

Performance of Macrolichens and Lichen Genera as Indicators of Lichen Species Richness and Composition

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Abstract: *In the search for cost-effective methods for measuring and monitoring lichen diversity, we tested the performance of two possible indicators: lichen genus diversity and macrolichen diversity. We studied the lichen vegetation of eight European countries situated in six different biogeographic regions. In each country, six land-use units (each 1 km²) representing a land-use gradient ranging from old-growth forest to farmland were sampled (n = 48) for terricolous, saxicolous, and epiphytic lichens at 16 plots each. We found 768 different lichen species belonging to 157 genera. Relationships between richness and density of genera and species, species and macrolichens, and crustose lichens and macrolichens were highly significant (p < 0.001) for all substrates combined and for epiphytic and saxicolous lichens. Richness and density of genera and macrolichens explained a large amount of variation of the species richness and density (R²: 71.9%–98.0%). The relationship between crustose lichens and macrolichens explained less of the variation (R²: 37.7%–70.1%). Effects of land-use intensity on the richness and density of genera, species, and crustose lichens were similar, except for a strong difference between the forested and the more open land-use units for epiphytic crustose lichens. For epiphytic macrolichens there were fewer significant effects. Detrended correspondence analysis indicated similar ordering of sites along the major gradients and similar length of these gradients for genera, species, macrolichens, and crustose lichens. Both genera and macrolichens are useful indicators of total lichen species richness and density. Macrolichens, however, are more suitable indicators than genera owing to (1) their*

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more stable taxonomy of species than of genera, (2) the potential that nonspecialists could do the sampling, (3) the limited use of genera data for species conservation, and (4) the fact that species extinctions will not be indicated by nonmonotypic genera.

Key Words: biodiversity indicator, crustose lichens, land-use intensity, species composition

El Funcionamiento de Géneros de Macrolíquenes y Líquenes como Indicadores de la Riqueza y Composición de Especies de Líquenes

Resumen: *En la búsqueda de métodos rentables para la medición y el monitoreo de la diversidad de líquenes, probamos el funcionamiento de dos posibles indicadores: diversidad de géneros de líquenes y diversidad de macrolíquenes. Estudiamos la vegetación de líquenes en ocho países europeos situados en seis regiones biogeográficas diferentes. En cada país, muestreamos los líquenes terrestres, saxícolas y epífitos en 16 parcelas ubicadas en seis unidades de uso de suelo (1 km² cada una) que representaban un gradiente de uso de suelo desde bosque maduro hasta tierras agrícolas (n = 48). Encontramos 768 especies diferentes de líquenes pertenecientes a 157 géneros. Las relaciones entre riqueza y densidad de géneros y especies, especies y macrolíquenes y líquenes costrosos y macrolíquenes fueron altamente significativos (p < 0.001) para todos los sustratos combinados y para líquenes epífitos y saxícolas. La riqueza y densidad de géneros y macrolíquenes explicaron una buena proporción de la variación de la riqueza y densidad de especies (R²: 71.9%–98.0%). La relación entre líquenes costrosos y macrolíquenes explicó menos de la variación (R²: 37.7%–70.1%). Los efectos de la intensidad de uso de suelo sobre la riqueza y densidad de géneros, especies y líquenes costrosos fueron similares, excepto por una fuerte diferencia entre terrenos boscosos y las unidades de uso de suelo más abiertas en cuanto a líquenes costrosos epífitos. Hubo menor efecto significativo para macrolíquenes epífitos. Los análisis de correspondencia indicaron un ordenamiento similar de sitios a lo largo de los gradientes principales y una longitud similar de estos gradientes para géneros, especies, macrolíquenes y líquenes costrosos. Los géneros y los macrolíquenes son indicadores útiles de la totalidad de la riqueza y densidad de especies de líquenes. Sin embargo, los macrolíquenes son indicadores más adecuados que los géneros debido a (1) su taxonomía de especies de más estable que la de géneros, (2) el potencial de que el muestreo no haya sido realizado por especialistas, (3) el uso limitado de datos de géneros para la conservación de especies y (4) el hecho de que las extinciones de especies no serán indicadas por géneros no monotípicos.*

Palabras Clave: composición de especies, indicador de biodiversidad, intensidad de uso de suelo, líquenes costrosos

Introduction

Species richness is a fundamental measure of biodiversity, and current trends of declining species richness in many regions of the world are a major ecological, economical, and cultural problem (see text of the Convention of Biodiversity at www.biodiv.org). The European Union aims to stop the loss of biodiversity by 2010 (European Commission 2001). Monitoring species richness over large geographic regions is, therefore, an urgent task for assessing the success of nature conservation policies or agroenvironmental schemes intended to stop this decline (Kleijn et al. 2001).

Gathering data on species richness of nearly any taxon, however, is expensive and time consuming in most regions of the world (e.g., Lawton et al. 1998). Thus, cost-effective methods that enable the prediction of species richness have to be developed. A popular approach is to identify some sort of indicator that correlates with the species richness of a particular group or even with overall species richness. Several methods have been suggested for finding such indicators (Gaston 1996; Duelli & Obrist

1998). These methods are based on assumed relationships between (1) environmental variables and species richness (e.g., Gaston 2000; Turner et al. 2003), (2) the richness of different, often unrelated taxa such as birds and plants or invertebrates (e.g., Prendergast et al. 1993; Lawton et al. 1998; Negi & Gadgil 2002; Vessby et al. 2002), or (3) numbers of species and numbers of supraspecific taxa such as genera or families (e.g., Williams & Gaston 1994; Andersen 1995; Balmford et al. 2000). Another promising approach is to search for species richness indicators within taxonomic groups. For example, Oliver and Beattie (1996) found that richness within some beetle families is highly correlated with overall beetle richness.

Here we focus on the last two approaches (i.e., the performance of phylogenetically related groups as indicators of species richness). By restricting the comparisons to phylogenetically related groups, a higher covariance between the numbers of species of the groups is expected (Beccaloni & Gaston 1995; but see Ricketts et al. 2002). This view is also supported by Prendergast et al. (1993), who found larger overlap of species-rich areas for more

related taxa that share climatic requirements (e.g., butterflies and dragonflies) than for unrelated taxa.

Furthermore, the taxon under consideration and its species-richness indicator should experience the same level of complementarity (i.e., spatial species turnover should follow the same gradients and turnover rates should be similar). If the ecological amplitude of the two taxa is too different, compositional changes in one group may not adequately reflect changes in the other group. If they experience the same level of specialization, however, the indicator will be broadly applicable in nature conservation issues such as designing efficient reserve networks (Balmford et al. 2000) and monitoring shifts in community composition (McCune et al. 1997). Again, more closely related groups or taxa are expected to exhibit higher covariance (Oliver & Beattie 1996).

We focused on the potential for lichen genera and macrolichen diversity to serve as indicators of total lichen diversity (*diversity* is used as a comprehensive term that includes species composition and richness). Lichens are a species-rich group (approximately 7000-8000 species in Europe) occurring in various habitats where, in some instances, their biomass and species richness may even outperform those of vascular plants.

However, lichens are rather laborious to sample and identify and, thus, are often neglected despite their important contribution to local species richness. This is especially true for crustose lichens, for which thin-layer chromatography analyses of the secondary chemical compounds are often necessary for identification. Macrolichens, on the other hand, are much easier to sample and to identify than crustose lichens. Many authors studying lichen species richness focus on macrolichens only, assuming, although not explicitly stating, that crustose lichens show the same patterns. Crustose lichens, however, may be as diverse or even more diverse than macrolichens in many regions (e.g., Dietrich & Scheidegger 1997; Eversman et al. 2002).

Specifically, we asked the following questions: (1) Can total lichen species richness be predicted by the richness of macrolichens or lichen genera alone? (2) Are effects of land-use intensity on total lichen species richness predictable by macrolichen richness or genera richness? (3) Do macrolichens, or lichen genera, alone reflect compositional shifts in lichen communities?

Methods

Study Area and Sampling Design

This study is part of a larger project funded by the European Union (BioAssess) that aims to develop biodiversity indicators across land-use gradients in Europe. Lichen vegetation data were sampled in eight European countries situated in six different biogeographic zones (Alpine,

Switzerland; Atlantic, Ireland and United Kingdom; Boreal, Finland; Continental, France; Mediterranean, Portugal and Spain; Pannonic, Hungary). Within each country one study region was selected. Within each study region, 6 study sites or land-use units (LUUs) with an area of 1 km² (1 × 1 km) each were established for a total of 48 LUUs. The six LUUs within each region represented different degrees of land-use intensity: natural forest (land-use intensity 1), managed forest (intensity 2), mixed-use landscape dominated by forest or woodland (intensity 3), mixed-use landscape not dominated by a single land-use (intensity 4), mixed-use landscape dominated by pasture (intensity 5), and mixed-use landscape dominated by arable crops (intensity 6).

The overall study design is randomized complete blocks (Sokal & Rohlf 1995) with eight blocks (countries) and six treatments (land-use intensity with six levels). In each of the 48 LUUs, a regular grid with mesh size 200 m was set up. The grid established 16 intersections that were at least 200 m away from the border of the LUUs. At each of these intersections a circular plot of 1 ha (56.4 m radius) was established. Within each plot 12 collecting sites at fixed distances and bearings from the center of the plot were surveyed. According to a standardized, complex scheme (Scheidegger et al. 2002), lichen vegetation was surveyed at each collecting site. All terricolous, saxicolous, and epiphytic lichen species were considered. At each collecting site, an area of 0.4 × 0.5 m (for each substrate, if available) was searched for lichens. Specimens not identified in the field were collected and species identity was confirmed in the laboratory (if necessary with thin-layer chromatography of the secondary chemical compounds).

Taxa were determined with a number of identification keys listed in Nimis and Martellos (2003). We also followed their generic concept, which splits large, heterogeneous genera such as *Parmelia* into smaller groups. Specimens were deposited in the following herbaria: Natural History Museum (London), Hungarian Natural History Museum (Budapest), University of Helsinki (Helsinki), Museu Nacional de História Natural (Lisboa), Universidad Complutense (Madrid), University College Dublin (Dublin), and at the Swiss Federal Research Institute (WSL). Field work was conducted in 2001 and 2002. In each country a different subgroup of the coauthors of this study carried out the lichen sampling and determination.

Data Analysis

We performed various tests to analyze the potential of macrolichen diversity and genera diversity as indicators of total lichen diversity. All analyses were performed for all taxa (*taxon* is used as a common term for species or genera), for taxa found on living trees (epiphytic taxa), and for taxa found on stones (saxicolous species). Terricolous taxa were not analyzed separately because on

the terricolous plots, lichens were also sampled on small trees, bushes, pebbles, rocks <50 cm × 40 cm, and on any other substrate. Thus, not all our terricolous taxa were growing on soil; therefore, they constitute an ecologically rather dissimilar group.

Total lichen species richness is the sum of macrolichen and crustose lichen species richness. Thus, coefficients of correlations between macrolichen and total lichen species richness cannot be low if macrolichen richness is much higher than crustose lichen richness. This is true even if there is no correlation between macrolichen species richness and crustose lichen species richness. We considered macrolichens good indicators of total richness, however, only if there was also a high correlation between macrolichens and crustose lichens. We therefore also analyzed the relationship between macrolichen and crustose lichen species richness. A similar problem arises if one uses genera richness as an indicator of total richness because obviously these two measures are not independent. There is no way, however, to circumvent this.

We calculated taxon richness, taxon density (mean taxon richness per plot and LUU, including plots without taxa), and beta diversity for each LUU. The term *total taxon richness* is used for describing overall richness patterns.

We used the beta-1 index of Harrison et al. (1992) to quantify beta diversity. Beta-1 is calculated as

$$\beta = [(S/D - 1)/(n - 1)] \times 100,$$

where S is the total number of taxa per LUU, D is corrected taxon density (i.e., taxon density per occupied plot, plots with no taxa or LUUs with just one occupied plot were omitted), and n is the number of occupied plots. For the calculation of beta diversity, LUUs with no taxa were omitted. Beta-1 is a modification of the original beta diversity measure of Whittaker (1960). It accounts for differing numbers of replication through division of the numerator in the above equation by its maximal possible value (which is $n - 1$). Beta-1 ranges from 0 (complete similarity) to 100 (complete dissimilarity). Because beta-1 depends on floristic similarities between plots within LUUs, it can be interpreted in terms of within-LUU habitat diversity as experienced by the different groups.

We used regression models to test the potential of our indicator groups (i.e., macrolichens and lichen genera) to predict species richness and species density. To account for effects of countries and land-use intensities, richness and density data for all species, macrolichen species, crustose species, and genera were corrected for effects of countries and land-use intensities prior to the regression analyses. This was done by regressing these variables on the factors "country" and "land-use intensity." For all further regression analyses we used the residuals of these regressions. Because performance of indicators may vary according to substrate type, we also performed all anal-

yses independently for epiphytic and saxicolous species. Significant deviations from zero of the regression slopes, percentage of variance explained by the regressions (adjusted $R^2 = 100 \times [1 - (\text{residual mean square})/(\text{total mean square})]$), and visual inspection of the 95% prediction intervals were used to evaluate the potential of the indicators.

We used analysis of variance (ANOVA) with orthogonal, linear contrasts for testing the effects of land-use intensity on species richness, species density, and beta diversity of the considered groups (genera, species, macrolichens, crustose lichens). Degrees of freedom for land-use intensity were five. These could be split into five orthogonal contrasts (see Table 2). The countries were included as blocking factors ($df = 7$, except for saxicolous species $df = 4$; see below). Both factors were tested against the residual mean squares. For the effects of land-use intensity (fixed factor) this is the correct test; for the effects of countries (random factor) this test is correct only if there is no significant interaction between the two factors (Sokal & Rohlf 1995). If there is significant interaction, the test is conservative (i.e., it is harder to reject the null hypothesis of no effect). Good indicators are expected to show the same effects of land-use intensities as the group for which they are indicators. Results of the ANOVAs are presented in an abbreviated form because we were interested only in whether the different groups show the same effects or not and not in the effects and their ecological meanings themselves. The ANOVAs will be presented and discussed in greater detail elsewhere.

To compare within-site habitat heterogeneity as experienced by the different taxon groups, we performed Mann-Whitney U tests with beta-1 values corrected for effects of countries and LUUs because we were not interested in (disturbing) effects of these covariables.

To study possible covariation in species composition of the different groups (genera, species, macrolichens, crustose lichens) and length of the main ecological gradients, we used detrended correspondence analyses (DCA). Covariation in species composition was quantified by means of Spearman rank correlations of site scores of DCA axes. Length of gradient, as revealed by DCA, is measured in standard deviation units (ter Braak 1995) and can be used as a measure of compositional turnover or beta diversity. However, it is not necessarily correlated to beta-1 because gradient length as measured by DCA depends on among-site similarity in species composition, whereas beta-1 depends on floristic similarity among plots within sites. Because second and higher DCA scores are often meaningless because of detrending (Legendre & Legendre 1998), we used only first axes site scores for all correlations and comparisons. Separate canonical correspondence analyses (CCA) indicated that both "design" variables (countries and LUUs) had significant effects on lichen species composition (results not presented). Therefore, we used partial DCAs with these

Table 1. Richness (total and per LUU*), density (mean taxon richness per plot), and beta diversity (beta-1 after Harrison et al. 1992) for lichen genera, lichen species, macrolichen species, and crustose lichen species.

Group	Taxon richness			Taxon density		Beta diversity	
	total	per LUU	±SE	per LUU	±SE	per LUU	±SE
All lichens							
genera	157	41	2.77	15.9	1.39	13.4	1.29
species	768	86.5	7.12	25.9	2.84	19.4	1.49
macrolichens	221	31.6	2.54	10.5	1.13	21.1	3.04
crustose lichens	547	54.9	4.99	15.4	1.86	22.5	2.27
Epiphytic lichens							
genera	114	29	1.85	10.9	0.98	13.8	1.33
species	433	51.9	3.95	15.6	1.63	19.5	1.50
macrolichens	131	20.6	1.63	7.3	0.82	18.9	2.62
crustose lichens	302	31.3	2.67	8.3	0.91	21.7	1.67
Saxicolous lichens							
genera	119	31.1	1.69	9.8	1.15	18.4	2.71
species	446	60.7	4.49	15.3	2.07	26.6	2.25
macrolichens	141	21	1.82	4.7	0.73	30.8	2.86
crustose lichens	305	39.7	3.52	10.5	1.55	24.3	2.66

*LUU = land-use unit (1 × 1 km).

variables as covariables to investigate correspondence in compositional covariation and to compare length of gradients. The following stepwise procedure was applied. First, we ran a DCA without covariables and then we ran a partial DCA with the countries as covariables followed by a partial DCA with the countries and the land-use intensities as covariables. As input data for both DCA and CCA we used presence-absence matrices.

Because there were no or almost no stones on plots in Ireland, Hungary, and Portugal, we omitted these countries from all analyses of saxicolous lichens. Owing to very intensive agricultural use of one LUU in Portugal (land-use intensity 6), not even a single lichen species was found on plots in that LUU. This LUU was therefore omitted from all ordinations, but not from analyses concerning taxon richness or density.

In all ordinations rare species were downweighted by the standard downweighting function of CANOCO. Otherwise, default settings for ordinations in CANOCO 4.5 were used (ter Braak & Smilauer 1997-2002). All ANOVAs, Spearman correlations, and Mann-Whitney *U* tests were carried out with the GENSTAT 5.0 program (release 3.2, Payne et al. 1993). Regressions and the calculations of 95% confidence and prediction intervals were done with R 1.8.1 (R Development Core Team 2003).

Results

Genera and Species Richness

We found 768 different lichen species that belonged to 157 genera (Table 1). Distribution of species among genera was highly skewed, with more than 40% of the genera represented by only one species (Fig. 1). The most

species-rich genus was *Lecanora* with 52 species. Total species and genera richness of epiphytic and saxicolous species was similar. Both epiphytic and saxicolous species accounted for approximately 60% of the total species richness and approximately 75% of the total genera richness. For both richness (LUU scale) and density (plot scale), the differences between genera and species were less pronounced for all groups (Table 1). The species-to-genera ratio was lower for taxon density than for taxon richness.

For total taxon richness, the ratio of the number of macrolichen species to the number of crustose lichen species was similar for all lichens (0.40), epiphytic lichens

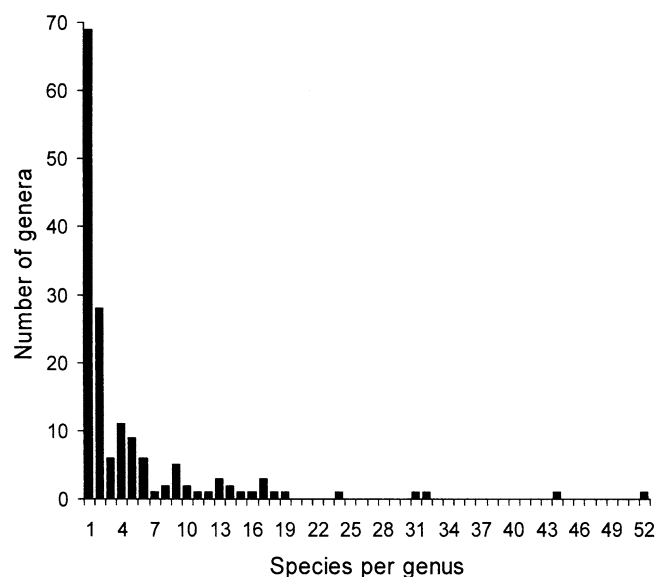


Figure 1. Distribution of lichen species per genus over all 48 land-use units.

(0.43), and saxicolous lichens (0.46). For taxon richness these ratios were higher (0.57 for all lichens, 0.66 for epiphytic lichens, and 0.53 for saxicolous lichens), and there was an additional increase of two of these ratios for taxon density (0.78 for all lichens, 0.88 for epiphytic lichens). However, for saxicolous lichen the species density ratio was only 0.45.

For both taxon richness and taxon density, all relationships ($p < 0.001$) between genera or macrolichens and all species were positive and highly significant (Fig. 2). For all regressions R^2 values were high (range: 71.9–98.0). The R^2 values for the relationships between genera and species richness were slightly higher than between macrolichen and species richness (+8.33 on average). Richness and density of crustose lichens were highly significantly related to macrolichen richness and density ($p < 0.001$ for all regressions, Fig. 3). However, the relationships for all lichens and epiphytic lichens revealed low R^2 values (range: 37.7–51.6).

Land-use intensity had significant, or at least marginally significant, overall effects on taxon richness and density for all lichens and epiphytic lichens but not for saxicolous lichens (Table 2). Overall, effects of land-use intensities were stronger for taxon density than for taxon richness. Effects on genera richness, species richness, and crustose lichen richness were similar, except for a strong effect of land-use intensities 1 and 2 versus 3, 4, 5, and 6 on richness of epiphytic crustose lichens (Table 2). For macrolichen richness, there were fewer and less significant effects of land-use intensities, in particular for the epiphytic species.

Regarding taxon density, patterns of significance that resembled those for genera, species, macrolichens, and crustose lichens appeared (Table 2). However, epiphytic macrolichens again showed fewer significant effects. The amount of variance explained by country in the ANOVAs was between 1.14 and 15.69 times larger than the amount explained by land-use intensity (mean = 5.21). The effects of country were significant in all ANOVAs except for density of all saxicolous lichen species and genera, saxicolous macrolichens, and richness of saxicolous macrolichens.

Genera and Species Assemblages

Beta diversity corrected for effects of country and land-use intensity revealed no significant differences between genera and species, between macrolichens and species, or between macrolichens and crustose lichens. This was true for all lichens, epiphytic species, and saxicolous lichens ($p > 0.13$ for all comparisons). Therefore, taxon turnover among plots within LUUs seems to be similar for the compared groups (Table 1).

Most correlations performed with the DCA site scores revealed highly significant relationships (Table 3). Only three correlations were not significant. Two of these were

between site scores of macrolichens and crustose lichens corrected for effects of the two covariables. The highest correlations were between the site scores of DCA axis 1 with country as a covariable. These correlations were all highly significant ($p < 0.001$), thus indicating that the groups responded in a similar way to the underlying main gradient after accounting for variation due to climatic or biogeographic differences. After fitting two covariables, the correlations of the resulting site scores were lower, suggesting that the groups did not correspond equally well along minor floristic gradients as along the major gradient. Length of gradients as revealed by DCA with country as covariable was similar for the compared groups (Table 4). The high value for genera was largely due to one LUU. Eliminating this LUU reduced length of gradient for genera considerably, revealing only minor differences.

Discussion

Macrolichens as Indicators

Our results suggest that macrolichens may be good indicators of lichen species richness because of the many highly significant relationships. Furthermore, species turnover within LUUs was very similar for all lichens and macrolichens and for macrolichens and crustose lichens, indicating similar ecological or habitat heterogeneity within LUUs for all groups. Considering the main species compositional gradients, site scores for all lichens and macrolichens and for macrolichens and crustose lichens were significantly correlated, and the lengths of gradients were quite similar. This result indicates that both macrolichen and crustose lichen assemblages respond to the same main gradients and that both groups will respond in a similar way to habitat alterations. Thus, there seems to be a high potential for the use of macrolichens alone as indicators of the condition of the entire lichen community. This is an important finding because in many surveys only macrolichens are considered.

Moreover, macrolichens were less species rich than crustose lichens. This was true for all lichens and epiphytic and saxicolous lichens. High species richness of crustose lichens, as compared with macrolichens, seems to be a common pattern in many surveys at widely differing geographic locations (Dietrich & Scheidegger 1996; Pharo & Beattie 1997; Eversman et al. 2002). Recording only macrolichens would therefore considerably reduce the amount of work both in the field and later in the laboratory for the determination.

Nevertheless, we cannot unconditionally recommend macrolichens as indicators of lichen species richness. Although highly significant, the relationships between the species richness of macrolichens and crustose lichens for all lichens and epiphytic lichens explained rather low

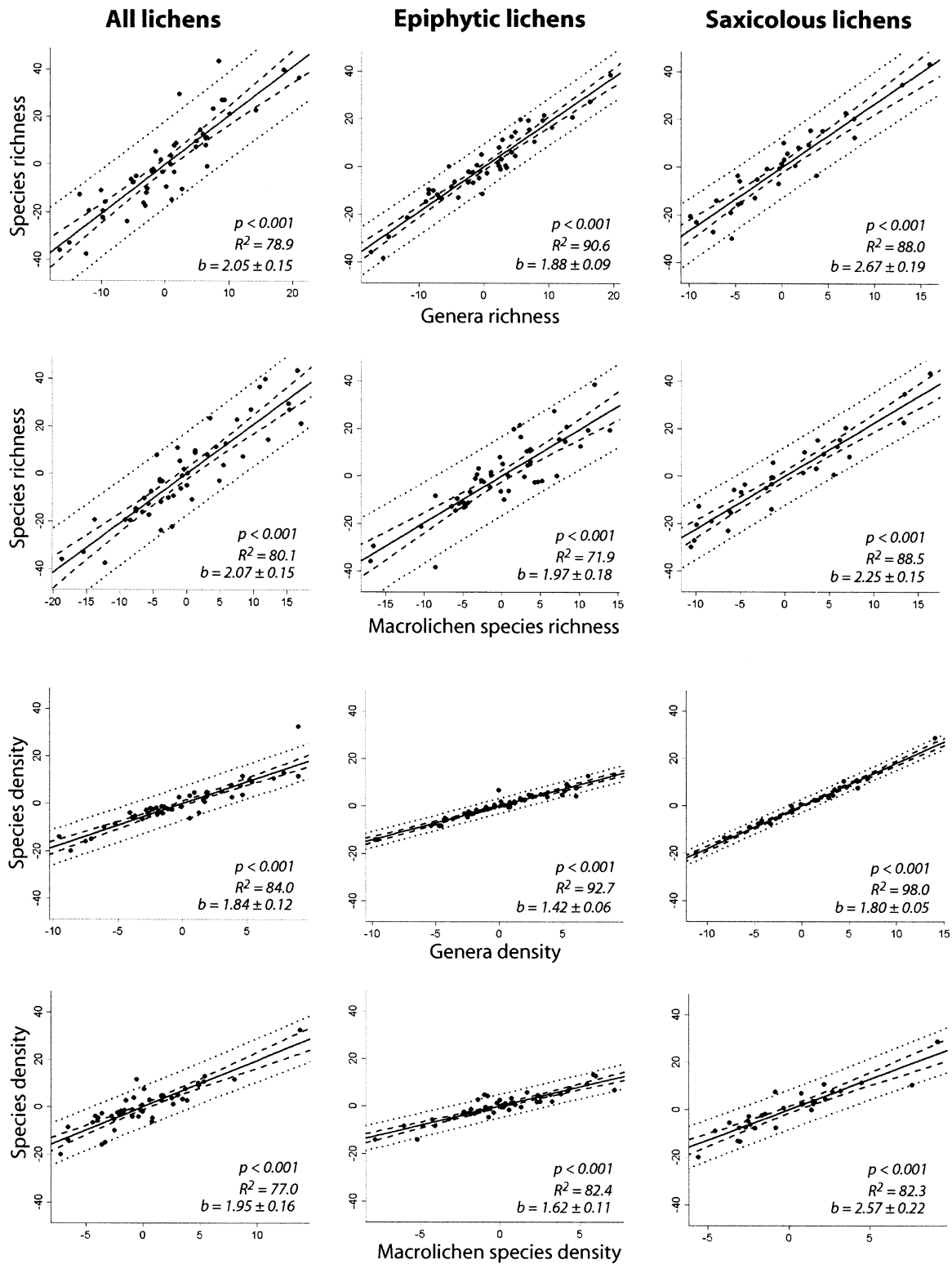


Figure 2. Relationships between richness and density of genera and species and between macrolichens and species for all lichens, epiphytic lichens, and saxicolous lichens. The x and y values are residuals from a regression of taxon richness and density, respectively, on country and land-use intensity. Inner dashed lines indicate the 95% CI, outer dotted lines the 95% prediction interval, and b is regression slope \pm SE.

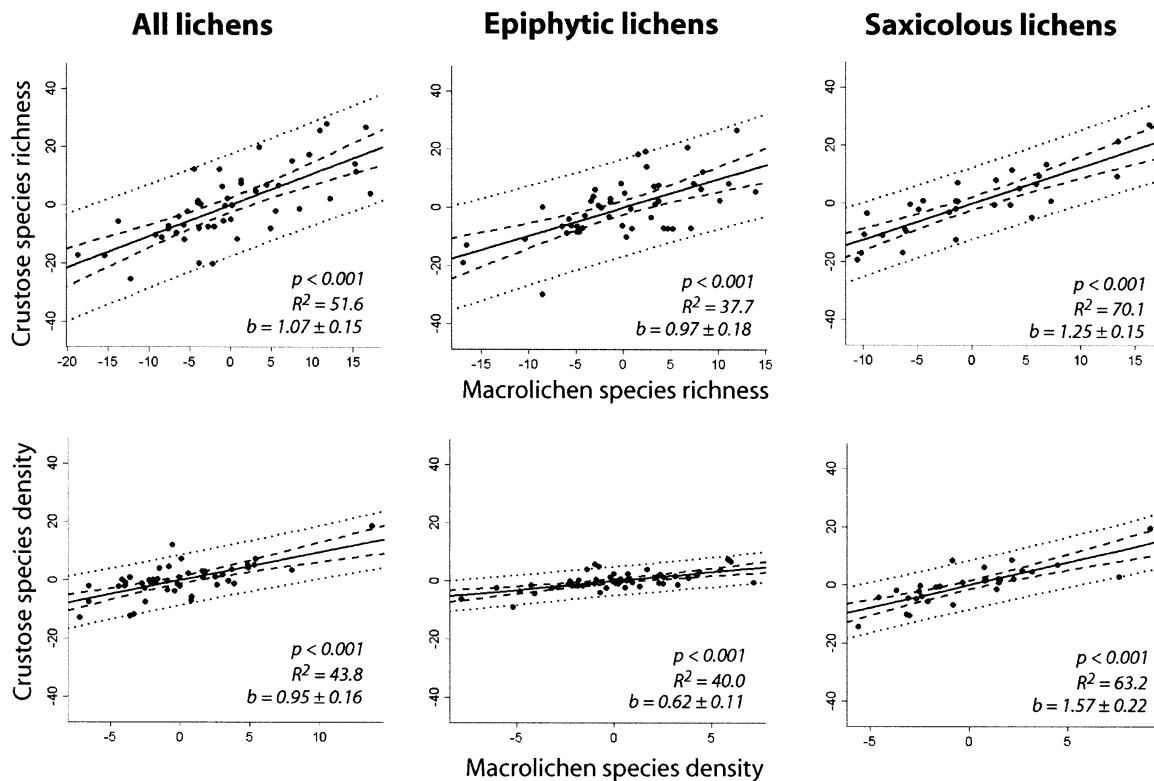


Figure 3. Relationships between richness and density of macrolichens and crustose lichens for all lichens, epiphytic lichens, and saxicolous lichens. The x and y values are residuals from a regression of taxon richness and density, respectively, on country and land-use intensity. Inner dashed lines indicate the 95% CI, outer dotted lines the 95% prediction interval, and b is regression slope \pm SE.

amounts of variation and the predictions were highly imprecise. Furthermore, effects of land-use intensity differed between epiphytic crustose lichens and epiphytic macrolichens, even though our land-use intensity classes followed a rather coarse gradient. Therefore, species richness or density of macrolichens and crustose lichens may respond differently to changes in land use. Moreover, variations of macrolichen and crustose lichen communities were not correlated or only weakly correlated after accounting for both country and land-use intensity.

Ecological differences between macrolichens and crustose lichens are sometimes obvious. For example, lichen assemblages on bark receiving no direct precipitation or on exposed rocks in harsh environments are often dominated by crustose lichens (Obermayer 1997). Lower lichen-species richness at forest edges compared with forest interior is mainly due to the absence of some crustose species (Hilmo & Holien 2002). Dietrich and Scheidegger (1996) found that sites with few lichens are often dominated by sorediate crustose species, but they did not find a significant negative correlation between richness of sorediate species and total number of species. Therefore, in more mesic sites crustose lichens and macrolichens may be quite rich in species.

Lichen Genera as Indicators

The relationship between richness and density of lichen genera and species was close. For epiphytic and saxicolous lichens the explained variation was higher than for all lichens. Moreover, the effects of land-use intensity on genus richness were almost identical to those on species richness. The close relationships imply that genus richness is a good indicator of species richness. In the only other known study exploring the applicability of (macro-) lichen genera richness as a surrogate for species richness (Negi & Gadgil 2002), the relationship was also highly significant. Furthermore, genus richness is a good indicator of species richness for a variety of other taxa such as vascular plants and bryophytes (Negi & Gadgil 2002), fungi (Balmford et al. 2000), and invertebrates (Pik et al. 1999; Cardoso et al. 2004). However, the relationship may depend on whether the comparisons have been made within or between habitats or regions. Andersen (1995) found a strong relationship between species and genus richness of ants within regions but not between regions. This was largely an area effect because sampling area varied within the regions. In our study, the genera-to-species ratio also depended on the area considered, with the genus curve flattening off much earlier than the

Table 2. Summary of analysis of variance (*p* values) with orthogonal contrasts for effects of land-use intensity on richness and density of lichen genera, all lichens, macrolichens, and crustose lichens.^a

Explanatory variable	Richness				Density			
	all genera	all species	macrolichens	crustose lichens	all genera	all species	macrolichens	crustose lichens
All lichens								
land-use intensity ^b	≤0.05	≤0.05	≤0.05	≤0.05	≤0.01	≤0.01	≤0.01	≤0.05
1,2 vs.3,4,5,6					≤0.01	≤0.01	≤0.05	≤0.05
1 vs. 2	≤0.01	≤0.01	≤0.05	≤0.01	≤0.05	≤0.05	≤0.05	≤0.1
3,4 vs. 5,6	≤0.1	≤0.1		≤0.1				
3 vs. 4								
5 vs. 6	≤0.05	≤0.1	≤0.05		≤0.1		≤0.1	
Epiphytic lichens								
land-use intensity	≤0.01	≤0.01	≤0.1	≤0.001	≤0.001	≤0.001	≤0.05	≤0.001
1,2 vs.3,4,5,6				≤0.01	≤0.001	≤0.01		≤0.001
1 vs. 2	≤0.001	≤0.001	≤0.05	≤0.001	≤0.01	≤0.001	≤0.01	≤0.001
3,4 vs. 5,6	≤0.05	≤0.05		≤0.01	≤0.05	≤0.05		≤0.01
3 vs. 4								
5 vs. 6	≤0.1							
Saxicolous lichens								
land-use intensity	≤0.1							
1,2 vs. 3,4,5,6	≤0.05			≤0.1				
1 vs. 2								
3,4 vs. 5,6								
3 vs. 4								
5 vs. 6								

^aThe blocking factor country (random factor, *df* = 7, except for saxicolous lichens with *df* = 4) is included in all analyses. For land-use intensity *df* = 5 in all analyses.

^bLand-use intensity: 1, natural forest; 2, managed forest; 3, mixed-use landscape dominated by forest or woodland; 4, mixed-use landscape not dominated by a single land use; 5, mixed-use landscape dominated by pasture; 6, mixed-use landscape dominated by arable crops.

species curve (Fig. 4). Thus, our study was more complete for genera as opposed to species.

Although genus richness was much lower than species richness, turnover (corrected for effects of country and land-use intensity) within LUUs was not significantly different. Furthermore, the length of compositional gradients and site ranking along the first DCA axis were similar for both species and genera. Thus, it seems to be sufficient to monitor lichen genera to detect effects of ma-

ior environmental changes on species composition. This was to some extent expected because ecological similarity within genera is often higher than between genera. For example, most species within the genera *Usnea* or *Bryoria* have similar ecological requirements.

A possible bias in our data set may stem from the fact that the genera lists were based on the species lists, implying that we did not have independent measures of genera and species richness. Therefore, the genera lists are

Table 3. Correlations of site scores of axis 1 of separately run detrended correspondence analyses with no covariable, country, or country and land-use intensity as covariables.

Lichen	Correlations	Covariables					
		no covariable	p	country	p	country + land-use intensity	p
All (<i>n</i> = 47)*	genera—species	0.74	≤0.001	0.77	≤0.001	-0.37	≤0.01
	species—macrolichens	0.92	≤0.001	0.93	≤0.001	0.60	≤0.001
	macrolichens—crustose lichens	0.56	≤0.001	0.86	≤0.001	0.15	
Epiphytic (<i>n</i> = 46)	genera—species	0.89	≤0.001	0.93	≤0.001	0.52	≤0.001
	species—macrolichens	0.86	≤0.001	0.90	≤0.001	-0.71	≤0.001
	macrolichens—crustose lichens	0.76	≤0.001	0.82	≤0.001	0.07	
Saxicolous (<i>n</i> = 30)	genera—species	-0.18		0.92	≤0.001	-0.79	≤0.001
	species—macrolichens	-0.96	≤0.001	0.95	≤0.001	0.70	≤0.001
	macrolichens—crustose lichens	-0.41	≤0.05	0.89	≤0.001	-0.45	≤0.01

*Land-use units without species are omitted; hence, the different number of replicates.

Table 4. Length of gradients as standard deviation units of first axes of detrended correspondence analyses (with country as covariable) as measure of lichen species, genera, macrolichen, and crustose lichen turnover.

	Length of gradient		
	<i>all lichens</i> ^a	<i>epiphytic lichens</i>	<i>saxicolous lichens</i>
Genera	3.06 (2.22) ^b	2.48	1.86
Species	1.88	2.14	2.41
Macrolichens	2.39	2.91	2.57
Crustose lichens	2.69	2.19	2.57

^an = 47 for *all lichens*, n = 46 for *epiphytic lichens*, and n = 30 for *saxicolous lichens*.

^bGradient length without one outlying land-use unit.

probably more complete than they would be if we considered only genera in the field.

A problem arising from the applicability of lichen genera as a surrogate for species richness may be that lichen taxonomy is continually changing (Nimis 1998). In some groups there is a considerable lack of consensus about the number of genera (e.g., *Cetraria* s. lat., *Rinodina* s. lat., *Buellia* s. lat. or *Parmelia* s. lat.). More so than species, genera are artificial units and their circumscription changes over time. Thus, the relationship between genera and species richness has to be reevaluated from time to

time, particularly after major taxonomic changes. Moreover, generic concepts often differ between countries or continents. This means that the exact relationship between genera and species richness has to be established for each area of interest.

Additionally, one must be aware that a data set composed of genera only is of limited use for further analyses because of its restricted information content. For conservation issues, species-level identifications are often inevitable. For example, the criteria of the IUCN Red List (IUCN 2001) can be applied only to taxonomic units at or below the species level.

A further problem may occur with some crustose species for which the genera cannot be recognized in the field and for which it is necessary to determine first the species before it is clear to which genus the species belongs. Obviously, such species do not contribute to cost-reduction of genera-level surveys. This has also been reported to be a problem in other taxa that are rather poorly known and hard to determine (e.g., spiders, Cardoso et al. 2004).

Effects of Country

In all analyses, country had a large effect. In the ANOVAs, the variance explained by country was always higher than the variance explained by land-use intensity. However, the latter variance may contain a further variance component caused by an interaction between country and land-use intensity. Owing to the design of the study, it was not possible to test whether there was a significant interaction (Sokal & Rohlf 1995). Despite the significant effects of country in most cases, the tests to reveal this significance were rather conservative because the residual mean squares would be too large if there were a significant interaction between country and land-use intensity. Moreover, correcting variables for effects of country improved DCAs and regression analyses. Although many lichens have a large distribution area (Lücking 2003), the effects of country on lichen richness, density, and composition were expected because the countries belonged to six widely different biogeographical regions.

Experience of Field Personnel

Large-scale studies or monitoring studies over a longer time period will have different field personnel among sites and over time. Diverging experience among field workers could bias the results. For example, in Switzerland a nonspecialist recorded fewer than one-third the species (including crustose species) that a lichen expert found (Will-Wolf et al. 2002). McCune et al. (1997), however, have shown that compositional gradients of macrolichen communities are robust with respect to the collector of the data (i.e., the influence of observer differences has minimal effects on the results). Therefore, differences in lichen field experience are believed to be

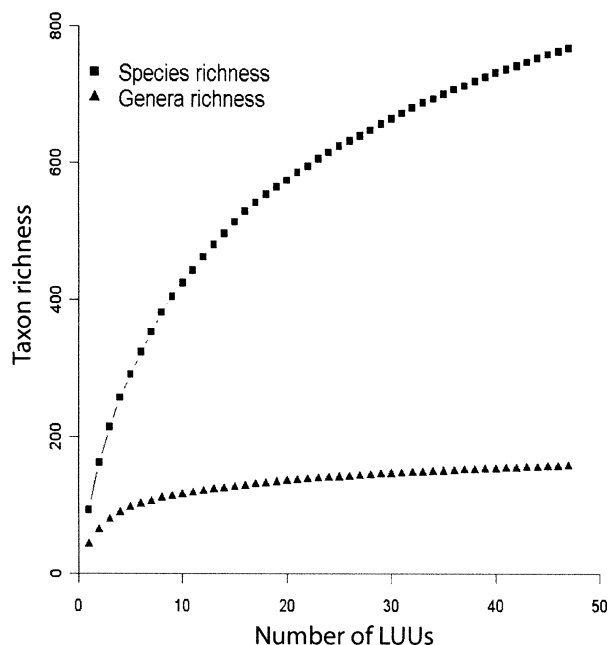


Figure 4. Lichen species and genera accumulation curves. Taxon richness is the observed species or genera richness. Curves are plotted from the means of 100 randomizations of sample (land-use unit, LUUs) accumulation order. Curves were calculated with EstimateS 6.0 (Colwell 2000).

more evident for crustose lichens than for macrolichens and so would affect lichen genera (including crustose lichens) as indicators more than macrolichens.

In our study all field workers were experienced lichenologists with at least some years of practice in collecting and determining lichens. Moreover, in all countries a different group of lichenologists sampled and identified the lichens, and bias introduced by different experiences of these groups was eliminated by correcting all data by effects of country. Therefore, the highly variable relationship between macrolichen and crustose lichen richness seems unlikely to be caused by a biased data set.

Conclusions

Genera and macrolichens may be used as indicators of total lichen species richness. It is also to be expected that complementary site selection based on either of the indicators alone would represent most of the species because both the indicators almost fully represent turnover at the species level. This has been shown for a related, species-rich group, namely the macrofungi, where hypothetical genus-based reserve networks capture a high percentage of the species represented when species-level data are used (Balmford et al. 2000).

Overall, macrolichens seem to be better suited as indicators of total lichen species richness than genera because (1) they have a more stable taxonomy of species than of genera, (2) they can be sampled by nonspecialists, (3) the genera data are of limited use for species conservation, and (4) species extinctions will not be indicated by nonmonotypic genera. However, identifying species extinctions may also be a serious drawback in the applicability of macrolichens alone as indicators. For example, if a habitat dominated by crustose lichens is eradicated, its disappearance will not necessarily be detected by monitoring macrolichens.

Eventually, one must be aware that no indicator is perfect, and even if there are close relationships between the richness of the indicator and that of the indicated group, one will rarely know anything about how such a relationship may change over time. Although the probability of related groups to react similarly to environmental variation (e.g., to climate change) is expected to be high because of similar ecological requirements, we must regularly determine whether the relationship between the indicator and the indicated group remains the same.

Finally, because neither richness of macrolichen species nor richness of genera may be an adequate measure on which to base conservation decisions, a more promising approach may be to optimize sampling strategies in such a way that even in resource-limited situations it would be possible to sample representative species-level data.

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