Perspectives in Plant Ecology, Evolution and Systematics 69 (2025) 125904

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Resampling epiphytic lichens in coniferous forests of the Southern Alps: Veteran trees promote compositional stability

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ARTICLE INFO

Keywords:
Alectorioid lichens
Compositional changes
Micro-refugia
Resampling
Temporal β-diversity
Thallus growth forms

ABSTRACT

In this study, by means of resampling epiphytic lichens in a timespan of fifteen years in forest stands of the Paneveggio-Pale di San Martino Natural Park (N Italy – Southern Alps), we aim at detecting changes in lichen assemblages by comparing temporal β-diversity patterns between tree individuals of different ages and considering the response pattern of thallus growth forms. Our results indicate that on veteran trees lichen composition seems to be more stable over time. This view is corroborated by lower values of temporal beta-diversity as compared to young trees which are more prone to changes of their lichen biota. In this perspective, dynamics of gains and losses, that translate into compositional changes over time, seem to be more rapid on young than on veteran trees. While the results on the overall dynamics of gains and losses in terms of taxonomic changes are still difficult to interpret, the frequency changes of different thallus growth forms are more explicit in the time frame of our study, indicating a decline in broad-lobed foliose and alectorioid lichens. Overall, our results further support the importance of retaining and increasing the occurrence of veteran trees for long term lichen conservation.

1. Introduction

Epiphytic lichens are increasingly recognized as threatened by climate change (Ellis et al., 2014; Di Nuzzo et al., 2022), with both direct and indirect effects through alterations of their habitats (Ellis et al., 2009; Nascimbene et al., 2020; Saiz et al., 2021), thus likely weakening their biodiversity and contribution to ecosystem functioning in the future. Lichens are poikilohydric organisms that strictly depend on environmental water availability (Nascimbene et al., 2019). However, their sensitivity to climate change is mediated by some functional traits that may differ across taxa (Ellis and Coppins, 2006; Gauslaa, 2014; Nimis et al., 2020; Di Nuzzo et al., 2022). For example, in temperate regions, cyanobacterial photobionts seem to make species more sensitive and threatened, whereas trentepohlioid photobionts, are expected to foster success in coping with climate change (Aptroot and van Herk, 2007; Rubio-Salcedo et al., 2016). One of the most responsive traits is the thallus growth form, i.e., the shape of the lichen thallus. By varying the thallus surface exposed to the atmosphere and the surface that adheres to tree bark, the different growth forms greatly influence lichen physiology and survival under climate change (Merinero et al., 2014; Ellis et al., 2021). Fruticose lichens, especially the alectorioid forms (i.e., those with filamentous thalli, like the genera *Bryoria* and *Usnea*), and broad-lobed foliose lichens have most of their thallus surface directly exposed to the atmosphere and scarcely adherent to the substrate. In contrast, narrow-lobed and squamulose and crustose lichens strongly adhere to the substrate, being also smaller and therefore exposing a smaller absolute and relative surface to the atmosphere. The exposed surface and the adherence to substrate increase the interception of stem-flow and directly influence water storage capability (Esseen et al., 2015), which is fundamental for physiological efficiency (Gauslaa, 2014). This suggests that fruticose and broad-lobed foliose species can be more negatively impacted by climate change due to stronger desiccation than smaller forms.

However, epiphytic lichens are also strongly influenced by local processes, as in the case of forest management (Nascimbene et al., 2013; Łubek et al., 2018). In particular, in temperate regions, weakening long-term connectivity and ecological continuity, and the scarcity of veteran trees are among the main management-related factors that negatively impact epiphytic lichens. Veteran trees, with their microhabitat diversity, large size, and temporal persistence, are crucial for lichen biodiversity in forest ecosystems, functioning as “lifeboats” where species may accumulate over time (Sillet and Goslin, 1999; Tews et al.,

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https://doi.org/10.1016/j.ppees.2025.125904
Received 30 May 2025; Received in revised form 24 October 2025; Accepted 27 October 2025
Available online 31 October 2025

2004; Ranius et al., 2008; Fritz et al., 2009; Marmor et al., 2011; Lindenmayer et al., 2013; Lundström et al., 2013; Hofmeister et al., 2016; Skarpaas et al., 2017; Zemanova et al., 2017; Pasques and Munné-Bosch, 2024). This may provide a chance both for long term-survival of several sensitive species, and for subsequent colonization events in the surroundings. In a climate change perspective, the role of veteran trees may translate into a micro-refugia effect (Ellis, 2020; Ellis and Eaton, 2021; Di Nuzzo et al., 2022; Porada et al., 2023), which may delay the negative impact of climate warming by providing more stable conditions which are less quickly affected by ongoing changes.

The interplay between climate change and forest management may exacerbate the negative impact on epiphytic lichens (Moning et al., 2009; Nascimbene et al., 2013, 2019). While reversing the trend of climate change today still seems a remote event, a rapid re-orientation of forest management towards biodiversity conservation could still leave time to slow down the local extinction of many species and compositional shifts. In the case of epiphytic lichens, this aspect is particularly crucial in the coniferous forests of the Southern Alps, since, on the one hand, the rate of climate change is faster than in low elevation areas and other parts of the Alps (Pepin et al., 2015; Kotlarski et al., 2023), and, on the other hand, there is still a level of biodiversity that is difficult to match in more anthropized areas at lower elevations (Gheza et al., 2023). This implies that, while in central European forests many species have already been lost in the past due to atmospheric pollution and intensification of forest management (Hauck, 2009; Hauck et al., 2013; Łubek et al., 2018), in alpine coniferous forests much more can be lost in the coming years, and this should be avoided.

In this study, by means of resampling epiphytic lichens in a timespan of fifteen years in forest stands of the Paneveggio-Pale di San Martino Natural Park (N Italy – Southern Alps), we aim at detecting changes in lichen assemblages by comparing temporal β-diversity patterns between tree individuals of different ages and considering the response pattern of thallus growth forms. We expect that, under the influence of the ongoing climate change, growth forms frequencies are changing, favouring the less sensitive ones. Furthermore, we expect higher stability of epiphytic lichen assemblages on older trees, which could therefore serve as “lifeboats” for richer and more stable communities.

2. Materials and methods

2.1. Study area

The study was carried out in the Paneveggio forest (Paneveggio-Pale di San Martino Natural Park, N-Italy, Trentino-Alto Adige; 46°18_N, 11°45_E), extending over a 6.000 ha surface.

The average annual temperature is 2.4°C, annual rainfall is c. 1.200–1.300 mm y^{-1}.

The bedrock is porphyry, the soils are rankers and podsols (Bizzarini, 2009).

The lichen survey was carried out in five 1-ha coniferous forest plots devoted to long-term monitoring since 1993 (Motta, 2002; Motta et al., 2002). Two plots were in dense mono-layered spruce stands which were not managed in the last 60 years and whose establishment started after an intensive logging activity. Two plots were in multi-layered, open-canopied spruce-dominated stands which were not managed in the last 70 years. One plot was in a mixed larch-stone pine stand that was managed in the past (until approximatively 80 years ago) as grazed forest in which single trees were occasionally cut.

2.2. Data collection

The first lichen survey was carried out in the summer of 2006 and 2007 (Nascimbene et al., 2008, 2009) using the standardized sampling protocol of the Forest BIOTA project (Giordani et al., 2006), which was based on the European guidelines for lichen monitoring (Asta et al., 2002; Scheidegger et al., 2002) to provide statistically robust data. Lichen diversity was sampled using four standard frames of 10 cm× 50 cm as sampling grids, subdivided into five 10 cm× 10 cm quadrats, which were attached to the tree trunk at the cardinal points with the shorter lower side at 100 cm from the ground. All lichen species inside the frames were listed and their frequency was computed as the number of 10 cm× 10 cm quadrats in which the species occurred. Tree selection was based on tree age, aiming at proportionally representing the whole gradient of tree age (about 50–450 years; Motta, 2002, Motta et al., 2002). The resampling was carried out in summer 2020 and 2021. Since in the five forest plots each single tree individual was numbered in the field and mapped, we precisely re-allocated the sampling grid on the same position and on the trees as in the original survey. For the resampling we selected a sub-sample of trees in each plot trying to respect the age proportions. A total of 91 trees out of 149 in the original dataset was resampled, spanning an age gradient between 55 and 447 years: 14 (spruce) in plot 1, 15 (spruce) in plot 2, 16 (spruce) in plot 3, 26 (17 spruce, 7 larch, 2 stone pine) in plot 4, and 20 (8 larch, 12 stone pine) in plot 5.

Nomenclature and species’ traits refer to ITALIC 8.0 (Nimis et al., 2025).

2.3. Data analysis

To investigate changes in species richness over time, for each plot we calculated the number of species gained, the number of species lost, and the net change between the two surveys. Differences among forest types were tested using the Kruskal–Wallis test (Vargha and Delaney, 1998). When significant, we performed post-hoc pairwise comparisons with Dunn’s test and Bonferroni correction (package FSA; Ogle et al., 2022).

Changes in species composition were assessed with Non-Metric Multidimensional Scaling (NMDS) based on the Jaccard dissimilarity index, using the function metaMDS of the vegan package (Oksanen et al., 2022). The analysis was run with 500 random starts in three dimensions, and the final solution was selected based on stress values and stability across runs. For each plot, the magnitude of temporal change was quantified as the Euclidean distance between the coordinates of the historical and current survey in the NMDS space, while the orientation of the connecting vector represented the direction of change.

To explore shifts in functional groups, we calculated for each species the difference in the number of occupied plots between the two surveys, separately for each forest type. We then modelled the frequency variation using Generalized Linear Mixed Models (GLMMs) implemented with the glmer function of the lme4 package (Bates et al., 2015). The response variable was the frequency variation, functional group was included as a fixed effect, and forest type as a random intercept. Models were fitted assuming Gaussian error distribution and identity link. Model assumptions were evaluated by inspection of residual plots.

Temporal beta diversity was quantified for each historical/current plot pair using the Jaccard dissimilarity index with the function beta.temp from the betapart package (Baselga et al., 2017). Since our goal was to quantify overall temporal compositional change at the plot level, we only focused on total beta diversity without partitioning it into turnover and nestedness components (Baselga, 2010). To test whether stand structure mitigated community shifts, we modelled temporal beta diversity as a function of log-transformed tree age, using GLMMs with Gaussian error and identity link (lme4::glmer). Forest type was included as a random intercept. DBH was not included jointly with age due to strong collinearity (Pearson’s $r > 0.8$), which can bias parameter estimation in GLMMs (Zuur et al., 2007). The log transformation was applied because relative age differences are ecologically more relevant among young than among old trees.

All analyses were performed in R version 4.3.3 (R Core Team, 2024), using the packages vegan (Oksanen et al., 2022), betapart (Baselga et al., 2017), lme4 (Bates et al., 2015), and FSA (Ogle et al., 2022).

The codes used for the analyses are available as Supplementary File 1.

3. Results

In total, 96 epiphytic lichen taxa were recorded: 87 in the 2006–2007 sampling and 89 in the 2020–2021 sampling. Between the two censuses, both species gains and species losses were detected (Fig. 1). Seven taxa were lost (i.e., *Cetraria sepincola*, *Calicium pinicola*, *C. tigillare*, *Frutidella furfuracea*, *Parmelia omphalodes*, *Protoparmelia oleagina*, *Strangospora deplanata*) and nine were gained (i.e., *Catillaria nigroclavata*, *Chaenotheca phaeocephala*, *C. stemonea*, *Cladonia sp.*, *Coenogonium pineti*, *Lepraria sp.*, *Melanohalea exasperatula*, *Micarea prasina* s. lat., *Ramalina pollinaria*). The overall richness did not vary significantly between the first sampling and the resampling.

The frequency of alectorioid fruticose lichens, i.e., the group including *Alectoria sarmentosa*, *Bryoria spp.*, *Evernia divaricata*, *Ramalina thrausta*, and *Usnea spp.*, decreased noticeably (Fig. 2; Table 1; Supplementary Files 2, 3). The decline was more evident in widespread species with many occurrences in the dataset, e.g., *Bryoria spp.* and *Usnea hirta*, but it was evident also in the other alectorioid species with fewer occurrences. Broad-lobed foliose lichens decreased noticeably as well (Fig. 2; Table 1; Supplementary Files 2, 3), whereas non-alectorioid fruticose lichens and crustose lichens remained more or less stable (Fig. 2; Table 1; Supplementary Files 2, 3). On the other hand, the frequency of narrow-lobed foliose lichens, i.e., *Imshaugia aleurites*, *Parmeliopsis ambigua*, and *P. hyperopta*, and squamulose lichens, i.e., *Hypocenomyce scalaris*, significantly increased (Fig. 2; Table 1; Supplementary Files 2, 3).

The NMDS (stress 0.103) showed that relevant changes occurred within the assemblages between the first sampling and the resampling (Fig. 3). Even though these changes are quite consistent among plots, a few show opposite trends and/or slight changes.

A significant non-linear negative relationship ($P < 0.05$) was detected between temporal total β-diversity and tree age (Fig. 4; Supplementary Files S4, S5). The curve has a steeper slope at low tree ages that decreases at increasing tree age, indicating that temporal β-diversity is higher between young trees and lower between old trees. It also indicates that the same age span corresponds to higher β-diversity in younger trees, but to lower β-diversity in old trees.

4. Discussion

Our resampling study indicates that, besides the role of veteran trees as lifeboats of lichen diversity enhancing species accumulation over time (Fritz et al., 2009), the composition of their lichen biota also seems to be more stable over time. This view is corroborated by lower values of temporal beta-diversity as compared to young trees, which are more prone to changes of their lichen biota. In this perspective, dynamics of gains and losses, that translate into compositional changes over time, seem to be more rapid on young than on veteran trees. This could be related not only to a larger surface to colonise, but also to a higher heterogeneity of microhabitats (Pasques and Munné-Bosch, 2024), that is crucial for organisms like lichens (Gignac and Dale, 2005; Hofmeister et al., 2024). Furthermore, the larger size of veteran trees is likely more efficient in protecting lichens from mechanical stresses originating in the surrounding environment, e.g., from the action of wind or incident rainfall. This finding further emphasizes the potential role of veteran trees for long-term conservation of epiphytic lichens even in a climate change scenario, acting as microrefugia that may delay local exctinctions (Di Nuzzo et al., 2022).

Retaining veteran trees, which are themselves sensitive to environmental alterations (Lindenmayer et al., 2012, 2013; Lindenmayer, 2017; Lindenmayer and Laurance, 2016; Skarpaas et al., 2017), should thus be prioritized in forest management, at least in protected areas. This can greatly benefit biodiversity in general (Siitonen and Ranius, 2015; Horák, 2017; Piovesan et al., 2022; Van Steenis, 2023), but also promote

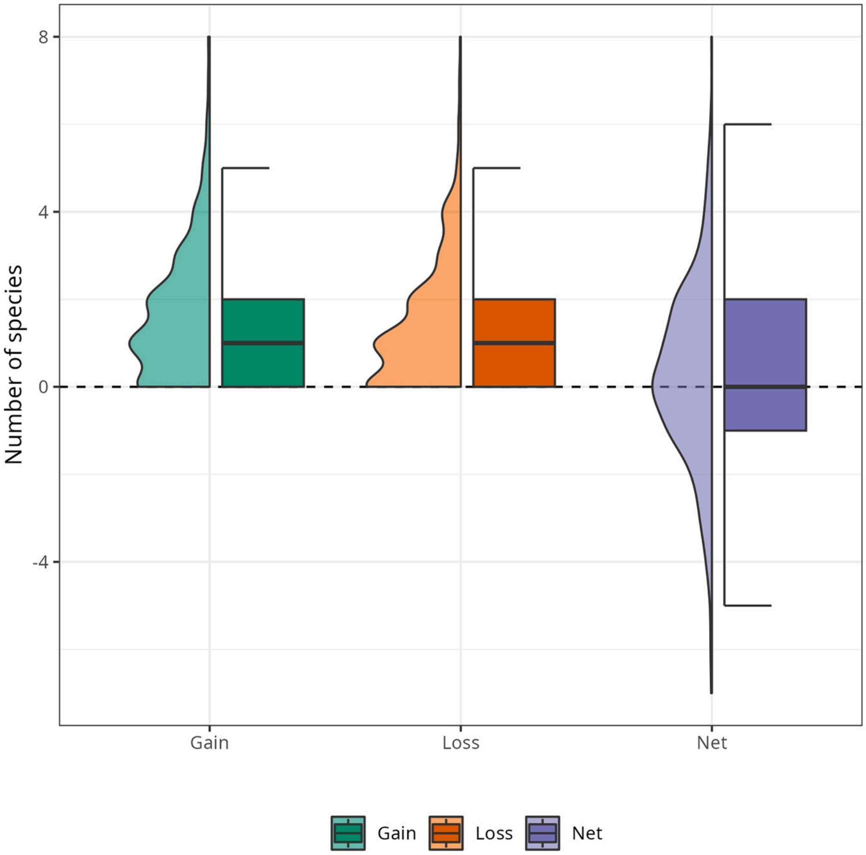

Fig. 1. Species losses, species gains and overall variation between the first sampling and the resampling.

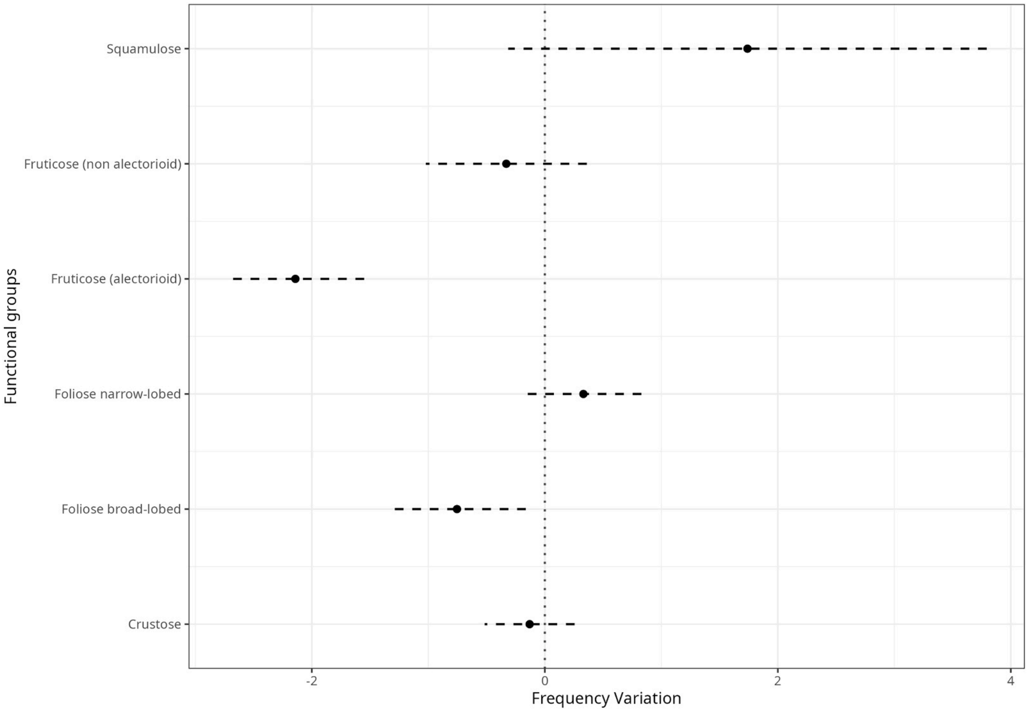

Fig. 2. Frequency variation in the growth forms functional groups between the first sampling and the resampling.

Table 1
Predicted effects (± standard error) of the mixed-effects model (GLMM, glmer) on the occurrence changes over time of different lichen functional groups. Reported values are model predictions (logit scale), with associated standard errors (Std. Error) and 95 % confidence intervals (Conf. Low–Conf. High). Significant effects are indicated when the 95 % confidence interval does not overlap zero.

FUNCTIONAL GROUP	PREDICTED	STD. ERROR	CONF. LOW	CONF. HIGH
Crustose	–0.13	0.20	–0.52	0.26
Foliose broad-lobed	–0.75	0.30	–1.35	–0.16
Foliose narrow-lobed	0.33	0.25	–0.17	0.83
Fruticose (alectorioid)	–2.14	0.30	–2.73	–1.55
Fruticose (non-alectorioid)	–0.33	0.35	–1.02	0.36
Squamulose	1.74	1.05	–0.31	3.79

heterogeneity in forest structure that can improve ecosystem functionality and help in building a better resilience against climate change effects (Piovesan et al., 2022; Pasques and Munné-Bosch, 2024). Furthermore, aside from maintaining already existing veteran trees, fostering the establishment of additional ones by selecting healthy individuals to be spared from felling in the long term would be an intelligent and farsighted strategy.

While the results on overall gain and loss dynamics in terms of taxonomic changes are still difficult to interpret, and perhaps will be more informative when more years have passed, changes of frequency of different thallus growth forms are already more explicit in the timespan of our study. Our results suggest that fruticose-alectorioid and broad-lobed foliose lichens can be more impacted than narrow-lobed foliose and crustose species by environmental alterations linked to climate change. The decrease of fruticose-alectorioid and broad-lobed foliose lichens is consistent with the model predictions of Nascimbene and Marini (2015). Despite the fact that these lichens are also influenced by local level factors, as stand structure and edge-effects (Jaakkola et al., 2006; Esseen, 2006, 2019), climatic alterations are likely to be relevant for their decline (Francesconi et al., 2025), due to longer and more frequent desiccation periods related to the combined effect of increasing temperatures and altered rainfall regimes (Nascimbene et al., 2019; Di Nuzzo et al., 2022). Air pollution could also play a role: some of these growth forms are particularly sensitive to it (Nascimbene et al., 2019) and, although being located in a territory well-known for its high environmental and lichenological value (Nascimbene et al., 2022), the study area could be affected by the increasing tourism in the last decade, as well as from the consequences of the “Vaia Storm” (which occurred in autumn 2018), that caused a thinning of the forest which could have modified the circulation patterns of pollutants.

In contrast, squamulose and narrow-lobed foliose lichens increased their frequency, corroborating their higher tolerance to warming in relationship with their lower exposure to the atmosphere and higher adherence to the substrate that likely prolongs the beneficial effect of stem-flow to thallus hydration. Moreover, their increased frequency may also be related to tree-level dynamics, taking advantage of the decreased frequency of larger lichens (e.g., alectorioid and large-lobed foliose species) which leaves more space free for their colonization without being outcompeted.

Besides the expected local extinction of several species currently composing the lichen biota of coniferous forests of the Southern Alps (mainly boreal-montane species) that may be replaced by “winners” that are crustose and with trentepohlioid photobiont, as in the emblematic case of *Coenogonium pineti* (Nascimbene et al., 2018), the pattern revealed by our results implies compositional changes that may negatively impact on both forest ecosystem functioning and macro-evolutionary processes. Alectorioid and large-lobed foliose lichens significantly contribute to the epiphyte biomass in boreo-montane coniferous forests of temperate Europe (Renhorn and Esseen, 1995; Esseen et al., 1996; Gauslaa et al., 2008; Nascimbene et al., 2019), including the Southern Alps, and are therefore crucial to multiple trophic networks and to the provision of ecosystem services related to nutrient and water cycling (Nascimbene et al., 2019; Porada et al., 2023). These lichens also belong to lineages (i.e., Parmeliaceae) with a higher speciation rate as compared to small crustose lichens (i.e., Lecanoraceae, Teloschistaceae) and their decline may trigger the depletion of gene pools that may rapidly generate further biodiversity in the future. In this regard, the genus *Bryoria* (alectorioid lichens) is an

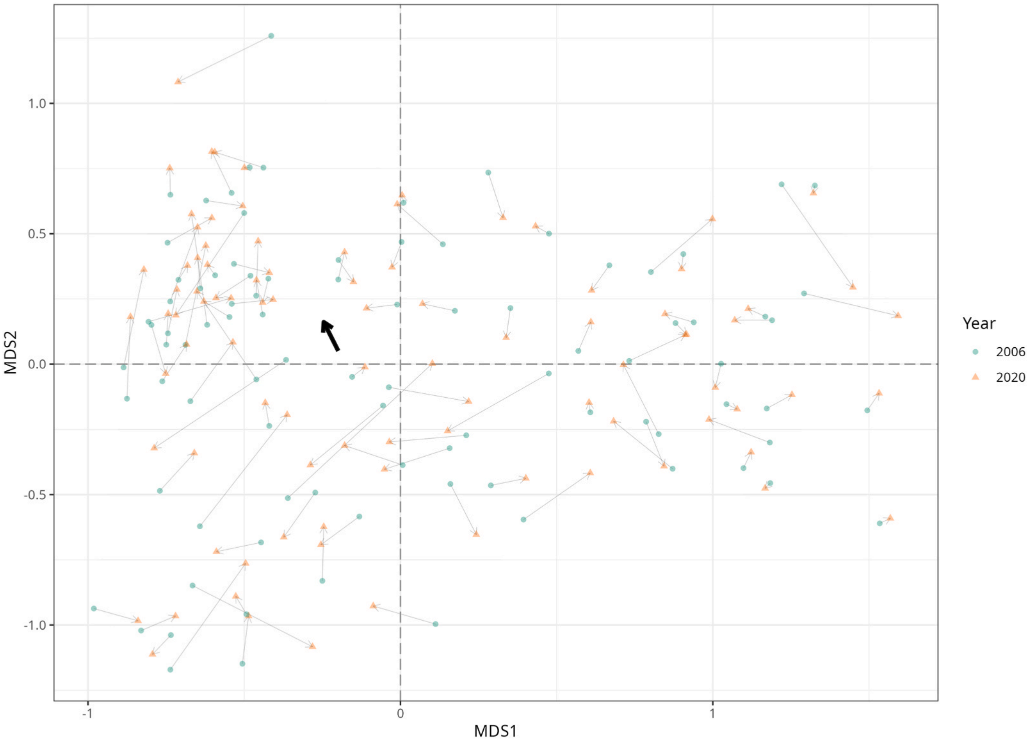

Fig. 3. NMDS scatterplot.

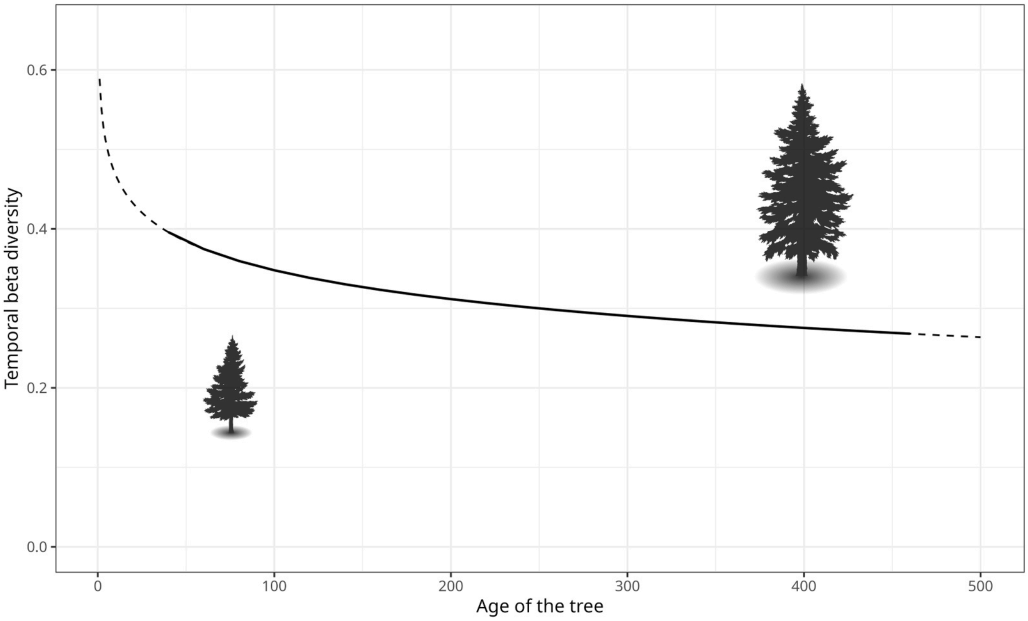

Fig. 4. Relationship between temporal β-diversity and tree age. Full line represents the actual data; dotted line represents the extrapolation.

emblematic case among the most threatened taxa in spruce forests of the Alps (Nascimbene et al., 2018), because it is considered of recent diversification and includes several still undescribed species (Myllys et al., 2023).

5. Conclusions

Resampling after just 15 years allowed to detect the fundamental role of veteran trees as “lifeboats” of epiphytic lichen diversity in coniferous forests of the Southern Alps by enhancing both species accumulation over time and communities stability. While resampling studies are increasingly available for vascular plants, demonstrating their usefulness to monitor and predict the trajectories of biodiversity in a global change scenario (e.g., Loeb, 1990; Dullinger et al., 2003; Knollová et al. 2005; Haveman and Janssen, 2008; Gillet et al., 2016; Lelli et al., 2020), those on lichens are still scanty (e.g., Aptroot and van Herk, 2007). Although our results are clear, the unambiguous interpretation of the general patterns could be somehow limited by the short timespan between censuses and the not very broad study area. Future research aimed at improving the topic should focus on (1) longer-term monitoring, to better capture temporal trends; (2) investigation of microclimatic factors, that can be relevant in influencing lichen diversity patterns (Renhorn et al., 1996; Canters et al., 2007); (3) comparative studies in other mountainous regions, to better generalise the findings; and (4) exploring the possible roles of biotic interactions between species, i.e., competition and facilitation, that can include physiological mechanisms and secondary metabolites (Mikhailova, 2006; Armstrong and Welch, 2007; Belinchón et al., 2015; Spicer and Woods, 2022).

CRediT authorship contribution statement

Michele Di Musciano: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Juri Nascimbene:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Gabriele Gheza:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the managing body of the Paneveggio-Pale di San Martino Natural Park, in particular to Maurizio Salvadori.

Supplementary files

Supplementary File 1. Codes used for the analyses.

Supplementary File 2. Frequency variation of epiphytic lichen species between the first sampling and the resampling.

Supplementary File 3. Predicted occurrence changes over time of lichen species obtained from the generalized linear mixed-effects model (glmer). Values are given on the logit scale as predicted percentiles (5th, 25th, 50th, 75th, 95th) obtained from the model's prediction intervals.

Supplementary File 4. Fixed effects estimated by the generalized linear mixed-effects model (glmer). Reported are regression coefficients (Beta) with 95 % confidence intervals (CI) on the logit scale. Random effects are reported as the standard deviation of the intercept across tree species (Tree_sp) and residual variance across observations.

Supplementary File 5. Results of the generalized linear mixed-effects model (glmer) testing the effect of tree age on temporal beta diversity. Reported are the estimated regression coefficient (Beta) for log-transformed age with 95 % confidence intervals (CI), and the variance components of the random effects: standard deviation of the intercept across tree species (tree_sp) and residual variance across observations.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2025.125904.

Data availability

The codes are available in the Supplementary Files.

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