


## 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

(Accepted 5 June 2023)

### 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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**Cite this article:** Gheza G, Di Nuzzo L, Giordani P, Chiarucci A, Benesperi R, Bianchi E, Canali G, Francesconi L, Vallese C and Nascimbene J (2023) Species–area relationship in lichens tested in protected areas across Italy. *Lichenologist* 55, 431–436. <https://doi.org/10.1017/S0024282923000488>

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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 epigeaic, 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).

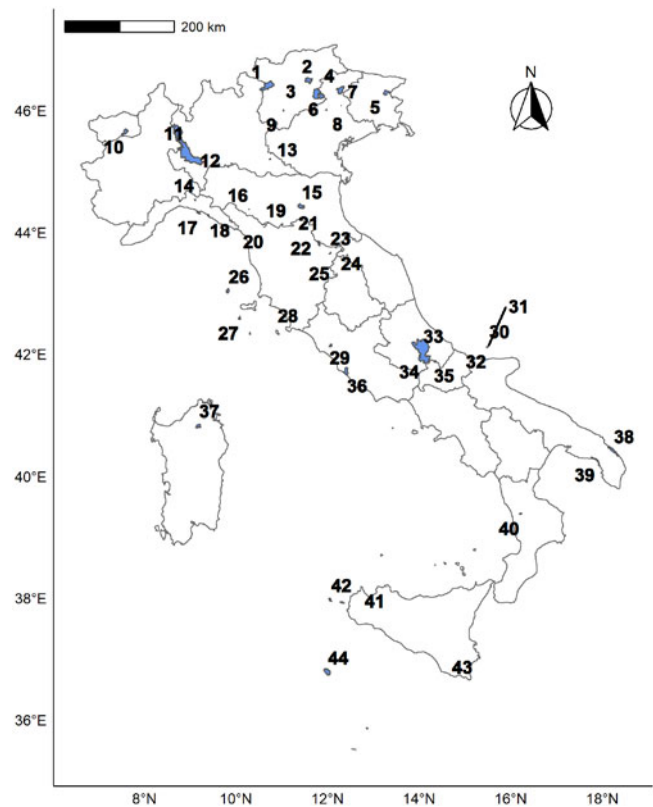
For each area, we extracted separate lists of the three guilds (i.e. species growing on the three main substratum types colonized by lichens: bark and wood (epiphytic), rock and bryophytes on rock (epilithic), and soil, bryophytes on soil and plant debris (epigeaic)). Species lists were not available for all substrata within each protected area, which resulted in 40 lists of epiphytic species, 37 of epilithic and 37 of epigeaic 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 (km<sup>2</sup>) 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 km<sup>2</sup> are shown in blue/shaded. In colour online.

## Results

The 44 protected areas investigated have an average area size of 60.1 km<sup>2</sup>, the smallest area measuring 0.04 km<sup>2</sup> and the largest 970.9 km<sup>2</sup>. 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 epigeaic (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 epigeaic 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 km<sup>2</sup>), as indicated by the *c* value of the SAR (59.7 species), followed by the epilithic (49.9 species) and epigeaic (16.9 species) guilds. Epigeaic 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
<b>Species richness</b>				
Epiphytic	81.0	257	7	53.0
Epilithic	78.1	458	10	79.4
Epigaeic	28.9	116	2	27.9
<b>Environmental variables</b>				
Area (km <sup>2</sup> )	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 km<sup>2</sup>) 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

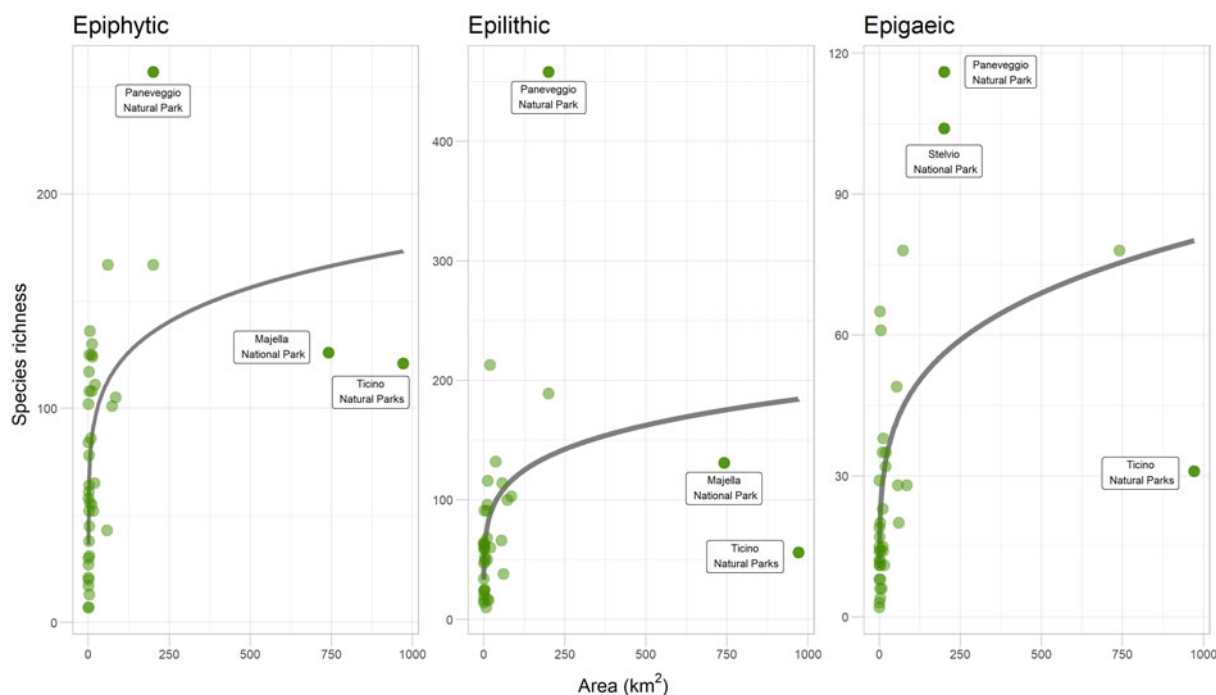
the Paneveggio-Pale di San Martino and Stelvio Parks) are positive outliers, whereas the Padanian ecoregion (in which most of the Ticino River area is located) represents a negative outlier. The case of Majella Park also highlights the limitations of not-so-exhaustive inventories when investigating SARs, 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 km<sup>2</sup>) 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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**Supplementary Material.** The Supplementary Material for this article can be found at <https://doi.org/10.1017/S0024282923000488>.

## References

- Arrhenius O (1921) Species and area. *Journal of Ecology* **9**, 95–99.
- Azovsky AI (2011) Species–area and species–sampling effort relationships: disentangling the effects. *Ecography* **34**, 18–30.
- Bässler C, Cadotte MW, Beudert B, Heibl C, Blaschke M, Bradtka JH, Langbehn T, Werth S and Müller J (2016) Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography* **39**, 689–698.
- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S and Magin G (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909–923.
- Bruun HH, Moen J, Virtanen R, Grytnes J, Oksanen L and Angerbjörn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science* **17**, 37–46.
- Buckley HL (2005) Vascular plant and epiphytic lichen communities in Canadian aspen parkland: scale-dependence of species–area relationships. *Community Ecology* **3**, 59–67.
- Chiarucci A, Bacaro G, Filibeck G, Landi S, Maccherini S and Scoppola A (2012) Scale dependence of plant species richness in a network of protected areas. *Biodiversity and Conservation* **21**, 503–516.
- Chiarucci A, Fattorini S, Foggi B, Landi S, Lazzaro L, Podani J and Simberloff D (2017) Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports* **7**, 1–11.
- Connor EF and McCoy ED (1979) The statistics and biology of the species–area relationship. *American Naturalist* **113**, 791–833.
- Connor EF and McCoy ED (2017) Species–area relationships. In Levin SA (ed.), *Encyclopedia of Biodiversity*, 2nd Edn. New York: Elsevier, pp. 640–650.
- D’Antraccoli M, Roma-Marzio F, Carta A, Landi S, Bedini G, Chiarucci A and Peruzzi L (2019) Drivers of floristic richness in the Mediterranean: a case study from Tuscany. *Biodiversity and Conservation* **28**, 1411–1429.
- de Bello F, Lepš J and Sebastià M-T (2007) Grazing effects on the species–area relationship: variation along a climatic gradient in NE Spain. *Journal of Vegetation Science* **18**, 25–34.
- Dembicz I, Dengler J, Steinbauer MJ, Matthews TJ, Bartha S, Burrascano S, Chiarucci A, Filibeck G, Gillet F and Janišová M (2021) Fine-grain beta diversity of Palaearctic grassland vegetation. *Journal of Vegetation Science* **32**, e13045.
- Dengler J, Matthews TJ, Steinbauer MJ, Wolfrum S, Boch S, Chiarucci A, Conradi T, Dembicz I, Marcenò C and García-Mijangos I (2020) Species–area relationships in continuous vegetation: evidence from Palaearctic grasslands. *Journal of Biogeography* **47**, 72–86.
- Desmet P and Cowling R (2004) Using the species–area relationship to set baseline targets for conservation. *Ecology and Society* **9**, 11.
- Di Nuzzo L, Vallese C, Benesperi R, Giordani P, Chiarucci A, Di Cecco V, Di Martino L, Di Musciano M, Gheza G, Lelli C, *et al.* (2021) Contrasting multitaxon responses to climate change in Mediterranean mountains. *Scientific Reports* **11**, 4438.
- Di Nuzzo L, Benesperi R, Nascimbene J, Papini A, Malaspina P, Incerti G and Giordani P (2022) Little time left. Microrefuges may fail in mitigating the effects of climate change on epiphytic lichens. *Science of The Total Environment* **825**, 153943.
- Dolnik C and Breuer M (2008) Scale dependency in the species–area relationship of plant communities. *Folia Geobotanica* **43**, 305–318.
- Drira S, Lasram FBR, Jenhani ABR, Shin YJ and Guilhaumon F (2019) Species–area uncertainties impact the setting of habitat conservation targets and propagate across conservation solutions. *Biological Conservation* **235**, 279–289.
- Ellis CJ (2020) Microclimatic refugia in riparian woodland: a climate change adaptation strategy. *Forest Ecology and Management* **462**, 118006.
- Ellis CJ, Asplund J, Benesperi R, Branquinho C, Di Nuzzo L, Hurtado P, Martínez I, Matos P, Nascimbene J, Pinho P, *et al.* (2021) Functional traits in lichen ecology: a review of challenge and opportunity. *Microorganisms* **9**, 766.
- Fattorini S (2020) Beetle species–area relationships and extinction rates in protected areas. *Insects* **11**, 646.
- Fattorini S, Borges PAV, Dapporto L and Strona G (2017) What can the parameters of the species–area relationship (SAR) tell us? Insights from Mediterranean islands. *Journal of Biogeography* **44**, 1018–1028.
- Gheza G, Di Nuzzo L, Vallese C, Benesperi R, Bianchi E, Di Cecco V, Di Martino L, Giordani P, Hafellner J and Mayrhofer H (2021) The lichens of the Majella National Park (Central Italy): an annotated checklist. *Mycologia* **78**, 119.
- Giordani P, Malaspina P, Benesperi R, Incerti G and Nascimbene J (2019) Functional over-redundancy and vulnerability of lichen communities decouple across spatial scales and environmental severity. *Science of The Total Environment* **666**, 22–30.
- Gleason HA (1922) On the relation between species and area. *Ecology* **3**, 158–162.
- Greiser C, Ehrlén J, Luoto M, Meineri E, Merinero S, Willman B and Hylander K (2021) Warm range margin of boreal bryophytes and lichens not directly limited by temperatures. *Journal of Ecology* **109**, 3724–3736.
- Grytnes JA, Heegaard E and Ihlen PG (2006) Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecologica* **29**, 241–246.

- Halley JM, Sgardeli V and Monokrousos N (2013) Species–area relationships and extinction forecasts. *Annals of the New York Academy of Sciences* **1286**, 50–61.
- Hanski I, Zurita GA, Belloq MI and Rybicki J (2013) Species–fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 12715–12720.
- Hoffmann S (2022) Challenges and opportunities of area-based conservation in reaching biodiversity and sustainability goals. *Biodiversity and Conservation* **31**, 325–352.
- Hulshof CM and Umaña MN (2023) Power laws and plant trait variation in spatio-temporally heterogeneous environments. *Global Ecology and Biogeography* **32**, 310–323.
- Krauss J, Klein A-M, Steffan-Dewenter I and Tschardt T (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation* **13**, 1427–1439.
- Lawrey JD (1991) The species–area curve as an index of disturbance in saxicolous lichen communities. *Bryologist* **94**, 377–382.
- Löhmus A, Löhmus P and Vellak K (2007) Substratum diversity explains landscape-scale co-variation in the species-richness of bryophytes and lichens. *Biological Conservation* **135**, 405–414.
- Löhmus P, Leppik E, Motiejunaite J, Suija A and Löhmus A (2012) Old selectively cut forests can host rich lichen communities – lessons from an exhaustive field survey. *Nova Hedwigia* **95**, 493–515.
- Lomolino MV (2000) Ecology's most general, yet protean 1 pattern: the species–area relationship. *Journal of Biogeography* **27**, 17–26.
- Lücking R, Rivas Plata E, Chaves JL, Umaña L and Sipman HJ (2009) How many tropical lichens are there... really? *Bibliotheca Lichenologica* **100**, 399–418.
- Marini L, Nascimbene J and Nimis PL (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, d'Agostino M, Chiarucci A, Nimis PL and Nascimbene J (2020) Lichen distribution patterns in the ecoregions of Italy. *Diversity* **12**, 294.
- Martínez I, Carreño F, Escudero A and Rubio A (2006) Are threatened lichen species well-protected in Spain? Effectiveness of a protected areas network. *Biological Conservation* **133**, 500–511.
- Matthews TJ, Triantis KA, Whittaker RJ and Guilhaumon F (2019) sars: an R package for fitting, evaluating and comparing species–area relationship models. *Ecography* **42**, 1446–1455.
- Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues AS, Stolton S, Visconti P, Woodley S, Kingston N and Lewis E (2020) Area-based conservation in the twenty-first century. *Nature* **586**, 217–227.
- Metcalf K, Delavenne J, Garcia C, Foveau A, Dauvin J-C, Coggan R, Vaz S, Harrop SR and Smith RJ (2013) Impacts of data quality on the setting of conservation planning targets using the species–area relationship. *Diversity and Distributions* **19**, 1–13.
- Moradi H, Fattorini S and Oldeland J (2020) Influence of elevation on the species–area relationship. *Journal of Biogeography* **47**, 2029–2041.
- Nascimbene J, Thor G and Nimis PL (2012) Habitat types and lichen conservation in the Alps: perspectives from a case study in the Stelvio National Park (Italy). *Plant Biosystems* **146**, 428–442.
- Nascimbene J, Gheza G, Hafellner J, Mayrhofer H, Muggia L, Obermayer W, Thor G and Nimis PL (2021) Refining the picture: new records to the lichen biota of Italy. *MycoKeys* **82**, 97–137.
- Nascimbene J, Gheza G, Bilovitz PO, Francesconi L, Hafellner J, Mayrhofer H, Salvadori M, Vallese C and Nimis PL (2022) A hotspot of lichen diversity and lichenological research in the Alps: the Paneveggio-Pale di San Martino Natural Park (Italy). *MycoKeys* **94**, 37–50.
- Nimis P (1993) *The Lichens of Italy. An Annotated Catalogue*. Torino: Museo Regionale di Scienze Naturali.
- Nimis PL (2016) *The Lichens of Italy. A Second Annotated Catalogue*. Trieste: EUT Edizioni Università di Trieste.
- Nimis PL and Martellos S (2022) *ITALIC: the information system on Italian lichens. Version 7.0*. Department of Biology, University of Trieste [WWW document] URL <https://dryades.units.it/italic> [Accessed 10 November 2022].
- Patiño J, Weigelt P, Guilhaumon F, Kreft H, Triantis KA, Naranjo-Cigala A, Sólymos P and Vanderpoorten A (2014) Differences in species–area relationships among the major lineages of land plants: a macroecological perspective. *Global Ecology and Biogeography* **23**, 1275–1283.
- Pebesma EJ (2018) Simple features for R: standardized support for spatial vector data. *The R Journal* **10**, 439–446.
- Porada P, Bader MY, Berdugo MB, Colesie C, Ellis CJ, Giordani P, Herzschuh U, Ma Y, Launiainen S and Nascimbene J (2023) A research agenda for non-vascular photoautotrophs under climate change. *New Phytologist* **237**, 1495–1504.
- Powell KI, Chase JM and Knight TM (2013) Invasive plants have scale-dependent effects on diversity by altering species–area relationships. *Science* **339**, 316–318.
- QGIS Development Team (2022) *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. [WWW document] URL <http://qgis.osgeo.org>
- R Core Team (2022) *R: a Language and Environment for Statistical Computing. Version 4.2.2*. R Foundation for Statistical Computing, Vienna, Austria. [WWW resource] URL <https://www.R-project.org>.
- Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Rubio-Salcedo M, Martínez I, Carreño F and Escudero A (2013) Poor effectiveness of the Natura 2000 network protecting Mediterranean lichen species. *Journal for Nature Conservation* **21**, 1–9.
- Scheidegger C, Clerc P, Dietrich M, Frei M, Groner U, Keller C, Roth I, Stofer S and Vust M (2002) *Lista Rossa delle Specie Minacciate in Svizzera. Licheni Epifiti e Terricoli*. Bern, Birmensdorf: UFAP and Istituto Federale di Ricerca WSL.
- Scheiner SM, Chiarucci A, Fox GA, Helmus MR, McGlenn DJ and Willig MR (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs* **81**, 195–213.
- Silva JB, Sfair JC, dos Santos ND and Pôrto KC (2018) Bryophyte richness of soil islands on rocky outcrops is not driven by island size or habitat heterogeneity. *Acta Botanica Brasiliica* **32**, 161–168.
- Triantis KA, Guilhaumon F and Whittaker RJ (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography* **39**, 215–231.
- Vallese C, Di Musciano M, Muggia L, Giordani P, Francesconi L, Benesperi R, Chiarucci A, Di Cecco V, Di Martino L, Di Nuzzo L, et al. (2022) Water–energy relationships shape the phylogenetic diversity of terricolous lichen communities in Mediterranean mountains: implications for conservation in a climate change scenario. *Fungal Ecology* **60**, 101189.
- Vondrák J, Svoboda S, Malicek J, Palice Z, Kocourkova J, Knudsen K, Mayrhofer H, Thues H, Schultz M and Kodnar J (2022) From Cinderella to princess: an exceptional hotspot of lichen diversity in a long-inhabited central-European landscape. *Preslia* **94**, 143–181.
- Weibull H and Rydin H (2005) Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. *Biological Conservation* **122**, 71–79.
- Yu J, Li D, Zhang Z and Guo S (2020) Species–area relationship and small-island effect of bryophytes on the Zhoushan Archipelago, China. *Journal of Biogeography* **47**, 978–992.