

Exploring patterns of commonness and rarity in lichens: a case study from Italy (Southern Europe)

Pier Luigi NIMIS, Stefano MARTELLOS, Daniel SPITALE and
Juri NASCIMBENE

Abstract: This paper, based on data from the latest checklist of Italy, analyzes the distribution patterns of rare and common lichen species within biogeographically homogeneous versus heterogeneous areas of Italy, and the relationships with some main drivers of rarity and commonness. The following data were used: 1) commonness-rarity values of 2565 species in nine ecoregions; 2) frequency of 353 nationally rare and 387 nationally common species in 21 administrative regions. The following functional and ecological traits were considered: growth form, photobiont(s), type of reproduction, substrata, bioclimatic range, ecological indicator values for aridity and eutrophication, and poleophoby. Within each ecoregion, rare species by far outweigh common species but about one third of these are common in other ecoregions. At the level of regional floras, rarity is significantly associated with epiphytic substrata, non-trebouxioid photobionts and high air humidity, while commonness is associated with saxicolous substrata, trebouxioid photobionts and eutrophication. Rarity seems to mainly depend on two factors, bioclimate (many rare species are outside the limit of their bioclimatic optima) and reduced availability of suitable habitats (e.g. old-growth forests), while commonness is mainly related to disturbance (eutrophication, creation of drier habitats). Most of the nationally rare lichens belong to an oceanic-suboceanic element with tropical affinities or to a small set of continental species with their optima in the dry steppe biome, which suggests that many rare species can persist in microrefugia, that is sites with microclimates that support small populations of species beyond the boundaries of the climatic limits of their main distributions.

Key words: bioclimate, disturbance, eutrophication, functional traits, microrefugia, photobionts

Accepted for publication 5 September 2017

Introduction

Commonness and rarity of species have been studied by biologists for decades (e.g. Preston 1948; Rabinowitz 1981), so that Kelly *et al.* (1996) have defined ecology as the study of commonness and rarity among and within species (Arellano *et al.* 2015). Both concepts are intrinsically “fuzzy” since they can be operationally expressed at different scales and along different ecological dimensions (Hanski 1982; Brown 1984; Rabinowitz *et al.* 1986; Pitman *et al.* 2001; Murray *et al.* 2002;

Kristiansen *et al.* 2009). For example, the abundance of a species in a sample, its frequency across a given region and the extent of its geographical distribution are three definitions of commonness/rarity at three different spatial scales (Gaston 1994). Species can also be ranked along other ecological dimensions, such as the variety of habitats, to distinguish different classes of commonness and rarity (Rabinowitz 1981; Rabinowitz *et al.* 1986).

In plants, commonness and rarity have been frequently related to species traits linked to environmental factors (Webb *et al.* 2010), providing insights into ecological processes which determine species distribution along environmental gradients (Diaz & Cabido 2001). For example, plant size was often correlated with commonness at different scales, from large scales across regions and continents (Ruokolainen & Vormisto 2000; Davidar *et al.* 2008; Kristiansen *et al.* 2009) to

P. L. Nimis and S. Martellos: Department of Life Sciences, University of Trieste, Via Giorgieri 10, I 34127 Trieste, Italy. Email: nimis@units.it

D. Spitale: Museum of Natural Sciences of South Tyrol, Via Bottai 1, I-39100 Bolzano/Bozen, Italy.

J. Nascimbene: Department of Biological, Geological and Environmental Sciences, University of Bologna, Via Imerio 42, I-40126 Bologna, Italy.

local scales (Nathan & Muller-Landau 2000; Moles & Westoby 2004; Wright *et al.* 2007; Kristiansen *et al.* 2009). The growth form of species could also influence their commonness and rarity patterns, particularly across different environments (e.g. Gentry 1991; Letcher & Chazdon 2012).

A well-known pattern is that most species are naturally rare, with only a few being common (Gaston 2010). However, the role of ecological processes shaping this pattern remains controversial: we still lack a detailed understanding of the mechanisms that produce this phenomenon (Roque *et al.* 2016), an issue that was listed among the 100 fundamental questions of ecology by Sutherland *et al.* (2013).

Understanding patterns of commonness and rarity is also important for conservation (Gaston 2010, 2012) because rarity is associated with extinction risk (Rabinowitz *et al.* 1986). In view of the dramatic decline of species due to human activities, a better understanding of how ecological traits vary among species in relation to commonness and rarity can provide a scientific basis for conservation strategies (Kunin & Gaston 1997; Arellano *et al.* 2015). Particularly relevant is the analysis of traits that allow species to escape rarity (Aizen & Patterson 1990; Murray & Westoby 2000), or those that are associated with persistence at low abundance (Kunin & Shmida 1997; Walck *et al.* 1999).

In contrast with the large number of studies devoted to the analysis of commonness and rarity in plants and animals, only a small number of papers deal specifically with this topic in lichenized fungi. On the one hand, we have abundant data on the relative occurrences of species in certain areas, such as those derived from mapping projects (e.g. see Seaward 1988, 1995; Wirth & Oberhollenzer 1990; Aptroot *et al.* 2004) or from field surveys at different geographical scales (e.g. Dietrich *et al.* 2000; Bielczyk *et al.* 2002; Edwards *et al.* 2005). On the other hand, only a small number of studies have looked for quantitative correlations between commonness/rarity and morpho-ecological traits of lichens, mostly at community level or at relatively small spatial scales (e.g. McCune *et al.* 1997; Ihlen *et al.* 2001; Edwards *et al.* 2004; Nascimbene *et al.*

2006, 2007, 2013; Allen & Lendemer 2016; Keim *et al.* 2017). This may create the risk of omitting adequate protection for a diverse and ecologically important group of organisms that contributes to the functioning of terrestrial ecosystems (Elbert *et al.* 2012; Asplund & Wardle 2017).

The starting point for the present paper was the publication of the new catalogue of the lichens of Italy by Nimis (2016), in which estimates of commonness/rarity in nine bioclimatic subdivisions of the country (ecoregions) were proposed for 2704 infrageneric taxa (2565 of which are lichenized), together with several morphological, ecological and distributional traits. The information provided by Nimis (2016) was swiftly transformed into a database where all of these parameters can be searched online (Martellos 2012; Nimis & Martellos 2017). The availability of such a wealth of data led us to carry out a study on the main traits and factors that might be related to the commonness and rarity of lichens at the level of a rich, varied, well-investigated and updated national flora, encompassing several bioclimatic regions.

The main questions we intended to answer were: 1) how consistent are patterns of commonness/rarity across different, biogeographically homogeneous versus heterogeneous regions and 2) are commonness and rarity associated with particular biological or ecological characteristics?

Data Sources and Methods

Data source

Data were retrieved from the latest catalogue of the lichens of Italy by Nimis (2016), covering the 2565 lichenized taxa which are known to occur in the country.

For each taxon, the following information was considered:

- (a) *Regional distribution.* Presence-absence in 21 administrative regions (Fig. 1): **VG**, Venezia Giulia; **Frl**, Friuli; **Ven**, Veneto; **TAA**, Trentino-Alto Adige; **Lomb**, Lombardia; **Piem**, Piemonte; **VA**, Valle d'Aosta; **Emil**, Emilia-Romagna; **Lig**, Liguria; **Tosc**, Toscana; **Marc**, Marche; **Umb**, Umbria; **Laz**, Lazio; **Abr**, Abruzzo; **Mol**, Molise; **Sar**, Sardegna; **Camp**, Campania; **Pugl**, Puglia; **Bas**, Basilicata; **Cal**, Calabria; **Si**, Sicilia. In addition, the

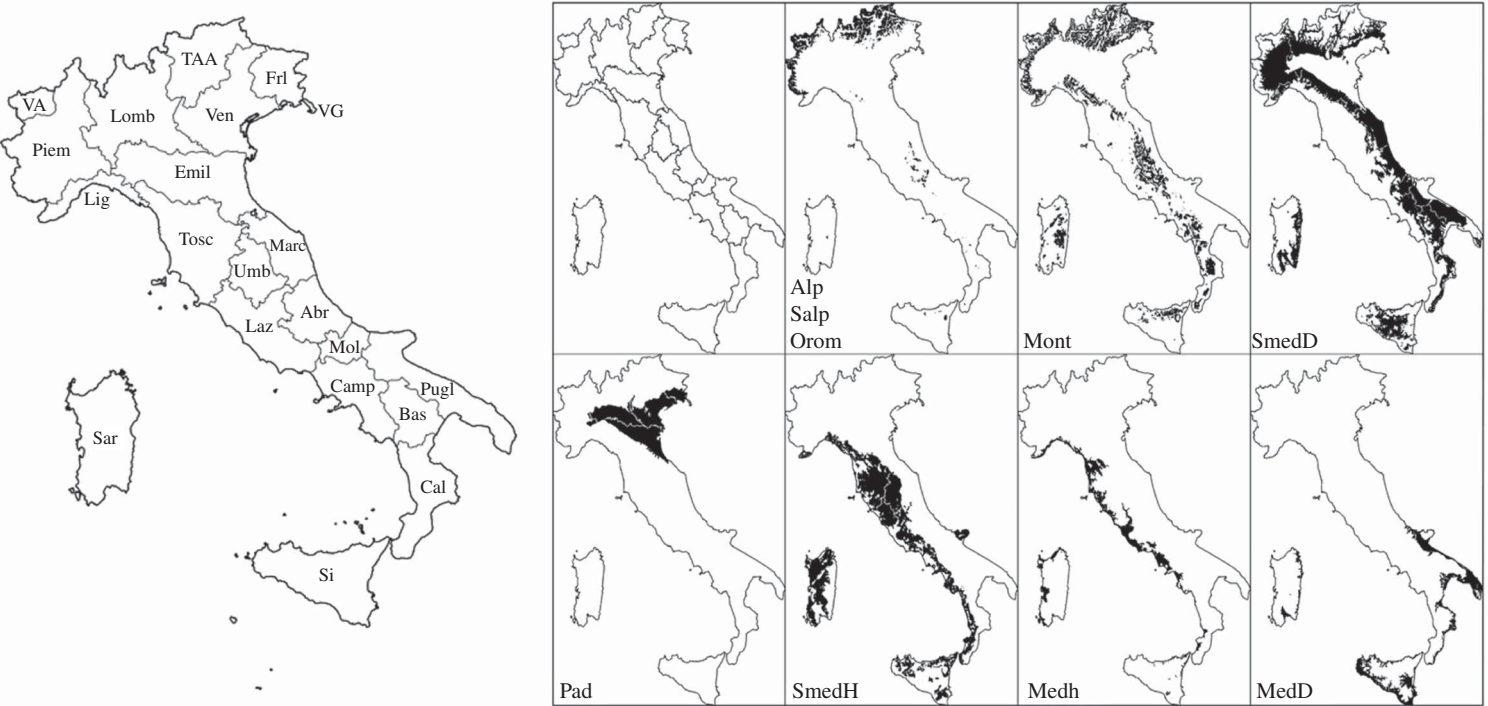


FIG.1. The 21 administrative regions of Italy (left) and the nine ecoregions used in this study. Regions and ecoregions are abbreviated as in Data Sources and Methods.

regional distribution was collapsed into 3 broad macroregions: Northern Italy, Adriatic peninsular Italy and Tyrrhenian peninsular Italy plus islands.

- (b) *Distribution in nine ecoregions.* Nine ecoregions were recognized by Nimis (2016) (Fig. 1) based on several thematic maps (elevation, precipitation, vegetation etc.) and taking into account the bioclimatic difference between the Tyrrhenian (humid) and Adriatic (dry) parts of the Italian Peninsula, which influences lichen distribution in Italy (Nimis & Tretiach 1995, 1999, 2004). The nine ecoregions (Fig. 1) are: **Alp**, Alpine (above treeline in the Alps and in Abruzzo); **Salp**, subalpine (near treeline in the Alps, oroboreal belt); **Orom**, oro-Mediterranean (above treeline outside the Alps except Abruzzo); **Mont**, montane (beech forest belt); **SmedD**, dry sub-Mediterranean (deciduous oak belt, excluding SmedH); **Pad**, padanian (the plains of the North, characterized by high urbanization, air pollution and almost total deforestation); **SmedH**, humid sub-Mediterranean (as SmedD but restricted to areas with a warm-humid climate, mostly Tyrrhenian); **MedH**, humid Mediterranean (mostly Tyrrhenian); **MedD**, dry Mediterranean.
- (c) *Commonness-rarity in each of the nine ecoregions.* This was calculated by Nimis (2016) on the basis of three main criteria: 1) number of specimens in the TSB lichen herbarium (% of the total for each ecoregion), 2) number of citations in the literature and 3) an expert assessment used in particular cases (e.g. that of recently-described taxa for which few literature records are available or to adjust the over-representation of studies on epiphytic lichens in urban/industrial areas). Commonness-rarity was expressed by Nimis (2016) on an 8-class scale, as follows: **er**, extremely rare; **vr**, very rare; **r**, rare; **rr**, rather rare; **rc**, rather common; **c**, common; **vc**, very common; **ec**, extremely common. The “er” class was adopted for lichens found less than five times and/or not found recently, excluding recently described species and taxonomically very poorly known taxa. Percentiles were used to delimit the other classes; for further details see Nimis & Martellos (2003).
- (d) *Growth form.* **Cr**, crustose; **Fol**, foliose and squamulose; **Fr**, fruticose.
- (e) *Photobiont.* **Ch**, Trebouxioid algae; **Tr**, Trentepohlioid algae; **Cy**, Cyanobacteria.
- (f) *Reproductive strategy.* **S**, mainly sexual; **Veg**, mainly asexual, by soredia or isidia.
- (g) *Substratum.* **Epiph**, bark and lignum; **Sax**, rocks; **Terr**, soil, terricolous mosses, and plant debris.
- (h) *Ecological indicator values.* These are “expert assessments” that are qualitative expressions of the ecological range of species with respect to different factors (e.g. Nimis & Martellos 2001; Wirth 2001, 2010). A 5-class ordinal scale was proposed by Nimis (2016) which was specific for each factor and each species. On testing, this scale was found to have high predictability (Nimis & Martellos 2001). The following two indicator values were considered in this study. *Xerophytism (aridity - X)*: 1, hydro- and hygrophytic, in

aquatic situations or in sites with frequent fog; 2, significantly hygrophytic, intermediate between 1 and 3; 3, mesophytic; 4, xerophytic, but absent from extremely arid stands; 5, very xerophytic. *Eutrophication (E* - including deposits of dust and nitrogen compounds): 1, not resistant to eutrophication; 2, resistant to very weak eutrophication; 3, resistant to weak eutrophication; 4, occurring in moderately eutrophicated situations; 5, occurring in highly eutrophicated situations.

- (i) *Bioclimatic range.* **oc**, restricted to humid-warm, oceanic areas; **suboc**, most common in areas with a humid-warm, suboceanic climate (e.g. most of Western Europe); **subc**, subcontinental, most common in areas with a dry-subcontinental climate (e.g. the Eurasiatic steppe biome).
- (j) *Poleotolerance.* This value represents the tendency of a lichen to occur in areas with different degrees of human disturbance. It is expressed by the following 4 classes: 3, species also occurring in heavily disturbed situations (e.g. large towns); 2, species also occurring in moderately disturbed situations (rural areas, small settlements etc.); 1, species mostly occurring in natural or semi-natural habitats; 0, species which occur exclusively on old trees in ancient, undisturbed forests. Contrary to the other values, this has been assigned only to epiphytic species, since it is useful to point out indicators of long ecological continuity in old-growth forests.

The analysis was carried out considering:

- 1) Commonness/rarity values of all species in each of the nine ecoregions (2565 taxa).
- 2) Two contrasting groups of lichens: a) “nationally rare” lichens (i.e. those having a value no higher than “er” in any of the nine ecoregions, for a total of 353 infrageneric taxa); b) “nationally common” lichens (i.e. those having a value ranging from “c” to “ec” in at least one ecoregion, for a total of 387 infrageneric taxa).

Statistical analyses

Four datasets were used in the statistical analyses. First, the frequency distribution of the eight classes of commonness-rarity within the ecoregions (% on the total flora of each ecoregion), to explore patterns within bioclimatically homogeneous areas. Second, the incidence of biological traits (growth form, photobiont type, reproductive strategy) and ecological traits (substrata, ecological indicator values for xerophytism and eutrophication, bioclimatic range) among nationally rare and nationally common species was analysed using contingency tables. The relationship between commonness/rarity and traits was tested with the χ^2 test. When significant differences were found for traits with multiple states, an additional pairwise comparison was carried out and the significance level was determined taking into account the Bonferroni correction. Lastly, presence-absence of nationally rare and nationally common species in the 21 administrative regions was used for

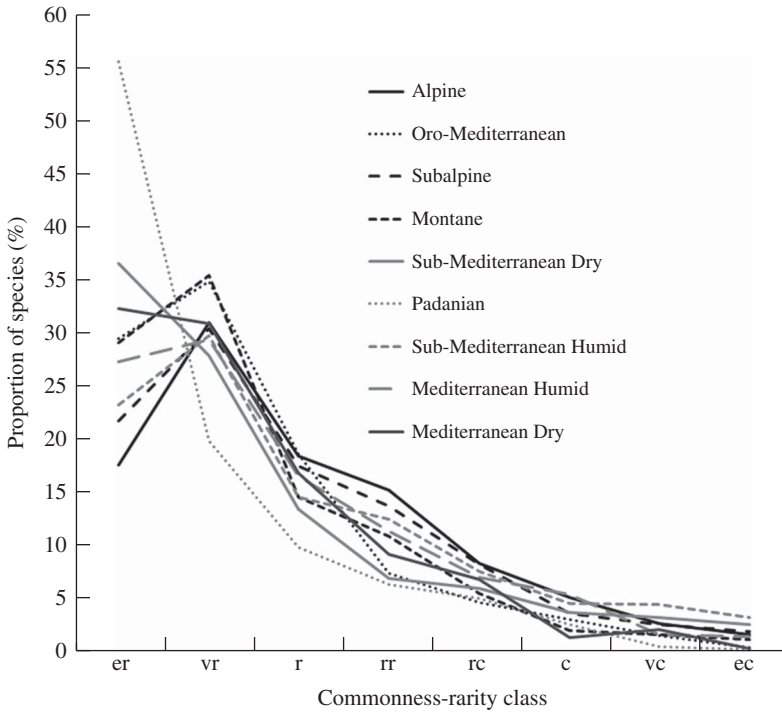


FIG. 2. Proportion of species in the 8 commonness-rarity classes in each of the 9 ecoregions expressed as a percentage of all species found in that region. Key to commonness-rarity classes: er, extremely rare; vr, very rare; r, rare; rr, rather rare; rc, rather common; c, common; vc, very common; ec, extremely common.

datasets 3 and 4 respectively. These two matrices were ordered using Principal Coordinate Analysis (PCoA, also known as metric multidimensional scaling), a technique which maintains the Euclidean representation of the objects (administrative regions). As a distance measure we used Jaccard's index, which is suited to binary data such as presence-absence species matrices (Legendre & Legendre 1998). The importance of three macroregions (Northern, Adriatic and Tyrrhenian peninsular Italy) was tested using Adonis (also known as Permutational Manova; Oksanen *et al.* 2017), a function which analyses and partitions sums of squares of the distance matrix. To inspect the PCoA ordination, we calculated the overall mean distance in the rare and common species, and the mean distance within and between groups. All statistical analyses were performed using R (R Development Core Team 2017).

Results

Commonness/rarity in the nine ecoregions of Italy

In the nine ecoregions, the frequency distribution of the eight commonness/

TABLE 1. Proportion of nationally common and nationally rare species in the nine ecoregions. Total for Italy: rare = 387, common = 353.

	Proportion of all species in each category (%)	
	Common	Rare
Alpine	52.7	11.6
Subalpine	75.9	24.8
Oro-Mediterranean	55.2	3.4
Montane	84.4	46.0
Dry sub-Mediterranean	70.5	23.8
Padanian	48.7	0.0
Humid sub-Mediterranean	70.3	31.5
Humid Mediterranean	62.3	40.6
Dry Mediterranean	53.3	6.5

rarity classes is similar (Fig. 2). Rare species are largely predominant after which there is a progressive, sharp decrease in percentage occurrence, with extremely common

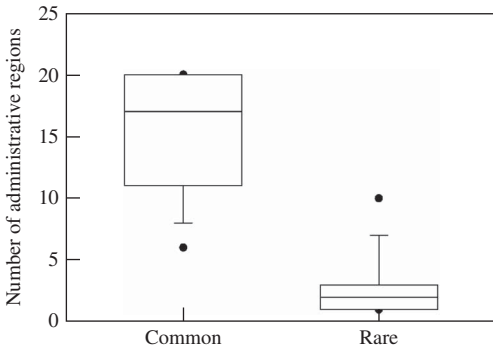


FIG. 3. The distribution of nationally rare versus nationally common species in the 21 regional floras. The bottom and top of the box are the first and third quartiles, while the line within the box is the median. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Outliers (5th and 95th percentiles) are shown as points.

species always being in a minority. Among epiphytic species restricted to old-growth forests (poleotolerance 0), the average percentage of those included in the “er” class (calculated excluding the Alpine and oro-Mediterranean ecoregions which do not host forest vegetation) is even higher (69%). In Fig. 2 the entire lichen biota of each ecoregion is considered, resulting in some species which are rare in a given ecoregion being common in another. The average percentage of “rare” species (from “er” to “rr”) in the ecoregions is 85.7% but around one third of these (29.3%) turn out to be “common” (from “rc” to “ec”) in other ecoregions, sometimes situated a few hundred metres downslope in the mountains.

TABLE 2. Comparison between nationally common and nationally rare lichen species for a range of morphological and ecological traits using χ^2 . For abbreviations see Data and Methods section. A significant χ^2 result was followed by a post-hoc pairwise test using the Bonferroni procedure. * = significant difference; (*) = marginally significant difference.

Traits	Number of species		χ^2	P
	Common	Rare		
Growth form			1.739	0.419
Crustose	232	270		
Foliose and squamulose	85	78		
Fruticose	36	39		
Photobiont			43.60	<0.0001
Trebouxioid alga	317	273		
Trentepohlioid alga (*)	17	31		
Cyanobacterium*	9	59		
Reproduction			3.044	0.081
Mainly asexual, by soredia or isidia	91	77		
Mainly sexual	262	302		
Substratum			51.852	<0.0001
Bark and lignum*	102	213		
Soil, terricolous mosses, and plant debris	61	46		
Rock*	190	128		
Bioclimatic range			109.88	<0.0001
Oc-Suboc	24	170		
Bioclimatic range			13.333	0.0002
Subc	5	25		
Xerophytism			151.08	<0.0001
1-2	26	218		
Eutrophication			24.275	<0.0001
3-5	69	22		
Poleotolerance			105.12	<0.0001
0-1	140	372		

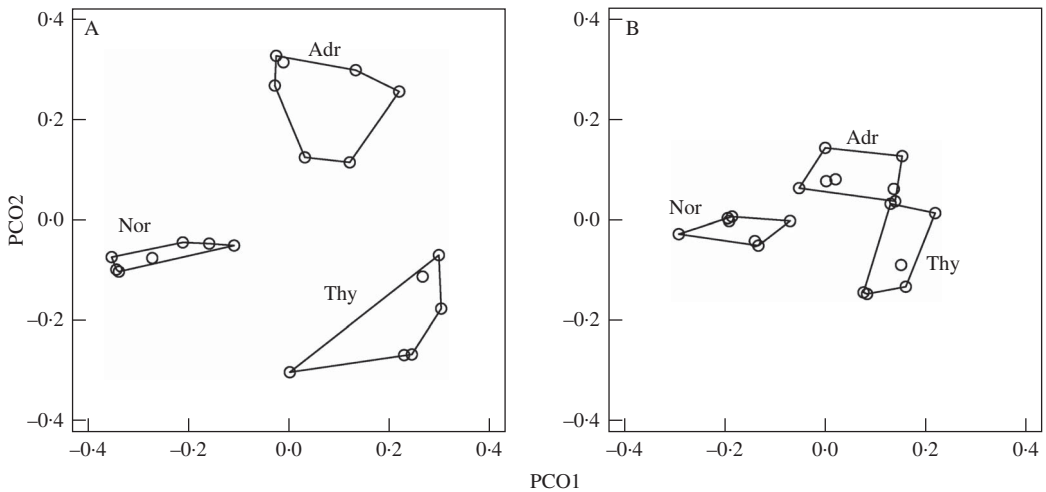


FIG. 4. Ordination diagrams (PCoA analysis) based on the presence/absence of nationally common (A) and rare (B) species in the 21 administrative regions. The regions are grouped in three macro-regions: Northern Italy (Nor), Adriatic peninsular Italy (Adr) and Tyrrhenian peninsular Italy and islands (Thy).

Comparison between nationally rare versus common species in the ecoregions and in the regional floras

Nationally rare species have the highest frequency in the least anthropized and/or more humid ecoregions (Table 1) (montane, subalpine and humid sub-Mediterranean), and the lowest frequency in areas which are the least favourable for lichens (the heavily polluted Padanian Italy and the dry Mediterranean ecoregion). Low frequencies in the oro-Mediterranean belt are probably due to this ecoregion of Italy being the only one that has been poorly explored by lichenologists.

The distribution of nationally rare versus common species in the 21 regional floras is markedly different (Fig. 3). Among common species, *c.* 60% occur in at least 75% of the regions while only 5% of rare species occur in at least 50% of the regions and *c.* 45% of them are known from only a single region. This pattern is also reflected in the significant difference in percentages of nationally rare (5.3 ± 1.8 ; mean \pm SD) and nationally common species (30 ± 6) in the 21 regional floras (*t*-test, $P < 0.001$). The lowest

percentage of rare species (<10%) is found in regions located along the Adriatic side of the Italian Peninsula.

Some biological and ecological traits differ significantly between rare and common species (Table 2). In particular, the type of photobiont is clearly different between these two groups, with a significantly higher frequency of trentepohlioid photobionts among rare species ($P < 0.001$). A similar pattern, even if only marginally significant, occurs for cyanobacterial photobionts ($P = 0.04$ and with the Bonferroni correction $P = 0.017$). Growth forms and reproductive strategies do not differ between rare and common species.

There are also differences in some ecological parameters (Table 2). Epiphytes are more frequent among rare species, and saxicolous lichens among common species. Lichens associated with natural or semi-natural habitats (poleotolerance = 0 and 1, respectively) have a higher proportion of the rarer species. Of the 194 rare epiphytic species, 97 (50%) are restricted to old-growth forests (poleotolerance = 0) while none are found in disturbed habitats (poleotolerance = 2 and 3). Conversely, 62.6% of

the common species occur in disturbed habitats. Nitrophytic lichens have greater representation among common species and hygrophytic lichens among rare species, which is also substantiated by the higher frequency of rare species with an oceanic/sub-oceanic distribution. The small set of species with a subcontinental distribution are also considerably more frequent among rare species.

Results of the PCoA analysis confirm the floristic differences among the three macro-regions in which the 21 administrative regions were grouped: a) Northern Italy, b) Adriatic peninsular Italy, c) Tyrrhenian peninsular Italy and islands (Fig. 4). Differences among macro-regions are supported by the Adonis results, both for rare and common species ($F=2.522$, $P<0.001$ and $F=10.221$, $P<0.001$, respectively). However, the three groups of regions are more scattered in the ordination diagram based on rare species (Fig. 4A; Euclidean distance between groups 0.84) than in that based on common species (Fig. 4B; Euclidean distance between groups 0.27) which indicates, for rare species, a lower number of shared species among macro-regions and a higher turnover in the regional floras.

Discussion

Gaston (2011) described rarity as “the state of having a low abundance and/or a small range size”. The second factor being almost irrelevant for broad-ranging organisms such as lichens, any definition of “rarity” for these organisms must answer the question “abundant where”? The spatial scale can vary from the level of a single biotope to the entire world. In our analysis, we have used two different definitions of “rarity”, reflecting the probability of finding a species a) within bioclimatically homogeneous areas (ecoregions), and b) within bioclimatically heterogeneous administrative regions. Depending on the definition, the results are slightly different. Within a given ecoregion, the observation that most species are naturally

rare and only a small number are common (Gaston 2010) proved to apply also to lichens; the number of rare species by far outweighs that of common species (i.e. the state of being common is itself rare). However, when we enlarge the scale to the entire country (i.e. across different ecoregions), it appears that many of the species which are “rare” in a given ecoregion are “common” in another. For this reason, the number of “rare” species is much lower in the national flora than within bioclimatically homogeneous ecoregions. This suggests that one of the main drivers for the rarity of species within bioclimatically homogeneous areas lies in the bioclimate itself, since several species bound to a different ecoregion survive in small populations within narrow microclimatic niches (Rodríguez *et al.* 2017). This might also be because lichens, as compared to vascular plants for example, have much wider geographical distributions and a very low number of narrow-ranging endemic species, rendering bioclimatic factors, especially air humidity, one of the main drivers of species distribution and abundance within a given area (Marini *et al.* 2011).

The analysis of rarity in the regional floras, encompassing several ecoregions, shows that nationally rare species are associated with epiphytic growth in undisturbed, natural or semi-natural forests, and with some morpho-functional traits such as trentepohlioid or cyanobacterial photobionts. Trentepohlioid photobionts occur in *c.* 10% of the lichens known from Italy, mostly in species growing in shaded and sheltered habitats within old forests (Marini *et al.* 2011) which often have subtropical to tropical affinities (Aptroot & van Herk 2007). Cyanobacterial lichens are an ecologically heterogeneous group comprising *c.* 10% of the Italian lichen flora. In terricolous lichens, Matos *et al.* (2015) found that the type of photobiont was particularly responsive to humidity-aridity gradients, with trentepohlioid algae and cyanobacteria clearly responding in contrasting ways to aridity. In our analysis, however, rare species tended to be associated with epiphytic growth, and cyanobacterial epiphytic lichens (with *Nostoc*) were shown

by Marini *et al.* (2011) to be significantly associated with old-growth forests in rainy areas. Common species, on the contrary, tend to be associated with saxicolous habitats and human disturbance.

There is no difference in reproductive strategy between nationally rare and common species, despite the fact that several extremely common lichens occurring in disturbed habitats reproduce vegetatively. Asexual reproduction is often regarded as a selective advantage as part of the “ruderal” strategy, such as in apomictic higher plants of disturbed habitats (Poelt 1994) where propagation strategy is typical of r-selected species (Rogers 1990). Similarly, some of the lichen flora of urban wastelands can be categorised as stress-tolerant ruderals (Gilbert 1990; Jahns & Ott 1997). However, according to Nimis & Martellos (2003), asexual species (*c.* 17% of the Italian flora), although including a few species which are very common and abundant in disturbed sites, mostly occur under humid, shaded, natural conditions and are relatively rare, which explains why asexual reproduction does not discriminate between rare and common species.

The analyses of regional floras based on nationally rare and common lichens show that both subsets are different among regions, revealing the important distinction between the more humid Tyrrhenian regions and those located along the Adriatic side of the Italian Peninsula (see Nimis & Tretiach 1995). However, the differences in composition are much more pronounced in rare species, indicating a much higher species turnover within the regional floras. Nationally rare species are less numerous in the regions located along the Adriatic side of the Italian Peninsula; these regions, compared to those located along the Tyrrhenian side, have a lower lichen diversity and are characterized by a less humid climate which is not favourable for the persistence of rare species with tropical affinities (see Nimis & Tretiach 1999). The behaviour of these two species pools is analogous to that of endemics with narrow ranges and invasive species in vascular plants (Myers *et al.* 2000; Qian &

Ricklefs 2006). Namely, the pool of nationally rare lichens contributes to the distinctiveness of the regional floras, whilst that of common lichens contributes to a floristic homogeneity across regions that is likely driven by human disturbance, as indicated by the high frequency of nitrogen-tolerant species in this group (Nascimbene *et al.* 2015).

In summary, the patterns revealed by our analyses reflect the environmental filters together with the morphological and ecological traits which determine rarity and commonness. Among Italian lichens, rarity appears to be related to two main factors. First, bioclimate (many rare species are outside the limit of their optimal bioclimatic conditions) and second, reduced availability of suitable habitats. Conversely, commonness is related mainly to human disturbance (eutrophication, creation of drier habitats). According to Nimis & Tretiach (1995), the high lichen diversity of Italy reflects clearly the climatic diversity of the country, from cold-alpine to warm suboceanic climates, with a prevalence of mild-temperate, moderately humid climates and an overall scarcity of truly oceanic or arid-continental climate types (Nimis 2016). The same phenomenon observed within homogeneous ecoregions (*i.e.* the high number of “rare” species being largely due to lichens which are at the margin of their bioclimatic range) seems to apply also at the national level. Most of the nationally “rare” species belong to biogeographical elements which are marginal with respect to Italy: an oceanic-suboceanic element with tropical affinities and a small set of continental species of the dry steppe biome. These survive only in habitats with particular bioclimatic conditions: the few remnants of old-growth forests (especially in Tyrrhenian Italy) and the dry Alpine valleys with a continental climate. Many rare species persist in microrefugia, sites with microclimates that support small populations of species beyond the boundaries of the climatic limits of their main distributions (Rull 2009; Dobrowski 2010). This suggests that, as already observed by Aptroot & van Herk (2007) in the Netherlands, climate change is also likely to modify the

patterns of rarity among the lichens occurring in Italy.

We are grateful to Chiara Lelli (PhD student, University of Bologna, BiGeA) for her support in preparing figure layouts.

REFERENCES

- Aizen, M. A. & Patterson, W. A. (1990) Acorn size and geographical range in the North American oaks (*Quercus* L.). *Journal of Biogeography* **17**: 327–332.
- Allen, J. L. & Lendemer, J. C. (2016) Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. *Biodiversity and Conservation* **25**: 555–568.
- Aptroot, A. & van Herk, C. M. (2007) Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environmental Pollution* **146**: 293–298.
- Aptroot, A., van Herk, C. M., Sparrus, L. B. & Spier, J. R. (2004) Checklist van de Nederlandse Korstmossen en korstmosparasieten. *Buxbaumia* **69**: 17–55.
- Arellano, G., Loza, M. I., Tello, J. S. & Macía, M. J. (2015) Commonness and rarity determinants of woody plants in different types of tropical forests. *Biodiversity and Conservation* **24**: 1073–1087.
- Asplund, J. & Wardle, D. A. (2017) How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* **92**: 1720–1738.
- Bielczyk, U., Cieslinski, S. & Faltynowicz, W. (eds) (2002) *Atlas Rozmieszczenia Geograficznego Porostów w Polsce*. 3. Kraków: Polish Academy of Sciences.
- Brown, J. H. (1984) On the relationship between abundance and distribution of species. *American Naturalist* **124**: 255–279.
- Davidar, P., Rajagopal, B., Arjunan, M. & Puyravaud, J. P. (2008) The relationship between local abundance and distribution of rain forest trees across environmental gradients in India. *Biotropica* **40**: 700–706.
- Diaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16**: 646–655.
- Dietrich, M., Stofer, S., Scheidegger, C., Frei, M., Groner, U., Keller, C., Roth, I. & Steinmeier, C. (2000) Data sampling of rare and common species for compiling a Red List of epiphytic lichens. *Forest, Snow and Landscape Research* **75**: 369–380.
- Dobrowski, S. (2010) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**: 1022–1035.
- Edwards, T. C. Jr, Cutler, D. R., Geiser, L., Alegria, J. & McKenzie, D. (2004) Assessing rarity of species with low detectability: lichens in Pacific Northwest forests. *Ecological Applications* **14**: 414–424.
- Edwards, T. C. Jr, Cutler, D. R., Zimmermann, N. E., Geiser, L. & Alegria, J. (2005) Model-based stratifications for enhancing the detection of rare ecological events. *Ecology* **86**: 1081–1090.
- Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O. & Pöschl, U. (2012) Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience* **5**: 459–462.
- Gaston, K. J. (1994) *Rarity*. London: Chapman & Hall.
- Gaston, K. J. (2010) Valuing common species. *Science* **327**: 154–155.
- Gaston, K. J. (2011) Common ecology. *BioScience* **61**: 354–362.
- Gaston, K. J. (2012) The importance of being rare. *Nature* **487**: 46–47.
- Gentry, A. H. (1991) The distribution and evolution of climbing plants. In *The Biology of Vines* (F. E. Putz & H. A. Mooney, eds): 3–49. Cambridge: Cambridge University Press.
- Gilbert, O. L. (1990) The lichen flora of urban wasteland. *Lichenologist* **22**: 87–101.
- Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**: 210–221.
- Ihlen, P. G., Gjerde, I. & Saetersdal, M. (2001) Structural indicators of richness and rarity of epiphytic lichens on *Corylus avellana* in two different forest types within a nature reserve in southwestern Norway. *Lichenologist* **33**: 215–229.
- Jahns, H. M. & Ott, S. (1997) Life strategies in lichens – some general considerations. *Bibliotheca Lichenologica* **67**: 49–67.
- Keim, J. L., Dewitt, P. D., Fitzpatrick, J. J. & Jenni, N. S. (2017) Estimating plant abundance using inflated beta distributions: applied learnings from a lichen-caribou ecosystem. *Ecology and Evolution* **7**: 486–493.
- Kelly, C., Woodward, F. & Crawley, M. (1996) Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philosophical Transactions: Biological Sciences* **351**: 1261–1269.
- Kristiansen, T., Svenning, J.-C., Grandez, C., Salo, J. & Balslev, H. (2009) Commonness of Amazonian palm (*Arecaceae*) species: cross-scale links and potential determinants. *Acta Oecologica* **35**: 554–562.
- Kunin, W. E. & Gaston, K. J. (1997) *The Biology of Rarity: Causes and Consequences of Rare-Common Differences*. London: Chapman & Hall.
- Kunin, W. E. & Shmida, A. (1997) Plant reproductive traits as a function of local, regional, and global abundance. *Conservation Biology* **11**: 183–192.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd ed. Amsterdam: Elsevier.
- Letcher, S. G. & Chazdon, R. L. (2012) Life history traits of lianas during tropical forest succession. *Biotropica* **44**: 720–727.
- Marini, L., Nascimbene, J. & Nimis, P. L. (2011) Large-scale patterns of epiphytic lichen species richness: photobiont dependent response to climate and forest structure. *Science of the Total Environment* **409**: 4381–4386.
- Martellos, S. (2012) From a textual checklist to an information system: the case study of ITALIC, the

- Information System on Italian Lichens. *Plant Biosystems* **146**: 764–770.
- Matos, P., Pinho, P., Aragón, G., Martínez, I., Nunes, A., Soares, A. M. V. M. & Branquinho, C. (2015) Lichen traits responding to aridity. *Journal of Ecology* **103**: 451–458.
- McCune, B., Rosentreter, R. & Debolt, A. (1997) Biogeography of rare lichens from the coast of Oregon. In *Conservation and Management of Native Plants and Fungi* (T. N. Kaye, A. Liston, R. M. Love, D. L. Luoma, R. J. Meinke & M. V. Wilson, eds): 234–241. Corvallis, Oregon: Native Plant Society of Oregon.
- Moles, A. T. & Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* **92**: 372–383.
- Murray, B. R. & Westoby, M. (2000) Properties of species in the tail of rank-abundance curves: the potential for increase in abundance. *Evolutionary Ecology Research* **2**: 583–592.
- Murray, B. R., Thrall, P. H., Gill, A. M. & Nicotra, A. B. (2002) How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Australian Ecology* **27**: 291–310.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
- Nascimbene, J., Martellos, S. & Nimis, P. L. (2006) Epiphytic lichens of tree-line forests in the central-eastern Italian Alps and their importance for conservation. *Lichenologist* **38**: 373–382.
- Nascimbene, J., Nimis, P. L. & Marini, L. (2007) Testing indicators of epiphytic lichen diversity: a case study in N Italy. *Biodiversity and Conservation* **16**: 3377–3383.
- Nascimbene, J., Nimis, P. L. & Ravera, S. (2013) Evaluating the conservation status of epiphytic lichens of Italy: a red list. *Plant Biosystems* **147**: 898–904.
- Nascimbene, J., Lazzaro, L. & Benesperi, R. (2015) Patterns of beta-diversity and similarity reveal biotic homogenization of epiphytic lichen communities associated with the spread of black locust forests. *Fungal Ecology* **14**: 1–7.
- Nathan, R. & Muller-Landau, H. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**: 278–285.
- Nimis, P. L. (2016) *The Lichens of Italy. A Second Annotated Catalogue*. Trieste: EUT.
- Nimis, P. L. & Martellos, S. (2001) Testing the predictivity of ecological indicator values. A comparison of real and 'virtual' relevés of lichen vegetation. *Plant Ecology* **157**: 165–172.
- Nimis, P. L. & Martellos, S. (2003) On the ecology of sorediate lichens in Italy. *Bibliotheca Lichenologica* **86**: 393–406.
- Nimis, P. L. & Martellos, S. (2017) *ITALIC – The Information System on Italian Lichens. Version 5.0*. Department of Life Sciences, University of Trieste. Available at: <http://dryades.units.it/italic>.
- Nimis, P. L. & Tretiach, M. (1995) The lichens of Italy – a phytoclimatical outline. *Cryptogamic Botany* **5**: 199–208.
- Nimis, P. L. & Tretiach, M. (1999) Itinera Adriatica – lichens from the eastern part of the Italian Peninsula. *Studia Geobotanica* **18**: 51–106.
- Nimis, P. L. & Tretiach, M. (2004) Delimiting Tyrrhenian Italy: a lichen foray in the SW part of the peninsula. *Bibliotheca Lichenologica* **88**: 465–478.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., et al. (2017) *vegan: Community Ecology Package. R package version 2.4-2*. Available at: <https://CRAN.R-project.org/package=vegan>.
- Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Nuñez, P. V., Neill, D. A., Cerón, C. E., Palacios, W. A. & Aulestia, M. (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**: 2101–2117.
- Poelt, J. (1994) Different species types in lichenized ascomycetes. In *Ascomycete Systematics. Problems and Perspectives in the Nineties* (D. L. Hawksworth, ed.): 273–278. New York: Plenum Press.
- Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology* **29**: 254–283.
- Qian, H. & Ricklefs, R. E. (2006) The role of exotic species in homogenizing the North American flora. *Ecology Letters* **9**: 1293–1298.
- R Development Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rabinowitz, D. (1981) Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation* (H. Synge, ed.): 205–217. New York: Wiley.
- Rabinowitz, D., Cairns, S. & Dillon, T. (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In *Conservation Biology: The Science of Scarcity and Diversity* (M. E. Soulé, ed.): 182–204. Sunderland, Massachusetts: Sinauer Associates.
- Rodriguez, J. M., Renison, D., Filippini, E. & Estrabou, C. (2017) Small shifts in microsite occupation could mitigate climate change consequences for mountain top endemics: a test analyzing saxicolous lichen distribution patterns. *Biodiversity and Conservation* **26**: 1199–1215.
- Rogers, R. W. (1990) Ecological strategies of lichens. *Lichenologist* **22**: 149–162.
- Roque, F. O., Zampiva, N. K., Valente-Neto, F., Menezes, J. F. S. & Hamada, N. (2016) Deconstructing richness patterns by commonness and rarity reveals bioclimatic and spatial effects in black fly metacommunities. *Freshwater Biology* **61**: 923–932.
- Rull, V. (2009) Microrefugia. *Journal of Biogeography* **36**: 481–484.
- Ruokolainen, K. & Vormisto, J. (2000) The most widespread Amazonian palms tend to be tall and habitat generalists. *Basic and Applied Ecology* **1**: 97–108.
- Seaward, M. R. D. (1988) Progress in the study of the lichen flora of the British Isles. *Botanical Journal of the Linnean Society* **96**: 81–95.

- Seaward, M. R. D. (1995) *Lichen Atlas of the British Isles, Fascicles 1–6*. London: British Lichen Society.
- Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C. *et al.* (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology* **101**: 58–67.
- Walck, J. L., Baskin, J. M. & Baskin, C. C. (1999) Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (*Asteraceae*). *American Journal of Botany* **86**: 820–828.
- Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I. & Poff, N. L. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* **13**: 267–283.
- Wirth, V. (2001) Zeigerwerte von Flechten. *Scripta Geobotanica* **18**: 221–243.
- Wirth, V. (2010) Ökologische Zeigerwerte von Flechten – erweiterte und aktualisierte Fassung. *Herzogia* **23**: 229–248.
- Wirth, V. & Oberhollenzer, H. (eds) (1990) Lichen mapping in Europe. *Stuttgarter Beiträge zur Naturkunde Ser. A (Biologie)* **456**: 1–200.
- Wright, I. J., Ackerly, D. D., Bongers, F. J. J. M., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A. *et al.* (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany* **99**: 1003–1015.