FREQUENCY, DIVERSITY AND ECOLOGICAL STRATEGIES OF EPIPHYTIC LICHENS IN THE SWISS CENTRAL PLATEAU AND THE PRE-ALPS

Michael DIETRICH★ and Christoph SCHEIDEGGER★

Abstract: To identify representative quantitative criteria for the creation of a future Red List of epiphytic lichens, 849 trees in 132 long-term ecological observation plots in the Swiss Central Plateau and the Pre-Alps were surveyed by standard sampling. Based on the trees, frequency data of the lichen taxa observed are described by the log series model, indicating the controlling effect of few ecological factors. Based on the plots, four classes of scarcity, each comprising 25% of the species, were established. As a contribution to the development of a national, representative survey of lichens, α-diversity (species richness, species density) and β-diversity (dissimilarity) were calculated in terms of region, vegetation formation, vegetation belt and for their combinations. Differences in lichen diversity between the Central Plateau and the Pre-Alps were caused by the bigger elevational range in the Pre-Alps, which resulted in a higher species richness. α-Diversity of forest and non-forest were similar, whereas each vegetation formation showed one third of its species restricted to it. The contributions to the total lichen diversity of crustose, foliose and fruticose as well as of generative and vegetative species was calculated. Specific features along the altitudinal gradient of vegetation belts emerged: the percentage of crustose and generative lichens declined with every altitudinal step, increased in fruticose and vegetative lichens, and was the same in foliose species.
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Introduction

The conservation of any group of organisms needs basic information on distribution diversity and dynamics. Representative data on the frequency of epiphytic lichens is of key importance when these organisms are used as bioindicators of air pollution or when Red Lists are to be established. In regional studies using epiphytic lichens as indicators of air pollution elaborate sampling designs have been proposed (Herzig & Urech 1991; Nimis *et al.* 1991). In conservation biology, however, the data used for creating Red Lists for lichens have so far always been of a qualitative nature (Thor 1995). International and national Red Lists have been published worldwide for many organisms. Based mainly on inventories of the organisms considered, the data used for establishing Red Lists are rarely representative. Unbiased inventories representative of large areas are difficult to carry out for many groups of organisms, either because of seasonality of sessile organisms or the translocation of vagrant organisms.

In Switzerland representative data collection was conducted as part of the Forest Inventory (EAFV 1988). For inconspicuous cryptogams a new method was proposed for the Inventory of the Swiss Bryophyte Flora (Urmi *et al.*

★Swiss Federal Institute for Forest, Snow and Landscape Research, CH–8903 Birmensdorf, Switzerland.

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1990). Switzerland's first Red List of macrolichens is based mainly on the personal field experience of the authors, as well as on herbaria and literature studies (Clerc *et al.* 1992). In this country, floristic studies on epiphytic lichens were sparse until recently, and mainly took the form of overall investigations of the flora of small, species-rich, forest areas (Camenzind & Wildi 1991; Dietrich 1991; Groner 1990; Scheidegger *et al.* 1991). However, the diversity of lichens reported in such studies is usually greatly biased by an unequal consideration of the organisms or the habitats. The first bias is often encountered when species difficult to identify are neglected in a survey, such as sorediate crustose lichens (Dietrich & Scheidegger 1996*a*). The second may lead to considerable errors when habitats of organisms with a narrow ecology are inaccurately represented.

This study is aimed at contributing to the development of a representative survey of the diversity, distribution and dynamics of epiphytic lichens. Floristic standard sampling (Clerc & Scheidegger 1990) will in future provide basic information on the epiphytic lichen flora at a regional level, in order to facilitate the compilation of a new Red List including all lichens.

Standardized surveys were conducted in the Swiss Central Plateau and the Pre-Alps. For comparability in time, data collection was carried out on long-term ecological observation plots (EAFV 1988). To be more representative stratified sampling was carried out according to region, vegetation formation (forest and non-forest) and vegetation belt, allowing comparisons of lichen diversity within particular interpretation units (a-diversity) or between them (β-diversity). Reliability of the sampling method in terms of species capture was estimated for a particular area known to be rich in lichens. The importance of the crustose, foliose and fruticose growth forms, as well as of the generative and vegetative dispersal types, was also analysed.

Materials and Methods

Study area and sampling

In 1993 and 1994 data from 849 trees on 132 long-term ecological observation plots (EAFV 1988) were sampled. The intersection points of the 1×1 km grid of the Swiss coordinate system were taken as plot centres. All the plots are situated in the two regions Central Plateau and Pre-Alps, comprising respectively 22·8% and 16·0% of the total surface of Switzerland (Bundesamt für Statistik 1980). Within these regions they are concentrated in the five areas (Fig. 1) established by Welten & Sutter (1982), ranging from 93 to 131 km² (Wohlgemuth pers. comm.).

Sampling was performed in terms of region (Central Plateau and Pre-Alps), vegetation formation (forest and non-forest), and vegetation belt (colline-submontane, lower and upper montane, and subalpine). Definitions of the strata follow those of the Swiss Forestry Inventory (EAFV 1988). In selecting the plots care was taken to ensure that at least ten were chosen for each combination of strata of which there were four in the Central Plateau and eight in the Pre-Alps. Within each combination, plots were selected arbitrarily, taking into account ease of access, but without any special attention to potentially rich habitats.

With an area of 93 km² extending through all four vegetation belts, Glaubenberg (Fig. 1) in the Pre-Alps (canton of Obwalden) was used as the area with the highest plot density (40 plots). To estimate the reliability of the sampling method in terms of species recorded, an overall investigation of the lichen flora of the Merli forest (Dietrich 1991) in Glaubenberg, with a surface of 1 km² covering the upper montane and the subalpine vegetation belt, as well as additional observations in this area (Dietrich, Frei, Groner & Scheidegger, unpubl.), were used as the basis for comparison.
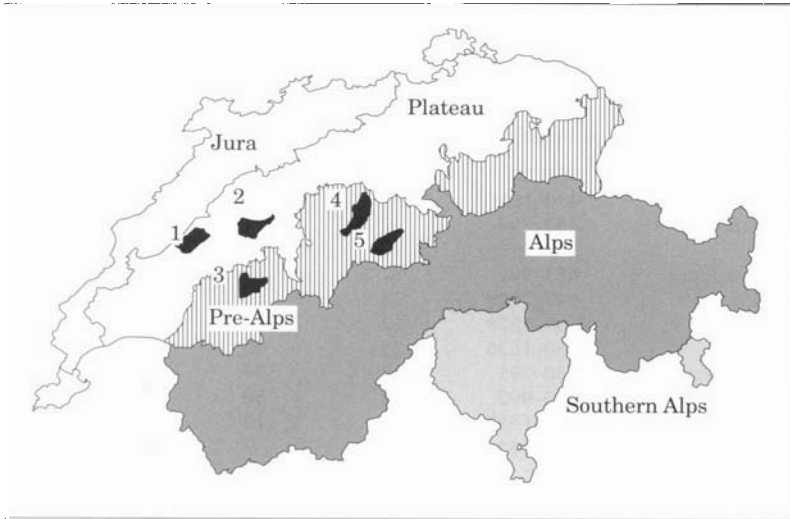
FIG. 1. The Central Plateau and the Pre-Alps of Switzerland with the five plot concentration areas: 1 = Payerne, 2 = Bern-West, 3 = Schwarzsee, 4 = Entlebuch, 5 = Glaubenberg.

Ecological plot data for the area of a circle of 500 m^2 (r = 12·62 m) were provided by the Swiss Forest Inventory (EAFV 1982). On each plot every tree with a diameter at breast height (dbh) ≥ 12 cm was normally sampled, although with a maximum of three individuals per phorophyte species and dbh-class of 12 cm.

The entire epiphytic lichen flora including the different species of *Lepraria* (Tønsberg 1992), was recorded for all trees (stem height of 0–170 cm) as cover percentage of the stem investigated (Dietrich & Scheidegger 1996b). The lichen flora of twigs and branches was not included. In addition to lichen data, phorophyte species, the dbh of every tree and the percentage of the overall cover of bryophytes was estimated. The two varieties of *Opegrapha vulgata* s. lat. and *Parmelia quercina* s. lat. as well as the two forms of *Lecanora allophana* s. lat. were treated in all calculations as distinct species. Affiliation of species to crustose, foliose and fruticose growth forms as well as to generative and vegetative dispersal types was determined according to Wirth (1992).

Data analysis

Data were analysed for 19 different interpretation units (Table 1): study area, eight strata, eight combinations of strata in the Pre-Alps, Lower Pre-Alps (colline-submontane and lower montane belt) and upper Pre-Alps (upper montane and subalpine).

The frequency distributions of lichen species were based on presence/absence data per tree and per plot. The determination of their pattern was based on classification on a linear scale as well as on species rank-abundance plots. Mathematical fit was tested according to Magurran (1988). The establishment of four classes of scarcity of lichens, each accounting for 25% of the total number of the species, was based on abundance of plots in which they occurred. The most frequent species were determined for the strata as well as for their 12 combinations.

α-Diversity was calculated for all interpretation units in terms of species richness, which is the number of species. The Shannon index, another index of α-diversity, was calculated using the formula $H' = -\Sigma(p_i * \ln p_i)$, where p_i is the percentage of plots with the lichen species i. The mean species number per plot and interpretation unit was calculated to give the species density. Species restricted to one interpretation unit are based on the occurrence in the corresponding level of stratification. β-Diversity between two interpretation units was calculated in terms of dissimilarity using the formula $d = 1 - 2n_{a+b}/(n_a + n_b)$, with d = dissimilarity, n_a = species number in one unit, n_b = species number in the other unit and n_{a+b} = species that both units have in common. β-Diversity between more than two interpretation units was determined for every unit as the average of the dissimilarities from each of the other units involved.

TABLE 1. *Altitude and phorophyte composition represented by the plots of the 19 different interpretation units*

Interpretation unit	Altitude (m)	Number of phorophyte species	Deciduous tree trunks (%)	Coniferous tree trunks (%)	Number of plots
Study area	430–1636	31	47	53	132
Central Plateau	430–799	22	70	30	44
Pre-Alps	483–1636	28	37	63	88
Lower Pre-Alps	483–992	27	63	37	44
Upper Pre-Alps	947–1636	8	11	89	44
Non-forest	483–1578	22	64	36	63
Forest	430–1636	21	40	60	69
Colline-submontane	430–791	27	79	21	44
Lower montane	620–992	22	50	50	44
Upper montane	947–1357	6	19	81	24
Subalpine	1322–1636	5	2	98	20
Pre-Alps, non-forest					
Colline-submontane	483–779	16	96	4	10
Lower montane	641–992	14	89	11	10
Upper montane	1010–1333	4	31	69	10
Subalpine	1328–1553	1	0	100	14
Pre-Alps, forest					
Colline-submontane	495–791	11	64	36	10
Lower montane	620–983	11	37	63	10
Upper montane	947–1357	5	13	87	14
Subalpine	1322–1636	5	3	97	10

For all interpretation units the mean percentage ± standard deviation of crustose, foliose and fruticose, as well as of generative and vegetative lichens was calculated per plot, by setting the flora of each plot at 100%, regardless of the number of species.

Results

Ecological plot data

Along the altitudinal gradient of vegetation belts, the ranges of altitude overlap up to 171 m (Table 1). As a result of higher tree density the number of trees examined was larger in forest (570) than in non-forest (279) areas. Numbers of different phorophyte species decrease distinctly along the altitudinal gradient of vegetation belts (Table 1). Of the 849 trees investigated 47% were deciduous and 53% coniferous. *Picea abies* dominates in each interpretation unit, from 25% (Central Plateau) to 100% of the tree trunks (Pre-Alps, subalpine, non-forest), except in the overall colline-submontane belt (*Fagus sylvatica* with 22%), the non-forest (*Malus*, 27%) and forest plots (*Fagus sylvatica*, 44%) of the colline-submontane belt in the Pre-Alps, and the non-forest plots of the lower montane belt in the Pre-Alps (*Salix alba*, 19%).

Frequency

The distributions of frequencies of lichens, calculated for plots and trees, have similar patterns. The 10% frequency classes based on the 849 trees show
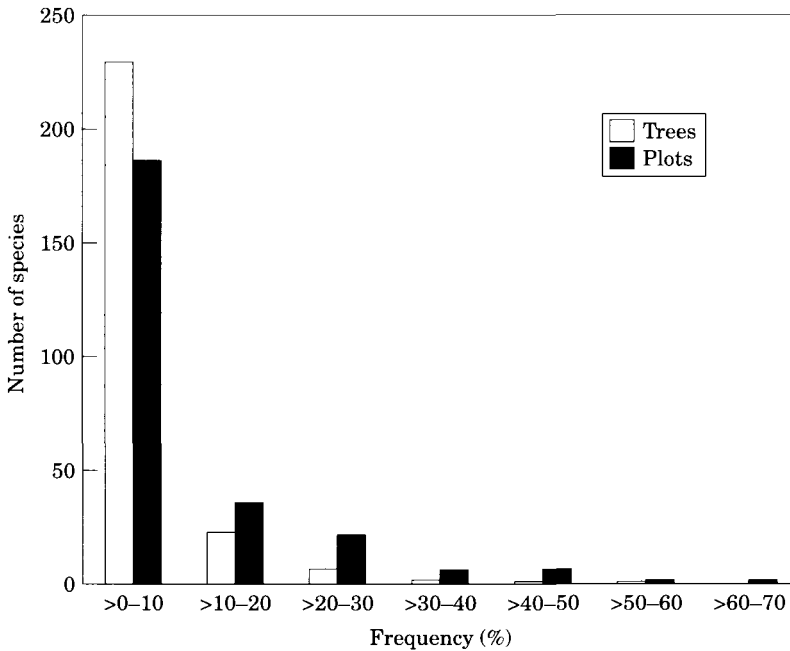
FIG. 2. Distribution of classified frequency of the 262 lichen species.

229 species (87%) in the lowest class (Fig. 2); 47 (18%) were found on one tree only. Based on the plots, 59 species (23%) were found on one plot. Only 18 species (6·9%) occurred on more than 30% of the plots (Fig. 2). Derived species rank-abundance plots based on trees and plots (Fig. 3) are both approximately linear, corresponding to the log series of species abundance models (Magurran 1988). However, testing of mathematical fit, only reveals a high value ($P>0·90$) for the frequencies based on trees, but not for the plots ($P=0·10$). Mathematical fit with the truncated log normal distribution of species abundance is $P<0·10$ for the trees, and $P<0·01$ for the plots.

As data from different trees of one plot are not independent, at regional level the frequency based on the plot level is more representative than that based on the tree level. Total study area, Central Plateau and Pre-Alps show similar distribution of species abundance (Fig. 4). They differ only with regard to the highest score (this probably originated from the different total number of plots investigated). The presence of the common frequency distribution enables us to create the same classes of scarcity for epiphytic lichen species. Each of the four classes (very rare, rare, moderately common and common) represents 25% of the total species number. To determine their boundaries, the relative sums of species occurring in the three regional interpretation units per relative number of plots were averaged. The boundaries correspond to the values of 25, 50 and 75% of species sum. Mathematically they are given by 1, 4 and 15% of the total number of plots investigated. Because the number of the plots
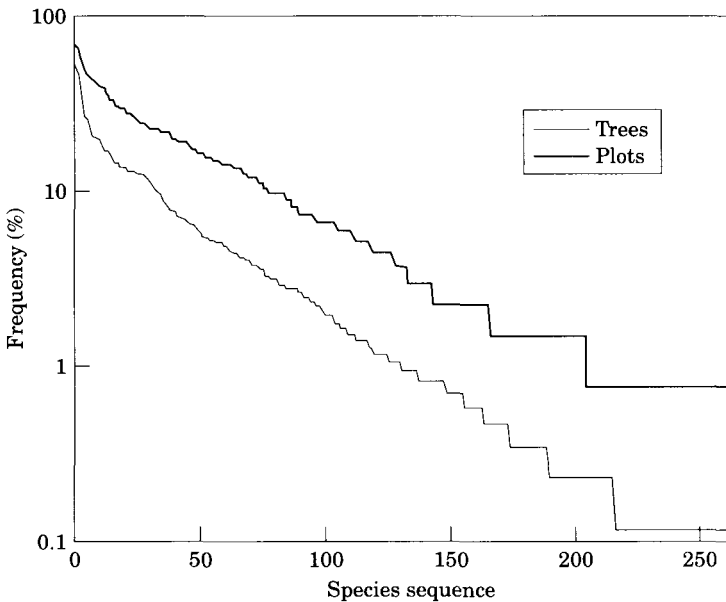
FIG. 3. Rank abundance plots showing the distribution of frequency of the 262 lichen species, based on 849 trees and 132 plots.

in Central Plateau and the Pre-Alps is below 100, correct processing of these classes is only possible for the entire study area (Table 2).

When considering each stratum individually, the number of species that occurred with the three highest scores in at least one of the strata is only ten (Table 3). For the ten most abundant species within the study area, only *Lepraria rigidula*, *Parmelia glabratula* and *Candelariella reflexa* must be added. A further abundant species, *Xanthoria parietina*, is restricted to non-forest in the lower vegetation belts (colline-submontane 100%, 90% of the plots in Central Plateau and Pre-Alps, respectively; lower montane in Central Plateau and Pre-Alps each 90%). *Cladonia digitata*, *Platismatia glauca* and *Hypogymnia farinacea* each have values of 100% in forest of the subalpine belt (Pre-Alps). In addition, the latter appears on 80% of the forest plots in the upper montane belt (Pre-Alps). In the forest plots of the colline-submontane and lower montane belt of the Pre-Alps, *Graphis scripta* has values of 90 and 86%, respectively. Finally *Arthonia radiata*, with 73%, has one of the highest scores in forest plots in the colline-submontane vegetation belt of the Central Plateau.

Diversity

Within the study area, species richness as an expression of α-diversity amounts to 262, including two species with two varieties and one species with two forms (Table 2). Nine taxa were not determined to species level. Their supposed systematic relationship is indicated where possible. Of the 182 crustose, 55 foliose and 25 fruticose taxa, the records of several sorediate
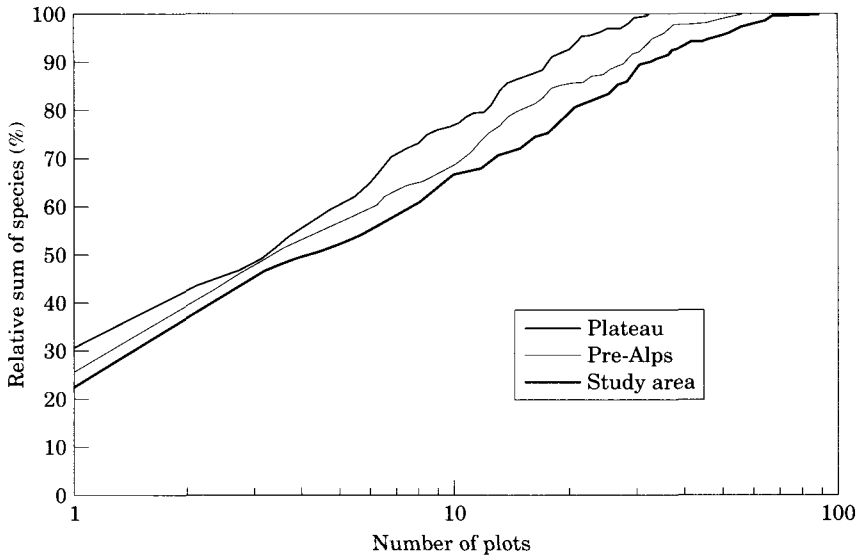
FIG. 4. Cumulative frequency within the regional interpretation units Central Plateau, Pre-Alps and in the entire study area.

crustose species are of particular floristic importance: 13 were reported as new to Switzerland, and seven taxa with distinctive chemistry could not be determined yet (Dietrich & Scheidegger 1996a). Furthermore, the sampling method revealed several taxa from the Red List of macrolichens of Switzerland (Clerc *et al.* 1992), whereas *Anaptychia ciliaris, Leptogium saturninum, Menegazzia terebrata* and *Parmelia acetabulum* were found on more than one plot. *Cladonia incrassata*, indicated as a species in danger of extinction, was found for the second time in Switzerland.

The 132 plots, with an average of six trees studied, showed a mean number of 24 species, corresponding to 9% of the total flora investigated. At least one species was observed on every plot, whereas the maximum number was 49 per plot and 35 per tree trunk. Comparing Central Plateau and Pre-Alps (Table 4), α-diversity expressed by the species richness (134, 243, respectively) was higher in the latter, with 53% of the taxa restricted to this region. In addition, species density measured by the number per plot was significantly higher (*t*-test, $P<0.001$), but the percentage of the corresponding total flora was higher in the Central Plateau (15%). Distinguishing lower from upper Pre-Alps in addition to the Central Plateau (Table 4), 48% of the taxa of the upper Pre-Alps were still restricted to this interpretation unit. Compared to the Central Plateau, species density is significantly higher only in the upper Pre-Alps ($P<0.001$).

Compared to the regional strata, the calculated differences in diversity between the strata of vegetation formation are very low (Table 4). Both, forest and non-forest revealed similar species densities, although the average number of trees investigated was four in non-forest and eight in forest.

TABLE 2. List of species in each of the four classes of scarcity, showing the number of plots they occurred on (see also text)‡

Very rare		Rare		Moderately common		Common	
Arthonia apatetica	1	Acrocordia gemmata	5	Arthonia spadicea	9	Amandinea punctata	39
A. dispersa	1	Anaptychia ciliaris	3	Arthothelium ruanum	16	Arthonia radiata	41
A. muscigena	1	Anisomeridium nyssaegenum	3	Bacidia naegelii	16	Bacidia rubella	21
A. punctiformis	1	Arthonia cinnabarina	3	B. subincompta	8	Buellia griseovirens	22
A. sp. 1 (*)	1	A. didyma	3	Bacidina aff. arnoldiana	15	Candelaria concolor	34
Bacidia arceutina	1	A. leucopellaea	2	B. caligans	7	Candelariella reflexa	54
Bacidina arnoldiana	1	Bacidia globulosa	2	Biatora chrysantha	9	C. xanthostigma	66
Bryoria nadvornikiana	1	Biatora efflorescens	3	Bryoria fuscescens	11	Chaenotheca chrysocephala	33
Buellia disciformis	1	B. helvola	2	Buellia schaereri	18	C. furfuracea	36
Candelariella aurella	1	Bryoria capillaris	2	Calicium parvum	9	C. trichialis	31
Catinaria atropurpurea	1	B. implexa	3	C. viride	7	Cladonia coniocraea	29
Chaenotheca brunneola	1	B. sp. 1 (*)	5	Caloplaca cerina	8	C. digitata	30
Cladonia furcata	1	Calicium lenticulare	2	C. cerinella	16	Dimerella pineti	52
C. glauca	1	Caloplaca citrina	2	C. chlorina	10	Evernia prunastri	30
C. incrassata	1	C. herbidella	4	C. holocarpa	6	Graphis scripta	40
C. norvegica	1	C. isidiigera	4	Catillaria nigroclavata	10	Hypogymnia farinacea	37
Cliostomum leprosum	1	C. obscurella	2	Chaenotheca ferruginea	11	H. physodes	57
Cyphelium karelicum	1	Candelariella vitellina	3	C. stemonea	10	Imshaugia aleurites	33
Fuscidea arboricola	1	Catillaria sp. (*)	2	Chrysothrix candelaris	19	Lecanora carpinea	53
Hypocenomyce scalaris	1	Cetrelia olivetorum	2	Cladonia fimbriata	19	L. chlarotera	50
Lecanactis abietina	1	Chaenotheca phaeocephala	3	C. pyxidata	7	L. expallens	21
Lecania fuscella	1	Cliostomum corrugatum	4	C. squamosa	9	L. aff. flavoleprosa (?)	20
Lecanora horiza	1	Eopyrenula leucoplaca	2	Evernia divaricata	13	L. rugosella	28
L. persimilis	1	Fuscidea praeruptorum	2	Gyalideopsis anastomosans	19	L. saligna	26
L. phaeostigma	1	F. pusilla	2	Hyperphyscia adglutinata	15	L. sambuci	25
L. sp. 2 (*)	1	Gyalecta truncigena	3	Hypocenomyce sorophora	13	Lecidella elaeochroma	29
Lecidella scabra	1	Haematomma ochroleucum var. ochroleucum	5	Hypogymnia bitteri	7	L. flavosorediata	30
Leptogium teretiusculum	1	Hypocenomyce leucococca	2	H. tubulosa	12	L. sp. 1 (?)	21
Lobaria pulmonaria	1	Hypogymnia vittata	2	Lecania cyrtella	11	L. sp. 2 (?)	60
Megalospora pachycarpa	1	Lecanora albella	2	Lecanora allophana f. allophana	10	Lepraria eburnea	26
Melaspilea aff. bagliettoana	1	L. allophana f. sorediata	5	L. argentata	9	L. elobata	20

Species	n	Species	n	Species	n	Species	n
Micarea cinerea	1	*L. cadubriae*	4	*L. pulicaris*	19	*L. lobificans*	90
M. melaena	1	*L. conizaeoides*	2	*L. subrugosa*	7	*L. rigidula*	64
M. nitschkeana	1	*L. impudens*	2	*Lecidea nylanderi*	6	*Loxospora elatina*	29
M. sp. 1 (?)	1	*L. norvegica*	2	*L. pullata*	6	*Micarea prasina*	68
Mycobilimbia epixanthoides	1	*L. subintricata*	3	*Lepraria incana*	13	*Mycoblastus fucatus*	23
Mycoblastus alpinus	1	*L. synuvicta*	3	*L. jackii*	8	*Ochrolechia androgyna*	27
M. sanguinarius	1	*L. sp. 1 (?)*	4	*L. obtusatica*	13	*Opegrapha rufescens*	22
Ochrolechia microstictoides	1	*Lecidea porphyrospoda*	3	*Leproloma vouauxii*	9	*O. vulgata*	23
Pannaria conoplea	1	*Leptogium saturninum*	2	*Micarea peliocarpa*	17	*Parmelia exasperatula*	24
Parmelia quercina var. *carporrhizans*	1	*Loxospora cismonica*	2	*Normandina pulchella*	18	*P. glabratula*	55
P. quercina var. *quercina*	1	*Megalaria pulverea*	3	*Opegrapha atra*	18	*P. saxatilis*	35
Parmotrema chinense	1	*Menegazzia terebrata*	3	*O. varia*	6	*P. subrudecta*	26
Peltigera collina	1	*Micarea lignaria*	2	*O. vermicellifera*	14	*P. sulcata*	45
Pertusaria borealis	1	*M. nigella*	2	*Parmelia acetabulum*	7	*P. tiliacea*	32
P. coccodes	1	*Mycobilimbia sabuletorum*	2	*P. caperata*	8	*Parmeliopsis ambigua*	37
P. constricta	1	*Mycoblastus affinis*	2	*P. revoluta*	7	*Pertusaria albescens*	22
P. hemisphaerica	1	*Ochrolechia alboflavescens*	2	*P. subargentifera*	17	*P. amara*	26
P. multipuncta	1	*O. arborea*	2	*P. subaurifera*	19	*Phaeophyscia orbicularis*	39
P. pustulata	1	*O. sp. 1 (?)*	2	*Parmeliopsis hyperopta*	13	*Phlyctis argena*	83
Phaeophyscia ciliata	1	*Opegrapha viridis*	3	*Phaeophyscia chloantha*	16	*Physcia adscendens*	29
Porpidia macrocarpa	1	*O. vulgata* var. *subsid.*	4	*P. endophoenicea*	10	*P. tenella*	58
Ramalina fraxinea	1	*O. sp. (*)*	2	*Physcia aipolia*	13	*Platismatia glauca*	27
Rinodina capensis	1	*Parmelia elegantula*	4	*Physconia distorta*	18	*Porina aenea*	20
R. sophodes	1	*P. glabra*	2	*P. grisea*	13	*Pseudevernia furfuracea*	41
s.K. 3 (?)	1	*P. pastillifera*	5	*Porina leptalea*	10	*Xanthoria fulva*	30
Usnea prostrata s. lat.	1	*Peltigera praetextata*	2	*Pyrenula nitida*	8	*X. parietina*	45
U. fulvoreagens	1	*Pertusaria leioplaca*	3	*P. nitidella*	8		
Xanthoria ulophyllodes	1	*P. pertusa*	2	*Ramalina pollinaria*	6		
		Phaeophyscia nigricans	2	*Rinodina pyrina*	9		
		Physcia stellaris	2	*Ropalospora viridis*	8		
		Physconia persidiosa	3	*Schismatomma pericleum*	6		
		Placynthiella icmalea	2	*Scoliciosporum chlorococcum*	9		
		Pyrenula laevigata	3	*Trapelia sp. (*)*	6		

TABLE 2. Continued‡

Very rare	Rare		Moderately common	
	Ramalina farinacea	4	Trapeliopsis gelatinosa	6
	Rinodina exigua	4	Usnea hirta	12
	R. griseosoralifera	2	U. subfloridana	14
	R. polyspora	3	U. sp. (*)	10
	Strigula affinis	2	Xanthoria fallax	6
	S. stigmatella	3		
	Tephromela atra	3		
	Thelotrema lepadinum	3		
	Trapelia corticola	5		
	Trapeliopsis flexuosa	3		
	Usnea filipendula	2		
	Vulpicida pinastri	4		
	Xanthoria polycarpa	2		

‡Very rare = observed on 1% or fewer of the plots; 59 species; rare = 1–4% of the plots, 77 species; moderately common = 4–15% of the plots, 69 species; common = on more than 15% of the plots, 57 species; ? = undetermined sorediate crustose lichen; * = undetermined lichen.

TABLE 3. *Relative frequency (%) of the most abundant species within the study area and in the strata of region, vegetation formation and vegetation belt, sorted according to decreasing frequency in the study area.*

	Study area	Central Plateau	Pre-Alps	Non-forest	Forest	Colline-sub-montane	Lower montane	Upper montane	Sub-alpine
Number of plots	132	44	88	63	69	44	44	24	20
Lepraria lobificans	68*	48	78*	48	87*	55	73*	88*	65
Phlyctis argena	63*	73*	58*	68*	58	86*	71*	50	10
Micarea prasina	52*	30	63*	19	81*	30	52	83*	60
Candelariella xanthostigma	50*	66*	42	79*	23	75*	57*	25	10
Lepraria rigidula	49*	41	52	32	64	41	48	79	35
Lecidella elaeochroma	46*	64	36	56	36	64	57*	25	5
Physcia tenella	44*	66*	33	73*	17	68*	57*	13	0
Hypogymnia physodes	43*	21	55	41	45	7	25	96*	100*
Parmelia glabratula	42*	32	47	37	46	32	48	42	50
Candelariella reflexa	41*	52	35	57	26	59	50	25	0
Dimerella pineti	39	39	40	3	71*	43	48	29	25
Pseudevernia furfuracea	31	9	42	41	22	5	11	70	100*
Parmeliopsis ambigua	28	0	42	24	32	0	0	71	100*

*The highest scores are starred (3 highest for each stratum, 10 highest for the study area).

TABLE 4. *Diversity within the strata of region, vegetation formation and vegetation belt, and within lower and upper Pre-Alps*

Interpretation unit	Species richness	Restricted to interpretation unit (%)	Mean species number per plot (species density)	Mean percentage per plot of flora of interpretation unit (%)	Number of plots
Central Plateau	134	14	20 ± 10	15 ± 7	44
Pre-Alps	243	53	26 ± 10	11 ± 4	88
Lower Pre-Alps	147	13	22 ± 7	18 ± 5	44
Upper Pre-Alps	184	48	30 ± 11	16 ± 6	44
Non-forest	195	31	25 ± 9	13 ± 4	63
Forest	202	33	23 ± 11	11 ± 6	69
Colline-submontane	141	17	22 ± 8	16 ± 6	44
Lower montane	145	9	20 ± 9	14 ± 6	44
Upper montane	160	20	30 ± 12	18 ± 7	24
Subalpine	114	16	30 ± 9	26 ± 8	20

TABLE 5. *Diversity along the altitudinal gradient of vegetation belts in the Pre-Alps region, non-forest and forest stratum separately*

Interpretation unit	Species richness	Mean species number per plot (species density)	Mean percentage per plot of flora of interpretation unit (%)	Number of plots
Non-forest				
Colline-submontane	78	25 ± 8	32 ± 10	10
Lower montane	78	25 ± 6	31 ± 8	10
Upper montane	110	26 ± 13	24 ± 11	10
Subalpine	77	26 ± 8	34 ± 11	10
Forest				
Colline-submontane	73	21 ± 8	29 ± 11	10
Lower montane	85	18 ± 6	22 ± 7	14
Upper montane	119	32 ± 11	27 ± 9	14
Subalpine	91	34 ± 9	38 ± 9	10

Along the altitudinal gradient (Table 4) species richness is highest in the upper montane (160) and lowest in the subalpine belt (114). In the latter the low total species number and the highest density result in a mean percentage of 26% per plot of its total flora. If forests and non-forest areas are distinguished in the Pre-Alps (Table 5), patterns of diversity along the vegetation belts do not change distinctly. In both areas species richness was clearly highest in the upper montane belt. The non-forest plots were responsible for the low species richness in the subalpine belt. Of all interpretation units, forest of the subalpine belt showed the highest species density (34).

TABLE 6. *Dissimilarity between Central Plateau, lower Pre-Alps and upper Pre-Alps*

Region	Lower Pre-Alps	Upper Pre-Alps	Average
Central Plateau	0·23	0·53	0·38
Lower Pre-Alps	0	0·47	0·35
Upper Pre-Alps		0	0·5

According to Magurran (1988) the Shannon indices of lichen diversity in all interpretation units are too high, reaching up to 4·91 for the entire study area. This is a result of the relatively low sampling size for heterogeneous units, in which no attention was paid to homogeneity in habitat or community. Nevertheless, ranking of Shannon indices always reflects the same order of the different interpretation units as the ranking of species richness.

For the estimation of species capture 40 plots were located in the Glaubenberg area, well known for the rich epiphytic lichen flora. The 40 plots revealed 205 lichen species. By adding observations from the lichen-rich Merli forest (Dietrich 1991) and other species from Glaubenberg (Dietrich, Frei, Groner & Scheidegger, unpublished) not observed in this study, the number of epiphytic species amounts to 296. Treating the 296 species found in Glaubenberg as its total epiphytic lichen flora, 69% of these were detected in the 40 plots investigated. By looking only at forest in the upper montane and subalpine belt of Glaubenberg, the flora of the corresponding 19 plots shows 134 species. With the additional Merli forest observations (Dietrich 1991), including species found only on branches and above a stem height of 1·70 m, richness increases to 231. Together, the 19 sites revealed 58% of this flora. In the Merli forest only one plot, with 43 different species, or 23% of the total forest lichen flora, was investigated in this study. The reliability of the sampling method, expressed by the species capture per plot for a given area, each with a well-known lichen flora, is evidently high: for the Glaubenberg area (93 km^2) one plot (500 m^2) revealed on average 11% of the flora, whereas forest in the upper montane and subalpine vegetation belt in the same area (24 km^2) yielded an average of 16%, and Merli forest (1 km^2) 23%.

As a measurement of β-diversity the calculated dissimilarity between the Central Plateau and Pre-Alps amounts of 0·38. Distinguishing again lower from upper Pre-Alps in addition to the Central Plateau (Table 6), the upper Pre-Alps on average shows the highest value of dissimilarity, as already reflected by the highest percentage of species restricted to this interpretation unit. Altitudinal division within one strata of region results in a much higher value of dissimilarity than regional division of the same altitudes.

Although the α-diversity of forest and non-forest plots was not significantly different, the calculated value of dissimilarity amounts to 0·32. This reflects the different species composition of the two strata, which have two thirds of the species in common.

Along the altitudinal gradient, dissimilarity in terms of β-diversity between the colline-submontane and each of the higher vegetation belts increases

TABLE 7. *Dissimilarity between the four vegetation belts and between the four vegetation belts in the Pre-Alps region, non-forest and forest stratum separately*

Interpretation unit	Lower montane	Upper montane	Subalpine	Average
Colline-submontane	0·21	0·5	0·65	0·45
Lower montane	0	0·42	0·58	0·4
Upper montane		0	0·34	0·42
Subalpine			0	0·52
Non-forest				
Colline-submontane	0·32	0·65	0·82	0·6
Lower montane	0	0·49	0·7	0·5
Upper montane		0	0·37	0·5
Subalpine			0	0·63
Forest				
Colline-submontane	0·33	0·55	0·62	0·5
Lower montane	0	0·51	0·59	0·48
Upper montane		0	0·33	0·46
Subalpine			0	0·51

continuously with altitude (Table 7). Dissimilarity from the subalpine to the lower belts increases with altitudinal distance as well. On average the subalpine belt has the highest β-diversity. As the lower montane belt shows a smaller dissimilarity to the colline-submontane (0·21) than to the upper montane (0·42), and the latter a smaller one to the subalpine (0·34) than to the lower montane (0·42), altitudinal division between the lower and upper montane belt reveals the greater differences in the flora of epiphytic lichens.

When forest areas are distinguished from non-forest areas in the Pre-Alps (Table 7), increasing floristic differences with altitudinal distance is more evident in non-forest. Here dissimilarity between the colline-submontane and the subalpine vegetation belt reaches the very high value of 0·82. Dissimilarity between non-forest and forest in each of the four vegetation belts decreases markedly with altitude, from 0·55 in the colline-submontane to 0·42 in the lower montane, 0·40 in the upper montane and 0·36 in the subalpine belt.

Ecological strategies

With a percentage of 70%, corresponding to 182 species, crustose lichens are by far the most abundant growth form (Table 8). For the study area, calculations of the mean contribution of each growth form to the flora per plot results in statistically significant ranking: Crustose>foliose (*t*-test, $P=<0·001$)>fruticose ($P=<0·001$).

Although generative and vegetative types of dispersal are almost equally distributed among the lichen species observed (Table 8), their mean percentages of the flora per plot differs significantly ($P<0·001$): 35% are constituted by generative lichen species. Only for crustose lichens is the number of generative species higher. Nevertheless, for vegetative dispersal the mean percentage of the flora per plot is significantly higher for foliose ($P=<0·001$) and fruticose lichens ($P=<0·001$).

TABLE 8. *Values of importance for growth forms and dispersal types in the study area*

Parameters	Number of species (%)	Mean percentage per plot (%)
Growth form		
Crustose	70	67 ± 19
Foliose	21	26 ± 17
Fruticose	9	7 ± 8
Dispersal type		
Vegetative	54	65 ± 17
Generative	46	35 ± 17
Growth and dispersal		
Crustose, vegetative	29	36 ± 14
Crustose, generative	41	32 ± 18
Foliose, vegetative	17	23 ± 14
Foliose, generative	4	3 ± 5
Fruticose, vegetative	8	6 ± 8
Fruticose, generative	1	$0{\cdot}24 \pm 0{\cdot}84$

All the following results are based on the mean percentages per plot. Absolute species numbers show only slight similarities, if at all. For the Central Plateau, Pre-Alps, forest, non-forest as well as for the colline-submontane, lower and upper montane and subalpine vegetation belts, the analysed mean percentages of growth forms and dispersal types show the same ranking of importance as for the entire study area: crustose>foliose $(P = < 0{\cdot}001) >$ fruticose growth form $(P \leqslant 0{\cdot}005)$, and vegetative>generative dispersal type $(P < 0{\cdot}001)$.

Comparing the Central Plateau with the Pre-Alps, significant differences within the growth forms were observed for the fruticose species only (2% and 9%, respectively; $P = 0{\cdot}003$). In addition, the calculated values for vegetative (55%, 70%) and for generative dispersal (45%, 30%; $P < 0{\cdot}005$) differ significantly.

For forest and non-forest, calculated values for dispersal types and fruticose species are similar to those of the entire study area. Differences between the two vegetation formations are obvious for crustose and foliose lichens. The former have a significantly higher mean percentage per plot in forest (79%) than in non-forest (55%; $P = < 0{\cdot}001$), while the latter show a significantly higher mean percentage in non-forest (39%) compared to forest (15%; $P = < 0{\cdot}001$).

Looking at the altitudinal gradient (Fig. 5), only for foliose lichens are the mean percentages per plot more or less the same in every vegetation belt. The importance of the crustose growth form decreases from colline-submontane to the higher belts (not significant). In contrast, the importance of the fruticose form increases from low to higher altitudes (not significant). A similar pattern is obvious for the two types of dispersal: values for vegetative lichens increase significantly with every altitudinal step, and as a consequence those of generative lichens decline in the same manner from the colline-submontane to

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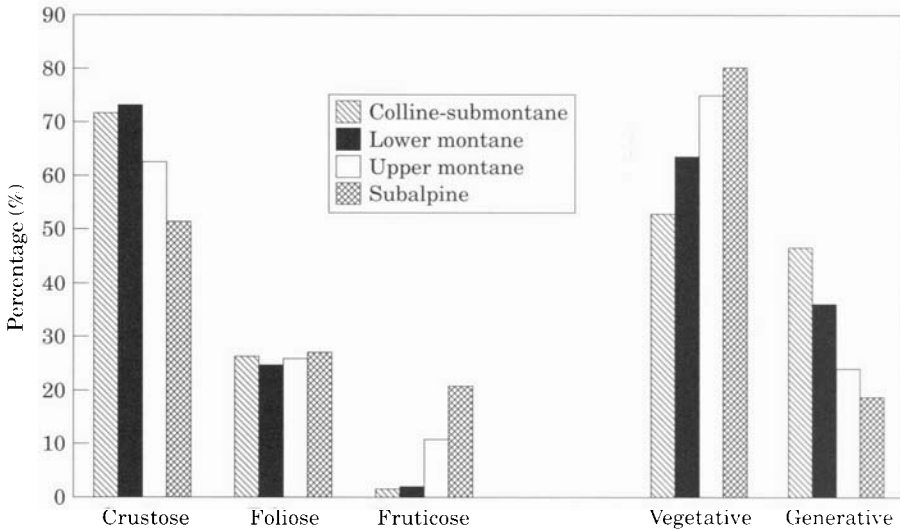
FIG. 5. Mean percentages per plot of crustose, foliose and fruticose lichens and of vegetative and generative dispersal type within the four vegetation belts.

the subalpine vegetation belt ($P \leqslant 0.013$). By distinguishing non-forest from forest in the four vegetation belts in the Pre-Alps, further differentiation is possible. Along the altitudinal gradient, forest plots in particular are responsible for the decrease in the importance of crustose lichens (Fig. 6), whereas in the colline-submontane belt the mean percentage per plot is extremely high (93%). With every altitudinal step its decrease is significant ($P < 0.045$). In non-forest the mean percentages in the four vegetation belts do not differ distinctly. In contrast, foliose lichens are of equal importance only if non-forest and forest are taken together. If separated, they show an opposite pattern of decrease and increase, although only the increase with every altitudinal step in forest areas is significant ($P < 0.05$). Fruticose lichens show similar increases in non-forest and forest.

Concerning the types of dispersal, the altitudinal patterns described above are more marked in forest than in non-forest (Fig. 7). As a consequence, significant differences for every altitudinal step exist only for forest ($P \leqslant 0.05$). The forest areas of the colline-submontane vegetation belt (Pre-Alps) are the only unit where the generative dispersal type reaches the same degree of importance as the vegetative one.

Discussion

Frequency

Inventories can provide important information for the conservation of organisms by indicating the existence of rare species, but also the abundance of common species. Beside the comparability of different mapping units, a necessarily representative inventory method should also support the
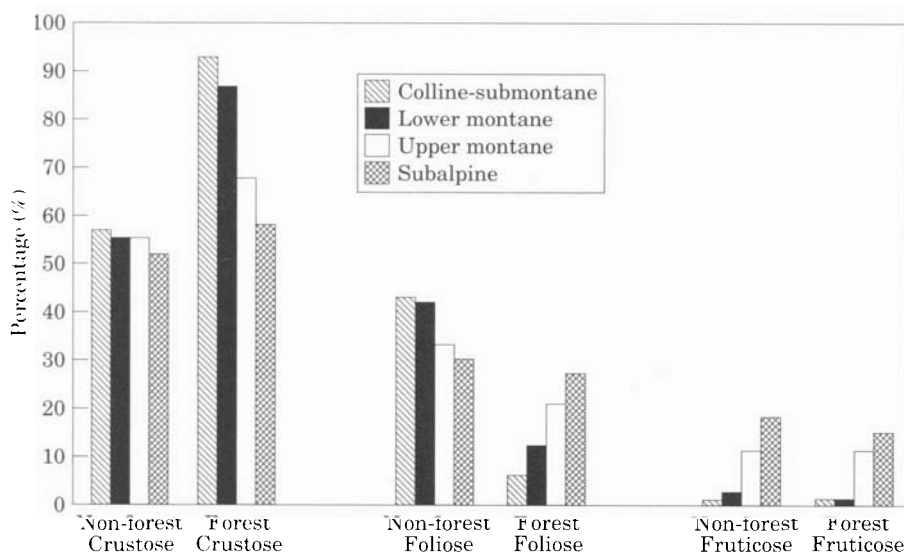
FIG. 6. Mean percentages per plot of crustose, foliose and fruticose lichens along the altitudinal gradient in the Pre-Alps, non-forest and forest strata separately.
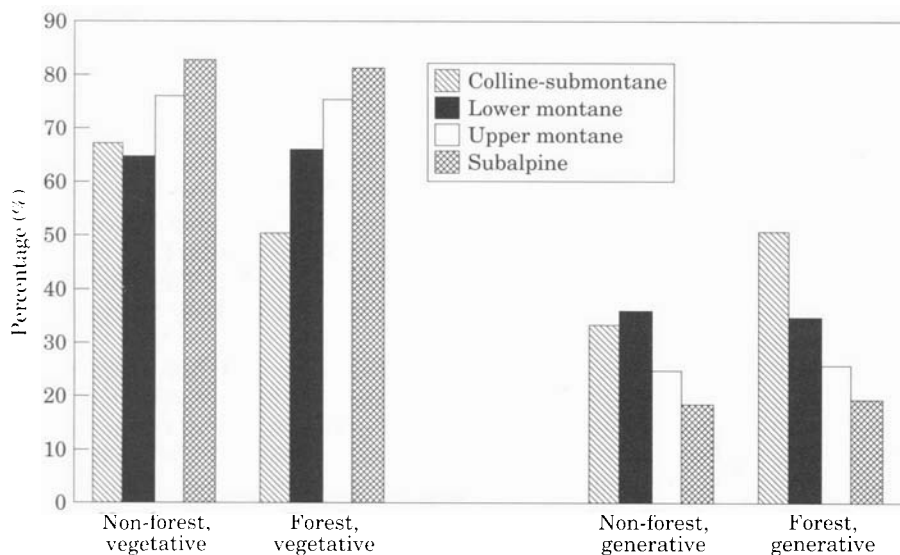

FIG. 7. Mean percentages per plot of vegetative and generative dispersal type along the altitudinal gradient in the Pre-Alps, non-forest and forest strata separately.

comparability of species frequencies. As demonstrated by Urmi *et al.* (1990), traditional mapping, theoretically represented by herbaria specimens, under-estimates the frequency of common species. A smallest scale programme,

combined with random sampling and stratification, counteracts this bias. In this study stratification by region, vegetation formation and vegetation belt, and arbitrary plot choice without any preconceived bias, resulted in a frequency distribution of lichen species that corresponds almost entirely with the 'law of frequencies' (Raunkiaer 1934). A few species are very abundant, some show medium abundance and most are represented by only a few observations. In general, the observed log series model of species abundance is typical for situations where one or a few factors control the ecology (Magurran 1988). In contrast, the log normal distribution of species abundance, one of the most consistent phenomena in multi-species samples (Huston 1994), indicates the effect of many independent factors (May 1975). This model of species abundance was recently shown for foliicolous lichens in Costa Rica (Lücking 1994) and lichens on *Salix caprea* in Finland (Kuusinen 1994).

The same distribution of species frequencies in the regional interpretation units (study area, Central Plateau and Pre-Alps) led to the establishment of four classes of scarcity, each comprising 25% of the species. Just as within phanerogams and pteridophytes (Landolt 1991), species are often in danger of extinction in one region but more common in others and, as suggested by Clerc *et al.* (1992), cannot therefore be satisfactorily classified at national level only. Out of the 55 foliose and 25 fruticose species found in this study, 11 foliose and five fruticose species are listed in the provisional red data list of macrolichens of Switzerland (Clerc *et al.* 1992). Even if sampling size in the two regions was lower than 100, it is evident that *Anaptychia ciliaris* (on 3 plots) and *Parmelia acetabulum* (6) are at least not very rare in the Central Plateau, *Leptogium saturninum* (3) and *Menegazzia terebrata* (3) are not very rare in the Pre-Alps. The proposed classification allows, for different interpretation units (sampling size ≥ 100), the comparable assessment of scarcity of individual lichen species at different times. In this way it has been demonstrated that of the 13 lichens found for the first time in Switzerland (Dietrich & Scheidegger 1996*a*), six are moderately common or common. Even among the seven undetermined sorediate crustose species, three seem to be common. Nevertheless, localities of very rare species may be revealed. This was the case with *Cladonia incrassata*, which was found growing at the base of a pine tree, for only the second time in Switzerland.

For the national survey of epiphytic lichens, the fact that frequency of common species will be estimated representatively by a representative plot choice will allow exclusion of those species not in danger of extinction at a regional or a national level. The quantitative criteria will be a lower threshold value of estimated absolute frequency for a given region (Jura, Central Plateau, Pre-Alps, Alps, Southern Alps) or the whole of Switzerland. This value has to be defined according to the international classification of extinction threats and, within certain confidence intervals, will separate at least those species with no risk of extinction.

Diversity

As no special priority was given to potentially rich habitats, the figures for species richness (262 epiphytic lichens for the entire study area, 134 for the

Central Plateau and 243 for the Pre-Alps) are high. About 700 epiphytic species are estimated for the whole of Switzerland. Regional surveys in the Swiss Central Plateau and the Pre-Alps focusing on epiphytic lichens revealed considerably smaller species numbers (Camenzind & Wildi 1991; Dietrich 1991; Groner 1990; Hilfiker 1989; Liebendörfer *et al.* 1991; Ruoss 1992; Scheidegger *et al.* 1991). Considering the restricted area of Glaubenberg, 42% of the expected epiphytic lichen flora of this country is found on only 2·3‰ of Switzerland's total area (*c.* 3‰ of the area below the timberline). In this small area, reliability of the sampling method is expressed by a species capture of 69% of the total epiphytic lichen flora by investigating the 40 plots. On average, 11% of the known flora of Glaubenberg was registered per plot.

Differences in α- and β-diversity between different interpretation units have several origins. Here, only the most evident reasons are considered. The higher species richness in the Pre-Alps is due to the wider altitudinal range (in contrast to the Central Plateau, elevations above 800 m are also covered), and to the greater sampling intensity. Wohlgemuth (1993) demonstrated higher species numbers for pteridophytes and phanerogams in the Pre-Alps than in the Central Plateau, depending significantly on the range of altitude. If the Pre-Alps are divided into a lower and an upper part, each with the same sampling size as for the central Plateau, phorophyte diversity is far lower in the upper Pre-Alps than in the Central Plateau and the lower Pre-Alps. Nevertheless, overall species number and mean number per plot are distinctly higher. The high precipitation in this interpretation unit favours different lichen species, comparable to oceanic areas (Degelius 1935; Schauer 1965). Almost half of the species were restricted to this zone and were not found in the Central Plateau nor in the lower Pre-Alps. The dissimilarity of the lower Pre-Alps to the upper Pre-Alps is greater than that to the Central Plateau. Phorophyte diversity in forest and non-forest is almost the same. As a result of the lower trunk density in non-forest, more trees per plot were investigated in forest. Nevertheless, the measurements of lichen diversity in forest and non-forest, including the number of lichen species per plot, have almost equal values. The only clear difference is in β-diversity, reflecting the different species composition (each stratum having one third of its flora restricted to it).

Looking at vegetation belts, the high species richness in the upper montane belt is striking. With 160 species, more than 60% of the flora found in the study area occurs in this vegetation belt. The plot with the highest value of 49 species, representing almost 20% of the total flora investigated, was located in this belt, too. Beside the suboceanic climate of this belt, forests with low anthropogenic influence (such as forest management and air pollution) promote a rich lichen flora (Rose 1976; Selva 1994). In contrast to the subalpine belt with the lowest overall species richness, *Fagus sylvatica* and *Abies alba* are frequent tree species along with the dominant *Picea abies*. Frey (1958) demonstrated in a number of different areas in Switzerland that *F. sylvatica* and *A. alba* favour a richer lichen flora than *P. abies*. Here, the higher habitat diversity in terms of phorophyte species coincides well with the higher species richness (Kuusinen 1994; Lücking 1994). Nevertheless, the

greater diversity of phorophyte species in colline-submontane and lower montane belts does not result in a higher lichen diversity compared to the upper montane belt. Detailed analysis of the lichen diversity of the different tree species are given in Dietrich & Scheidegger (1996*b*).

The low total species number with a high number per plot in the subalpine belt might be compared to the conditions of arctic lichen vegetation, where the species number is relatively low but the number of individuals is high (Henssen & Jahns 1973). In addition, the lichen flora of the subalpine belt shows easily the highest dissimilarity in forest as well as in non-forest. Increasing β-diversity with increasing altitudinal distance might be due mainly to larger climatic differences. Dissimilarity between forest and non-forest decreases markedly with every altitudinal step. This is due to the decreasing differences in phorophyte diversity.

Ecological strategies

Significant ranking of importance of different growth forms in terms of mean percentage per plot is the same in all strata. The higher percentage of fruticose lichens in the Pre-Alps compared to the Central Plateau is probably related to the higher precipitation, which supports intensive growth of this predominantly aerohygrophytic growth form. The greater light intensity at the lower tree trunk level in non-forest seems to be responsible for the higher percentage of foliose species per plot compared to forest. Higher air humidity in woodland seems to have a smaller effect on the importance of growth forms with a relatively large surface area. As foliose species are often competitive lichens with a high relative growth rate (Rogers 1990), their high mean percentage per plot in non-forest may be expected to result in lower diversity, as observed by Kuusinen (1994). Thus, species number per plot is slightly higher in non-forest. The decreasing importance of crustose growth forms with increasing altitude, especially in forest plots, could be influenced by decreasing ecological disturbance, as the more stress-tolerant crustose species showed the highest index of ruderality (Rogers 1990).

As an efficient adaptation to symbiotic life, vegetative reproduction in lichens is generally more abundant than generative reproduction (Henssen & Jahns 1973). In the study area, vegetative dispersal was found to be of greater importance for every growth form. In addition, the mean percentage per plot of lichens with vegetative dispersal was significantly higher. As Frey (1958) observed, recolonization of lichens by symbiotic diaspores in clear-cut second-growth forests from adjacent woodland takes a long time. Therefore, as the mean percentage of species with vegetative dispersal per plot is significantly higher in forest and non-forest, it is still more efficient than generative propagation.

As a methodological study, this work was aimed at contributing to the design of the national survey of epiphytic lichens. Standardized data sampling on the intersection points of the 1×1 km grid of the Swiss coordinate system have shown to be an appropriate tool for the evaluation of lichen diversity. From 1996 to 1999 slightly modified sampling will be used to collect data on 826 plots in the whole of Switzerland. Plot choice will be representative according to the strata of the region, vegetation formation and vegetation belt.

Within every stratum plots will be determined at random. Designed as long-term ecological observation, the national standardized survey will provide representative data on lichen frequency in order to facilitate the compilation of a new Red List of epiphytic lichens.

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