



Landscape patterns of indicator plants for soil acidity in the Bavarian Alps

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Abstract

Aim Electronic distribution atlases and lists of ecological indicator values are becoming important tools in plant geography. In this contribution, we combine a geographical and an ecological data bank, and map out patterns of indicator value spectra (instead of single or average values) across a physiographically complex landscape. For our study, we select indicators of soil pH and carbonate content as key environmental factors that strongly affect overall plant diversity patterns in the temperate zone. Our goal is to relate the distribution and diversity of plant groups that are indicators of soil pH and carbonate content to environmental controls at the landscape-scale, and thus contribute to a causal understanding of species pools.

Location We studied the Bavarian Alps, which represent the German portion of the Northern Alps.

Methods Based on the existing floristic survey, we calculated relative frequencies of nine classes of indicator plants for soil pH and carbonate content in grid cells. The resulting attribute matrix (cells by indicator class frequencies) was subjected to principal components analysis and to k-means clustering. Results were compared and mapped out in the grid array of the whole region, resulting in continuous and discrete representations of species pool structure. We used a geographical information system to derive physiological landscape properties from a geological map and a digital elevation model, and analysed their statistical relationship with the shapes of indicator spectra.

Results and Main conclusions Averages of indicator values for soil pH and carbonate content follow the geological structure quite closely. Surprisingly, the diversity of indicator plant groups does not appear to be a function of geological or topographic heterogeneity. Rather, it seems to be related to areas of high elevation with uniform geology. The effect is a matter of additional acidophytes in high mountain areas and, in the high calcareous Alps, extreme calciphytes, while species with intermediate requirements are rarer than usual. For explanation, we suggest two facts: (1) a frequent lack of mature soils at high elevations and (2) particularities in soil genetic processes occurring under the harsh climatic conditions of high mountains.

Keywords

Biodiversity, macroecology, Ellenberg values, floristic data base, indicator plants, landscape pattern, soil pH, carbonate content, altitudinal gradient.

INTRODUCTION

Knowledge about the distribution and the ecology of plants is steadily growing, and large electronic data bases offer

formidable tools for studying distributional and ecological phenomena. In the last decades of the twentieth century, national and supranational floristic data bases have been developed and atlases describing the landscape-scale distribution of vascular floras have been published (e.g. Jälas *et al.*, 1972–99; Haeupler & Schönfelder, 1989; Benkert *et al.*, 1996). Some of these data bases are becoming accessible via the Internet (e.g. Wohlgemuth *et al.*, 2001; Bundesamt für

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Naturschutz, 2002). In the same period, lists of indicator values (Ellenberg values) for ecological traits of plants have been supplied for several areas. They rank species by their estimated realized optima on environmental gradients of temperature, soil pH, carbonate content, water supply, etc., which are expressed on ordinal numerical scales (e.g. Ellenberg, 1974; Landolt, 1977; Klinka *et al.*, 1989; Ellenberg *et al.*, 1991; Borhidi, 1995; Kojić *et al.*, 1997; Hill *et al.*, 1999). In this contribution we combine a geographical and an ecological data bank, and map the complex pattern of indicator plants across the landscape. We exemplify the potential of our method by using plant indicators of soil pH and carbonate content, which are key environmental factors that have a strong influence on overall plant diversity patterns in the temperate zone in general (Pärtel, 2002) and the Alps in particular (Wohlgemuth, 2002). The aim of our study is to relate the diversity of indicator plant groups, as a special case of functional response groups (Lavorel & Garnier, 2002), to environmental controls acting at the scale of entire landscapes, and to contribute to a causal understanding of species pool structure.

STUDY AREA AND DATA

We studied the Bavarian Alps, which represent the German portion of the Northern Alps, a physiographically complex mountain region extending 230 km west to east and 10–40 km south to north. Elevations range from around 450 m up to 2962 m. The highest mountains are situated at the southern fringe of the region, where limestone and dolomite of the Triassic period prevail (hereafter referred to as calcareous rocks). The lower belts at the northern margin are constituted by non-calcareous material, the most important being cretaceous Flysch sandstones and marls.

Floristic distribution data were taken from the German floristic survey data base (Zentralstelle für Phytodiversität = Centre for Plant Diversity). We included all records of indigenous or established vascular plants from 1950 onwards. Survey data list all recorded plant taxa in grid cells of 5.0' in longitude and 3.0' in latitude (c. 6.2 × 5.5 km). To delimit the mountain area against its foreland, all grid cells not reaching an elevation of at least 1200 m were excluded from the analysis. All borderline grid cells that have more than 50% of their surface area in neighbouring Austria were omitted, because they had not been systematically included in the survey. The remaining number of grid cells was 133.

The indicator values used for this study originate from Ellenberg *et al.* (1991), who distinguish nine soil acidity indicator classes (R-indicator classes) ranging from indicators of acid soils to calciphilous plants (Table 1). These R-values correspond to certain ranges of soil pH and carbonate content (Ellenberg *et al.*, 1991; Diekmann, 1995; Ertsen *et al.*, 1998; Wamelink *et al.*, 2002). Geological data were taken from a geological map 1 : 500,000 (Bayerisches Geologisches Landesamt, 1998), and elevation data from a digital elevation model provided by the Bavarian Surveying Administration.

Table 1 The description of indicator values for soil pH and carbonate content as given by Ellenberg *et al.* (1991)

R1	Indicator of extreme acidity, never found on weakly acid or basic soils
R2	Between 1 and 3
R3	Acidity indicator, mainly on acid soils, but exceptionally on neutral ones
R4	Between 3 and 5
R5	Indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soils
R6	Between 5 and 7
R7	Indicator of weakly acid to weakly basic conditions; never found on very acid soils
R8	Between 7 and 9
R9	Indicator of basic reaction, always found on calcareous soils

METHODS

For each of the 133 grid cells we counted the indicator plants for soil pH and carbonate content (R-value) from the list of Ellenberg *et al.* (1991) and calculated average, standard deviation, evenness and Shannon diversity of R-values (Shannon, 1948). Relative frequencies of R classes in the grid cells (percentage of indicator species) were standardized. The resulting attribute matrix (133 grid cells by nine reaction indicator frequencies) was subjected to principal components analysis (PCA) and to the k-means algorithm with Euclidean distance measure and a predefined number of five clusters (performed in STATISTICA 5.5; StatSoft, Tulsa, OK, USA). While the PCA-ordination extracts and maps the regularities in the multivariate structure of indicator spectra in the form of continuous gradients (axes), clustering delimits discrete landscape units with more or less homogeneous species pool structure regarding R-indicators.

Physiographical characteristics of grid cells and clusters were derived by intersection with the geological map and with the digital elevation model in ArcView 3.2a (ESRI, Redlands, CA, USA). Areal proportions of stratigraphic geological units, of broad, edaphically important rock types and of elevation belts, as well as mean elevation, were derived as possible explanatory variables. Landscape heterogeneity was assessed by calculating numbers of occurring stratigraphic units, edaphic rock types and elevation belts per grid cell, as well as their evenness and Shannon diversity (Table 2).

Distribution and diversity of indicator plant groups for soil pH and carbonate content were related to landscape properties in several ways: in (1) PCA-biplot the first two principal components of species pool structure are correlated to environmental variables, which are represented as vectors in ordination space. We then computed (2) linear correlations between PCA-axes and statistical summary parameters of the R-indicator matrix (mean, standard deviation, evenness and Shannon diversity). We calculated (3) average characteristics of the grid cell clusters. And we provide a (4) *post hoc* illustration of the clusters by tabulating diagnostic

Table 2 Abbreviations for environmental and response variables (Fig. 3b, Table 4)

Mean in <i>R</i> -indicator values	mR
sd in <i>R</i> -indicators	sdR
Evenness of <i>R</i> -values	eR
Shannon diversity of <i>R</i> -values	dR
Mean elevation (m)	mE
Number of elevation belts	#EB
Evenness of elevation belts	eEB
Shannon diversity of elevation belts	dEB
Spatial proportions of non-calcareous rock types	%A
Spatial proportions of calcareous rock types	%C
Spatial proportions of mixed rock types	%M
Number of stratigraphic rock types	#SR
Evenness of stratigraphic rock types	eSR
Number of edaphic rock types	#ER
Evenness of edaphic rock types	eER
Shannon diversity of stratigraphic rock types	dSR
Shannon diversity of edaphic rock types	dER

species derived in indicator species analysis (Dufrene & Legendre, 1997), based on a Monte Carlo test with 999 permutations performed in PC-ORD 4 (MjM Software, Gleneden Beach, OR, USA; McCune & Mefford, 1998). In order to be included in the table, all taxa had to exceed a subjectively set minimum indicator value of 30. All listed

taxa passed a Monte Carlo test of statistical significance, with $P \leq 0.005$.

RESULTS

Overall frequency of indicator plant groups for soil pH and carbonate content

The floristic survey data base contained distributions of 1496 plant taxa occurring in our area and listed in the Ellenberg list of indicator values. A total of 1253 or 83.8% of these species are considered as indicators of soil pH and carbonate content, while the rest are judged as not fitting in any of the indicator classes (Table 1). For the flora of the whole study region the frequency of indicator taxa across reaction groups was unimodal (Fig. 1a), with a strong skew towards basiphytic (R7) and calciphilous plants (R8). This general pattern was more or less valid for all single grid cells (Fig. 1b). Absolute numbers of taxa ranged from 300 to above 700 per grid cell, with 70–85% reaction indicators (Fig. 2).

Gradients in the distributions of indicator plant groups for soil pH and carbonate content

R-spectra in individual grid cells, as modulations of the general picture, follow two independent gradients depicted

Figure 1 Frequency distribution of indicator taxa for soil pH and carbonate content as represented in the whole data set (a) and in the grid cells (b). The error bars show maximum and minimum values.

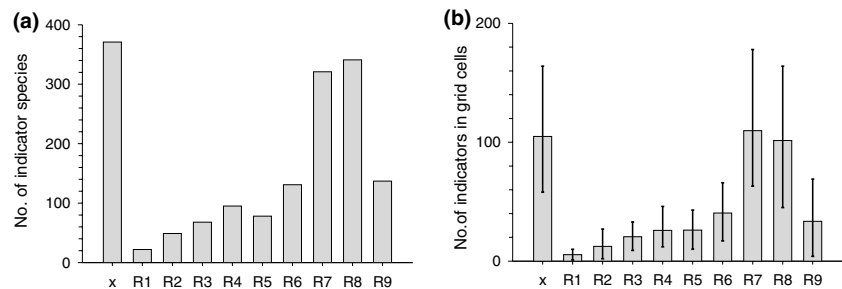
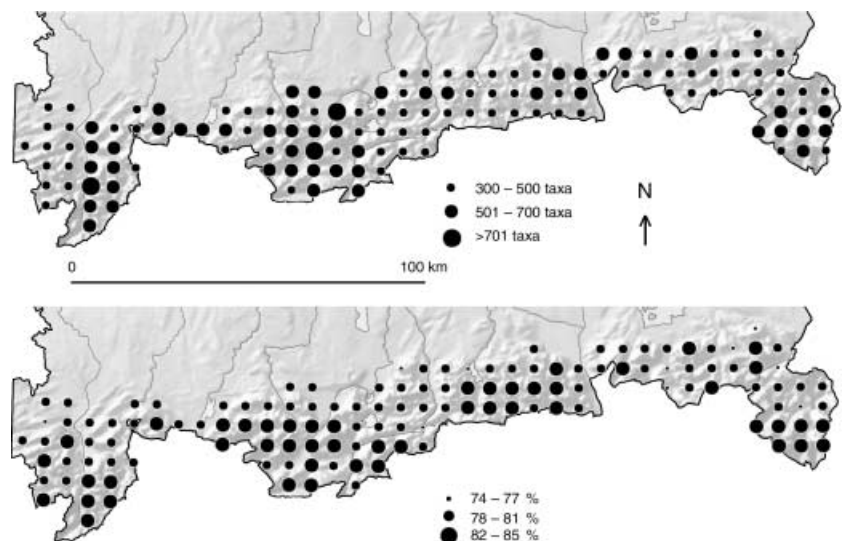


Figure 2 Grid cells of the floristic survey in the Bavarian Alps and the number of recorded taxa listed in the Ellenberg table (Ellenberg *et al.*, 1991); above: absolute number of taxa; below: percentage of indicators of soil pH and carbonate content in total species number.



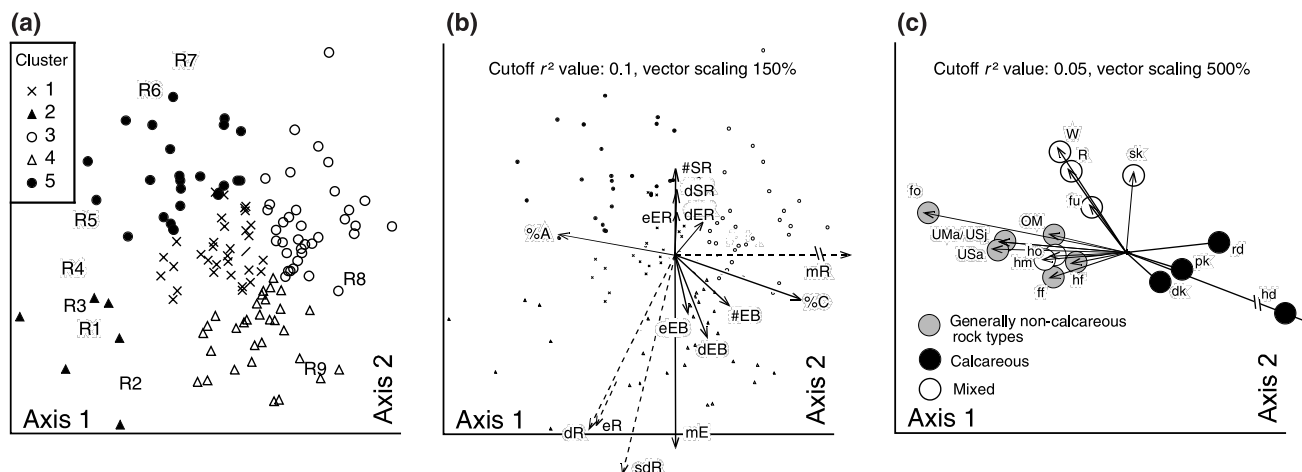


Figure 3 (a) Results of PCA showing the position of 133 grid cells in a space defined by two principal components, which are linear combinations of relative frequencies in nine indicator classes. Clusters C1-5 (resulting from k-means algorithm) are shown as symbols. The R-indicator loadings (R1-R9) were arranged in a circular manner: along axis 1, basiphytes increase at the expense of acidophytes. Clusters C2 and C5 are found at the beginning, C3 and C4 at the top of this axis. Species of both extreme ends of the spectrum increase along axis 2. At the beginning we find C3 and C5, at the top C4 and C2. (b) Joint plot of PCA with environmental variables and parameters of the R-indicator matrix (dashed vectors). (c) Joint Plot of PCA with stratigraphic rock types as variables. dk, *Dachsteinkalk*; ff, *Feuerstätter Flysch*; fo, *Rhenodanubischer Flysch: Untere Bunte Mergel or Ofterschwanger Schichten to Anthering-formation*; fu, *Rhenodanubischer Flysch: Tristelschichten to Quarzitserie*; hd, *Hauptdolomit and Dachsteindolomit*; hf, *Helvetikum, Ultrahelvetikum and Feuerstätter Flysch*; hm, *Schrautenkalk to Garschella-formation*; ho, *Seewer Kalk to Hachauer Schichten*; OM, *Obere Meeresmolasse, in the east with Obere Brackwassermolasse*; pk, *Plattenkalk*; R, moraines and outwash plains (riß); rd, *Ramsadolomit, Wettersteindolomit*; sk, alluvial fan, scree; UMa, *Untere Meeresmolasse, older part*; USa, *Untere Süßwassermolasse, older part*; USj, *Untere Süßwassermolasse, younger part*; W, moraines and outwash plains (würm) (Bayerisches Geologisches Landesamt, 1998).

by PCA: axis 1 is an increase of mean R-value (42% of total variance); axis 2, a decrease of standard deviation and diversity in R-values (31% of variance, cumulative 73%); axis 3, representing only 7% of the total variance is not discussed in the following. The first axis can be thought of as an increasing proportion of basiphytes at the expense of acidophytes, the second as an increasing proportion of extreme indicators (both basiphytes and acidophytes) at the expense of more moderate indicators (Fig. 3a), a pattern that we call polarization. The distinct horseshoe arrangement of variables R1-R9 in PCA (Fig. 3a) is no numerical artefact (Jongman *et al.*, 1987; Legendre & Legendre, 1998), but a meaningful expression of the nonlinear structure in indicator frequencies – an interpretation that is supported by the complete absence of a horseshoe in grid cell positions and the even distribution of explained variance among both axes.

The five groups obtained by k-means clustering were represented in the two-dimensional space of PCA without much overlap, indicating a good representation of multivariate Euclidean space by the two ordination axes (Fig. 3a). Corresponding to its central position in the PCA, cluster C1 had approximately average mean R-spectra (Fig. 4). C2 and C3, and C4 and C5, had complementary mean spectra corresponding to their diagonally opposite position in the PCA. C2 has many extreme acidophytes, C3 has an inverse and more moderate spectrum. C4 has a lot of extreme calciphytes, while C5 is moderate, with a relative paucity of calciphytes.

While scores on PCA-axis 1 increased from the western towards the eastern part of the study area, scores on axis 2 formed a spatial gradient from the southern interior to the northern fringe of the German Alps (Fig. 5). Mean R-values form a pattern very similar to PCA-axis 1, standard deviation and Shannon diversity (Fig. 5) of R-values to PCA-axis 2.

The same spatial pattern becomes very obvious when depicted as clusters (Fig. 6): the northern fringe and the far west (Allgäu) belong to clusters C5 and C2, whereas clusters C3 and C4 occupy much of the interior of the mountain range.

Environmental variables and their relation to indicators of soil pH and carbonate content

The biplot in Fig. 3b provides an illustration of the potential of the environmental variables considered (plotted as solid lines) to explain the variance in the R-indicator matrix, while dashed lines represent the parameters of the matrix itself.

One group of environmental variables is associated with the first axis of PCA and therefore with the mean R-values of grid cells. The most important of these variables are the distributions of calcareous vs. non-calcareous rock types. Figure 3c presents individual stratigraphic units with a major influence on this gradient and groups them by rock type. Clusters C2 and C5 (both with more acidophytes and fewer calciphytes) are associated with younger sedimentary

Figure 4 Characterization of cluster areas by means of their *R*-indicator spectra. The figure shows deviations from the mean proportions of *R*-classes: values above 100% signify more indicators, values below 100% fewer indicators than average.

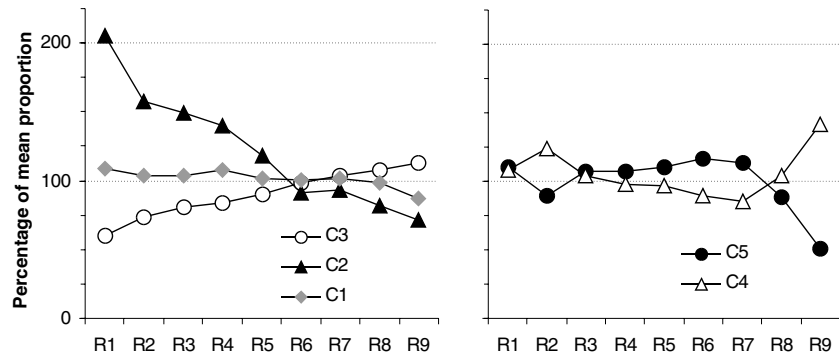


Figure 5 Maps of Shannon diversity of *R*-values and PCA axes scores of grid cells. The PCA axes represent the major differences in indicator spectra across the region. While scores on PCA-axis 1 increase from the western towards the eastern part of the study area, scores on axis 2 form a spatial gradient from the southern interior to the northern fringe of the German Alps. Shannon diversities of *R*-values increase to the contrary from the northern fringe to the southern interior with a skew towards the western parts.

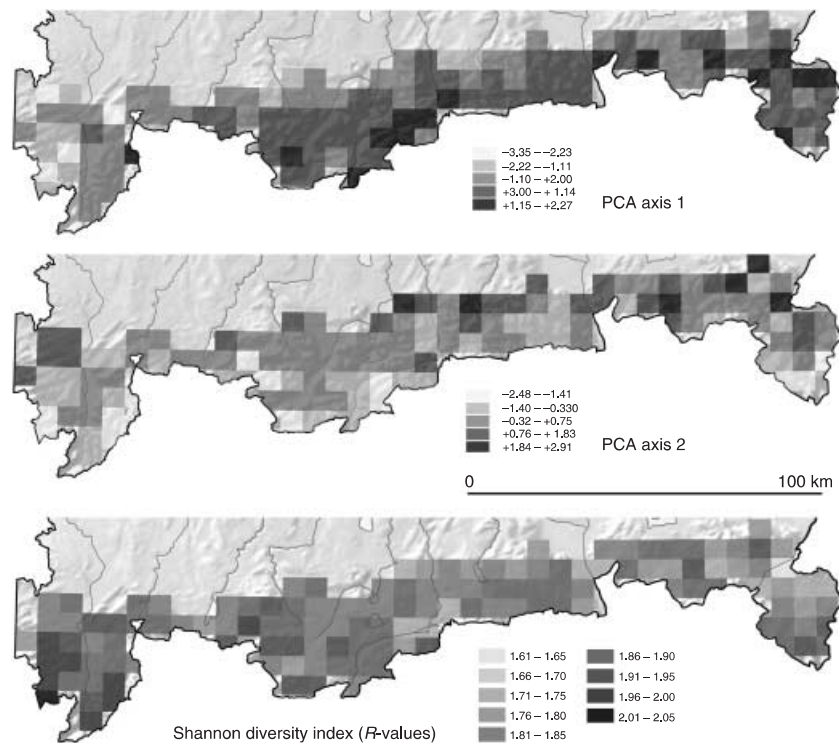
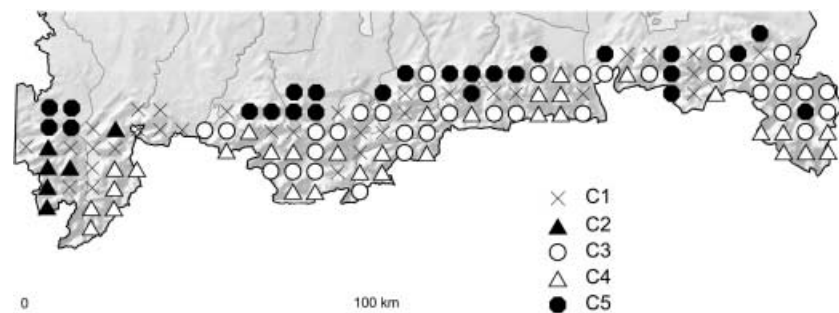


Figure 6 Map of cluster areas. Clustering delimits discrete landscape units with more or less homogeneous species pool structure regarding *R*-indicators. The map reflects the same differences between western and eastern, northern and southern parts as the gradients shown in Fig. 5.



rocks and sediments (cretaceous to pleistocene), which tend to contain considerable amounts of non-calcareous material, the most important being Flysch sandstones and marls (fo).

Clusters C4 and C3 (more calciphytes, fewer acidophytes), on the other hand, are tied to the occurrence of older (Triassic to Jurassic) pure carbonate rocks (limestones and

dolomites), the most widespread being Hauptdolomit (hd). Cluster C1 has no marked preference for any particular parent material.

Mean elevation as the most important environmental variable is related to the second axis and therefore to standard deviation and diversity of *R*-values. Alternatively, this part of the variance can be related to the proportions of single elevation belts (not shown). Diversity and evenness of elevation belts point in a similar direction as mean elevation. Clusters C2 and C4 have relatively high proportions of area close to or above timberline, C3 and C5 have relatively high proportions at low elevations. Once again C1 takes an intermediate position. Stratigraphic units and rock types are more numerous in lower areas, which, however, has no apparent positive effect on the diversity of *R*-values. Contrary to expectation, polarized spectra with high standard deviation and diversity of *R*-values (low scores on the second PCA-axis) are more often found in geologically uniform than in diverse areas, as long as these have high proportions of high-elevation terrain. Thus, they are less explained by geological gradients but rather more by elevation.

Among all considered environmental variables (Table 3), mean elevation of grid cells (Fig. 7) contributes most to

R-diversity (Pearson $r = 0.63$, $P = 0.000$). An apparently much smaller portion is explained by diversity and evenness of elevation belts (Pearson $r = 0.26/0.25$, $P = 0.000$). Correlations with the diversity of stratigraphic units and rock types are even significantly negative. Mean *R*-values are positively related to the spatial proportions of calcareous rock types and to the number of elevation belts, a fact that reflects a more accentuated relief in areas with calcareous rocks.

Characteristics of cluster areas

The most important characteristics of the cluster areas have been mentioned in the previous sections. We can summarize (see Table 4) by saying that C5 is a low elevation, predominantly non-calcareous area with relatively low averages in *R*-values and a relative lack of indicators of extreme soil pH and carbonate content. C3 is another low elevation area with low diversity in *R*-indicators, but with high proportions of calcareous rocks, which is clearly reflected by the highest average *R*-values of all clusters. C4 is a high elevation, predominantly calcareous area with high averages in *R*-values and a high proportion of indicators of extreme soil pH and

Table 3 Correlations among parameters of the *R*-matrix and environmental variables (see Table 2 for abbreviations)

	sdR	eR	dR	mE	#EB	eEB	dEB	%A	%C	%M	#SR	eSR	dSR	#ER	eER	dER
mR	-0.51	-0.58	-0.60	-0.01	0.40	0.20	0.31	-0.62	0.62	-0.18	0.10	0.10	0.13	0.35	0.04	0.29
<i>P</i>	0.00	0.00	0.00	0.91	0.00	0.02	0.00	0.00	0.00	0.04	0.25	0.25	0.15	0.00	0.67	0.00
sdR		0.93	0.96	0.70	0.15	0.29	0.30	-0.01	0.08	-0.11	-0.39	-0.22	-0.37	-0.14	-0.33	-0.36
<i>P</i>		0.00	0.00	0.00	0.08	0.00	0.00	0.87	0.34	0.21	0.00	0.01	0.00	0.11	0.00	0.00
eR			0.98	0.64	0.15	0.26	0.28	0.06	-0.02	-0.04	-0.33	-0.17	-0.31	-0.15	-0.32	-0.36
<i>P</i>			0.00	0.00	0.09	0.00	0.00	0.52	0.83	0.63	0.00	0.05	0.00	0.08	0.00	0.00
dR				0.63	0.12	0.25	0.26	0.07	-0.03	-0.03	-0.33	-0.17	-0.30	-0.13	-0.34	-0.36
<i>P</i>				0.00	0.18	0.00	0.00	0.45	0.70	0.74	0.00	0.05	0.00	0.13	0.00	0.00
mE					0.46	0.59	0.65	-0.27	0.40	-0.28	-0.43	-0.21	-0.39	-0.06	-0.32	-0.27
<i>P</i>					0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.49	0.00	0.00
#EB						0.46	0.77	-0.37	0.48	-0.28	-0.15	-0.07	-0.14	0.18	-0.06	0.10
<i>P</i>						0.00	0.00	0.00	0.00	0.00	0.08	0.45	0.12	0.04	0.46	0.25
eEB							0.91	-0.25	0.33	-0.19	-0.17	0.00	-0.11	0.18	-0.26	-0.07
<i>P</i>							0.00	0.00	0.00	0.03	0.05	0.96	0.23	0.04	0.00	0.43
dEB								-0.35	0.45	-0.26	-0.20	-0.04	-0.15	0.20	-0.21	-0.01
<i>P</i>								0.00	0.00	0.00	0.02	0.67	0.09	0.02	0.01	0.91
%A									-0.75	-0.09	0.05	0.07	0.08	-0.32	0.28	-0.03
<i>P</i>									0.00	0.30	0.54	0.45	0.35	0.00	0.00	0.74
%C										-0.59	-0.32	-0.27	-0.35	0.22	-0.28	-0.05
<i>P</i>										0.00	0.00	0.00	0.00	0.01	0.00	0.56
%M											0.41	0.32	0.43	0.07	0.09	0.11
<i>P</i>											0.00	0.00	0.00	0.43	0.32	0.19
#SR												0.36	0.82	0.35	0.11	0.27
<i>P</i>												0.00	0.00	0.00	0.23	0.00
eSR													0.82	0.13	0.29	0.30
<i>P</i>													0.00	0.14	0.00	0.00
dSR														0.29	0.23	0.34
<i>P</i>														0.00	0.01	0.00
#ER															-0.07	0.55
<i>P</i>															0.40	0.00
eER																0.76
<i>P</i>																0.00

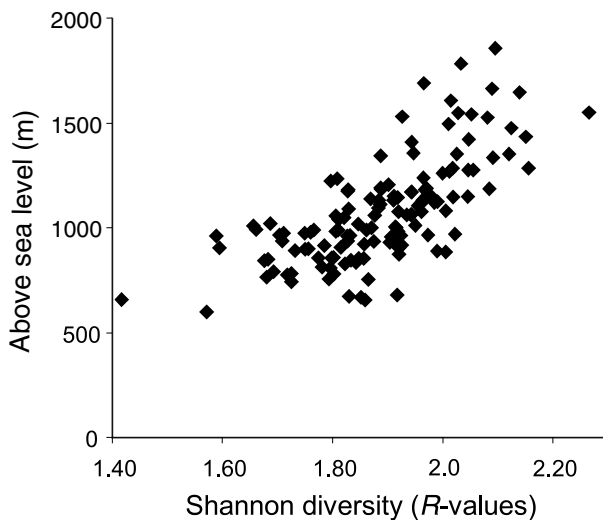


Figure 7 Relationship between medium elevation of grid cells and Shannon diversity of *R*-values.

carbonate content, i.e. polarized spectra. C2 occupies the second highest elevations and also has high proportions of indicators of extreme soil pH and carbonate content, but with a lack of calcareous rocks and corresponding low averages in *R*-values. C1 takes an intermediate position in all respects.

Based on the relative amounts of indicators, our classification of grid cells is quite abstract. To make it more tangible to those familiar with the flora of the Alps, we provide a table of individual taxa that are typical for the clusters (Table 5). Certainly, these taxa do not necessarily cause the *R*-value-clustering, but are simply a *post hoc* illustration of particularly characteristic ecological conditions by diagnostic elements in the cluster floras.

C2 and C4 are floristically well defined by many diagnostic taxa; C3 is poorly defined, C1 and C5 have no diagnostic taxa that passed our criteria. Diagnostic plant species of C2 are mainly sub-alpine and alpine species adapted to non-calcareous soils; *Bupleurum ranunculoides* L. and *Trifolium badium* Schreb., being calciphilous plants, are the only odd ones out. Because of the small number of grid cells, the floristic inventory of C2 is prone to surveying artefacts (this is a plausible explanation for the complete lack of otherwise frequent acidophytes like *Calamagrostis villosa* (Chaix) J.F.Gmel. or *Agrostis rupestris* All. Preferential taxa of C3 are thermophilous, calciphilous plants of the lower belts. C4 is characterized by an extraordinary number of calciphilous plants of the alpine belt, however its diagnostic taxa cover the entire *R*-spectrum and include many acidophytes.

DISCUSSION

This study identifies relationships between the diversity of indicator plants for soil acidity and broad landscape

Table 4 Short characterization of grid cell clusters in terms of their *R*-indicator plants and landscape properties (see Table 2 for abbreviations)

	C1	C2	C3	C4	C5
# Grid cells	33	6	37	32	25
mR	6.45	6.02	6.73	6.56	6.34
SD	0.09	0.12	0.08	0.12	0.12
Mean sdR	1.91	2.12	1.76	2.02	1.83
SD	0.06	0.08	0.11	0.07	0.08
Mean dR	1.87	1.97	1.79	1.9	1.83
SD	0.03	0.03	0.05	0.04	0.04
Mean eR	0.88	0.87	0.85	0.88	0.87
SD	0.04	0.02	0.06	0.05	0.04
mE (m)	1009	1295	980	1370	872
SD	120	130	159	227	133
Mean #EB	4.52	4.5	5.16	5.34	3.56
SD	0.99	0.5	0.92	0.73	0.7
Mean dEB	0.89	1.17	1.14	1.37	0.72
SD	0.33	0.23	0.26	0.24	0.21
Mean eEB	0.59	0.78	0.69	0.82	0.57
SD	0.18	0.13	0.10	0.12	0.15
Mean #SR	10.76	7.33	10.05	8.09	10.88
SD	2.58	1.25	2.63	2.64	3.23
Mean dSR	1.81	1.44	1.74	1.41	1.69
SD	0.33	0.26	0.36	0.39	0.42
Mean eSR	0.77	0.72	0.76	0.69	0.72
SD	0.08	0.11	0.10	0.12	0.13
Mean #ER	2.70	2.00	2.86	2.66	2.52
SD	0.46	0.00	0.34	0.47	0.50
Mean dER	1.24	1.21	1.23	1.19	1.28
SD	0.03	0.05	0.04	0.06	0.04
Mean eER	0.83	0.73	0.77	0.74	0.76
SD	0.15	0.20	0.17	0.15	0.15
Mean %C	0.27	0.00	0.51	0.63	0.07
SD	0.25	0.00	0.24	0.18	0.13
Mean %A	0.27	0.60	0.13	0.06	0.43
SD	0.22	0.27	0.13	0.08	0.27
Mean %M	0.46	0.40	0.36	0.31	0.49
SD	0.18	0.27	0.17	0.16	0.21

properties. In interpreting the results it is crucial to emphasize that relating entire floras to landscape attributes yields results at a broad spatial scale, which is only a starting point (albeit we believe a highly valid one) for the development of hypotheses about ecological processes occurring at finer scales.

General limitations of ecological indicator values and cumulative floristic surveys

The general problems of ecological indicator values have been discussed at length in the literature (e.g. by Durwen, 1982; Böcker *et al.*, 1983; Kowarik & Seidling, 1989; Dierschke, 1994; Englisch & Karrer, 2001; Wamelink *et al.*, 2002). We admit that our method may suffer from some of these general limitations, such as changing ecological behaviour of species in different places or under environmental change, and incorrect judgements on individual species

Table 5 Table of plants typical for clusters. *R*: indicator values for soil pH and carbonate content according to Ellenberg *et al.* (1991); *IV*: observed fidelity according to Dufrene & Legendre (1997); the value combines information on the frequency of a species in the cluster area and on its limitation to this cluster area; *P*: result of a Monte Carlo test of significance with 999 permutations (proportion of randomized trials with indicator value equal to or exceeding the observed indicator value)

	<i>R</i>	<i>IV</i>	<i>P</i>
C2			
<i>Bupleurum ranunculoides</i> L.	9	31	0.002
<i>Trifolium badium</i> Schreb.	8	33	0.005
<i>Achillea macrophylla</i> L.	6	52	0.001
<i>Dianthus sylvestris</i> s. <i>sylvestris</i> Čel.	4	45	0.001
<i>Gnaphalium norvegicum</i> Gunn.	4	44	0.001
<i>Hieracium aurantiacum</i> L.	4	43	0.001
<i>Gnaphalium sylvaticum</i> L.	4	32	0.005
<i>Carex brunnescens</i> (Pers.) Poir.	3	69	0.001
<i>Plantago alpina</i> L.	3	62	0.001
<i>Potentilla aurea</i> L.	3	31	0.002
<i>Gentiana purpurea</i> L.	3	31	0.005
<i>Dryopteris expansa</i> Fras.-Jenk. et Jermy	2	36	0.002
<i>Viola palustris</i> L.	2	36	0.010
<i>Gentiana punctata</i> L.	2	35	0.001
<i>Pseudorchis albida</i> (L.) A. et D. Löve	2	35	0.001
<i>Campanula barbata</i> L.	1	62	0.001
<i>Hieracium alpinum</i> L.	1	37	0.002
<i>Juncus squarrosus</i> L.	1	35	0.005
<i>Gentiana lutea</i> L.	x	33	0.001
C3			
<i>Laserpitium siler</i> L.	9	38	0.002
<i>Carex humilis</i> Leyss.	8	36	0.003
<i>Hepatica nobilis</i> Mill.	7	30	0.001
C4			
<i>Salix reticulata</i> L.	9	50	0.001
<i>Chamorchis alpina</i> (L.) Rich.	9	45	0.001
<i>Thlaspi rotundifolium</i> (L.) Gaud.	9	43	0.001
<i>Athamantia cretensis</i> L.	9	43	0.001
<i>Helianthemum alpestre</i> (Jacq.) DC.	9	40	0.001
<i>Hutchinsia alpina</i> (L.) R. Br.	9	40	0.001
<i>Gentiana aspera</i> (Heget.) Dost. ex Skal.	9	40	0.004
<i>Saxifraga aphylla</i> Sternb.	9	39	0.001
<i>Arabis ciliata</i> Clairv.	9	37	0.001
<i>Gypsophila repens</i> L.	9	37	0.001
<i>Leucanthemum atratum</i> (Jacq.) DC.	9	35	0.004
<i>Pedicularis rostratocapitata</i> Crantz	9	34	0.005
<i>Erigeron polymorphus</i> Scop.	9	34	0.005
<i>Rhamnus pumilus</i> Turra	9	33	0.002
<i>Saxifraga caesia</i> L.	9	32	0.001
<i>Androsace chamaejasme</i> Wulf.	9	32	0.002
<i>Carex mucronata</i> All.	9	32	0.001
<i>Kernera saxatilis</i> (L.) Rchb.	9	32	0.001
<i>Valeriana saxatilis</i> L.	9	31	0.001
<i>Silene pusilla</i> W. et Kit.	9	31	0.001
<i>Saxifraga androsacea</i> L.	8	49	0.001
<i>Silene acaulis</i> (L.) Jacq.	8	47	0.001
<i>Cystopteris regia</i> (L.) Dev.	8	44	0.001
<i>Achillea atrata</i> L.	8	43	0.001
<i>Festuca rupicaprina</i> (Hack.) Kern.	8	42	0.001
<i>Gnaphalium hoppeanum</i> Koch	8	41	0.001
<i>Veronica aphylla</i> L.	8	39	0.001

Table 5 *continued*

	<i>R</i>	<i>IV</i>	<i>P</i>
<i>Hedys. hedys.</i> (L.) Schz. et Thell.	8	39	0.004
<i>Potentilla caulescens</i> L.	8	38	0.001
<i>Poa minor</i> Gaud.	8	37	0.002
<i>Sedum atratum</i> L.	8	36	0.001
<i>Linaria alpina</i> (L.) Mill.	8	36	0.001
<i>Taraxacum alpinum</i> Hegetschw. s.l.	8	33	0.005
<i>Salix waldsteiniana</i> Willd.	8	33	0.005
<i>Pulsatilla alpina</i> (L.) Del.	8	32	0.002
<i>Globularia nudicaulis</i> L.	8	32	0.001
<i>Gentiana bavarica</i> L.	8	32	0.002
<i>Euphrasia salisburgensis</i> Hoppe	8	31	0.001
<i>Galium anisophyllum</i> Vill.	8	31	0.001
<i>Phleum hirsutum</i> Honck.	7	44	0.001
<i>Rumex scutatus</i> L.	7	37	0.001
<i>Peucedanum ostruthium</i> (L.) Koch	7	36	0.002
<i>Moebria ciliata</i> (Scop.) DT.	7	35	0.004
<i>Biscutella laevigata</i> L.	7	35	0.001
<i>Anthericum ramosum</i> L.	7	34	0.001
<i>Gentiana nivalis</i> L.	7	33	0.004
<i>Festuca pulchella</i> Schrad.	7	31	0.004
<i>Epilobium alsinifolium</i> Vill.	6	45	0.001
<i>Carex atrata</i> L. ssp. <i>atrata</i>	6	41	0.003
<i>Agrostis alpina</i> Scop.	6	32	0.002
<i>Euphrasia picta</i> Wimm.	6	31	0.010
<i>Saxifraga stellaris</i> L.	5	36	0.004
<i>Ligusticum mutellina</i> (L.) Crantz	5	36	0.005
<i>Hieracium picroides</i> Vill.	4	42	0.001
<i>Minuartia sedoides</i> (L.) Hiern	4	37	0.002
<i>Clematis alpina</i> (L.) Mill.	3	38	0.001
<i>Agrostis rupestris</i> All.	2	43	0.001
<i>Calamagrostis villosa</i> (Chaix) Gmel.	2	34	0.002
<i>Anthoxanthum alpinum</i> A. et D. Löve	2	31	0.004
<i>Veronica fruticans</i> Jacq.	x	45	0.001
<i>Arctostaphylos alpinus</i> (L.) Spreng.	x	33	0.004

responses. However, we are confident that the size and completeness of our data set offers a sound basis to study broad landscape patterns that should not be too sensitive to these problems.

The considerable differences in total recorded richness per grid cell (Fig. 2) could have two explanations: they may represent real gradients in richness, or they may be a result of varying surveying intensity – both in terms of time and personnel. It appears practically impossible to isolate the contributions of the two components. The lack of standardization in surveying intensity is a general weakness of cumulative surveys, like the German floristic atlas, when it comes to deriving diversity patterns (Haeupler & Schönfelder, 1989). Analysing proportions of species groups with a similar response to the environment should be much less prone to this bias. We therefore assume that the spatial patterns of *R*-spectra represent real gradients rather than surveying artefacts. The fact that the clusters formed by indicator proportions map out in a coherent pattern, with a clear relationship to physiographical landscape structures, supports this assumption.

Ecological background of species pool structure

Much of the variance in *R*-spectra can be neatly explained by the prevalence of certain rock types giving rise to soils of varying pH and base status (Fig. 3b,c). In fact, this study lends strong support to a grouping of stratigraphic units into rock types that has been developed in earlier ecological analyses of the Bavarian Alps (Freyer 1986, 1988; Ewald, 1997): rather acid rocks rich in quartz (sandstones, siliceous limestones, radiolarite), pure carbonates (limestone, dolomite), and a group of intermediate rocks (mudstones, marls) and loose pleistocene sediments. Areal proportions of these rock types account for the major differences in mean *R*-values of the grid cells.

Another considerable amount of variance in *R*-spectra can be described as differences in standard deviation and diversity of *R*-values. In the Bavarian Alps, instead of geological or topographic diversity, elevation *per se* appears to be the broad-scale key driver of diversity in soil conditions and corresponding plant groups. The *R*-indicator proportions in high mountain clusters C2 and C4 (Fig. 4) suggest that this effect is a matter of additional acidophytes and, in the high calcareous Alps, extreme calciphytes, while species with intermediate requirements are rarer than usual. The importance of these effects come out even more clearly when *R*-indicator frequencies are plotted in strata defined by temperature indicators for the entire Central European flora (Fig. 8; data from Ellenberg *et al.*, 1991; *T*-values 1–3 denote species of subalpine to alpine altitudinal distribution). We are not aware of an earlier recognition of this fact, that can also be observed in other floras, e.g. the Croatian (data from Kojić *et al.*, 1997). What are the causes? We hypothesize that two major drivers account for higher proportions of extreme *R*-indicators at higher elevations: (1) a frequent lack of mature soils at high elevations and (2)

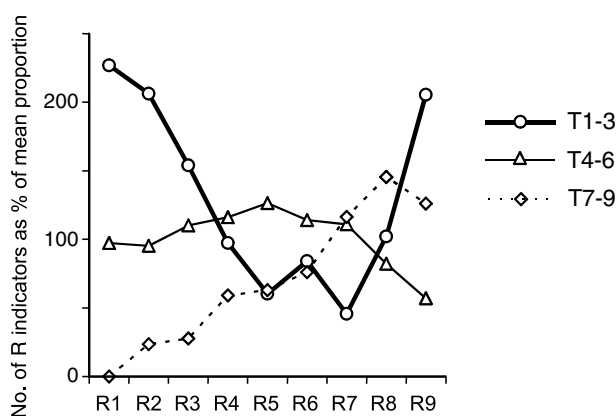


Figure 8 Proportions of *R*-indicator classes for temperature indicator classes in the whole data set of the central European vascular flora, as listed in Ellenberg *et al.* (1991). *T*-values from T1 = indicator of cold climate, only in the alpine belt, to T9 = indicators of very warm places. Values above 100% signify more indicators, values below 100% fewer indicators than average

particularities in soil genetic processes occurring under the harsh climatic conditions of high mountains.

(1) The rugged terrain of the alpine and subalpine belt, a result of relatively recent intensive glaciation, causes high erosion rates in many places. Cold climate imposes low chemical weathering. As a result, high elevations have an unusual preponderance of raw parent materials that have undergone limited chemical changes, like acidification and leaching of base cations.

(2) On the other hand, decreasing temperatures and increasing precipitations favour decreasing soil pH and increasing organic C concentrations at higher elevations (e.g. Hanawald & Whittaker, 1976; Dahlgren *et al.*, 1997). In the absence of advanced mineral soil development, cold, high-precipitation climates cause the accumulation of large stocks of organic carbon, that undergo rapid acidification from both atmospheric and internal sources. The depth of such well-drained Follic Histosols is highest around timberline, where intricate soil mosaics with marked vertical and lateral gradients of soil chemistry prevail (Bochter, 1984). In calcareous areas, they favour the coexistence of contrasting indicator plants even within the same plant communities (Ewald, 1999; Frankl, 2001). A similar heterogeneity can be caused by the patchy loam residuals of carbonate corrosion.

The uneven distribution of plant richness along the soil acidity gradient as a prominent feature of the flora of the Bavarian Alps (Fig. 1) accords with a wealth of published reports, chiefly from the arctic (Gough *et al.*, 2000), boreal (Tyler, 1999) and temperate zones (Pärtel, 2002), including other parts of the Alps (Wohlgemuth, 2002). It must be borne in mind that plant species richness in individual grid cells of the Bavarian Alps is recruited from that larger species pool of predominantly basiphytic or calciphytic taxa, whereas a considerably smaller number of acidophytes is regionally available. Frequency differences in rare *R*-indicator groups have more bearing on Shannon diversity than differences in large *R*-indicator groups. Because of the generally skewed distribution of *R*-indicators, the addition of acidophytes has the greatest influence on diversity in *R*-spectra, as we can see in C2 with the maximum in acidophytes, standard deviation and diversity in *R*-values. This same effect results in a negative correlation between average *R*-values and *R*-diversity in grid cells (Table 3). The combined effects of climate, edaphic processes and species pools, deserve further investigations, including field studies and analyses of the plant community patterns.

Landscape-scale analyses of indicator values

Linking plant species distributions and their ecological preferences as expressed in indicator values is an obvious way of interpreting floristic patterns on the landscape level, and it can help us to understand plant biodiversity (Austin, 1999). The correlation between averages of indicator values and measured site factors has often been demonstrated at the community scale (references in Ellenberg *et al.*, 1991). The combination of floristic grid cells and physiographical layers

in geographical information system enabled us to study such a relationship at the landscape-scale. We were well aware of the fact that large grid squares are much more heterogeneous than the usual community quadrat. Therefore we did not restrict our analysis to single values or averages, but devised a method to relate the multivariate spectra of indicator value frequencies to environmental quality and diversity. The analysis of single values or averages on landscape-scale levels has been done several times before (e.g. Orschied, 1994; Chytrý *et al.*, 1999; Korsch, 1999; Scheuerer & Schönfelder, 2000), an analysis of entire spectra has so far only been applied once (Durwen, 1982).

CONCLUSION

Linking plant geography and the ecology of individual taxa proves to be particularly useful in detecting and analysing biodiversity patterns. We are convinced that increased data availability offers considerable opportunities for establishing novel links between autecology, community ecology, macroecology and geographical landscape ecology, and we hope that similar multivariate analyses of indicator floras will promote the causal understanding of biodiversity patterns in the future.

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