


Standard Paper

Species–area relationship in lichens tested in protected areas across Italy

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Abstract

The species–area relationship (SAR) states that species richness increases with the increase of the sampled area, although other factors can influence the pattern. SARs have been tested on many different organisms, but only rarely on lichens. We aimed to test the SAR, across a wide range of area sizes, for three main substratum-related guilds of lichens, namely epiphytic, epilithic and epigeaic. The test was performed using data from lichen inventories carried out in 44 protected areas of various sizes across Italy. We found a positive correlation of species richness with area size for all three guilds, better fitted by the logarithmic function for epilithic lichens and by the power function for epiphytic and epigeaic lichens. Our results support the fundamental role of area size as the main driver for lichen diversity, suggesting that in an area-based conservation framework, larger protected areas are fundamental to support high lichen species richness. However, finer scale investigations are also required to better elucidate whether and how other environmental factors could interact with area size and modify SAR patterns. Exhaustive lichen inventories could be useful information sources to more robustly test such relationships, and therefore better inform conservation practices.

Keywords: biodiversity; conservation; ecology; lichen inventories; species richness

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Introduction

The ‘species–area relationship’ (SAR) is one of the oldest studied and most widely recognized patterns in ecology, being well established since the 1920s (Arrhenius 1921; Gleason 1922). In simple terms, it states that species richness increases with an increase in sampled area size (Connor & McCoy 1979, 2017; Rosenzweig 1995; Lomolino 2000). Various hypotheses have been suggested to explain the causes of this pattern and its underlying mechanisms (Connor & McCoy 1979, 2017; Scheiner *et al.* 2011; Moradi *et al.* 2020). Furthermore, other factors, such as habitat diversity or edge effect, can simultaneously act through increases in area size and themselves modify species richness (Connor & McCoy 2017). SARs have been tested for different variations of the concept of ‘area’: 1) islands (Yu *et al.* 2020), 2) contiguous (Dengler *et al.* 2020) or fragmented (Hanski *et al.* 2013) habitat patches, 3) ecoregions (Martellos *et al.* 2020), and also 4) administratively defined territories, such as protected areas (Fattorini 2020). The SAR can also be used as an effective tool in biodiversity conservation, for example to predict the biodiversity loss related to habitat loss or fragmentation (Brooks *et al.* 2002; Halley *et al.* 2013; Hanski *et al.* 2013), to test

long-term changes in species diversity (Chiarucci *et al.* 2017), or to disentangle the combined effect of area size, climate and disturbance on plant species richness (de Bello *et al.* 2007).

SARs have been studied for almost all taxa, for example vascular plants (Krauss *et al.* 2004; Powell *et al.* 2013; Patiño *et al.* 2014; D’Antraccoli *et al.* 2019; Dengler *et al.* 2020) and bryophytes (Weibull & Rydin 2005; Silva *et al.* 2018; Yu *et al.* 2020), but have been poorly investigated in lichens. The positive effect of increasing area size on lichen richness has been highlighted in some papers, but with these mainly considering the area of suitable habitat. For example, in forest habitats, an increase in forested surface area has been shown to correlate with increasing species richness of epiphytic lichens (Marini *et al.* 2011), and the increase in good quality forested habitat has had a positive effect on lichen richness together with the diversity of available substratum types (Löhmus *et al.* 2007). Alteration of SARs has been investigated in epilithic lichens in relation to increased levels of pollution (Lawrey 1991). When considering broader areas, such as ecoregions, SARs remain detectable, albeit affected by habitat heterogeneity (Martellos *et al.* 2020). SARs of lichens have also been addressed at local scales, usually in plots in which many taxa were recorded (e.g. Löhmus *et al.* 2012; Dengler *et al.* 2020; Dembicz *et al.* 2021). Some studies have considered SARs in lichens as part of investigations into disturbance processes (Lawrey 1991), but very few studies have examined broader scales with a biogeographical or macroecological focus (Buckley 2005; Lücking *et al.* 2009).

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In the present paper, we aim to fit traditional SAR models using data for three main substratum-related guilds of lichens, namely epiphytic, epilithic and epigaeic, obtained from exhaustive floristic inventories carried out in protected areas across Italy, and to test different functions to find which are the best in describing SARs for the different guilds. This has never been carried out before, to the best of our knowledge. A better understanding of the role of area size on lichen richness can be useful to inform area-based conservation (Maxwell *et al.* 2020; Hoffmann 2022), and to highlight further knowledge gaps in the study of SARs for lichens, for example the comparison between poorly investigated versus well-studied areas, or between well-preserved natural areas versus areas located in anthropized landscapes.

Materials and Methods

Lichen inventories

Italy is an environmentally heterogeneous country, ranging from the Alpine chain to the centre of the Mediterranean Sea, in which lichenological studies have been widely carried out over the last four decades (Nimis 1993, 2016; Nimis & Martellos 2022). We retrieved 44 sources reporting exhaustive lichen inventories carried out mainly in well-defined protected areas of various sizes within this context, over the last 25 years. Most inventories were retrieved from published papers, each dealing with a single protected area; for the area of the Ticino River, we merged the Piedmont and the Lombardy Ticino Natural Parks, since the multiple data sources referring to this area often lacked precise locality details for the species (G. Gheza, unpublished data). The distribution of the 44 areas is shown in Fig. 1 and their metadata is provided in Supplementary Material File S1 (available online).

For each area, we extracted separate lists of the three guilds (i.e. species growing on the three main substratum types colonized by lichens: bark and wood (epiphytic), rock and bryophytes on rock (epilithic), and soil, bryophytes on soil and plant debris (epigaeic)). Species lists were not available for all substrata within each protected area, which resulted in 40 lists of epiphytic species, 37 of epilithic and 37 of epigaeic species.

Data analysis

Polygons of most of the areas were retrieved from regional or national databases. When the relevant polygon was not available, the area was digitized by hand using QGIS 3.28 (QGIS Development Team 2022) based on the information available in the relevant paper.

All the subsequent analyses were performed using R v. 4.2.2 (R Core Team 2022). The area of each polygon (km²) was calculated using the 'st_area' function in the *sf* package (Pebesma 2018). In cases where the area calculated using the available or digitized polygon differed from that declared in the paper, we retained the latter, presuming this to be the more accurate calculation of the true area surveyed.

We compared three commonly used SAR models: 1) the Gleason model (Gleason 1922), where *S* (number of species) is a function of LogA (area), 2) the Arrhenius power function and 3) the linear model. All models were fitted using the *sars* package (Matthews *et al.* 2019), using 'sar_loga', 'sar_pow' and 'sar_linear' for the Gleason (LogA), Arrhenius (Power) and linear (Linear) models respectively. The three models were compared using the Akaike information criterion corrected for small sample sizes (AICc).

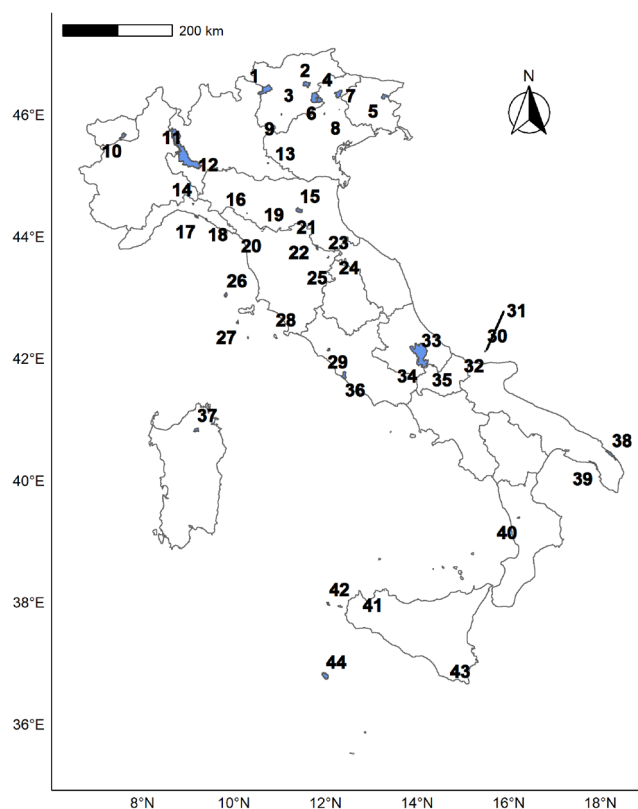


Figure 1. A map of Italy showing the areas considered in this study. The numbers refer to the area identification code (ID) used in Supplementary Material File S1 (available online). Sites with an area > 50 km² are shown in blue/shaded. In colour online.

Results

The 44 protected areas investigated have an average area size of 60.1 km², the smallest area measuring 0.04 km² and the largest 970.9 km². In the lichen inventories there were reported an average of 81.0 epiphytic (min. 7, max. 257), 78 epilithic (min. 10, max. 458) and 28 epigaeic (min. 2, max. 116) species (Table 1).

A SAR based on the LogA model was the best fit in the case of the epiphytic guild, while in the epilithic and epigaeic species the Power model fitted better (Fig. 2; Table 2). In all three cases the Linear model resulted in a poor fit. Given the small differences in AICc, all subsequent comparisons were carried out using the Power model, which was the best performing model in two out of the three cases. The amount of variance in species richness explained by the SAR models was constantly low (< 36%), indicating that area size significantly affected lichen species richness but that other factors probably contributed to a higher amount of species richness variation for the three lichen guilds. Using the Power model, the epiphytic guild presented the highest number of species found per unit area (1 km²), as indicated by the *c* value of the SAR (59.7 species), followed by the epilithic (49.9 species) and epigaeic (16.9 species) guilds. Epigaeic lichens had the higher slope values (0.23), followed by epilithic (0.19) and epiphytic (0.15) species.

Discussion

Our results indicate that area size has a significant effect on species richness for all three guilds of lichens, albeit with different

Table 1. Species richness and area of the sites in Italy where the 44 lichen inventories were made, that were used in the analysis. SD = Standard deviation.

	Mean	Max	Min	SD
Species richness				
Epiphytic	81.0	257	7	53.0
Epilithic	78.1	458	10	79.4
Epigaeic	28.9	116	2	27.9
Environmental variables				
Area (km ²)	60.1	970.9	0.04	182.9

patterns. In fact, we found support for a positive correlation between species richness and area size, thus confirming the general validity of SARs in lichens, with major differences according to the substratum guild. In particular, epigaeic lichens were revealed to have the lowest species richness at the unit area (1 km²) and the highest increase in species richness with increasing area size. On the other hand, species richness of epiphytic and epilithic lichens showed high values at the unit area and a lower increase with increasing area size. These findings are consistent with the suggestion that availability of the different substratum types could be expected to vary with the increase in area size, for example depending on the geographical zone. However, larger areas are more likely to include a higher habitat heterogeneity (Scheiner *et al.* 2011; Connor & McCoy 2017; Drira *et al.* 2019; Martellos *et al.* 2020; Moradi *et al.* 2020), which leads to a greater diversity in climate, substrata and microhabitats available for lichen colonization, than small areas. Larger areas could also be expected to include wider elevational spans, and lichen assemblages are known to vary along altitudinal gradients (Bruun *et al.* 2006; Grytnes *et al.* 2006; Bässler *et al.* 2016; Di Nuzzo *et al.* 2021; Vallese *et al.* 2022), thus promoting species richness as broader gradients are considered. Interestingly, the form of a SAR can be directly influenced by elevation: at increasing elevations, plant species richness decreases due to an increase of bare rock (Moradi *et al.* 2020). This could imply a decrease in epiphytic lichens but, on the other hand, it could increase the diversity of epilithic lichens owing to the greater substratum availability, and also of epigaeic species that can easily colonize the thin bare soil layer often developed in rock crevices.

Our analysis highlighted the presence of a small number of remarkable outliers in the dataset. The Paneveggio-Pale di San Martino Natural Park hosts a far higher richness for all three guilds than expected, given its area, confirming its claimed role as a 'lichen diversity hotspot'. This is explained by the high environmental heterogeneity but also by its long history of lichenological exploration (Nascimbene *et al.* 2022). A similar pattern is highlighted, even if only for epigaeic species, for the Trentino sector of the Stelvio National Park (Nascimbene *et al.* 2012). However, two outliers show a far lower richness than expected given their areas, probably for two different reasons. The Majella National Park (Gheza *et al.* 2021) is probably under-investigated, whereas the area of the Ticino Natural Parks lies within the western Po Valley, a territory that is largely a plain and severely impacted by human activities. Indeed most of its extent is covered by urbanized and agricultural lands, which has led to a depletion of its lichen biota (Nimis 1993). These results are consistent with the analysis by Martellos *et al.* (2020), who tested SARs with lichens in the ecoregions of Italy, finding that the Montane and Subalpine ecoregions (the most represented in

the Paneveggio-Pale di San Martino and Stelvio Parks) are positive outliers, whereas the Padanian ecoregion (in which most of the Ticino River area is located) represents a negative outlier. The case of Majella Park also highlights the limitations of not-so-exhaustive inventories when investigating SARs, which requires as comprehensive data as possible, especially when considering territories with a high environmental heterogeneity; good quality data from extensive fieldwork are therefore crucial to reliably test SAR.

The *c* value (i.e. the number of species per km²) seems to depend, among other factors, on the overall number of species within the guild considered (Triantis *et al.* 2012; Fattorini *et al.* 2017). The whole lichen biota of Italy is composed of a low number of epigaeic (326) species and an intermediate number of epiphytic (663) species, while epilithic species represent the highest number (1352). This is partially consistent with our results, as the *c* value is lowest for the epigaeic (17) guild, while a different pattern is found for epilithic (44) and epiphytic (58) species. This difference between the epilithic and epiphytic guilds could be partially explained by the area effectively available for each guild. For example, in regions where forests were prevalent, the surface/substratum area available for epiphytic colonization was higher than that available for epilithic species, which are restricted to rocks not covered by vegetation. By contrast, except for high altitude zones, at least some trees that can harbour epiphytic species are always present in the areas considered. The lower number of epigaeic lichens could be due to this effect, and also to their overall lower diversity, which is probably driven by multiple factors, including higher competition with vascular plants and/or their higher sensitivity to environmental alteration and habitat loss (Scheidegger & Clerc 2002).

However, in complex landscapes it will be difficult to disentangle the effects of area size from those of other environmental variables, such as climatic or habitat heterogeneity. Finer-scale data would be required to test this relationship fully, for example by comparing different areas selected *ad hoc* to include both size and environmental gradients in a balanced design. Furthermore, precise data on microclimate would also be required, since lichens are greatly influenced by this factor (Di Nuzzo *et al.* 2022).

Implications for conservation and future perspectives

Our results show that larger areas host more lichen species across all three substratum guilds, making larger protected areas more likely to display a higher species richness. Habitat heterogeneity and geographical context are expected to play a role in this, but area size itself seems quite crucial in the pattern. This supports the idea that mitigation of the main current threats to biodiversity conservation (i.e. habitat loss and global change) could be

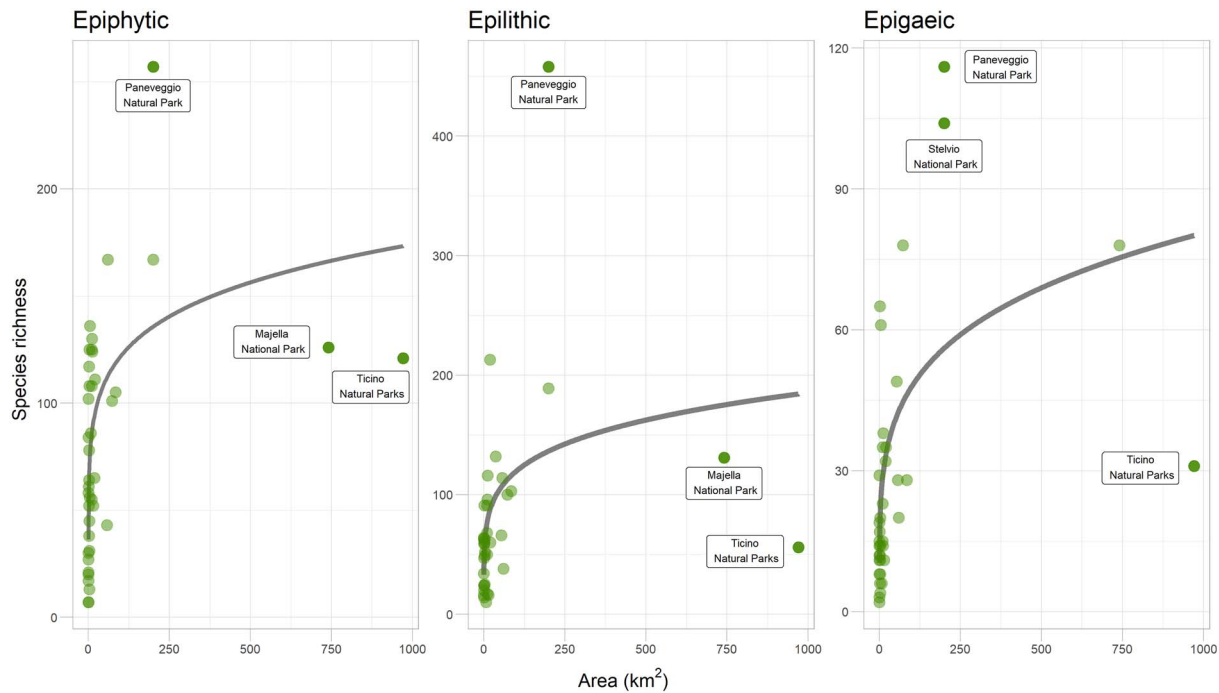


Figure 2. Species–area relationships (SAR) using the Power model for the three lichen guilds from inventories from the 44 protected areas from across Italy. Outliers discussed in the text are indicated. In colour online.

improved in the case of lichens by protecting larger areas, in a framework of area-based conservation. Larger areas are also more likely to include a higher number of so-called ‘microrefugia’, sites with locally favourable conditions that are placed outside the main range of a species or that are surrounded by unfavourable habitats, the preservation of which is considered one of the best strategies to mitigate the effects of climate change on sensitive lichens (Ellis 2020; Greiser *et al.* 2021; Porada *et al.* 2023), even with recognized limitations (Di Nuzzo *et al.* 2022). To date, there is contrasting evidence about the effectiveness of already

established protected areas in lichen conservation (Martínez *et al.* 2006; Rubio-Salcedo *et al.* 2013), even though in some cases protected areas have been recognized as lichen diversity hotspots (Nascimbene *et al.* 2022) or refugia for fragmented species at the border of their distributional range (Gheza *et al.* 2021). To verify this, however, a comparison of SAR patterns with non-protected areas, that sometimes can be included in area-based conservation frameworks (Hoffmann 2022), should also be made, to examine whether the protection regime could influence SAR.

Table 2. Parameters and model fitting of the three species–area relationship (SAR) models for the three lichen guilds from inventories of 44 protected areas from across Italy. For each SAR model, the c value, representing the intercept, and the z value, representing the slope of the fitting line, are reported in terms of the number of species. For both c and z , the lower and upper confidence intervals (CI) are also given. The last two columns show the model evaluation data as corrected Akaike’s information criterion (AICc) and R^2 .

	c	c - CI 95%	z	z - CI 95%	AICc	R^2
Epiphytic						
LogA	58.324	[42.387 - 74.262]	14.329	[8.643 - 20.015]	416.373	0.368
Power	59.735	[44.156 - 75.315]	0.155	[0.092 - 0.218]	417.019	0.358
Linear	75.126	[58.020 - 92.233]	0.092	[0.007 - 0.178]	432.133	0.063
Epilithic						
LogA	47.146	[17.389 - 76.903]	16.366	[6.451 - 26.281]	424.376	0.193
Power	49.925	[22.848 - 77.001]	0.190	[0.069 - 0.311]	424.235	0.196
Linear	72.015	[44.081 - 99.949]	0.085	[-0.049 - 0.220]	432.688	-0.011
Epigaeic						
LogA	15.931	[6.604 - 25.258]	7.233	[4.055 - 10.411]	339.684	0.335
Power	16.954	[8.996 - 24.911]	0.226	[0.127 - 0.324]	338.298	0.359
Linear	25.311	[16.021 - 34.601]	0.052	[0.008 - 0.097]	351.359	0.088

The study of the SAR itself can also be used as a powerful tool in biodiversity conservation, to set baseline targets for conservation based on area and/or species richness. In the latter case, however, these need to be set according to the local situation and studied considering alternate model frameworks (Desmet & Cowling 2004; Metcalfe *et al.* 2013; Drira *et al.* 2019). Obviously, the selection of potential protected areas cannot be based solely on their area size, since other factors must be taken into account (e.g. habitat diversity and heterogeneity, or elevational ranges), and species richness is not the only valid criterion with which to assess the conservation value of a site. Furthermore, the validity of the SAR is also dependent on scale (Dolnik & Breuer 2008; Chiarucci *et al.* 2012; Powell *et al.* 2013) and sampling effort (Azovsky 2011; Metcalfe *et al.* 2013), and this could also apply when considering lichens.

To better understand the processes underlying the SAR, making a transition from a taxonomically descriptive and pattern-based approach towards a more predictive and generalizable process-based ecological approach, could make functional traits a valuable tool (Ellis *et al.* 2021; Hulshof & Umaña 2023). An increase in traits variation with increasing area size has been demonstrated for lichens, although this is dependent not only on the area size but also on scale and environmental factors (Giordani *et al.* 2019).

The present work can be considered as a starting point towards a better knowledge of the multiple issues related to SARs applied to the study of lichen diversity patterns, and which need to be addressed to achieve a better understanding of the possible applications to conservation.

Finally, the present work highlights the importance of exhaustive species inventories, realized at different scales, to address ecological and conservation issues. Such endeavours are challenging, yet crucial for providing knowledge on the ecology and distribution of lichen species, and also for detecting diversity hotspots (Nascimbene *et al.* 2021, 2022; Vondrák *et al.* 2022). High quality floristic research should therefore be recognized as a key tool to support more applied tasks in lichenology.

Author Contributions. Gabriele Gheza and Luca Di Nuzzo contributed equally to this paper.

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