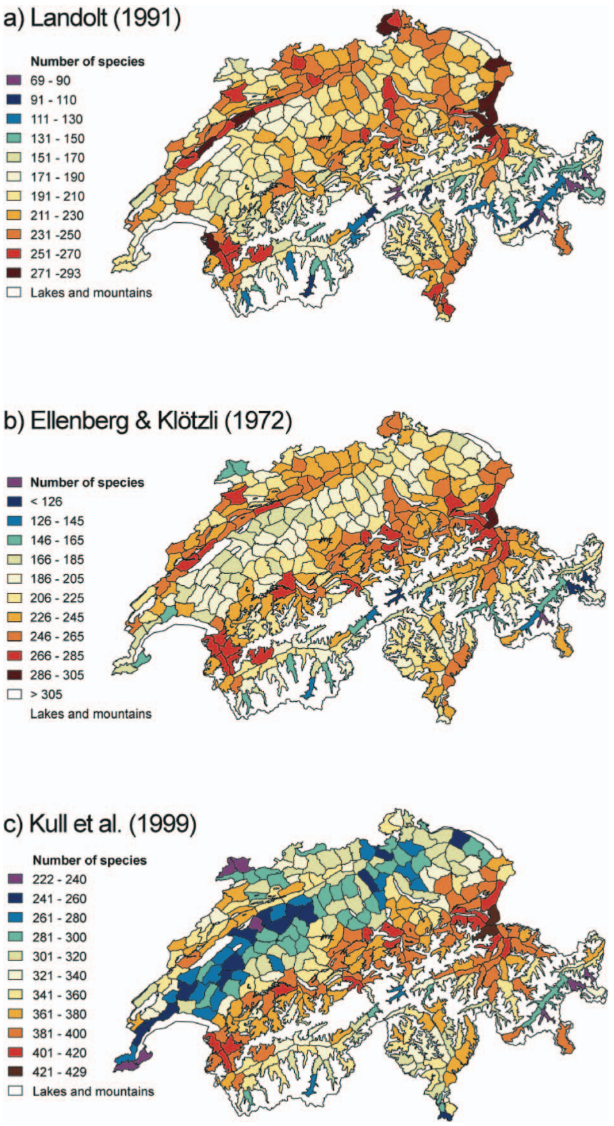

Figure 3. Richness of forest plant species in numbers per mapping unit according to different lists of forest species: (a) 388 frequent forest species according to the first Red List of vascular plants (Landolt 1991); (b) 350 frequent forest species according to the Swiss forest community system of Ellenberg and Klötzli (1972); (c) 466 frequent species in the systematic forest vegetation sample (Kull et al. unpubl.).

levels within a mapping area, as the best predictor of forest species richness (positive correlation). The influence of calcareous substrate and minimum precipitation is comparable to the results for the other species lists. Independently of the number of variables included in the model, the explained variation in species richness (adj. R^2) was always highest for the list derived from the systematic sample of Kull et al. (unpubl.), being 0.45, 0.56, 0.62 and 0.66 for 1- to 4-variable models, respectively.

The proportion of vegetation plots attributed to different plant communities is displayed in Figure 4. Accordingly, more than 50% of the forests are beech forests (*Eu-Fagion*, *Cephalanthero-Fagion*,

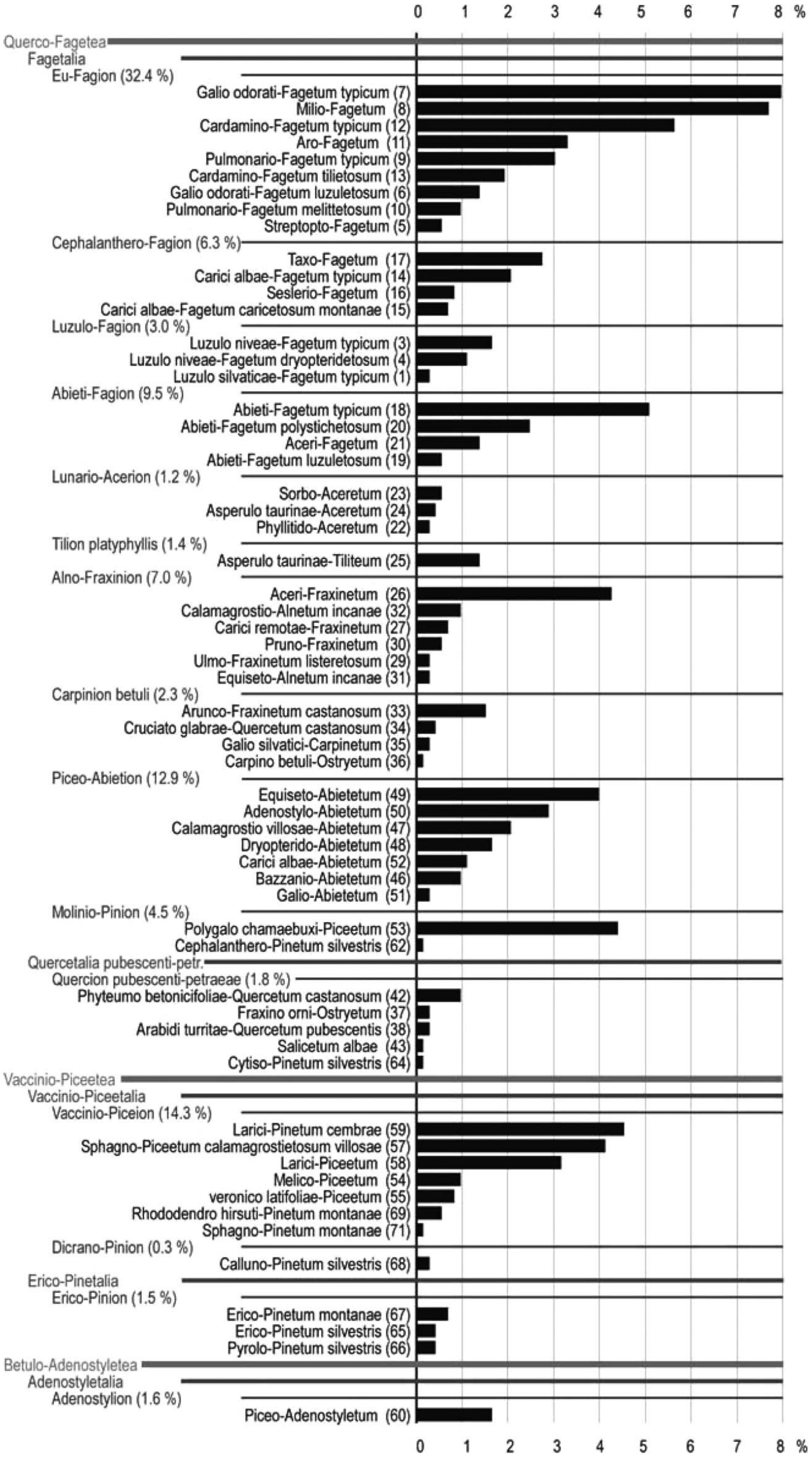

Figure 4. Proportion of forest communities in the systematic forest sample ($n = 729$; Kull et al. unpubl.). Classification of the relevés following the system of Ellenberg and Klötzli (1972).

Luzulo-Fagion and *Abieti-Fagion*), almost 14.3% Norway spruce forests (*Vaccinio-Piceion*) and 12.9% are forests with silver fir (*Picea-Abietion*). Eleven out of the 71 forest communities defined for the study area were not represented in the systematic vegetation sample.

The average community richness of vascular plants is 22.9 species at 30 m^2, 37.9 at 200 m^2 and 45.0 at

500 m^2. The linear models for community species richness generally had a smaller predictive power than those for landscape species richness (Table IV). Averaged indicator values returned the best results at all community scales. The combination of light availability (*L*), temperature (*T*), calcareous substrate (*R*) and/or nutrient rich places (*N*) explained most of the variance accounted for by the full model: 0.372, 0.477 and 0.486 for the 30, 200 and 500 m^2-circle, respectively. With biophysical variables, the model power was smaller. For all plot sizes, the canopy of trees of the 500 m^2-circles (CT5) was the best fitting variable and negatively correlated with species richness. In models with more than one variable, CT5 was followed by pH, precipitation in January (P1) and further variables such as soil skeleton (SK), slope (SL), northness (NN), degree-days > 5.56° (DD5) or continentality (CO). Models with disturbance variables had only a small predictive power. Of the four variables, only pasture intensity (PA) showed a significant, albeit weak influence.

Discussion

Forest species richness at the landscape scale

In mountainous landscapes such as the Alps and their foothills, the variation in total plant species richness at the landscape scale is correlated with topographical heterogeneity (Wohlgemuth 1993; Heikkinen & Birks 1996), energy/climate (Hawkins & Pausas 2004; Moser et al. 2005) or substrate (Wohlgemuth 2002; Bruun et al. 2003). Therefore, we expected that forest species richness in Switzerland would mainly be affected by a combination of these factors. Models with the species list of Kull et al. (unpubl.) returned the best explanatory power. Here, the variable RTL (range of temperature levels) generally addresses landscape or topographical heterogeneity. RCC (rocky outcrops, with higher weights for calcareous substrate) was found to be the second most important variable at the landscape level. At this scale, most forest species are found in areas with calcareous substrate, which corresponds

Table IV. Regression models for community richness on different sampling scales.

30 m^2 SR: 22.9 ± 12.4			200 m^2 SR: 37.9 ± 17.7			500 m^2 SR: 45.0 ± 21.5		
Variables	*F*	*R*^{2} adj.	Variables	*F*	*R*^{2} adj.	Variables	*F*	*R*^{2} adj.
Averaged indicator values								
L	205.3	**0.224**	L	288.8	**0.289**	L	293.7	**0.293**
C	109.7	0.133	C	136.6	0.161	C	135.1	0.159
R	48.5	0.063	R	54.7	0.071	R	68.6	0.087
L, N	121.4	**0.254**	L, N	216.3	**0.378**	L, N	230.4	**0.394**
L, R	112.3	0.239	L, R	187.8	0.346	L, R	198.8	0.359
L, T	108.7	0.234	L, M	154.7	0.303	L, M	155.5	0.304
L, T, R	114.5	**0.325**	L, T, N	165.1	**0.411**	L, N, M	177.5	**0.428**
L, T, N	113.5	0.323	L, T, R	163.6	0.408	L, T, N	172.0	0.421
T, R, C	89.1	0.272	L, N, M	158.0	0.400	L, T, R	168.6	0.416
L, T, R, N	105.8	**0.372**	L, T, R, N	162.0	**0.477**	L, T, N, M	168.1	**0.486**
L, T, R, M	92.6	0.341	L, T, N, M	148.6	0.455	L, T, R, N	168.0	0.486
L, T, N, M	89.7	0.334	L, T, R, M	128.7	0.419	L, N, M, C	143.9	0.447
Full model	71.33	*0.374*	Full model	119.1	*0.501*	Full model	133.1	*0.529*
Biophysical variables								
CT5	195.1	**0.215**	CT5	202.0	**0.221**	CT5	171.3	**0.194**
DD5	62.6	0.080	DD5	61.7	0.079	DD5	58.5	0.075
DD3	56.3	0.075	DD3	50.7	0.066	pH	51.1	0.070
CT5, pH	131.8	**0.281**	CT5, pH	145.0	**0.301**	CT5, pH	136.0	**0.288**
CT5, P1	120.6	0.253	CT5, P1	120.8	0.253	CT5, P1	100.9	0.220
CT5, NN	101.4	0.221	CT5, NN	106.4	0.230	CT5, NN	90.2	0.202
CT5, pH, P1	101.1	**0.310**	CT5, pH, P1	108.8	**0.326**	CT5, pH, P1	99.8	**0.307**
CT5, pH, P7	90.6	0.287	CT5, pH, SL	101.2	0.310	CT5, pH, SL	95.1	0.297
CT5, pH, DD5	90.3	0.286	CT5, pH, DD5	99.3	0.306	CT5, pH, DD5	94.5	0.296
CT5, pH, P1, NN	77.0	**0.313**	CT5, pH, P1, SL	85.0	**0.335**	CT5, pH, P1, SL	78.2	**0.316**
CT5, pH, P1, SK	76.9	0.313	CT5, pH, P1, NN	83.6	0.331	CT5, pH, SL, DD5	76.9	0.312
CT5, pH, P1, SL	76.9	0.312	CT5, pH, P1, SK	83.3	0.330	CT5, pH, P1, Co	76.7	0.312
Full model	26.8	*0.317*	Full model	30.7	*0.348*	Full model	28.85	*0.334*
Disturbance								
PA	42.1	**0.055**	PA	54.2	**0.070**	PA	59.1	**0.076**
AM	0.0	0.000	AM	1.8	0.001	AM	3.8	0.004
EF	0.0	0.000	EF	0.8	0.000	AGE	1.9	0.002
Full model	9.7	*0.057*	Full model	10.7	*0.063*	Full model	12.0	*0.071*

The best models with one, two, three and four variables are displayed. SR, species richness (mean ± SD); *F*, F-ratio.

with findings for total species richness of vascular plants (Ewald 2003; Wohlgemuth & Gigon 2003). As a third variable, precipitation below a minimum annual threshold decreased forest species richness. In the models using the species lists of Landolt (1991) and Ellenberg and Klötzli (1972), maximum temperature in January replaced RTL. Mild temperatures in January correspond to energy, i.e. low elevated places or regions within a mapping area explain variation in forest species richness better than heterogeneity with these species lists.

In summary, the highest numbers of forest species are found in landscapes with a wide elevational range. Such landscapes stretch from low elevated places towards the timberline and reflect a wide ecological amplitude. Therefore, the places with the highest species numbers are found along the northern Pre-Alps, and especially in the regions of Chablais and the Rhine valley, where mapping areas extend from deep valley bottoms to high elevated timberlines. The results may be explained by both the energy hypothesis (Moser et al. 2005) and the environmental heterogeneity hypothesis (Shmida & Wilson 1985; Rosenzweig 1995). In addition, limestone landscapes such as the Jura Mountains and the Northern Pre-Alps host more forest species than landscapes where this substrate is missing. In general, there are more different forest communities defined on calcareous substrate in Switzerland, and these communities are more species rich than acidic forest communities (Wohlgemuth & Gigon 2003). According to the list of Kull et al. (unpubl.), small or smallest numbers of forest species are found in landscapes of the Central Plateau. The finding best reflects the low total plant species richness in these topographically homogenous landscapes (Wohlgemuth 1998). All three graphs of Figure 3 show that forest species richness is small in high elevated valleys of the Alps. This is basically due to the increasing growth limitations in higher altitudes (e.g. Körner 1999).

The variety of forest communities

In Switzerland, the best reference to compare forest communities nationwide is the dataset of Kull et al. (unpubl.), because the data were assessed consistently and on a systematic sampling grid. According to the results from this assessment, most abundant site conditions in Switzerland are suitable for *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Fraxinus excelsior* and *Larix decidua*. In contrast to this result, the Swiss forest inventory (Brassel & Brändli 1999) found following numbers for most frequent living trees (DBH $\geq$12 cm) in Switzerland: *Picea abies* (196×10^6), *Fagus sylvatica* (95×10^6), *Abies alba* (55×10^6), *Larix decidua* (21×10^6), *Fraxinus excelsior* (19×10^6). With respect to the principle of potential natural vegetation that was applied to define the forest association (Tüxen 1956; Brzeziecki et al. 1993), the high portion of *Picea abies* – especially also in beech forests – found by the Swiss forest inventory reflects its use in forestry for timber production.

Species richness at the community scale

In agreement with other studies (Bacaro et al. 2008; Ewald 2008), the richness of vascular plants in forests is best explained by local-scale factors, in particular available light that in many forests resulted from disturbance such as stand management or windthrow. To some extent, the systematic assessment accounts for this result because strict phytosociological criteria such as plot homogeneity (e.g. canopy homogeneity) were not followed. Using averaged Landolt's indicator values, light availability was the best correlate of species richness (negatively correlated), followed by temperature (negative) and reaction (positive). Consequently, community richness at higher elevations (lower *T*-values) was higher than at lower elevation. The resulting species richness can be understood as an effect of more open canopies in communities of higher elevations and may also be explained by the big species pool at mid-elevations and containing many light-demanding grassland species and early colonisers. The species pool peaks between 1200 and 1300 m asl. (Wohlgemuth et al. 2008). In many of the models with three and more variables, the averaged *R*-value follows the *L*- and *T*-values. In correspondence to the species richness at the landscape scale, the presence of calcareous substrate increases forest species richness at the community scale, too (Wohlgemuth & Gigon 2003). The use of averaged indicator values as a surrogate of primary factors that are difficult to measure has been debated for years (Diekmann 2003). However, the performance of these variables is very similar to that of the biophysical factors, where the canopy of trees (CT5) is the most important variable, followed by pH and precipitation in January. The results confirm that plant species richness in forest communities is driven by light, substrate and energy. As substrate does not change within centuries, and energy (warmth) does not change within decades (Thuiller et al. 2006), disturbance by extreme events or by management may be the only factor to trigger changes in forest species richness in the short term (Wohlgemuth et al. 2002). In our models, disturbance variables had only a very small statistical power, though. This is basically due to the fact that disturbance was found only in a small number of relevés.

Our results of community forest species richness confirm to some extent the outcomes of the recently published study on species richness in Swiss forests, which is based on three hundred and eighty-one 10 m^2-plots (Brändli et al. 2007). Because of the larger sample and the wider spectrum of plot sizes, our models are more powerful.

Climatic and substrate heterogeneity, energy and sufficient precipitation determine forest species richness at the landscape scale. At the community scale, light, calcareous substrate and sufficient precipitation enrich species numbers in forest communities. Regarding conservation strategies, it has been suggested to open up forests in Switzerland to increase species richness at the community scale (Wohlgemuth et al. 2002). Our results imply that such management supports the spread of light-demanding species but does not change the number of forest species at the landscape scale. At this scale, the underlying species list has proven to be crucial for the outcome of the species richness patterns. It follows that there is neither a "best scale" nor a "best species group" to be applied for strategies in conservation. Instead, the variety of different results confirms the diversity of aspects to consider. For conservation strategies, value systems, which are currently widely neglected by ecologists, need to be integrated (Duelli et al. 2007).

Acknowledgements

We thank Iris Gödickemeier and Sandra Limacher for their help in the field, Walter Keller for defining the plant associations for all relevés, two anonymous reviewers for valuable comments, and Charles Mitchell for revising the English.

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