Species richness of lichen functional groups in relation to land use intensity

Silvia STOFER, Ariel BERGAMINI, Gregorio ARAGÓN, Palmira CARVALHO, Brian J. COPPINS, Simon DAVEY, Michael DIETRICH, Edit FARKAS, Kati KÄRKKÄINEN, Christine KELLER, László LÖKÖS, Sampsa LOMMI, Cristina MÁGUAS, Ruth MITCHELL, Pedro PINHO, Víctor J. RICO, Anne-Marie TRUSCOTT, Patricia A. WOLSELEY, Allan WATT and Christoph SCHEIDEGGER

Abstract: Changing land use has a major impact on lichen diversity. This study attempts to identify patterns or trends of lichen functional groups along a land use gradient, ranging from natural forests to open agricultural landscape. In eight countries, covering six main European biogeographic regions, lichen vegetation was assessed according to a standardized scheme. Data on reproductive, vegetative and ecological traits was compiled and relative species richness for all classes of all traits calculated. Relationships between the land use gradient and relative species richness of trait classes were analysed. Open and intensively managed landscapes harbour more fertile species while sterile species are relatively more important in forests. This finding is also supported by analyses of different classes of dispersal propagules. The importance of species with the principal photobiont *Trebouxia* s.l. increases linearly with intensification of land use. A converse pattern is revealed by species with *Trentepohlia*. Concerning substratum specialization only generalists show an effect along the land use intensity gradient. Their relative species richness decreases from landscapes dominated by forests to open agricultural landscape. A considerable decline in the rare lichen species richness as a result of land intensification is predicted.

Key words: Europe, functional groups, land use intensity, lichen diversity

Introduction

Several studies have shown that the influence of human activities on biodiversity is unprecedented as natural habitats have been

S. Stofer, A. Bergamini, C. Keller and C. Scheidegger: Swiss Federal Research Institute WSL, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland.
G. Aragón: Área de Biodiversatión y Conservatión, ESCET, Universidad Rey Juan Carlos, c/Tulipán s.n., 28933 Móstoles (Madrid), Spain.
P. Carvalho: Museu Nacional de História Natural, Jardim Botanico, Rua da Escola Politécnica, 58, 1250-102 Lisboa, Portugal.
B. J. Coppins: Royal Botanic Garden Edinburgh, Inverleith Row, Edinburgh, EH3 5LR, United Kingdom
S. Davey: Stable Flat, Downsland Court, 115 East End Lane, Ditchling, Hassocks, Sussex, BN6 8UR, United Kingdom or Dept. of Zoology, University College Dublin, Belfield, Dublin 4, Ireland.
M. Dietrich: I de Böde, CH-6010 Kriens, Switzerland.
E. Farkas: Institute of Ecology and Botany, Hungarian Academy of Sciences, H-2163 Vacratot, Hungary.
K. Kärkkäinen: Department of Ecology and Systematics, P.O. Box 65, 00014 University of Helsinki, Finland.

L. Lökös: Department of Botany, Hungarian Natural History Museum, H-1476 Budapest, Pf. 222, Hungary.
S. Lommi: The Finnish Forest Research Institute, Vantaa Research Centre, Vantaa Unit, PL 18, 01301 Vantaa, Finland.
C. Máguas and P. Pinho: FCUL, Centro de Ecologia e Biologia Vegetal, Depto. de Biologia Vegetal, Bloco 2C, Campo Grande, 1749-016, Lisboa, Portugal.
R. Mitchell, A.-M. Truscott and A. Watt: Centre for Ecology and Hydrology (CEH), Banchory, Hill of Brathens, Banchory, Aberdeenshire, AB31 4BW, Scotland, United Kingdom.
V. J. Rico: Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, E-28040 Madrid, Spain.
P. A. Wolseley: Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

displaced by human disturbance on at least 50% of the global land surface (Hannah *et al.* 1994; Sanderson *et al.* 2002; Turner II 2002), and it is predicted that land use change and habitat conversion will continue in future (Sala *et al.* 2000; Tilman *et al.* 2001). In Europe only 15.6% of the land surface remained undisturbed (Hannah *et al.* 1994), largely restricted to the most unproductive regions. Changes in land use have a strong influence on species diversity and species composition (Rosenzweig 1995; Hacker & Gaines 1997; Turner *et al.* 2001) which in turn clearly depend on the pool of species of the regions studied. Thus, studying effects of environmental variables on species composition reveals no generalizable insights because of the limited geographical distribution of most species. Although lichen species have a larger distribution area than, for example, vascular plants, lichen floras of different biogeographic regions within Europe show considerable differences (Bergamini *et al.* 2005). Therefore, a better strategy for understanding and predicting effects of land use changes on lichen vegetation may be to study effects on the distribution of functional traits rather than effects on the distribution of species.

In comparison to better known groups such as vascular plants (Diaz *et al.* 2004), we still know very little about functional traits in lichens and their response to various impacts such as land use, disturbance or climate change. There has been little effort so far to build functional classifications of lichens or to fit them into existing schemes (Rogers 1990; During 1992; Jahns & Ott 1997; Wolseley 1997), mainly because relevant information on important traits such as competitive ability or relative growth rate are not readily available. The relevance of functional classifications may depend further on environmental conditions, for example traits sensitive to land use change or disturbance may be quite different to those sensitive to climate change. There may also be some regional dependence of the importance of some traits (Diaz *et al.* 2002), reducing the usefulness of general classifications. For example a species may be a good competitor in one region, but a bad one in other regions.

In this paper we explore whether there are patterns or trends in the relative importance of various lichen traits along a land use gradient. The land use gradient was replicated in eight European countries and ranged from closed natural forests to open agricultural landscapes (A. Watt, personal communication). Previous work (Bergamini *et al.* 2005) showed that this land use gradient had significant effects on lichen species richness and composition. We collected a diverse range of data from various literature resources on different ecological, vegetative and reproductive lichen traits for which a functional relationship to land use was hypothesized.

Methods

Study area and sampling design

This study is part of the EU-funded project BioAssess which aims to develop biodiversity indicators across land use gradients in Europe. Fieldwork was performed in eight countries and six main biogeographic regions of Europe (Alpine, Switzerland; Atlantic, Ireland and United Kingdom; Boreal, Finland; Continental, France; Mediterranean, Portugal and Spain; Pannonic, lowlands of the Danube river plain in Hungary, characterized by warm and dry summers and cold winters). In each country one study region was selected. Within each study region six 1 km^2 land use units (LUUs) were chosen, one in each of the following land use classes: old-growth, more or less unmanaged forest (LUU1); managed, mainly secondary forest (LUU2); woodland dominated landscape (LUU3); mixed-use landscape (LUU4); pasture dominated landscape (LUU5); farmland (LUU6). In each LUU lichen vegetation was assessed according to a complex scheme (for details see Scheidegger *et al.* 2002). In brief, we established in each LUU a regular grid (mesh size 200 m) resulting in 16 intersections. Each intersection was the centre of a circular sampling plot of 1 ha (56·4 m radius). Within each sampling plot twelve randomly selected collecting sites served as the starting point for three lichen relevés (total area of 50×40 cm each), one on each of the following substrata: rocks, bark of living trees, and "other" (including soil, bryophytes, small pebbles, dead wood, shrubs, and saplings). All lichenized fungi with a minimum size of 5 mm, except parasites were considered. When species could not be identified in the field, specimens were collected for further identification in the laboratory (microscopy and thin-layer chromatography). Keys listed in Nimis & Martellos (2004)

TABLE 1. *Reproductive, vegetative and ecological traits recorded for each lichen species*

Trait	Description
Reproductive traits	
1. Fertility	Two classes: 1: mostly sterile; 2: mostly fertile (regularly producing ascospores).
2. Propagules	Five classes of lichen propagules and their combinations: 1: symbiotic propagules (soredia and/or isidia); 2: soredia; 3: isidia; 4: fungal propagules (ascospores and/or conidia); 5: conidia; small thallus fragments were considered as isidia.
3. Spore length and shape	Four classes (combination of two spore length and two spore shape classes): 1: short and globose to ellipsoid; 2: short and elongate; 3: long and globose to ellipsoid; 4: long and elongate.
	Definition of two spore length classes: short spores ($\leq 15\ \mu$m) and long spores ($>15\ \mu$m). Two spore shape classes were defined by the ratio of average spore length/average spore width: globose to ellipsoid spores (ratio $\leq 2\cdot5$) and elongate spores (ratio$>2\cdot5$). Shape terminology modified from Kirk *et al.* (2001). Species of the class 'mostly fertile' from trait 1 were considered only.
4. Spore septation	Four classes: 1: no septum; 2: 1-septate; 3: 3-septate or more; 4: muriform. Species of the class 'mostly fertile' from trait 1 were considered only.
Vegetative traits	
5. Growth form	Five classes modified from Büdel & Scheidegger (1996): 1: crustose; 2: foliose-adpressed; 3: foliose ascendant; 4: fruticose-erect; 5: fruticose-pendulous.
6. Photobiont	Three classes: 1: green algae (excluding *Trentepohlia*); 2: *Trentepohlia*; 3: *Nostoc*. In tripartite lichens only the green algal photobiont was considered.
Ecological traits	
7. Substratum specialization	Three classes: 1: specialist (restricted to one substratum); 2: intermediate type (growing on two or three different substrata); 3: generalist (growing on more than three substrata). Rock, soil, living trees, deadwood and bryophytes were considered as possible substrata.
8. Rarity	Three classes modified from Rabinowitz (1981): 1: wide distribution and high abundance in most areas; 2: wide distribution and high abundance in some areas, but rare in others; 3: narrow distribution, high or low abundance. Reference area was Europe.

were used for species identification. Specimens were deposited in the following herbaria: BM, BP, H, MAF, DBN, LISU (abbreviations after Holmgren *et al.* 1990) and at the Federal Research Institute WSL. Field work was carried out in 2001 and 2002. Different groups of co-authors of this study were responsible for sampling and determination in their country.

Species traits

We compiled data on reproductive, vegetative and ecological traits for each of the 768 lichen species found in the study (Table 1). A multitude of literature was used to assemble the data. The most important data sources were Purvis *et al.* (1992), Clauzade & Roux (1985), Poelt (1969), Poelt & Vězda (1977, 1981) and (Wirth 1995). Determinations for the trait 'fertility' and the trait 'rarity' were based on expert opinion. See Appendix for the complete species list with assigned trait values for each species.

Data analysis

For each class of each trait (Table 1) relative species richness (called 'relative richness' in the following for convenience) was calculated as follows: first the species number of all classes of a certain trait for each of the 48 LUUs were summed. Then the species numbers of each class of that trait was divided by this sum. This provided relative richness for that trait class in that LUU. One LUU6, farmland of Portugal, was excluded from all analyses of relative richness because no lichens at all were found in this LUU and therefore no relative richness could be calculated. Changes in relative richness along the land use gradient for a certain trait class reflect the changing dominance of groups of species exhibiting that trait class. However, one has to be aware that the changing dominance measured in that way is always in terms of species richness and not abundance.

Analysis of variance (ANOVA) was used to study the relationships between the land use gradient and relative

richness of trait classes. In all the analyses, countries were included as blocking factor. In a first series of ANOVAS, the land use gradient was considered as a fixed factor with six levels. If the overall effect of the land use gradient was at least marginally significant ($P \leq 0.1$), we used Tukey's HSD procedure for pair wise comparisons of means of relative richness between levels of the land use gradient. In a second series of ANOVAS the land use gradient as an ordered factor was considered. For these ANOVAS LUU2 (managed forest) was omitted. We performed the same analyses as in the first series, but now we tested for linear trends of the land use gradient on relative richness. By this procedure, it was possible to detect significant trends in the data which were not detected by pair wise comparisons. In all ANOVAS homogeneity of variances was checked graphically by Tukey-Anscombe plots, and normality of the residual distribution by normal probability plots. If variances were not homogeneous and/or residuals not normally distributed, we used the arcsine transformation for relative richness which considerably improved residual distributions in these cases. This is the standard transformation used for proportions (Sokal & Rohlf 1995). Despite this transformation, outlying values in some analyses were problematic. To cope with these LUUs, we constructed for each outlier a new variable with only two values: 1 for the outlying LUU, zero for all other LUUs. If there were problems with an outlying LUU, we included the respective variable as an additional covariable into the ANOVA. Transformations used and covariables included are indicated in Table 2. All analyses revealed that LUU2 of Portugal (*Eucalyptus*-forest) was very different from all other LUUs and was therefore excluded from the analyses.

Because many univariate ANOVAS were performed, the probability of reporting significant results just by chance was increased. Therefore, results with *P* values >0·01 should be interpreted with caution.

All analyses were carried out with R 2.3.0 (R Development Core Team 2006).

Results

For all species groups defined on the various trait classes we found highly significant block (= country) effects. This remained true even if we considered block effects as random and not fixed, because a possible treatment (=LUU) × block interaction would only increase the residual mean squares and the treatment mean squares but not the block mean squares; i.e. F-values for blocks are either correct or too low (Sokal & Rohlf 1995; Hulbert 2004).

For all species, we found a significant overall effect of land use ($F_{5,34} = 2.75$, $P = 0.034$) on lichen species richness and a significant linear trend with decreasing species richness along the gradient. Differences in means, however, were only significant between extremes of land use – LUU1 and LUU6 (Bergamini *et al.* 2005). The relationships between the land use gradient and relative richness of trait classes as revealed by analyses of variance are summarized in Table 2. In the following paragraphs we concentrate on significant effects of land use units on relative richness of the trait-defined groups. Where results of pair wise comparisons were significant, figures showing means of the land use units are presented.

Reproductive traits

Relative richness of mostly sterile species exhibited a clear pattern. It decreased linearly along the gradient (Table 2). Pair wise comparisons revealed that LUU6 (farmland) in particular had a lower mean (Fig. 1A). A similar pattern was revealed looking at the different classes of symbiotic propagules. Relative richness of species capable of producing symbiotic propagules, soredia only or isidia only was significantly lower in LUU6 (farmland). Furthermore, relative richness of these trait classes decreased linearly from LUU1 to LUU6 (Table 2; Fig. 1B–D).

In contrast, relative richness of fertile species increased linearly along the land use gradient. Pair wise comparisons revealed that LUU6 (farmland) in particular had a higher mean (Fig. 1E). The same pattern was revealed by species producing fungal propagules (Fig. 1F). Relative richness of conidia producing species, however, was indifferent to the gradient (Table 2).

Relative richness of species with short and globose to ellipsoid spores increased along the gradient (Table 2). Species with long spores, on the other hand, were relatively more important in forests as revealed by the pair wise comparisons and the linear contrasts (Table 2, Fig. 1D & H). The number of species with unicellular or with 1-septate spores remained more or less constant across the gradient (Table 2). Relative richness of species with 2- or more septate spores

TABLE 2. *Effects of the land-use gradient on* relative richness *of trait classes as revealed by ANOVA*

Traits	Trait class	Transformation†	Covariables‡	F	Trend§	Sign of trend§
Reproductive traits						
Fertility	Mostly sterile	–/–	–/–	6·46***	***	–
	Mostly fertile	–/–	–/–	7·58***	***	+
Propagules	Symbiotic prop.	–/asin	–/–	5·75***	***	–
	Soredia	asin/–	–/–	3·61*	**	–
	Isidia	asin/asin	–/Ire 6	2·92*	***	–
	Fungal prop.	–/–	Hun5/Hun5	8·09***	***	+
	Conidia	–/asin	–/–	0·49		
Spore length & shape	Short & glob./ellip.	–/–	Hun5/Hun5	3·72**	**	+
	Long & glob./ellip.	–/–	Hun6/Hun6	4·01**	*	–
	Short & elongate	–/–	–/–	0·59		
	Long & elongate	asin/asin	Hun4/–	4·23**	**	–
Spore septation	No septation	–/–	–/–	1·29		
	1-septate	–/–	–/–	1·72		
	3-septate or more	asin/asin	–/–	3·04*	*	–
	muriform	asin/asin	Ire2/Ire6	1·95	**	–
Vegetative traits						
Growth form	Crustose	–/–	Hun5/Hun5	1·19		
	Fol.-adpressed	–/–	Hun5/Hun5	11·00***	***	+
	Fol.-ascendant	–/–	Hun5/Hun5	1·71		
	Frut.-erect	–/–	–/–	4·10**	***	–
	Frut.-pend.	–/asin	–/–	1·42		
Photobiont	Green algae (excl. *Trentepohlia*)	asin/asin	–/–	2·44**	**	+
	Trentepohlia	asin/asin	–/–	2·86*	**	–
	Nostoc	asin/asin	Spa1/Spa1	1·52		
Ecological traits						
Substratum specialization	Specialists	–/–	Hun5/–	2·16		
	Intermediates	–/–	–/–	0·39		
	Generalists	–/asin	Hun6/Hun6	6·22***	***	–
Rarity	Wide, abundant	asin/asin	Hun5/Hun5	7·13***	***	+
	Wide, partly rare	asin/–	Hun5/Hun5	6·72***	***	–
	Narrow	asin/asin	–/–	3·01*	**	–

†Transformations of relative richness and additional covariables are indicated for the ANOVAs of the first series before the slash, and for the ANOVAs of the second series (trend analyses) after the slash; asin: arcsine.

‡Ire2: Ireland LUU2 Ire6: Ireland LUU6, Hun5: Hungary LUU5, Hun6: Hungary LUU6, Spa1: Spain LUU1, *P≤0·05, **P≤0·01, ***P≤0·001.

§Significance and sign of trends of the second ANOVA series. Residual degrees of freedom for ANOVAs of the first series are usually 33, and for the second series are usually 27. If a covariable is included, these values are reduced by one.

significantly decreased along the gradient (Table 2).

Vegetative traits

Only three classes of the trait growth form revealed linear trends along the land use gradient. While relative richness of foliose-adpressed lichens increased along the gradient, fruticose-erect species decreased in importance from LUU1 to LUU6 (Table 2). Results of pair wise comparisons between means of relative richness of foliose-adpressed and fruticose-erect lichens are shown in Fig. 2A and B.

The importance of species with green algae (excl. *Trentepohlia*) as the principal photobiont increased linearly along the
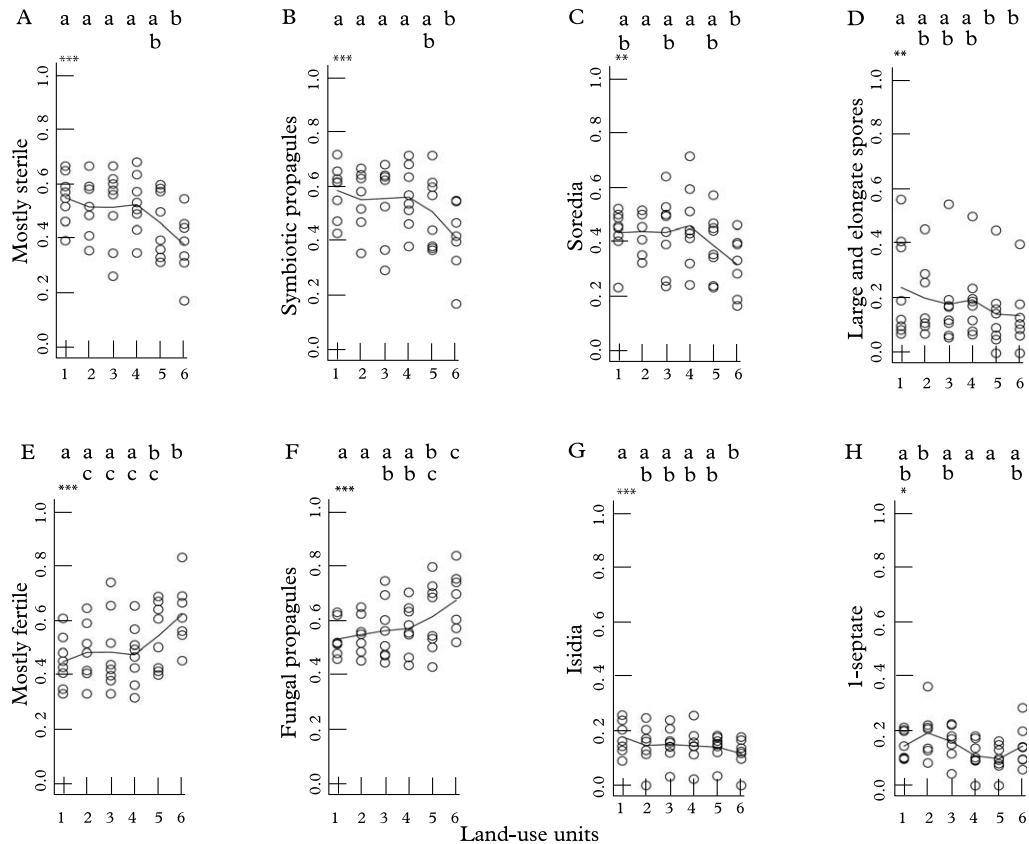
FIG. 1. Effects of land use units on relative richness of classes defined by *fertility* (A & E), *propagules* (B, C, F & G), *spore length & shape* (D & H). See Table 1 for details of classes. Mean relative richness values with the same letter (top x-axis) are not significantly different at the $P \leq 0.05$ level as revealed by pair wise comparisons (Tukey HSD). Lines connect means for land use units. Significance of trends is indicated by stars in the upper left corner of each diagram (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). Note that for the calculation of trends LUU2 was omitted. Land use unit 1: old-growth forest, 2: secondary forest, 3: mixed-use landscape, dominated by forest, 4: mixed-use landscape with an equal share of forest and open land, 5: pasture, 6: farmland.

gradient while the importance of species with *Trentepohlia* decreased linearly (Table 2; Fig. 2C & D). Contrary to expectations, the land use units had no effects on relative richness of species with *Nostoc* (Table 2).

Ecological traits

Considering substratum specialization, only the substratum generalists showed a significant overall effect of the land use units on their relative richness. Moreover, only the generalists exhibited a clear trend along the gradient (Fig. 2E; Table 2). Interestingly, their relative richness decreased from

forests (LUU1 and LUU2) to the open farmland.

Overall effects of land use units on relative richness of all three rarity classes were significant. Widespread, abundant species increased in importance from the old-growth forest to the farmland while widespread, but in some areas rare species decreased (Table 2). While relative richness of the former increased from around 40% to 57%, that of the latter decreased from 53% to 39% (Fig. 2F & G). Relative richness of narrowly distributed species, which may be rare or abundant in their distribution area, also showed a linear decrease from the
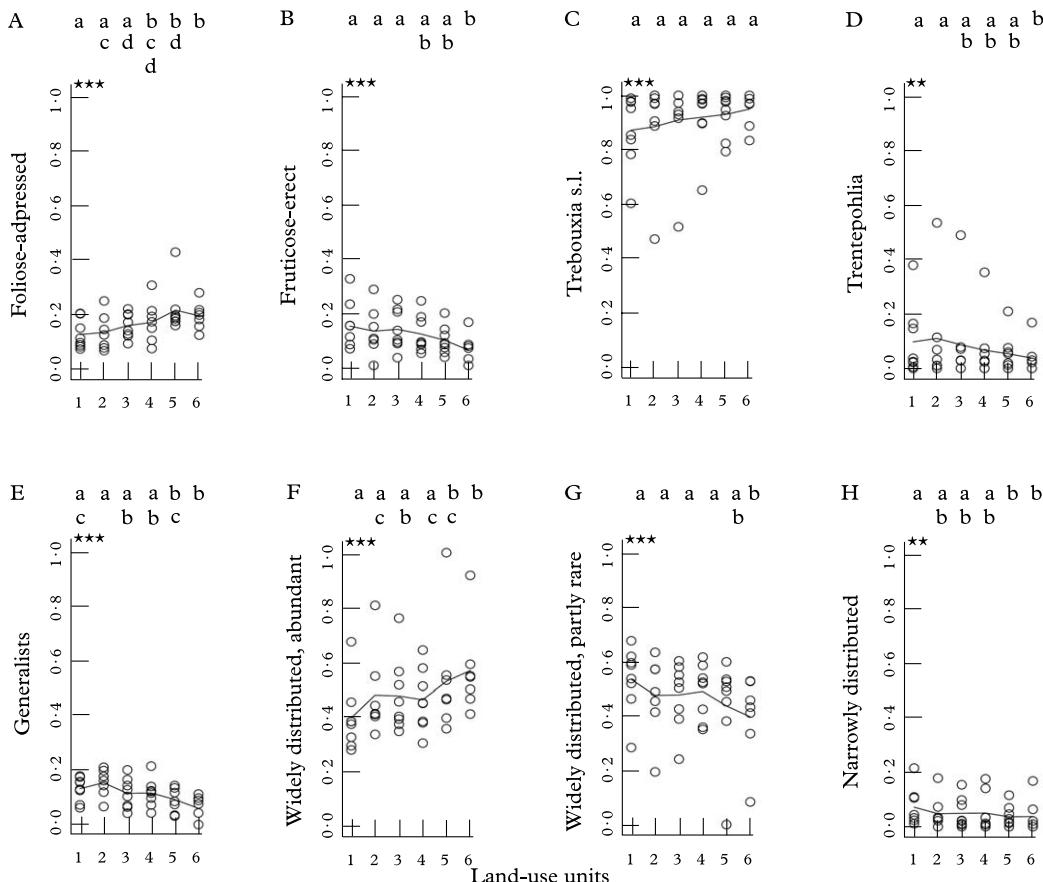
FIG. 2. Effects of land use units on relative richness of classes defined by *growth form* (A & B), *photobiont* (C & D), *substratum specialization* (E) and *rarity* (F–H). See Table 1 and legend for Fig. 1 for further details.

old-growth forest (LUU1) to the farmland (LUU6; Fig. 2H).

Discussion

We found significant relationships between many of the reproductive, vegetative and ecological traits considered and land use-intensity. This was to some extend expected since land use intensity has a clear effect on lichen species composition (Bergamini *et al.* 2005). Furthermore, the considered land use gradient was rather broad ranging from natural or semi-natural forests to intensively used agricultural landscapes. Lack of basic knowledge of physiological, reproductive and ecological aspects of many lichen species prevented the compilation of data for many preferable traits such as growth rate, generation length and so on. Nevertheless, our analyses give a valuable basis for the selection of traits for building context-specific functional classifications.

Reproductive traits

The results show that species which usually produce fungal propagules, were more often found in open and more intensively managed land use units while forests or landscapes with a high proportion of forest cover harboured more species with

vegetative symbiotic propagules. Moreover, fertile lichens with multiseptate and long spores appeared more frequently in forested landscapes, independently of spore shape.

There are some fundamental differences between fungal propagules and symbiotic propagules of lichens. Fungal propagules are usually much smaller than symbiotic propagules and they are self-liberating as well as self-transporting over small distances (excluding those of the *Caliciales*). After dispersal they have to find favourable conditions for germination, and at a later stage a compatible photobiont to establish a new symbiotic phenotype. On the other hand, symbiotic diaspores are usually larger than fungal propagules, they are dispersed by passive means only, but they disseminate the whole lichen symbiosis (Bailey 1976; Lawrey 1984; Tibell 1994). These differences are likely to have consequences on dispersal and establishment. For example, dispersal by wind is influenced by size, shape and volume of the propagules (Tibell 1994; Bjelland 2001). Soredia are likely to be carried farther than isidia but not as far as spores (Pyatt 1973). It is thus suggested that species with small propagules are better adapted to long distance dispersal between suitable habitats whereas species with larger (mostly asexual) propagules are adapted to short-distance dispersal. This is also confirmed by Hedenås & Ericson (2000) who found sexually dispersed species appearing earlier in successional forests than asexually dispersed species. Furthermore, Walser (2004) found evidence of very limited dispersal of symbiotic propagules in *Lobaria pulmonaria* by means of molecular analyses. In the non-forested land use units, where suitable localities are more isolated, it may thus be advantageous for lichens to exhibit a sexual reproductive strategy with small spores. Higher establishment capacity of asexual compared to sexual propagules might be advantageous within forests, where establishment rather than dispersal might be limiting as suggested by Hedenås *et al.* (2003) and Werth *et al.* (2006).

Vegetative traits

As expected, land use intensity had pronounced effects on relative richness of the different growth forms. Bergamini *et al.* (2005) demonstrated that land use intensity affected species richness and density of crustose lichens.

Our studies revealed that with increasing land use intensity the importance of green algae (excl. *Trentepohlia*) as lichen photobiont increased while it decreased for *Trentepohlia*. In contrast, we found no effects of land use intensity on lichens with *Nostoc* as primary photobiont. Little is known about lichen ecology with respect to photobionts except for cyanolichens. Several studies describe a pronounced association of epiphytic cyanolichens with old growth forests (Rose 1976; Gauslaa 1985; Kuusinen 1996; Sillett & McCune 1998; Goward & Arsenault 2000). Moreover, cyanolichens play an important role in calcareous rock communities. Therefore, any effects of old-growth forests in our study may have been obscured by occurrences of cyanolichens growing on calcareous rocks in any other land use unit along the intensity gradient. In fact, saxicolous cyanolichens were much more evenly distributed over the different land use units than epiphytic cyanolichens (results not shown). Epiphytic cyanolichens were found in only seven of the 48 land use units and just four times in old growth forests. Not every old-growth forest in Europe may be a suitable habitat for cyanolichens. Other factors such as climatic conditions, species composition of forest trees, and insolation of the forest stand may affect occurrence of cyanolichens in forest ecosystems (Hedenås & Ericson 2000).

Ecological traits

We found a linear decrease of substratum generalists from the forested land use units to the agricultural landscapes. There may be a close relationship between this pattern and the decrease of sorediate and/or isidiate species along the same gradient. Bowler & Rundel (1975) found some evidence that sorediate species have broader ecological

amplitudes than closely related species that disperse by sexual spores only. They argued that asexual propagules can germinate in a broader habitat range since they do not have to re-build the symbiosis. Additional support for this hypothesis comes from Hedenås *et al.* (2003) who found that a very high proportion of species which occur on a wide range of trees are asexually dispersed.

Rabinowitz (1981) constructed flexible categories of rarities taking into consideration geographic range, habitat specificity and local population size of a species. Only species with a large geographic range, wide habitat specificity and dominant local populations were not defined as rare. Our results showed that widespread, abundant species were more likely to occur with increasing land use intensity, while relative richness of widespread, but in some areas rare species and species showing a narrow distribution decreased. They predict a considerable decline of many rare species if there is a further intensification of already extensively used landscapes.

Limitations

There are some limitations for the interpretation of our results, which should be kept in mind. First, all the relationships we found are of a correlative nature and are by no means a proof of a functional relationship. The adaptive value of the traits studied with respect to the land use gradient can only be assumed. It might well be that several of the traits studied are correlated with other traits, for example physiological traits such as drought tolerance, which are directly under a selection pressure.

A second point concerns the dependence of data points. Lichen species have been treated as independent data points, however, the predominance of a trait in a certain land use unit may occur for reasons other than its functional or adaptive value. The relative importance of a trait may result from groups of closely related species sharing this trait. This might cause spurious correlations between land use intensity and relative importance of traits.

Finally, we used only species presence/absence data, i.e. abundance measures were not considered. Therefore, importance of traits is always measured as relative richness of species sharing a certain trait. It does not mean that species with a dominant trait in a certain land use unit are also the dominant species.

REFERENCES

Bailey, R. H. (1976) Ecological aspects of dispersal and establishment in lichens. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds): 215–247. London: Academic Press.

Bergamini, A., Scheidegger, C., Stofer, S., Carvalho, P., Davey, S., Dietrich, M., Dubs, F., Farkas, E., Groner, U., Kärkkäinen, K., Keller, C., Lökös, L., Lommi, S., Máguas, C., Mitchell, R., Pinho, P., Rico, V. J., Aragón, G., Truscott, A.-M., Wolseley, P. A. & Watt, A. (2005) Performance of macrolichens and lichen genera as indicators of lichen species richness and composition. *Conservation Biology* **19:** 1051–1062.

Bjelland, T. (2001) Comparative studies of the distribution and ecology of some oceanic species in the genus *Leptogium* (Lecanorales, Ascomycotina) in Norway. *Nova Hedwigia* **72:** 1–44.

Bowler, P. A. & Rundel, P. W. (1975) Reproductive strategies in lichens. *Botanical Journal of the Linnean Society* **70:** 325–340.

Büdel, B. & Scheidegger, C. (1996) Thallus morphology and anatomy. In *Lichen biology* (T. H. Nash III, ed.): 37–64. Cambridge: Cambridge University Press.

Clauzade, G. & Roux, C. (1985) *Likenoj de Okcidenta Europo. Ilustrita Determinlibro.* Royan.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Marti,

G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M. R. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15:** 295–304.

Diaz, S., McIntyre, S., Lavorel, S. & Pausas, J. G. (2002) Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. *New Phytologist* **154:** 7–9.

During, H. J. (1992) Ecological classifications of bryophytes and lichens. In *Bryophytes and Lichens in a Changing Environment* (J. W. Bates & A. M. Farmer, eds): 1–31. Oxford: Clarendon Press.

Gauslaa, Y. (1985) The ecology of *Lobarion pulmonariae* and *Parmelion caperatae* in *Quercus* dominated forests in South-West Norway. *Lichenologist* **17:** 117–140.

Goward, T. & Arsenault, A. (2000) Cyanolichen distribution in young unmanaged forests: a dripzone effect? *Bryologist* **103:** 28–37.

Hacker, S. D. & Gaines, S. D. (1997) Some implication of direct positive interactions for community species diversity. *Ecology* **78:** 1990–2003.

Hannah, L., Lohse, D., Hutchinson, C., Carr, J. L. & Lankerani, A. (1994) A preliminary inventory of human disturbance of world ecosystems. *Ambio* **23:** 246–250.

Hedenås, H. & Ericson, L. (2000) Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biological Conservation* **93:** 43–53.

Hedenås, H., Bolyukh, V. O. & Jonsson, B. G. (2003) Spatial distribution of epiphytes on *Populus tremula* in relation to dispersal mode. *Journal of Vegetation Science* **14:** 233–242.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. (1990) *Index Herbariorum. Part I: The Herbaria of the World*. 8th Edition. New York: New York Botanical Garden.

Hulbert, S. H. (2004) On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. *Oikos* **104:** 591–597.

Jahns, H. M. & Ott, S. (1997) Life strategies in lichens—some general considerations. In *New Species and Novel Aspects in Ecology and Physiology of Lichens. In Honour of O. L. Lange* (L. Kappen, ed.): 49–67. Berlin: Cramer.

Kirk, P. M., Canon, P. F., David, J. C. & Stalpers, J. A. (2001) *Ainsworth & Bisby's Dictionary of the Fungi*, 9th Edition. Wallingford: CABI Publishing.

Kuusinen, M. (1996) Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biological Conservation* **75:** 43–49.

Lawrey, J. D. (1984) *Biology of Lichenized Fungi*. New York: Praeger Publishers.

Nimis, P. L. & Martellos, S. (2004) *Keys to the Lichens of Italy. I. Terricolous Species*. Trieste: Edizioni Goliardiche.

Poelt, J. (1969) *Bestimmungsschlüssel Europäischer Flechten*. Lehre: J. Cramer.

Poelt, J. & Vězda, A. (1977) *Bestimmungsschlüssel Europäischer Flechten. Ergänzungsheft I*. Vaduz: J. Cramer.

Poelt, J. & Vězda, A. (1981) *Bestimmungsschlüssel Europäischer Flechten. Ergänzungsheft II*. Vaduz: J. Cramer.

Purvis, O. W., Coppins, B. J., Hawksworth, D. L., James, P. W. & Moore, D. M. (Eds) (1992) *The Lichen Flora of Great Britain and Ireland*. London: Natural History Museum Publications.

Pyatt, F. B. (1973) Lichen propagules. In *The Lichens* (V. Ahmadjian & M. E. Hale, ed.): 117–145. New York: Academic Press.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rabinowitz, D. (1981) Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation: Proceedings of an International Conference* (H. Synge, ed.): 205–217. Chichester: Wiley

Rogers, R. W. (1990) Ecological strategies of lichens. *Lichenologist* **22:** 149–162.

Rose, F. (1976) Lichenological indicators of age and environmental continuity in woodlands. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds): 279–307. London and New York: Academic Press.

Rosenzweig, M. L. (1995) *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000) Biodiversity – Global biodiversity scenarios for the year 2100. *Science* **287:** 1770–1774.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience* **52:** 891–904.

Scheidegger, C., Groner, U., Keller, C. & Stofer, S. (2002) Biodiversity assessment tools—lichens. In *Monitoring with Lichens—Monitoring Lichens* (P. L. Nimis, C. Scheidegger & P. A. Wolseley, eds): 359–365. Dordrecht: Kluwer.

Sillett, S. C. & McCune, B. (1998) Survival and growth of cyanolichen transplants in douglas-fir forest canopies. *Bryologist* **101:** 20–31.

Sokal, R. R. & Rohlf, F. J. (1995) *Biometry*, 3rd Edn. New York: W. H. Freeman and Company.

Tibell, L. (1994) Distribution patterns and dispersal strategies of Caliciales. *Botanical Journal of the Linnean Society* **116:** 159–202.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science* **292:** 281–284.

Turner II, B. L. (2002) Toward integrated land-change science: advances in 1.5 decades of sustained international research on land-use and land-cover changes. In *Challenges of a Changing Earth: Proceedings of the Global Change Open Science Conference, Amsterdam, The Netherlands*, 10 – 13 July 2001 (W. Steffen, J. Jäger, D. J. Carson & C. Bradshow, eds): 21–26. Berlin: Springer.

Turner, M. G., Gardner, R. H. & O'Neill, R. V. (2001) *Landscape Ecology in Theory and Practice: Pattern and Process*. New York: Springer Verlag.

Walser, J. C. (2004) Molecular evidence for limited dispersal of vegetative propagules in the epiphytic lichen *Lobaria pulmonaria*. *American Journal of Botany* **91:** 1273–1276.

Werth, S., Wagner, H., Gugerli, H., Holderegger, R., Csencsics, D., Kalwij, J. & Scheidegger, C. (2006) Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology*, in press.

Wirth, V. (1995) *Die Flechten Baden-Württembergs*. Stuttgart: Ulmer.

Wolseley, P. A. (1997) Response of epiphytic lichens to fire in tropical forests of Thailand. In *Progress and Problems in Lichenology in the Nineties* (R. Türk & R. Zorer, eds): 165–176. Berlin: J. Cramer.

Appendix

Species list with assigned trait values (see Table 1 for details)

Fertility	1: mostly sterile; 2: mostly fertile (producing regularly ascospores); na: not available
Propagules	*Symbiotic propagules* (soredia and/or isidia): 0: lacking; 1: existing; na: not available
	Soredia: 0: lacking; 1: existing; na: not available
	Isidia: 0: lacking; 1: existing (small thallus fragments were considered as isidia); na: not available
	Fungal propagules (ascospores and/or conidia): 0: lacking; 1: existing; na: not available
	Conidia: 0: lacking; 1: existing; na: not available
Spore length & shape	1: short and globose to ellipsoid; 2: short and elongate; 3: long and globose to ellipsoid; 4: long and elongate; na: not available; –: species of the class 'mostly fertile' from trait '*fertility*' were considered only
Spore septation	1: no septum; 2: 1-septate; 3: 3-septate or more; 4: muriform; na: not available; –: species of the class 'mostly fertile' from trait '*fertility*' were considered only
Growth form	1: crustose; 2: foliose-adpressed; 3: foliose ascendant; 4: fruticose-erect; 5: fruticose-pendulous
Photobiont	1: green algae (excl. *Trentepohlia*); 2: *Trentepohlia*; 3: *Nostoc*; na: not available
Substrate specialization	1: specialist (restricted to one substratum); 2: intermediate type (growing on two or three different substrata); 3: generalist (growing on more than three substrata); na: not available (rock, soil, living trees, deadwood and bryophytes were considered as possible substrata)
Rarity	1: wide distribution and high abundance in most areas; 2: wide distribution and high abundance in some areas, but rare in others; 3: narrow distribution, high or low abundance; na: not available

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Acarospora badiofusca	2	0	0	0	1	0	1	1	1	1	1	2
A. cervina	2	0	0	0	1	na	na	1	1	1	na	1
A. fuscata	2	0	0	0	1	0	2	1	1	1	1	1
A. glaucocarpa	2	0	0	0	1	0	2	1	1	1	1	2
A. heppii	2	0	0	0	1	0	1	1	1	1	1	2
A. impressula	2	0	0	0	1	0	1	1	1	1	1	2
A. modenensis	2	0	0	0	1	na	1	1	1	1	1	2

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Acarospora nitrophila	2	0	0	0	1	0	2	1	1	1	1	1
A. oligospora	2	0	0	0	1	na	1	1	1	1	1	2
A. scotica	2	0	0	0	1	na	1	1	1	1	1	2
A. smaragdula	2	0	0	0	1	0	2	1	1	1	2	2
A. sulphurata	2	0	0	0	1	na	1	1	1	1	1	3
A. veronensis	2	0	0	0	1	0	2	1	1	1	1	2
Acrocordia gemmata	2	0	0	0	1	1	3	2	1	2	1	2

Species													Species												
Acarospora macrospora	2	0	0	0	1	1	3	2	1	2	1	2	*Bacidia beckhausii*	2	0	0	0	1	1	4	3	1	1	1	2
A. salweyi	2	0	0	0	1	1	3	2	1	2	1	2	*B. biatorina*	2	1	0	1	1	0	4	3	1	1	1	2
Agonimia tristicula	na	1	0	1	0	0	–	–	1	1	3	1	*B. chloroticula*	2	0	0	0	1	1	4	3	1	1	2	2
Amandinea punctata	2	0	0	0	1	1	1	2	1	1	2	1	*B. circumspecta*	2	0	0	0	1	1	4	3	1	1	2	2
Anaptychia ciliaris	2	0	0	0	1	0	3	2	4	1	2	2	*B. delicata*	2	1	1	0	1	1	4	3	1	1	2	2
Anisomeridium biforme	na	0	0	0	1	1	2	2	1	2	1	2	*B. globulosa*	2	1	1	0	1	1	2	3	1	1	1	2
Arthonia cinnabarina	2	0	0	0	1	1	4	3	1	2	1	2	*B. incompta*	2	1	1	0	1	1	4	3	1	1	1	2
A. didyma	2	0	0	0	1	1	4	2	1	2	1	2	*B. inundata*	2	0	0	0	1	1	4	3	1	1	1	2
A. elegans	2	0	0	0	1	0	4	3	1	2	1	2	*B. laurocerasi*	2	0	0	0	1	1	4	3	1	1	1	2
A. intexta	2	0	0	0	1	1	2	3	1	–	1	1	*B. naegelii*	2	0	0	0	1	0	4	3	1	1	2	2
A. lapidicola	2	0	0	0	1	1	1	2	1	2	1	2	*B. phacodes*	2	0	0	0	1	1	4	3	1	1	1	2
A. leucopellaea	2	0	0	0	1	0	2	3	1	2	1	2	*B. rosella*	2	0	0	0	1	1	4	3	1	1	1	2
A. mediella	2	0	0	0	1	1	2	3	1	2	1	2	*B. rubella*	2	1	0	1	1	1	4	3	1	1	2	2
A. pruinata	2	0	0	0	1	1	4	3	1	2	2	3	*B. trachona*	1	0	0	0	1	1	–	–	1	1	2	2
A. radiata	2	0	0	0	1	1	4	3	1	2	1	1	*Baeomyces carneus*	2	0	0	0	1	na	na	1	1	1	2	2
A. spadicea	2	0	0	0	1	1	2	2	1	2	1	1	*B. rufus*	na	1	1	0	0	0	–	–	1	1	3	1
A. vinosa	2	0	0	0	1	1	2	2	1	2	1	2	*Bagliettoa baldensis*	2	0	0	0	1	0	3	1	1	1	1	2
Arthopyrenia antecellens	2	0	0	0	1	1	4	2	1	–	1	3	*Bellemerea cinereofusca*	2	0	0	0	1	na	1	1	1	1	1	2
A. cinereopruinosa	2	0	0	0	1	1	4	2	1	–	1	2	*Biatora chrysantha*	1	1	1	0	0	0	–	–	1	1	2	2
A. fraxini	2	0	0	0	1	1	4	2	1	–	1	2	*B. efflorescens*	1	1	1	0	1	1	–	–	1	1	2	2
A. lapponina	2	0	0	0	1	1	4	2	1	–	1	1	*B. helvola*	2	0	0	0	1	1	2	1	1	1	1	2
A. orustensis	2	0	0	0	1	na	3	2	1	na	na	3	*B. subduplex*	2	0	0	0	1	1	2	1	1	1	1	2
A. punctiformis	2	0	0	0	1	0	4	2	1	–	1	1	*Bryoria capillaris*	1	1	1	0	0	0	–	–	5	1	1	2
A. ranunculospora	2	0	0	0	1	1	2	2	1	2	1	3	*B. fuscescens*	1	1	1	0	0	na	–	–	5	1	1	2
A strontianesis	2	0	0	0	1	0	3	2	1	–	na	2	*B. implexa*	1	1	1	0	1	1	–	–	5	1	1	2
Arthrosporum populorum	2	0	0	0	1	1	2	3	1	1	1	2	*B. subcana*	1	1	1	0	0	na	–	–	5	1	1	2
Aspicilia bricconensis	2	0	0	0	1	1	3	1	1	1	1	2	*Buellia aethalea*	2	0	0	0	1	1	1	2	1	1	2	1
A. caesiocinerea	2	0	0	0	1	1	3	1	1	1	1	1	*B. alboatra*	2	0	0	0	1	na	3	4	1	1	2	2
A. calcarea	2	0	0	0	1	0	3	1	1	1	1	1	*B. anomala*	2	0	0	0	1	na	1	2	1	1	2	3
A. cinerea	2	0	0	0	1	1	3	1	1	1	1	1	*B. arnoldii*	2	0	0	0	1	1	3	2	1	1	1	3
A. contorta	2	0	0	0	1	1	3	1	1	1	1	1	*B. badia*	2	0	0	0	1	0	1	2	1	1	1	2
A. crespiana	2	0	0	0	1	1	3	1	1	1	2	3	*B. disciformis*	2	0	0	0	1	1	4	2	1	1	1	2
A. grisea	1	1	1	0	0	0	–	–	1	1	1	2	*B. epipolia*	2	0	0	0	1	1	3	2	1	1	1	2
A. intermutans	2	0	0	0	1	1	3	1	1	1	1	2	*B. erubescens*	2	0	0	0	1	1	3	2	1	1	1	2
A. laevata	2	0	0	0	1	1	3	1	1	1	1	2	*B. griseovirens*	1	1	1	0	0	0	–	–	1	1	2	1
A. recedens	2	0	0	0	1	1	1	1	1	1	1	2	*B. iberica*	2	0	0	0	1	na	na	2	1	1	na	3
A. simoensis	1	1	0	1	0	0	–	–	1	1	1	2	*B. leptocline*	2	0	0	0	1	1	1	2	1	1	1	2
Bacidia absistens	2	1	1	0	1	0	4	3	1	1	1	2	*B. ocellata*	2	0	0	0	1	1	1	2	1	1	1	2
B. arceutina	2	0	0	0	1	0	4	3	1	1	3	2	*B. schaereri*	2	0	0	0	1	1	1	2	1	1	2	2
B. arnoldiana	na	1	1	0	1	1	–	–	1	1	2	1	*Buellia stellulata*	2	0	0	0	1	1	1	2	1	1	1	2
B. assulata	2	0	0	0	1	0	4	3	1	1	1	2	*B. subdisciformis*	2	0	0	0	1	1	1	2	1	1	1	3

Appendix. *Continued*

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Buellia triseptata	2	0	0	0	1	na	na	2	1	1	na	2
Calicium abietinum	2	0	0	0	1	0	1	2	1	1	2	2
C. glaucellum	2	0	0	0	1	1	1	2	1	1	2	2
C. montanum	2	0	0	0	1	0	1	2	1	1	2	2
C. parvum	2	0	0	0	1	1	1	2	1	1	2	2
C. trabinellum	2	0	0	0	1	1	1	2	1	1	2	2
C. viride	2	0	0	0	1	0	1	2	1	1	2	2
Caloplaca aractina	2	0	0	0	1	0	1	2	1	1	1	3
C. biatorina	2	0	0	0	1	0	1	2	1	1	1	2
C. carphinea	2	0	0	0	1	0	1	2	1	1	1	3
C. cerina	2	0	0	0	1	0	1	2	1	1	3	1
C. cerinella	2	0	0	0	1	0	1	2	1	1	1	1
C. chalybaea	2	0	0	0	1	0	1	2	1	1	1	2
C. chlorina	1	1	1	0	0	0	–	–	1	1	1	2
C. chrysodeta	1	1	1	0	0	0	–	–	1	1	1	2
C. cirrochroa	na	1	1	0	0	0	1	2	1	1	1	2
C. citrina	1	1	1	0	0	0	–	–	1	1	3	1
C. conglomerata	2	0	0	0	1	0	1	2	1	1	1	2
C. crenularia	2	0	0	0	1	0	1	2	1	1	1	2
C. crenulatella	2	0	0	0	1	0	3	2	1	1	1	2
C. diphyodes	2	0	0	0	1	1	1	2	1	1	1	2
C. dolomiticola	2	0	0	0	1	0	1	2	1	1	1	2
C. ferruginea	2	0	0	0	1	0	1	2	1	1	1	1
C. festivella	2	0	0	0	1	0	1	2	1	1	1	2
C. flavescens	2	0	0	0	1	0	1	2	1	1	2	1
C. flavorubescens	2	0	0	0	1	0	3	2	1	1	2	2
C. flavovirescens	2	0	0	0	1	0	3	2	1	1	1	1
C. haematites	2	0	0	0	1	0	1	2	1	1	1	2
C. herbidella	na	1	0	1	0	0	–	–	1	1	1	2
Caloplaca holocarpa	2	0	0	0	1	0	1	2	1	1	2	1
C. hungarica	2	0	0	0	1	0	1	2	1	1	1	1
C. irrubescens	2	0	0	0	1	0	1	2	1	1	1	2
C. lactea	2	0	0	0	1	0	3	2	1	1	1	1
C. nubigena	2	0	0	0	1	0	2	2	1	1	1	3
C. pyracea	2	0	0	0	1	0	1	2	1	1	2	1
C. sinapisperma	2	0	0	0	1	0	3	2	1	1	2	2
C. subpallida	2	0	0	0	1	0	4	2	1	1	1	2
C. teicholyta	2	1	1	0	1	0	3	2	1	1	1	1
C. variabilis	2	0	0	0	1	0	1	2	1	1	1	1
Candelaria concolor	1	1	0	1	1	1	–	–	3	1	2	1
Candelariella aurella	2	0	0	0	1	0	2	1	1	1	2	1
C. coralliza	1	1	0	1	0	0	–	–	1	1	1	2
C. deflexa	2	0	0	0	1	0	2	1	1	1	1	2
C. medians	1	1	0	1	0	0	–	–	1	1	1	2
C. reflexa	1	1	1	0	0	0	–	–	1	1	1	1
C. vitellina	na	0	0	0	1	1	–	–	1	1	2	1
C. xanthostigma	1	1	0	1	0	0	–	–	1	1	1	1
Carbonea vorticosa	2	0	0	0	1	1	2	1	1	na	1	2
Catapyrenium cinereum	2	0	0	0	1	0	4	1	2	1	2	2
C. rufescens	2	0	0	0	1	1	3	1	2	1	2	2
C. squamulosum	2	0	0	0	1	1	1	1	2	1	1	3
Catillaria atomarioides	2	0	0	0	1	0	2	1	1	1	1	2
C. chalybeia	2	0	0	0	1	1	2	2	1	1	2	2
C. nigroclavata	2	0	0	0	1	0	2	2	1	1	1	2
C. pulverea	1	1	1	0	0	0	–	–	1	2	3	2
Cetraria aculeatum	1	1	0	1	0	0	–	–	4	1	2	2
C. chlorophylla	1	1	1	0	1	1	–	–	4	1	2	1
C. islandica	1	1	0	1	1	1	–	–	4	1	1	2

Cetraria merillii	1	1	0	1	0	0	–	–	4	1	na	3	*Cladonia merochlorophaea*	2	1	1	1	1	1	–	–	4	1	2	1
C. muricatum	1	1	0	1	1	1	–	–	4	1	3	2	*C. metacorallifera*	2	1	1	1	1	1	–	–	4	1	2	2
Cetrelia cetrarioides agg.	1	1	1	0	0	0	–	–	3	1	1	2	*C. phyllophora*	1	1	1	1	1	1	–	–	4	1	2	2
Chaenotheca brunneola	2	0	0	0	1	0	1	1	1	1	2	2	*C. pleurota*	2	1	1	0	1	1	–	–	4	1	2	2
C. chrysocephala	2	0	0	0	1	0	1	1	1	1	2	2	*C. polydactyla*	2	1	1	0	1	1	–	–	4	1	2	2
C. ferruginea	2	0	0	0	1	0	1	1	1	1	2	2	*C. portentosa*	1	1	0	1	0	0	–	–	4	1	1	2
C. furfuracea	2	1	1	0	1	0	1	1	1	1	2	2	*C. pyxidata*	2	1	1	0	1	1	–	–	4	1	3	1
C. phaeocephala	2	0	0	0	1	0	1	1	1	1	2	2	*C. ramulosa*	2	1	1	1	1	1	–	–	4	1	2	2
C. stemonea	2	1	1	0	1	0	1	1	1	1	2	2	*C. rangiferina*	1	1	0	1	1	1	–	–	4	1	2	2
C. trichialis	2	0	0	0	1	0	1	1	1	1	2	2	*C. rangiformis*	1	1	0	1	1	1	–	–	4	1	1	2
C. xyloxena	2	0	0	0	1	0	1	1	1	1	1	2	*C. squamosa*	1	1	0	1	1	1	–	–	4	1	3	2
Chrysothrix candelaris	1	1	1	0	0	0	–	–	1	1	2	2	*C. stellaris*	1	1	0	1	1	1	–	–	4	1	1	2
C. chlorina	1	1	1	0	0	0	–	–	1	1	2	2	*C. subcervicornis*	2	1	0	1	1	1	–	–	4	1	2	2
C. flavovirens	1	1	1	0	0	0	–	–	1	1	na	3	*C. subulata*	1	1	1	1	1	1	–	–	4	1	2	2
Cladonia acuminata	1	0	0	0	1	1	–	–	4	1	na	3	*C. sulphurina*	1	1	1	0	1	1	–	–	4	1	2	2
C. amaurocraea	1	0	0	0	1	1	–	–	4	1	1	2	*C. symphycarpa*	1	1	0	1	1	1	–	–	4	1	1	1
C. arbuscula	1	1	0	1	1	1	–	–	4	1	1	2	*C. uncialis*	1	1	0	1	1	1	–	–	4	1	2	3
C. bellidiflora	2	0	0	0	1	1	–	–	4	1	1	2	*Clauzadea monticola*	2	0	0	0	1	0	1	1	1	1	1	2
C. borealis	1	na	na	na	1	1	–	–	4	1	3	3	*Clauzadeana macula*	2	0	0	0	1	0	1	1	1	1	1	2
C. botrytes	2	0	0	0	1	1	–	–	4	1	1	2	*Cliostomum griffithii*	2	0	0	0	1	1	2	2	1	1	2	2
C. carneola	1	1	1	0	1	1	–	–	4	1	2	2	*Coelocaulon crespoae*	na	1	0	1	0	na	–	–	4	1	na	3
C. cenotea	1	1	1	0	1	1	–	–	4	1	2	1	*Collema auriforme*	1	1	0	1	0	0	–	–	2	3	2	2
C. cervicornis	1	1	0	1	1	1	–	–	4	1	1	2	*C. crispum*	1	1	0	1	0	0	–	–	3	3	2	1
C. coccifera	2	1	1	0	1	1	–	–	4	1	3	2	*C. cristatum*	2	1	0	1	1	0	3	4	2	3	2	1
C. coniocraea auct.	1	1	1	0	1	1	–	–	4	1	2	1	*C. fasciculare*	2	0	0	0	1	0	4	3	2	3	2	2
C. convoluta	1	1	0	1	1	1	–	–	4	1	1	2	*C. flaccidum*	1	1	0	1	0	0	–	–	2	3	2	2
C. cornuta	1	1	1	1	1	1	–	–	4	1	2	2	*C. furfuraceum*	1	1	0	1	0	0	–	–	2	3	2	2
C. crispata	2	1	0	1	1	1	–	–	4	1	1	2	*C. fuscovirens*	1	1	0	1	0	0	–	–	2	3	1	2
C. deformis	1	1	1	0	1	1	–	–	4	1	2	2	*C. nigrescens*	2	0	0	0	1	0	4	3	2	3	2	2
C. digitata	1	1	1	0	1	1	–	–	4	1	2	2	*C. parvum*	1	1	0	1	1	1	–	–	2	3	1	2
C. diversa	1	1	1	1	1	1	–	–	4	1	2	2	*C. polycarpon*	2	0	0	0	1	0	4	na	3	3	1	1
C. fimbriata	1	1	1	0	1	1	–	–	4	1	2	1	*C. subflaccidum*	1	1	0	1	0	0	–	–	2	3	2	2
C. foliacea	1	1	0	1	1	1	–	–	4	1	2	2	*C. subnigrescens*	2	0	0	0	1	0	4	3	2	3	2	2
C. furcata	2	1	0	1	1	1	–	–	4	1	2	2	*C. tenax*	2	1	0	1	1	1	4	na	2	3	2	1
C. glauca	1	1	1	0	1	1	–	–	4	1	2	2	*C. undulatum*	2	0	0	0	1	0	4	3	2	3	1	1
C. gracilis	1	1	0	1	1	1	–	–	4	1	2	2	*Cystocoleus ebeneus*	1	1	0	1	0	0	–	–	1	2	2	2
C. luteoalba	1	1	1	0	1	1	–	–	4	1	3	2	*Degelia atlantica*	1	1	0	1	0	0	–	–	2	3	2	3
C. macilenta	2	1	1	0	1	1	–	–	4	1	3	2	*D. plumbea*	2	0	0	0	1	1	3	1	2	3	2	3
C. macroceras	1	1	0	1	1	1	–	–	4	1	1	2	*Dendriscocaulon umhausense*	1	1	0	1	0	0	–	–	4	3	na	3
C. macrophylla	2	1	0	1	1	1	–	–	4	1	2	2	*Dermatocarpon miniatum*	2	0	0	0	1	1	1	1	3	1	1	2
C. magyarica	1	1	1	1	1	1	–	–	4	1	na	3	*Dibaeis baeomyces*	2	1	0	1	1	1	4	1	1	1	1	1

Appendix. *Continued*

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Dimerella lutea	2	0	0	0	1	1	2	2	1	2	3	2
D. pineti	2	0	0	0	1	1	2	2	1	2	3	1
Diploicia canescens	1	1	1	0	1	1	1	2	1	1	2	2
Diploschistes euganeus	2	0	0	0	1	0	3	4	1	1	1	2
D. gypsaceus	2	0	0	0	1	0	3	4	1	1	1	2
D. muscorum	2	0	0	0	1	0	3	4	1	1	2	1
D. scruposus	2	0	0	0	1	1	3	4	1	1	1	1
Enterographa crassa	2	0	0	0	1	1	4	3	1	2	2	3
Evernia divaricata	1	0	0	0	0	0	–	–	5	1	1	2
E. prunastri	1	1	1	0	0	0	–	–	4	1	3	1
Farnoldia jurana	2	0	0	0	1	1	3	1	1	1	1	2
Fellhanera bouteillei	2	1	1	0	1	1	2	2	1	1	1	2
Fuscidea arboricola	1	1	1	0	0	0	–	–	1	1	1	2
F. cyathoides	2	0	0	0	1	1	1	1	1	1	2	2
F. lightfootii	2	1	1	0	1	0	1	1	1	1	1	2
F. praeruptorum	1	1	1	0	0	0	–	–	1	1	1	2
F. pusilla	1	1	1	0	0	0	–	–	1	1	1	2
Graphina anguina	2	0	0	0	1	0	3	3	1	2	1	3
Graphis elegans	2	0	0	0	1	0	4	3	1	2	2	3
G. scripta	2	0	0	0	1	1	4	3	1	2	1	1
Gyalecta flotowii	2	0	0	0	1	0	1	3	1	2	1	2
G. jenensis	2	0	0	0	1	0	1	4	1	2	2	1
G. truncigena	2	0	0	0	1	0	4	4	1	2	1	2
Gyalideopsis anastomosans	1	1	0	1	0	0	–	–	1	1	3	2
Haematomma ochroleucum	1	1	1	0	1	1	–	–	1	1	2	2
Halecania giraltiae	1	1	1	0	1	1	–	–	1	1	na	3
H. viridescens	1	1	1	0	0	0	–	–	1	1	1	2
Heterodermia obscurata	1	1	1	0	0	0	–	–	2	1	3	3
H. speciosa	1	1	1	0	0	0	–	–	2	1	2	3
Hyperphyscia adglutinata	1	1	1	0	1	1	–	–	2	1	2	2
Hypocenomyce caradocensis	1	0	0	0	1	1	–	–	1	1	2	2
H. friesii	2	0	0	0	1	1	1	1	1	1	2	2
H. scalaris	1	1	1	0	0	0	–	–	1	1	2	2
H. sorophora	1	1	1	0	0	0	–	–	1	1	2	2
H. stoechadiana	1	1	1	0	0	0	–	–	1	1	2	3
Hypogymnia bitteri	1	1	1	0	0	0	–	–	2	1	1	2
H. farinacea	1	1	1	0	1	1	–	–	2	1	2	2
H. physodes	1	1	1	0	1	1	–	–	3	1	3	1
H. tubulosa	1	1	1	0	1	1	–	–	3	1	2	1
H. vittata	1	1	1	0	0	0	–	–	3	1	1	3
Icmadophila ericetorum	2	0	0	0	1	1	4	2	1	2	2	2
Immersaria athroocarpa	2	0	0	0	1	1	3	1	1	1	1	2
Imshaugia aleurites	1	1	0	1	1	1	–	–	2	1	2	2
Ionaspis epulotica	2	0	0	0	1	1	3	1	1	2	1	2
I. melanocarpa	2	0	0	0	1	1	3	1	1	2	1	2
Japewia carrollii	2	0	0	0	1	0	1	1	1	1	1	3
Koerbera biformis	2	1	0	1	1	0	4	1	1	3	1	3
Lasallia pustulata	1	1	0	1	1	1	–	–	3	1	1	2
Lecanactis abietina	na	0	0	0	1	1	–	–	1	2	2	2
L. latebrarum	1	1	1	0	0	0	–	–	1	2	1	3
L. lyncea	2	0	0	0	1	0	4	3	1	2	1	3
L. premnea	2	0	0	0	1	1	4	3	1	2	2	3
L. umbrina	1	1	1	0	0	0	–	–	1	2	1	2
Lecania cyrtella	2	0	0	0	1	1	2	2	1	1	1	1
L. fuscella	2	0	0	0	1	0	4	3	1	1	1	2
L. inundata	2	0	0	0	1	0	2	2	1	1	1	3
Lecanora aff. *expallens*	1	1	1	0	0	0	–	–	1	1	1	2
L. albella	2	0	0	0	1	0	1	1	1	1	1	2

Species												
Lecanora albescens	2	0	0	0	1	1	1	1	1	1	1	2
L. allophana	2	0	0	0	1	0	3	1	1	1	1	2
L. argentata	2	0	0	0	1	0	1	1	1	1	1	2
L. bolcana	2	0	0	0	1	0	1	1	1	1	1	2
L. cadubriae	2	0	0	0	1	1	2	1	1	1	2	2
L. caesiosora	1	1	1	0	1	1	–	–	1	1	1	2
L. campestris	2	0	0	0	1	1	4	1	1	1	2	1
L. carpinea	2	0	0	0	1	1	1	1	1	1	2	1
L. cenisia	2	0	0	0	1	0	1	1	1	1	1	2
L. chlarotera	2	0	0	0	1	1	1	1	1	1	2	1
L. circumborealis	2	0	0	0	1	0	1	1	1	1	2	2
L. compallens	1	1	1	0	0	0	na	1	1	na	na	2
L. confusa	2	0	0	0	1	0	2	1	1	1	2	2
L. conizaeoides	na	1	1	0	1	1	–	–	1	1	3	2
L. dispersa	2	0	0	0	1	0	1	1	1	1	2	1
L. expallens	na	1	1	0	0	0	–	–	1	1	2	2
L. expersa	1	1	1	0	1	1	–	–	1	1	2	3
L. farinaria	1	1	1	0	0	0	–	–	1	na	2	3
L. gangaleoides	2	0	0	0	1	0	1	1	1	1	2	2
L. hagenii aggr.	2	0	0	0	1	1	1	1	1	1	2	1
L. hispanica	na	0	0	0	0	na	–	–	1	1	na	3
L. horiza aggr.	2	0	0	0	1	0	1	1	1	1	1	2
L. hypoptella	2	0	0	0	1	1	2	1	1	1	2	2
L. intricata	2	0	0	0	1	1	1	1	1	1	2	2
L. intumescens	2	0	0	0	1	0	1	1	1	1	1	2
L. jamesii	1	1	1	0	0	0	–	–	1	1	2	2
L. leptyrodes	2	0	0	0	1	0	1	1	1	1	1	2
L. meridionalis	2	0	0	0	1	0	1	1	1	1	2	2
L. muralis	2	0	0	0	1	1	1	1	1	1	2	1
L. norvegica	1	0	0	0	0	0	–	–	1	na	1	2
L. orosthea	1	1	1	0	1	1	–	–	1	1	2	2
L. persimilis	2	0	0	0	1	0	1	1	1	1	1	2
L. piniperda	2	0	0	0	1	1	2	1	1	na	2	2
L. polytropa	2	0	0	0	1	1	1	1	1	1	2	1
L. populicola	2	0	0	0	1	0	1	1	1	1	1	2
L. praesistens	2	0	0	0	1	0	1	1	1	1	1	3
L. pulicaris	2	0	0	0	1	0	1	1	1	1	2	1
L. rubicunda	2	0	0	0	1	0	1	1	1	na	na	2
L. rugosella	2	1	0	1	1	0	1	1	1	1	2	2
L. rupicola	2	0	0	0	1	1	1	1	1	1	1	1
L. saligna	2	0	0	0	1	1	1	1	1	1	2	2

Species												
Lecanora sambuci	2	0	0	0	1	1	1	1	1	1	1	1
L. soralifera	1	1	1	0	0	0	–	–	1	1	2	2
L. strobilina	2	1	1	0	1	1	1	1	1	1	2	2
L. subcarpinea	2	0	0	0	1	1	1	1	1	1	1	2
L. subintricata	2	0	0	0	1	1	1	1	1	na	2	2
L. subrugosa	2	0	0	0	1	1	1	1	1	1	1	1
L. sulphurea	2	0	0	0	1	1	1	1	1	na	1	2
L. symmicta aggr.	2	0	0	0	1	1	2	1	1	1	2	1
L. varia	2	0	0	0	1	1	1	1	1	1	2	2
Lecidea albohyalina	2	0	0	0	1	0	2	1	1	1	1	2
L. amaurospoda	1	1	1	0	0	0	–	–	1	1	2	2
L. auriculata	2	0	0	0	1	1	2	1	1	na	1	2
L. botryosa	2	1	1	0	1	0	2	1	1	na	2	2
L. cinnabarina	1	1	1	0	0	0	–	–	1	1	1	2
L. confluens	2	0	0	0	1	1	1	1	1	1	1	2
L. exigua	2	0	0	0	1	0	1	1	1	1	1	2
L. fuscoatra	2	0	0	0	1	1	1	1	1	1	2	2
L. hypopta	2	0	0	0	1	1	1	1	1	1	2	2
L. lactea	2	0	0	0	1	1	1	1	1	1	2	2
L. lapicida	2	0	0	0	1	1	1	1	1	1	1	1
L. lithophila	2	0	0	0	1	1	1	1	1	1	2	2
L. lurida	na	0	0	0	1	1	–	–	1	1	2	2
L. nylanderi	1	1	1	0	0	0	–	–	1	1	2	2
L. plana	2	0	0	0	1	1	1	1	1	1	1	2
L. sarcogynoides	2	0	0	0	1	1	2	1	1	1	1	2
L. swartzioidea	2	0	0	0	1	1	1	1	1	1	1	2
L. symmictella	2	0	0	0	1	1	2	1	1	1	1	2
Lecidella carpathica	2	0	0	0	1	0	1	1	1	1	1	1
L. elaeochroma	2	0	0	0	1	0	1	1	1	1	2	1
L. flavosorediata	1	1	1	0	0	0	–	–	1	1	1	2
L. pulveracea	1	1	1	0	0	0	–	–	1	1	1	2
L. scabra	1	1	1	0	0	0	–	–	1	1	2	2
L. stigmatea	2	0	0	0	1	0	1	1	1	1	1	1
L. subincongrua	2	0	0	0	1	1	1	1	1	1	2	2
Lepraria caesioalba	1	1	1	0	0	0	–	–	1	1	2	2
L. eburnea	1	1	1	0	0	0	–	–	1	1	3	2
L. elobata	1	1	1	0	0	0	–	–	1	1	3	2
L. incana	1	1	1	0	0	0	–	–	1	1	2	1
L. jackii	1	1	1	0	0	0	–	–	1	1	3	1
L. lobificans	1	1	1	0	0	0	–	–	1	1	3	1
L. neglecta	1	1	1	0	0	0	–	–	1	1	2	2

Appendix. *Continued*

| Species | Fertility | Propagules | | | | | Spore length & shape | Spore septation | Growth form | Photobiont | Sub. specialization | Rarity |
		Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia						
Leparia rigidula	1	1	1	0	0	0	–	–	1	1	3	1
Leprocaulon microscopicum	1	1	1	0	0	0	–	–	1	1	3	2
Leproloma membranaceum	1	1	1	0	0	0	–	–	1	1	3	2
L. vouauxii	1	1	1	0	0	0	–	–	1	1	3	2
Leptochidium albociliatum	2	1	0	1	1	0	4	2	3	3	2	2
Leptogium corniculatum	1	1	0	1	0	0	3	4	3	3	3	2
L. gelatinosum	2	0	0	0	1	0	3	4	3	3	3	2
L. intermedium	2	1	0	1	1	0	3	4	3	3	3	2
L. lichenoides	1	1	0	1	0	0	–	–	3	3	3	2
L. saturninum	1	1	0	1	0	0	–	–	3	3	2	2
L. subtile	2	0	0	0	1	0	3	4	3	3	2	2
L. tenuissimum	1	1	0	1	0	0	–	–	3	3	2	2
L. teretiusculum	1	1	0	1	0	0	–	–	3	3	2	2
Leptorhaphis epidermidis	2	0	0	0	1	1	4	2	1	2	1	2
Lobaria pulmonaria	1	1	1	1	1	1	–	–	3	1	2	2
Lobothallia radiosa	2	0	0	0	1	1	1	1	1	1	1	2
Loxospora cismonica	2	0	0	0	1	0	4	3	1	1	1	2
L. elatina	1	1	1	0	1	1	–	–	1	1	2	2
Megaspora verrucosa	2	0	0	0	1	0	3	1	1	1	2	2
Menegazzia terebrata	1	1	1	0	1	1	–	–	2	1	2	2
Micarea bauschiana	2	0	0	0	1	1	2	1	1	1	2	2
M. botryoides	2	1	1	0	1	1	2	2	1	1	3	2
M. cinerea	2	0	0	0	1	1	4	3	1	1	2	2
M. coppinsii	1	1	1	0	1	1	–	–	1	1	1	2
M. denigrata	2	0	0	0	1	1	1	2	1	1	3	1
M. erratica	2	0	0	0	1	1	1	1	1	1	1	2
M. lignaria	2	0	0	0	1	1	4	3	1	1	1	2
M. lithinella	2	0	0	0	1	1	2	1	1	1	2	2
M. melaena	2	1	1	0	1	1	4	3	1	1	3	2
Micarea myriocarpa	2	1	1	0	1	1	2	2	1	1	2	2
M. nitschkeana	2	0	0	0	1	1	2	3	1	1	2	2
M. peliocarpa	2	0	0	0	1	1	4	3	1	1	3	2
M. prasina agg.	1	1	1	0	1	1	–	–	1	1	3	1
M. sylvicola	2	0	0	0	1	1	1	1	1	1	2	2
M. synotheoides	2	1	1	0	1	1	4	3	1	1	2	2
M. turfosa	2	0	0	0	1	1	4	2	1	1	1	2
Microcalicium arenarium	2	0	0	0	1	0	2	2	1	–	2	2
Miriquidica deusta	2	0	0	0	1	0	1	1	1	1	1	2
M. leucophaea	2	0	0	0	1	0	1	1	1	1	1	2
Mycobilimbia carneoalbida	2	0	0	0	1	0	4	3	1	1	2	2
M. epixanthoides	1	1	1	0	0	0	–	–	1	1	2	2
M. hypnorum	2	0	0	0	1	0	1	3	1	1	3	2
M. sabuletorum	2	0	0	0	1	0	4	3	1	1	3	1
M. sanguineoatra	2	0	0	0	1	0	2	3	1	1	2	2
Mycoblastus alpinus	1	1	1	0	0	0	–	–	1	1	2	2
M. caesius	1	1	1	0	0	0	–	–	1	1	2	2
M. fucatus	1	1	1	0	0	0	–	–	1	1	2	2
M. sanguinarius	2	1	1	0	1	0	3	1	1	1	3	2
Nephroma laevigatum	na	1	0	1	1	1	4	3	3	3	1	2
N. parile	1	1	1	0	1	1	–	–	3	3	2	2
Normandina pulchella	1	1	1	0	0	0	–	–	1	1	2	2
Ochrolechia alboflavescens	1	1	1	0	0	0	–	–	1	1	1	2
O. androgyna agg.	1	1	1	0	0	0	–	–	1	1	2	2
O. arborea	1	1	1	0	0	0	–	–	1	1	1	1
O. microstictoides	1	1	1	0	0	0	–	–	1	1	1	2
O. pallescens	2	0	0	0	1	0	3	1	1	1	1	2
O. parella	2	0	0	0	1	0	3	1	1	1	1	2
O. subviridis	1	1	0	1	0	0	–	–	1	1	1	2

Ochrolechia szatalaensis	2	0	0	0	1	0	3	1	1	1	1	2
O. tartarea	2	0	0	0	1	0	3	1	1	1	2	3
O. turneri	1	1	1	0	0	0	–	–	1	1	2	2
Omphalina umbellifera	1	0	0	0	0	0	–	–	1	1	2	2
Opegrapha atra	2	0	0	0	1	1	2	3	1	2	2	1
O. corticola	1	1	1	0	0	0	–	–	1	2	1	3
O. fumosa	1	1	1	0	0	0	–	–	1	2	1	3
O. ochrocheila	2	0	0	0	1	1	4	3	1	2	2	2
O. rufescens	2	0	0	0	1	1	4	3	1	2	1	1
O. sorediifera	1	1	1	0	1	1	–	–	1	2	1	2
O. varia	2	0	0	0	1	1	4	3	1	2	2	1
O. viridis	2	0	0	0	1	1	4	3	1	2	1	2
O. vulgata	2	0	0	0	1	1	4	3	1	2	1	1
Ophioparma ventosa	2	0	0	0	1	1	4	3	1	3	1	2
Pachyphiale carneola	2	0	0	0	1	1	4	3	1	2	1	2
P. fagicola	2	0	0	0	1	1	4	3	1	2	1	2
Pannaria conoplea	1	1	1	0	0	0	–	–	2	3	2	2
P. ignobilis	2	0	0	0	1	0	3	1	1	3	1	3
P. mediterranea	1	1	1	0	0	0	–	–	1	3	1	3
P. pezizoides	2	0	0	0	1	0	4	1	1	3	3	2
P. rubiginosa	2	0	0	0	1	0	3	1	1	3	2	3
P. sampaiana	1	1	1	0	0	0	–	–	1	3	2	3
Parmelia acetabulum	na	0	0	0	1	1	–	–	2	1	2	2
P. borreri	1	1	1	0	1	1	–	–	2	1	2	2
P. caperata	1	1	1	0	0	0	–	–	2	1	2	2
P. centrifuga	na	0	0	0	0	0	–	–	2	1	1	2
P. conspersa	na	1	0	1	1	1	–	–	2	1	1	2
P. discordans	1	0	0	0	1	1	–	–	2	1	2	2
P. disjuncta	1	1	1	0	0	0	–	–	2	1	1	2
P. elegantula	1	1	0	1	0	0	–	–	2	1	1	2
P. exasperata	2	1	0	1	1	1	4	1	2	1	1	2
P. exasperatula	1	1	0	1	0	0	–	–	2	1	2	1
P. flaventior	1	1	1	0	0	0	–	–	2	1	na	2
P. glabra	2	0	0	0	1	0	1	1	2	1	2	2
P. glabratula	1	1	0	1	0	0	–	–	2	1	2	1
P. hypoleucina	1	1	1	0	0	na	–	–	3	1	1	3
P. laevigata	1	1	1	0	1	1	–	–	3	1	3	2
P. loxodes	1	1	1	0	0	0	–	–	2	1	1	2
P. mougeotii	1	1	1	0	1	1	–	–	2	1	1	2
P. olivacea	2	0	0	0	1	0	1	1	2	1	1	2
P. omphalodes	2	0	0	0	1	1	1	1	2	1	2	2

Parmelia panniformis	1	1	0	1	0	0	–	–	2	1	1	2
P. pastillifera	1	1	0	1	1	1	–	–	2	1	2	2
P. pokornyi	na	1	0	1	0	na	–	–	2	1	1	3
P. protomatrae	na	0	0	0	0	na	–	–	2	1	na	2
P. pulla	2	0	0	0	1	1	1	1	2	1	2	1
P. quercina	2	0	0	0	1	1	1	1	2	1	1	2
P. reticulata	1	1	1	0	1	1	–	–	3	1	2	2
P. revoluta	1	1	1	0	0	0	–	–	2	1	2	2
P. saxatilis	1	1	0	1	1	1	–	–	2	1	2	1
P. somloensis	2	0	0	0	1	0	1	1	2	1	2	2
P. soredians	1	1	1	0	0	0	–	–	2	1	2	2
P. sorediosa	1	1	1	0	0	0	–	–	2	1	1	2
P. stygia	2	0	0	0	1	1	1	1	2	1	1	2
P. subargentifera	1	1	1	0	0	0	–	–	3	1	1	1
P. subaurifera	1	1	1	1	1	1	–	–	2	1	2	2
P. submontana	1	1	1	1	0	0	–	–	3	1	1	2
P. subrudecta	1	1	1	0	1	1	–	–	2	1	2	2
P. sulcata	1	1	1	0	1	1	–	–	2	1	2	1
P. taylorensis	1	1	1	0	1	1	–	–	2	1	2	2
P. tiliacea	1	1	0	1	1	1	–	–	2	1	2	1
P. tinctina	1	1	0	1	1	1	–	–	2	1	1	2
P. verruculifera	1	1	1	0	0	0	–	–	2	1	1	2
Parmeliella triptophylla	1	1	0	1	0	0	–	–	1	2	2	2
Parmeliopsis ambigua	1	1	1	0	1	1	–	–	2	1	2	1
P. hyperopta	1	1	1	0	1	1	–	–	2	1	2	1
Parmotrema chinense	1	1	1	0	0	0	–	–	3	1	2	2
P. crinitum	1	1	1	0	0	0	–	–	3	1	2	2
Peltigera aphthosa	1	0	0	0	0	0	–	–	3	1	3	2
P. canina	1	0	0	0	0	0	–	–	3	3	1	1
P. degenii	1	1	0	1	0	0	–	–	3	3	3	2
P. didactyla	2	1	1	0	1	0	4	3	3	3	1	2
P. elisabethae	2	0	0	0	1	0	4	3	3	3	2	2
P. horizontalis	2	0	0	0	1	0	4	3	3	3	1	2
P. hymenina	2	0	0	0	1	0	4	3	3	3	3	2
P. leucophlebia	1	0	0	0	0	0	–	–	3	1	2	2
P. membranacea	2	0	0	0	1	0	–	–	3	3	3	2
P. neckeri	2	0	0	0	1	0	4	3	3	3	2	2
P. polydactyla	2	0	0	0	1	0	4	3	3	3	2	2
P. praetextata	2	1	0	1	1	0	–	–	3	3	3	1
P. rufescens	2	0	0	0	1	0	–	–	3	3	1	1
Pertusaria albescens	1	1	1	0	0	0	–	–	1	1	3	1

Appendix. *Continued*

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Pertusaria amara	1	1	1	0	0	0	–	–	1	1	2	1
P. amarescens	1	1	1	0	0	0	–	–	1	na	1	3
P. aspergilla	1	1	1	1	0	0	–	–	1	1	na	2
P. coccodes	1	1	0	1	0	0	–	–	1	1	2	2
P. corallina	1	1	0	1	0	0	–	–	1	1	2	2
P. coronata	1	1	0	1	0	0	–	–	1	1	1	2
P. excludens	1	1	1	0	0	0	–	–	1	1	1	2
P. ficorum	2	0	0	0	1	0	3	1	1	1	1	3
P. flavida	1	1	1	0	0	0	–	–	1	1	1	2
P. hemisphaerica	1	1	1	0	0	0	–	–	1	1	1	2
P. heterochroa	2	0	0	0	1	0	4	1	1	1	1	2
P. hymenea	2	0	0	0	1	1	3	1	1	1	2	2
P. lactea	1	1	1	0	1	1	–	–	1	1	1	2
P. leioplaca	2	0	0	0	1	1	3	1	1	1	1	2
P. leucosora	na	1	1	0	0	0	na	na	1	1	1	3
P. leucostoma	2	1	1	0	1	0	3	1	1	1	1	3
P. multipuncta	2	1	1	0	1	0	4	1	1	1	2	2
P. ophthalmiza	2	1	1	0	1	0	3	1	1	1	2	2
P. pertusa	2	0	0	0	1	1	4	1	1	1	2	2
P. pseudocorallina	1	1	0	1	0	0	–	–	1	1	1	2
P. pupillaris	1	1	1	0	0	0	–	–	1	1	1	2
P. pustulata	2	0	0	0	1	0	4	1	1	1	1	2
Petractis clausa	2	0	0	0	1	0	4	3	1	2	1	2
Phaeographis dendritica	2	0	0	0	1	0	4	3	1	2	1	3
Phaeographis lyellii	2	0	0	0	1	1	4	3	1	2	1	3
Phaeophyscia ciliata	2	0	0	0	1	0	3	2	2	1	1	2
P. endophoenicea	1	1	1	0	1	1	–	–	2	1	2	1
P. nigricans	1	1	1	1	1	1	–	–	2	1	2	1
P. orbicularis	na	1	1	0	1	1	–	–	2	1	2	1
Phlyctis agelaea	2	0	0	0	1	0	4	4	1	1	2	2
P. argena	1	1	1	0	0	0	–	–	1	1	2	1
Phyllopsora rosei	1	1	0	1	0	0	2	1	1	1	2	3
Physcia adscendens	1	1	1	0	0	0	–	–	2	1	2	1
P. aipolia	2	0	0	0	1	1	3	2	2	1	2	1
P. caesia	1	1	1	0	1	1	–	–	2	1	2	1
P. dubia	1	1	1	0	1	1	–	–	2	1	2	1
P. semipinnata	2	0	0	0	1	1	3	2	3	1	1	2
P. stellaris	2	0	0	0	1	1	3	2	2	1	2	1
P. tenella	1	1	1	0	1	1	–	–	3	1	2	1
P. tribacia	1	1	1	0	1	1	–	–	2	1	2	2
P. tribacioides	1	1	1	0	0	0	–	–	2	1	2	3
Physconia distorta	2	0	0	0	1	1	3	1	2	1	2	1
P. enteroxantha	1	1	1	0	1	1	–	–	2	1	2	2
P. grisea	1	1	1	0	1	1	–	–	2	1	2	2
P. perisidiosa	1	1	1	0	1	1	–	–	2	1	2	2
P. subpulverulenta	2	0	0	0	1	1	na	2	2	1	1	2
P. venusta	2	0	0	0	1	1	na	2	2	1	2	2
Placopsis gelida s.l.	1	1	1	0	0	0	–	–	1	1	1	2
Placopyrenium buceckii	2	0	0	0	1	1	1	1	2	1	1	3
Placynthiella dasaea	1	1	0	1	0	0	–	–	1	1	1	2
P. icmalea	2	1	0	1	1	0	–	–	1	1	3	1
P. uliginosa	2	1	0	1	1	0	1	1	1	1	2	1
Placynthium nigrum	2	1	0	1	1	0	2	3	1	–	1	2
Platismatia glauca	1	1	1	1	0	0	–	–	3	1	2	1
Polyblastia albida	2	0	0	0	1	0	3	4	1	1	1	2
P. cruenta	2	0	0	0	1	0	4	4	1	1	1	2
P. cupularis	2	0	0	0	1	0	3	4	1	1	1	2
P. sepulta	2	0	0	0	1	0	4	4	1	1	1	2

Species												
Polyblastia theleodes	2	0	0	0	1	0	3	4	1	1	1	2
Polychidium muscicola	1	0	0	0	1	1	–	–	4	3	2	2
Polysporina lapponica	2	0	0	0	1	0	1	1	1	1	2	2
P. simplex	2	0	0	0	1	0	2	1	1	1	1	1
Porina aenea	2	0	0	0	1	1	2	3	1	2	1	2
P. chlorotica	2	0	0	0	1	1	4	3	1	2	2	2
P. guentheri	2	0	0	0	1	1	4	3	1	2	1	2
P. lectissima	2	0	0	0	1	1	4	3	1	2	2	2
P. leptalea	2	0	0	0	1	1	4	3	1	2	2	2
P. linearis	2	0	0	0	1	1	4	3	1	2	1	2
Porpidia albocaerulescens	2	0	0	0	1	0	3	1	1	1	1	2
P. cinereoatra	2	0	0	0	1	0	1	1	1	1	1	2
P. crustulata	2	0	0	0	1	0	1	1	1	1	2	1
P. macrocarpa	2	0	0	0	1	0	3	1	1	1	2	1
P. musiva	2	0	0	0	1	0	3	1	1	1	1	2
P. soredizodes	1	1	1	0	0	0	–	–	1	1	2	2
P. speirea	2	0	0	0	1	0	1	1	1	1	1	3
P. superba	2	0	0	0	1	0	3	1	1	1	1	3
P. tuberculosa	1	1	1	0	0	0	–	–	1	1	2	2
Protoblastenia incrustans	2	0	0	0	1	0	1	1	1	1	1	2
P. rupestris	2	0	0	0	1	0	1	1	1	1	2	2
Protoparmelia badia	2	0	0	0	1	1	2	1	1	1	1	2
P. hypotremella	1	1	1	0	0	0	–	–	1	1	1	3
Pseudevernia furfuracea	1	1	0	1	0	0	–	–	4	1	2	1
Psilolechia lucida	2	1	1	0	1	0	2	1	1	1	2	2
Pyrenula chlorospila	2	0	0	0	1	0	3	3	1	2	1	3
P. laevigata	2	0	0	0	1	1	3	3	1	2	1	2
P. macrospora	2	0	0	0	1	0	4	3	1	2	1	3
P. nitida	2	0	0	0	1	0	4	3	1	2	1	2
Pyrrhospora lusitanica	2	0	0	0	1	0	2	1	1	1	1	3
P. quernea	1	1	1	0	0	0	–	–	1	1	2	2
Racodium rupestre	1	1	0	1	0	0	–	–	1	2	1	2
Ramalina calicaris	2	0	0	0	1	0	1	2	4	1	1	2
R. canariensis	1	0	0	0	0	0	–	–	4	1	2	3
R. duriaei	1	1	1	0	0	0	–	–	4	1	2	3
R. farinacea	1	1	1	0	0	0	–	–	4	1	2	1
R. fastigiata	2	0	0	0	1	0	1	2	4	1	2	2
R. fraxinea	2	0	0	0	1	0	1	2	4	1	1	2
R. implectens	1	0	0	0	0	0	–	–	4	1	1	3
R. obtusata	1	1	1	0	0	0	–	–	4	1	2	2
R. pollinaria	1	1	1	0	0	0	–	–	4	1	2	1

Species												
Ramalina pusilla	1	0	0	0	0	0	–	–	4	1	2	3
Ramonia interjecta	2	0	0	0	1	0	4	na	1	1	1	3
Reichlingia leopoldii	1	0	0	0	1	1	–	–	1	2	1	3
Rhizocarpon constrictum	2	0	0	0	1	0	3	4	1	1	1	2
R. eupetraeum	2	0	0	0	1	0	3	2	1	1	1	2
R. geminatum	2	0	0	0	1	0	3	4	1	1	1	2
R. geographicum	2	0	0	0	1	0	3	4	1	1	1	1
R. hochstetteri	2	0	0	0	1	0	3	2	1	1	1	2
R. lavatum	2	0	0	0	1	0	3	4	1	1	1	2
R. lecanorinum	2	0	0	0	1	0	3	4	1	1	1	2
R. macrosporum	2	0	0	0	1	0	3	4	1	1	1	2
R. obscuratum	2	0	0	0	1	0	3	4	1	1	1	1
R. oederi	2	1	1	0	1	0	2	3	1	1	1	2
R. petraeum	2	0	0	0	1	0	4	4	1	1	1	2
R. polycarpum	2	0	0	0	1	0	3	2	1	1	1	1
R. tetrasporum	2	0	0	0	1	0	3	4	1	1	1	2
R. umbilicatum	2	0	0	0	1	0	3	4	1	1	1	2
R. viridiatrum	2	0	0	0	1	0	3	4	1	1	1	2
Rimularia fusca	na	na	na	na	0	0	–	–	1	1	na	3
R. intercedens	1	1	0	1	0	0	–	–	1	1	1	2
Rinodina archaea	2	0	0	0	1	0	3	2	1	1	2	2
R. aspera	2	0	0	0	1	0	3	2	1	1	1	3
R. atrocinerea	2	0	0	0	1	1	3	2	1	1	1	2
R. bischoffii	2	0	0	0	1	0	3	2	1	1	1	2
R. capensis	2	0	0	0	1	0	3	2	1	1	1	2
R. colobina	2	0	0	0	1	0	3	2	1	1	1	2
R. confragosa	2	0	0	0	1	0	3	2	1	1	1	2
R. dubyana	2	0	0	0	1	0	1	2	1	1	2	2
R. efflorescens	1	1	1	0	0	0	–	–	1	1	1	2
R. exigua	2	0	0	0	1	0	3	2	1	1	1	2
R. gennarii	2	0	0	0	1	1	3	2	1	1	1	2
R. immersa	2	0	0	0	1	0	3	2	1	1	1	2
R. orculata	2	0	0	0	1	1	1	2	1	1	1	2
R. oxydata	2	0	0	0	1	0	3	2	1	1	1	2
R. polysporoides	2	0	0	0	1	0	1	2	1	1	1	2
R. pyrina	2	0	0	0	1	0	1	2	1	1	1	2
R. sophodes	2	0	0	0	1	0	3	2	1	1	1	2
R. sp. 1	2	0	0	0	1	1	3	2	1	1	1	na
R. subglaucescens	2	0	0	0	1	0	3	2	1	1	2	2
Ropalospora viridis	1	1	1	0	0	0	–	–	1	1	1	1
Sagiolechia protuberans	2	0	0	0	1	0	4	3	1	2	1	3

Appendix. *Continued*

Species	Fertility	Sym. prop.	Soredia	Isidia	Fung. prop.	Conidia	Spore length & shape	Spore septation	Growth form	Photobiont	Sub. specialization	Rarity
Sarcogyne regularis	2	0	0	0	1	0	1	1	1	1	2	2
Sarcosagium campestre	2	0	0	0	1	0	2	1	1	1	3	2
Schaereria cinereorufa	2	0	0	0	1	1	1	1	1	1	2	2
S. fuscocinerea	2	0	0	0	1	1	2	1	1	1	1	2
Schismatomma cretaceum	1	1	1	0	0	0	–	–	1	2	1	3
S. decolorans	1	1	1	0	0	0	–	–	1	2	1	2
S. pericleum	1	1	1	0	0	0	–	–	1	2	2	2
S. picconianum	2	0	0	0	1	0	4	3	1	2	1	2
Scoliosporum chlorococcum	2	1	1	0	1	0	4	3	1	1	1	1
S. gallurae	2	1	1	0	1	0	4	3	1	1	1	2
S. sarothamni	2	1	1	0	1	0	4	3	1	1	1	1
S. umbrinum	2	1	1	0	1	0	4	3	1	1	2	1
Sphaerophorus globosus	1	0	0	0	0	0	–	–	1	1	3	2
Staurothele frustulenta	2	0	0	0	1	0	3	4	1	1	1	2
S. guestphalica	2	0	0	0	1	0	4	4	1	1	1	2
S. rupifraga	2	0	0	0	1	0	3	4	1	1	1	2
Stereocaulon paschale	1	1	0	1	0	0	–	–	4	1	2	2
S. saxatile	1	1	0	1	0	0	–	–	1	1	2	2
Strangospora ochrophora	2	0	0	0	1	1	1	1	1	1	2	2
S. pinicola	2	0	0	0	1	1	1	1	1	1	2	2
Strigula stigmatella	2	0	0	0	1	1	4	3	1	2	2	2
S. taylorii	2	0	0	0	1	1	4	2	1	2	1	2
Tephromela atra	2	0	0	0	1	1	1	1	1	2	2	2
T. pertusarioides	1	1	1	0	0	0	–	–	1	1	1	2
Thelidium decipiens	2	0	0	0	1	0	3	2	1	1	1	2
T. minutulum	2	0	0	0	1	0	3	2	1	1	2	2
T. olivaceum	2	0	0	0	1	0	3	2	1	1	1	2
T. papulare	2	0	0	0	1	0	4	3	1	1	1	2
T. pyrenophorum	2	0	0	0	1	0	4	2	1	1	1	2
Thelocarpon laureri	2	0	0	0	1	0	1	1	1	1	2	2
Thelotrema lepadinum	2	0	0	0	1	0	4	4	1	2	1	2
Toninia sedifolia	na	0	0	0	0	0	–	–	1	1	2	2
T. taurica	na	0	0	0	0	0	–	–	2	1	1	2
Trapelia coarctata	2	0	0	0	1	0	3	1	1	1	2	1
T. corticola	1	1	1	0	0	0	–	–	1	1	2	2
T. involuta	2	0	0	0	1	0	3	1	1	1	2	1
T. mooreana	2	0	0	0	1	1	3	1	1	1	2	2
T. obtegens	1	1	1	0	0	0	–	–	1	1	2	1
T. placodioides	1	1	1	0	0	0	–	–	1	1	1	1
Trapeliopsis flexuosa	na	1	1	0	0	0	–	–	1	1	2	1
T. gelatinosa	2	1	1	0	1	0	1	1	1	1	1	2
T. granulosa	2	1	1	0	1	0	1	1	1	1	1	2
T. pseudogranulosa	1	1	1	0	0	0	–	–	1	1	2	2
Tremolecia atrata	2	0	0	0	1	0	1	1	1	1	1	1
Tylothallia biformigera	2	0	0	0	1	0	2	2	1	1	1	3
Umbilicaria cylindrica	2	0	0	0	1	0	1	1	3	1	1	2
U. deusta	1	1	0	1	0	0	–	–	3	1	1	2
U. grisea	1	1	1	0	0	0	–	–	3	1	1	2
U. polyphylla	1	0	0	0	1	1	–	–	3	1	1	2
U. polyrrhiza	1	0	0	0	1	1	–	–	3	1	1	2
Usnea ceratina	1	1	1	1	0	0	–	–	5	1	1	2
U. cornuta	1	1	1	1	0	0	–	–	5	1	2	3
U. esperantiana	1	1	1	1	0	0	–	–	5	1	1	3
U. filipendula	1	1	0	1	0	0	–	–	5	1	2	2
U. fulvoreagens	1	1	1	0	0	0	–	–	5	1	1	2
U. glabrata	1	1	1	1	0	0	–	–	5	1	1	2
U. hirta	1	1	0	1	0	0	–	–	5	1	2	2
U. lapponica	1	1	1	0	0	0	–	–	5	1	na	2

Usnea prostrata	1	1	0	1	0	0	–	–	5	1	na	2	*Verrucaria lecideoides*	2	0	0	0	1	0	3	1	1	1	1	2
U. rigida	2	0	0	0	1	0	na	1	5	1	na	2	*V. macrostoma*	2	0	0	0	1	0	3	1	1	1	1	1
U. rubicunda	1	1	1	1	0	0	–	–	5	1	1	3	*V. maculiformis*	2	0	0	0	1	0	3	1	1	1	1	2
U. subfloridana	1	1	0	1	0	0	–	–	5	1	1	2	*V. muralis*	2	0	0	0	1	0	3	1	1	1	1	1
U. wasmuthii	1	1	1	1	0	0	–	–	5	1	1	2	*V. nigrescens*	2	0	0	0	1	0	3	1	1	1	1	1
Verrucaria amylacea	2	0	0	0	1	0	3	1	1	1	1	2	*V. viridula*	2	0	0	0	1	0	3	1	1	1	1	2
V. aquatilis	2	0	0	0	1	0	1	1	1	1	1	2	*Vulpicida pinastri*	1	1	1	0	1	1	–	–	3	1	2	2
V. caerulea	2	0	0	0	1	0	4	1	1	1	1	2	*Xanthoria calcicola*	2	1	0	1	1	1	na	2	3	1	2	1
V. concinna	2	0	0	0	1	0	3	1	1	1	1	2	*X. candelaria* agg.	1	1	1	0	0	0	–	–	3	1	2	2
V. dolosa	2	0	0	0	1	0	2	1	1	1	1	2	*X. elegans*	2	0	0	0	1	0	1	2	2	1	1	1
V. dufourii	2	0	0	0	1	0	3	1	1	1	1	2	*X. parietina*	2	0	0	0	1	0	1	2	2	1	2	1
V. foveolata	2	0	0	0	1	0	3	1	1	1	1	2	*X. polycarpa*	2	0	0	0	1	0	1	2	3	1	2	1
V. fusconigrescens	2	0	0	0	1	0	3	1	1	1	1	2	*Xylographa vitiligo*	na	1	1	0	1	1	–	–	1	1	1	2
V. glaucina	2	0	0	0	1	0	1	1	1	1	1	2	*Zamenhofia hibernica*	1	1	0	1	0	0	–	–	1	2	2	3
V. hochstetteri	2	0	0	0	1	0	3	1	1	1	1	2													