RESEARCH ARTICLE

Networks of epiphytic lichens and host trees along elevation gradients: Climate change implications in mountain ranges

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Abstract

1. Several studies have evaluated lichen responses in terms of shifts in species climate suitability, species richness and community composition. In contrast, patterns of co-occurrence among species that could be related to complex species interactions have received less consideration. Biotic interactions play a major role in shaping species niches, fitness and adaptation to new environments. Therefore, considering the specific relationships among co-occurring species is essential to further deepen our knowledge of biodiversity response to climate change. In this perspective, the analysis of lichen ecological networks across elevational gradients may provide a powerful tool to understand how communities are structured and how biotic interactions are modulated by changing climatic conditions.

2. We evaluated the contribution of environmental and species biological attributes to the structure of epiphytic lichen–host tree networks. Specifically, we studied lichen communities considering two different network levels: the whole lichen community, and groups of lichen species that presented similar biological traits. In this framework, we (a) characterized the structure of the epiphytic lichen–host tree networks; (b) assessed how network structure varied with climate, forest attributes and community trait diversity and (c) evaluated the role that biological traits played in the connections established between co-occurring lichens.

3. On the one hand, results indicate that epiphytic lichen communities are dominated by local segregation, suggesting habitat specialization among lichens within their host tree, and that climatic conditions and, to a lesser extent, lichen diversity are the main drivers of community assemblage. On the other hand, the role of lichen species in the networks depends on their particular biological traits, supporting the hypothesis that biological traits contribute to shape network structure by influencing the ability of the species to interact between each other. These findings warn about the potential impact of climate change on epiphytic lichen communities.

4. Synthesis. This study builds towards a better understanding of lichen community assembly and on biodiversity response to climate change in forest alpine ecosystems. In particular, our results highlight the value of lichen–tree networks to inform about assemblage processes acting at different organizational levels and indicate...
1 | INTRODUCTION

Climate change is a major threat for natural ecosystems, posing concern for biodiversity conservation and ecosystem functioning (Bellard et al., 2012). For this reason, there is an increasing research interest in species' and communities' responses to changing climatic conditions. In alpine forests, epiphytic lichen communities contribute greatly to ecosystem biodiversity (Nascimbene et al., 2006, 2014), and underpin important ecological functions (Zedda & Rambold, 2015). However, due to their poikilohydric nature, epiphytic lichens are among the most sensitive organisms to climate change (Ellis, 2019; Nascimbene et al., 2020). This supposes a major threat for alpine ecosystems, which are predicted to be strongly affected by climate change (Gobiet et al., 2014). Several studies have evaluated lichen responses in terms of shifts in species climate suitability, species richness and community composition (Ellis et al., 2007, 2014; Hurtado et al., 2019; Nascimbene, Casazza, et al., 2016). In contrast, the effect of climate change on co-occurrence patterns among species that could be related to complex species interactions has received less consideration or has been only indirectly addressed (Nascimbene, Ackermann, et al., 2016). Biotic interactions play a major role in shaping species niches, fitness and adaptation to new environments (Hargreaves et al., 2020; Tomiolo et al., 2015; Wiens, 2011). Therefore, considering the specific relationships between co-occurring species is essential to further deepen our understanding of biodiversity response to climate change.

In this perspective, the analysis of lichen ecological networks across environmental gradients may provide a powerful tool to understand how communities are structured and how biotic interactions are modulated by changing climatic conditions (Tylianakis & Morris, 2017), especially under the current climate change scenarios. Among environmental gradients, elevation gradients are among the most suitable model templates for exploring the relationships between biodiversity and climate (Baniya et al., 2010; McCain & Grytnes, 2010), as they encompass rapid changes in several climatic variables over a short distance (Körner, 2007). Besides, the analysis of species co-occurrences patterns along environmental gradients may shed some light on how changing climatic conditions influence species interactions (Kapfer et al., 2013; López et al., 2013). In particular, climate change may modify some network structural features (e.g. modularity and nestedness) that are indicative of how biotic interactions are impacted (Dalsgaard et al., 2013).

Besides climate change-related stochastic events that can affect lichen communities in an instant, such as fires and insect outbreaks that may destroy large patches of forests (e.g. Miller et al., 2018), climate also affects epiphytic lichen communities at individual species scale. Lichen physiology is closely related to ambient temperature and moisture, which influences water saturation and desiccation tolerance (Gauslaa, 2014; Gauslaa & Arsenault, 2020; Green et al., 2011). Increasing temperature may then impact epiphytes due to increased respiratory carbon losses (Schroeter et al., 2000). Moreover, high temperature influences thallus rewetting and water content, inducing frequent and severe desiccation events that hamper the photosynthetic activity (Insarov & Schroeter, 2002). Importantly, lichens physiology is mediated by species traits (Benesperi et al., 2018; Hurtado et al., 2020), which may therefore have implications for structuring lichens occurrences on their host trees, influencing species ability to interact between each other. Hence, identifying key lichen traits shaping community structure would provide valuable information to anticipate the effects of climate change on natural communities. Altogether, evaluating the simultaneous influence of abiotic and biotic drivers on ecological networks will pave the way to address the role that biotic interactions play in ecosystems response to climate change.

Here, we evaluate the contribution of environmental and species biological attributes to the structure of epiphytic lichen–host tree networks. These are bipartite networks that gather information about the occurrences of lichen species on their host trees. Specifically, we studied lichen communities considering two different network levels: the whole lichen community, and groups of lichen species that presented similar biological traits. In this framework, we (a) characterized the structure (i.e. connectivity, checkerboard pattern, modularity, nestedness) of the epiphytic lichen–host tree networks; (b) assessed how network structure varied with climate, forest attributes and community trait diversity and (c) evaluated the role that biological traits (i.e. type of thallus, photobiont, and reproduction strategy) played in the connections established between co-occurring lichens. We hypothesize that epiphytic lichen–host tree networks present a non-random (modular and nested) structure, like other mutualistic and commensalistic ecological networks. Furthermore, this structure is modulated by environmental stress and lichens trait diversity. Limited niche availability (due to increasing environmental stress) together with high niche overlap (due to low trait diversity) will lead to an increase in lichen co-occurrences, resulting in networks with less segregation and modularity. Finally, we hypothesize that biological traits have a significant effect on lichen species roles in the network, with lichens showing traits associated with habitat specialization...
acting as hubs (i.e. co-occur with habitat specialist lichens) and habitat generalist lichens acting as connectors (i.e. co-occur with all lichens).

2 | MATERIALS AND METHODS

2.1 | Study area

We carried out the study in South Tyrol (N Italy), an alpine region covering 740,000 ha (Nascimbene & Marini, 2015). Elevation strongly influences the climatic conditions (Adler et al., 2015) that range from temperate in the Adige Valley (mean annual temperature of 11–12°C) to alpine tundra conditions above 1,700 m (mean annual temperature of 2–3°C). In this region also, precipitation varies considerably from <600 mm/year in the western part (Venosta valley) to 1,400 mm/year in the eastern part (Dolomites). The geological bedrock is very heterogeneous including hard siliceous, metamorphic, porphyric and carbonatic rocks. Soils are mainly podsols and rendzinas. Forests are the main vegetation type between 600 and 2,100 m and in particular 52% of the forest area is occupied by spruce forests managed for timber production in even-aged and multilayered, uneven-aged, stands. In both cases, management is based on progressive thinning and exploitation (1.6 m³ ha⁻¹ year⁻¹) of mature trees.

2.2 | Sampling design

Eight distinct sites were selected according to the distribution range of spruce-dominated forests along the elevation gradient (900–1,900 m). Site selection was made to span the entire regional rainfall gradient (c. 600–1200 mm/year). In each site, a pair of forest stands (one monoplane even-aged and one monoplane uneven-aged) with mature trees were selected at three different elevation steps: 900–1,200, 1,400–1,600, and 1,800–1,900 m. Three these elevation steps represented distinct climatic (temperature) belts in the study region (Table S1). Since the primary aim of this study was to evaluate the effect of climate, along the elevation gradient forest structural heterogeneity was minimized by selecting forest stands as similar as possible. Nevertheless, for each forest stand, we collected information about the forest age (extracting cores from the trees selected for the lichen survey by a Pressler-type increment borer; Sulc, 1967) and the canopy openness (using a spherical densitometer and averaging 20 records taken at the four cardinal points of each tree sampled for lichens) to control for potential effect of forest attributes in the community.

On each forest, a 13-m radius plot was randomly placed, in which five mature spruce individuals were randomly selected for the lichen survey, for a total of 240 trees (8 sites × 3 elevation steps × 2 paired forests stands × 5 trees). The lichen survey was conducted according to the European guidelines for lichen monitoring (Asta et al., 2002). Epiphytic lichen diversity was sampled using four standard frames of 10 × 50 cm divided into five quadrats, which were attached to the tree trunk at each cardinal point with the shorter lower side at 100 cm from the ground. To better capture lichen diversity, two additional standard frames were placed at the base of the trunk on north and south cardinal points. The frequency of all the species inside the frames, including sterile crustose lichens, was recorded as occurrence in each quadrat (ranging between 0 and 5 according with the number of the quadrats) and the total frequency of each species per forest stand was established as the sum of the frequencies considering all frames. Details on species identification methods are reported in Nascimbene and Marini (2015).

2.3 | Lichen functional traits

We collected lichen information regarding three biological traits: thallus growth form, photobiont type and reproductive strategy from Nimis and Martellos (2017). Lichens have four main thallus growth forms: crustose, squamulose, foliose and fruticose. Since in our dataset squamulose lichens are scarcely represented, we lumped them with crustose species. Lichens with a crustose growth form are expected to better resist drought events due to lower surface-to-volume ratio (i.e. less surface exposed to the atmosphere), resulting in a higher tolerance to desiccation (Büdel & Scheidegger, 2008). Photobiont type, that include chlorococcoid green algae, trentepohlioid green algae and cyanobacteria, strongly determines species performance under contrasting climatic conditions (Marini et al., 2011; Nimis et al., 2020). Finally, lichens may reproduce both sexually and asexually (i.e. vegetatively) and this influences the capability of the species to disperse and establish (Morando et al., 2019). Species were classified according to their main reproduction strategy as (a) sexually reproducing by spores (size c. 10–100 μm) or (b) asexually reproducing by different types of vegetative propagules (i.e. isidia and soredia, with sizes ranging from 50 to 200 μm to centimetres).

We then calculated trait diversity for each forest stand using the functional dispersion index (FDIS). Functional dispersion allows us to calculate diversity for qualitative traits and weights individual traits contribution based on species abundances. We calculated the observed functional dispersion (FDISexp) for each forest stand using the R package in R (Laliberté et al., 2010). To remove potential effects due to species richness on FDIS, we applied a null model where we randomized the abundances across all lichen species within each forest stand (Mason et al., 2013). Specifically, we ran 100 simulations per forest stand and calculated the expected functional dispersion (FDISexp) as the average of the functional dispersion calculated for each simulation. Finally, for each forest stand, we defined functional dispersion as FDIS = FDISexp – FDISexp.

2.4 | Network analysis

We built one epiphytic lichen–host tree network (hereafter network) for each forest stand, using the occurrence data of lichens on the different sampling frames. This bipartite network is
characterized by the adjacency matrix $A_{L \times T}$, where lichens richness ($L$) is the number of rows, the number of sampling frames on the trees ($T = 5$ trees $\times 6$ samples/tree = $30$ samples) is the number of columns and $a_{ij}$ represents the abundance of lichen $i$ in the sampling frame $j$. The connectivity of each network was measured with connectance ($C = $ number of presences of lichen species on sampling frames/$L \times T$).

For each network, we calculated the checkerboard pattern, nestedness and modularity. Checkerboard pattern (Check) evaluates the number of times that two lichen species do not co-occur in the same sampling frame, and we calculated it with the C-score index (Stone & Roberts, 1990). This index is a measure of the spatial segregation of lichens on their host trees (i.e. higher C-score = higher segregation), and can be interpreted as a proxy for niche differentiation or inter-specific competition. Nestedness ($N$) evaluates the presence of nested patterns in the community (sensu, rare species occur in a subset of the sampling frames occupied by common species) and is calculated with the weighted-interactions nestedness estimator (WINE, Galeano et al., 2009). On the other hand, modularity ($Q$) evaluates the presence of modules or highly connected blocks in the network, and is calculated with Newman's modularity index (Newman, 2006). These two indices ($N$ and $Q$) indicate the degree of niche specialization in the community, with nested patterns indicating that species are generalists in their niche preferences and modules indicating that species are divided into groups of similar preference. As these three indices are sensitive to network size (Dormann et al., 2009), for each network we simulated 1,000 random networks with the same link distribution as the real network, and compared network indices expected values (i.e. the 95% confidence interval for the indices calculated from simulated networks) against the observed ones.

We also calculated the role of each lichen species in the community using the modules found by modularity analysis. The role of each species was calculated based on the intra-module degree and the participation of each species on the networks (Guimera & Amaral, 2005). Intra-module degree ($I_m$) represents how a species connects to other species within the same module, while participation ($P$) represents how the species connects to different modules. The combination of these two indices allows the classification of the species based on their role in the network as hubs (i.e. species highly connected to other species in the same module) and connectors (i.e. species highly connected to species in different modules; Guimera & Amaral, 2005). All network indices were calculated with the bipartite package in R (Dormann et al., 2008).

2.5 | Statistical analysis

We evaluated the effect of environmental conditions, forest attributes and lichen diversity on the structure of the networks with a confirmatory path analysis (Shipley, 2009). In these models, we included elevation, rainfall, forest canopy openness, lichen richness ($L$), functional dispersion (FDIS) and the difference between the observed and simulated values for C-score, nestedness and modularity. We ran one model for each network index, where elevation, rainfall and forest canopy openness had a direct effect on $L$ and FDIS, and all variables had a direct effect on the network index. We then simplified each model performing a stepwise variable selection by removing at each step the path with less explanatory power. Finally, we selected the best model based on Akaike and Bayesian information criteria (Shipley, 2009). We also included locality as a random effect in all models. To evaluate the effect of biological traits on the role that lichen species had in networks, we ran ANOVA mixed models. Specifically, we ran one model for each biological trait. In each model, we included trait categories as explanatory variables, and network role indices ($I_m$ and $P$) together with lichen total abundance in the forest stand as dependent variables, with locality and species identity as random effects. When the effect of a trait was significant, we applied Tukey post-hoc tests to evaluate the differences between the different categories of the trait using the emmeans package in R (Lenth et al., 2019). All analyses were calculated with R 3.5.3 (R Development Core Team, 2014).

3 | RESULTS

Lichen-tree networks were quite variable in lichen richness, but presented a similar trait diversity (Table 1). Connectance was quite comparable between sites ($C = 0.181, 95\%$ confidence interval: 0.11–0.28). In general, networks were not randomly structured, presenting significantly more segregation between pairs of species (higher C-score) and being significantly more modular than expected by chance, while nested pattern was not significantly different from the expectation based on the null model (Table 1).

Network structure was influenced by environmental variables and functional dispersion, but each index was affected differently (Figures 1 and 2). Functional dispersion had a significant negative direct effect on checkerboard patterns. Thus, higher functional diversity was related to lower spatial segregation in the community. On the other hand, functional dispersion and rainfall had significant direct positive effects on nestedness. Finally, elevation had a significant direct negative effect on modularity indicating that lichens segregate in groups of coexisting species at higher elevation. Looking at the contribution of each variable (Figure 1), environmental conditions (i.e. elevation, rainfall) were the most influential for all network indices, while forest openness was the least. The effect of lichen diversity (taxonomic and trait) was as important as the environmental conditions for checkerboard patterns and nestedness while they did not influence modularity.

The analysis of biological traits showed that thallus growth form had a significant effect on lichen abundance, with foliaceous types being more abundant than crustose ($p < 0.05$, Figure 3). Reproduction type also had a marginal effect, showing higher abundance of lichens with asexual reproduction (Figure 3). Similarly, thallus growth form was the most relevant trait determining species role in the community, influencing both the
**TABLE 1** Description of the structure of the lichen–host tree networks along elevation gradients in South Tyrol (N Italy)

<table>
<thead>
<tr>
<th>Description</th>
<th>Observed value</th>
<th>Coefficient of variation</th>
<th>Obs - Exp value</th>
<th>Significant sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lichen richness (L)</td>
<td>24.44 (7, 40)</td>
<td>0.43</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Functional dispersion (FDIS)</td>
<td>0.28 (0.18–0.34)</td>
<td>0.16</td>
<td>−0.01 (~0.08, 0.02)</td>
<td>4 (0.08) 0 (0)</td>
</tr>
<tr>
<td>Connectance (C)</td>
<td>0.18 (0.11–0.28)</td>
<td>0.25</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C-Score (Check)</td>
<td>0.63 (0.51–0.68)</td>
<td>0.11</td>
<td>0.18 (0.08, 0.34)</td>
<td>2 (0.04) 45 (0.93)</td>
</tr>
<tr>
<td>Nestedness (N)</td>
<td>0.43 (0.23–0.64)</td>
<td>0.26</td>
<td>−0.08 (~0.23, 0.07)</td>
<td>19 (0.4) 2 (0.04)</td>
</tr>
<tr>
<td>Modularity (Q)</td>
<td>0.36 (0.25–0.56)</td>
<td>0.23</td>
<td>0.15 (0.1, 0.27)</td>
<td>0 (0) 48 (1)</td>
</tr>
</tbody>
</table>

Note: Observed value is the mean observed value (95% confidence interval) for all sites; Obs - Exp value is the mean difference between the observed and expected value based in simulations (95% confidence interval) for all sites; Significant sites is the number (proportion) of sites with observed significantly higher/lower than expected values. Numbers in bold indicate indices significantly different from the expectation based on simulations.

**FIGURE 1** Confirmatory path analysis for the effect of environmental variables on epiphytic lichen–host tree network structure. Panels on the left represent the CPA models for (a) C-score, (c) Nestedness and (e) Modularity. Solid/Dash arrows represent positive/negative paths between variables. Arrows in black represent paths with $p < 0.1$, while arrows in grey represent non-significant paths present in the selected model. Panels on the right represent network indices explained variance associated with (b) C-score, (d) Nestedness and (f) Modularity.
intra-module degree ($I_m$) and participation ($P$). Particularly, foliose lichens had higher $I_m$ and $P$ than the other types ($p < 0.05$; Figure 3), indicating that foliose species act as habitat generalists (i.e., they strongly coexist with other lichens, independently of their module). In addition, reproduction type had a significant effect on $P$, with lichens that reproduce sexually presenting lower $P$ than...
asexual ones \( (p < 0.05, \text{Figure } 3) \), indicating that sexual lichens tend to be habitat specialist (i.e. they only coexist with lichens in their same module). Finally, photobiont type had no influence on lichen species, with no effect on the abundance or the role that species played in the networks (Figure 3).

4 | DISCUSSION

Our analysis of epiphytic lichen–host tree networks along elevation gradients provides novel insights into epiphyte assemblages at the community and species scales. On the one hand, results indicate that epiphytic lichen communities are driven by local segregation (as shown by checkboard patterns and modularity), suggesting habitat specialization among lichens within their host tree, and that climatic conditions and, to a lesser extent, lichen diversity are the main drivers of community assemblage. On the other hand, the role of lichen species in the networks depends on their particular biological traits, supporting the hypothesis that biological traits contribute to shape network structure by influencing the ability of species to interact with each other. These findings point to the potential impact of climate change on epiphytic lichen communities by altering species niche preferences and the intraspecific interactions shaping community assemblages.

4.1 | Environmental effects on epiphytic lichen–host tree networks

Our results showed that lichen–tree networks had a non-random structure along the elevation gradients. Ecological networks, particularly those including positive interactions (e.g. mutualism, commensalism), usually share common structural properties that depart from randomness (i.e. low connectance, nested patterns; Ings et al., 2009), which contribute to increase the robustness of the community to random species extinctions (Memmott et al., 2004). In our case, lichen–tree networks had similar connectivity to typical mutualistic networks (Olesen & Jordano, 2002), but instead of a nested pattern, they showed high segregation and the presence of modules of co-occurring lichen species. Previous studies found that epiphyte-tree networks can have nested structure, but evidence is so far scarce (Blick & Burns, 2009; Burns, 2007; Taylor et al., 2016). The absence of nested patterns found here can be attributed to a relatively limited dispersal capacity of many lichens (Antoine & McCune, 2004; Morando et al., 2019), which precludes the presence of abundant early colonizers that dominate the community. Importantly, the structure of epiphytes networks can be influenced by the spatial scale of the co-occurrence (Burns & Zotz, 2010). For example, epiphyte networks showed a segregated structure when evaluated at within-tree scale (i.e. each host tree has several sampling units), in line with the pattern we found in our study. This segregation can be due to different mechanisms, reflecting, for instance, potential niche preferences for each species, or specific adaptations among species to avoid competition within host trees (Burns & Zotz, 2010). Overall, the analysis of lichen–tree networks suggest that lichen species have strong preferences that influences their within-tree coexistence. Thus, with the upcoming homogenization of ecological communities due to global change drivers (Gossner et al., 2016), the loss of microhabitats within ecosystems could result in a major threat to epiphyte lichen diversity (Boch et al., 2016; Miller et al., 2018).

Although lichen–tree networks showed a common structure characterized by lichen segregation, this structure was influenced by abiotic (climatic) and biotic attributes. In general, elevation showed a strong positive relationship with lichen richness, predicting more rich communities at higher elevation (Bässler et al., 2016). This is likely related to more stressful conditions at lower elevation where warmer temperature may hamper the effectiveness of eco-physiological functions of these poikilohydric organisms. Similarly, network modularity decreased at higher elevation. The more stressful dry conditions at lower elevation could lead to higher microhabitat specialization, resulting in the presence of specific groups of co-occurring species related to specific microhabitats. In contrast, at higher elevation, where the conditions are more favourable for lichens, generalist lichens are more widespread in the community. This probably limits the presence of exclusive groups of species associated with specific microhabitats. In addition, spatial segregation was influenced by lichen trait diversity, with higher functional dispersion leading to lower spatial segregation. This increase in co-occurrences can be explained by the limiting similarity mechanism, in which functionally contrasted rare species co-occur with abundant species, precluding functional over-redundancy (Giordani et al., 2019). In lichen communities, this pattern is emphasized by increasing water availability (Nimis et al., 2018), which may mitigate the effect of increasing temperature at the lower elevation (Vetaas, 2006; Whittaker et al., 2007).

Interestingly, we did not find any effect of forest attributes on lichen–tree network structure. Several explanations can be proposed. First, previous studies of epiphytic networks found that host tree characteristics played an important role in the structure of the system (Ceballos et al., 2016). As we did not find any effect of tree attributes at the forest level, our results suggest that the effect of host trees on the network exerted mainly at the host level and not within host, as in the present study. Second, in our study system, the gradient of forest structure is relatively short, reflecting homogeneous management conditions across the study area (di Bolzano, 2010). Third, our sampling design intended to mainly reveal the effect of climatic conditions on epiphytic lichen communities, targeting only mature trees, and thus avoiding the variability in species richness and composition related to a gradient of tree ages (Nascimbene, Ackermann, et al., 2016). Therefore, identifying the specific tree attributes that define the microhabitat diversity at the forest level could help to preserve biologically diverse lichen communities. However, the predicted reduction in precipitation associated with climate change in the coming years, including mountain regions (Gobiet et al., 2014), presents a major threat for lichen communities driven by the loss of generalist species.
4.2 | Functional traits effect on lichen species role in the network

We found that biological traits strongly influenced lichen species in the community. In particular, thallus growth form and reproduction type were the most important traits influencing both the lichens occupancy capability and role in the network. The higher abundance recorded for asexually reproducing and foliose lichens likely reflects a trade-off between local dispersal processes and thallus growth rates. Asexual reproduction allows effective local recruitment since the two symbionts (the mycobiont and the photobiont) are simultaneously dispersed, thus avoiding the uncertainty of re-establishing the lichen symbiosis, as in the case of sexually dispersed species whose spores have to meet a new photobiont. This situation is particularly favourable in forest ecosystems, where the vitality of vegetative propagules is not hampered by harsh conditions (Nimis & Martellos, 2003). Besides, foliose lichens are more competitive than both crustose and fruticose species, but due to contrasting reasons. On the one hand, foliose lichens usually have higher growth rates than crustose species (Armstrong & Bradwell, 2010), thus being more effective in spatial occupancy, which is also reflected by a higher abundance. On the other, they can also develop under relatively warm and dry conditions that prevent the colonization of fruticose species, as in the lower part of our elevation gradient (Nascimbene & Marini, 2015). The connection between these traits and the success of the lichens in the community highlights the importance of moving from a taxonomic to a functional approach where species traits are considered a key aspect of lichen communities.

Traits determining species abundance also lead to contrasting roles of the species in the networks, ultimately influencing lichens coexistence. In particular, foliose, asexually reproducing lichens behave as habitat generalists providing connections among the modules of the networks (network hubs). These lichens are able to rapidly form a dense lichen cover on trunks that may improve the water retention capacity of the substrate, providing more suitable micro-habitat conditions for species with small or thin thalli that have a low water holding capacity (Merinero et al., 2014). It is emblematic the case of Hypogymnia physodes (L.) Nyl. that contributes to the species composition of several lichen communities in montane-subalpine coniferous forests (Nascimbene, Ackermann, et al., 2016). In contrast, crustose, sexually reproducing species, as well as fruticose lichens, are segregated in their modules and behave as habitat specialists. Spatial segregation in crustose and fruticose lichens is probably related to tree-level heterogeneous microclimatic conditions (Benesperi et al., 2018). For example, crustose-calcioid species are found at the driest, underhanging, parts of the trunks that do not receive rain or stemflow (Nimis & Martellos, 2017), while fruticose-filamentous species prefer well lit conditions exposed to both rain and wind where they can maximize their metabolic activity (Coxson & Coyle, 2003; Gauslaa et al., 2008; Nascimbene et al., 2019). Despite its importance in determining lichen response to both micro and macro-climatic conditions (Aptroot & van Herk, 2007), photobiont type is not important in determining networks structure in our study system. This finding could be related to the fact that photobionts other than coccoid green algae are scarcely represented (e.g. in the case of trentepohlioid photobionts that occur only in the lower part of the elevation gradient) or almost missing (e.g. in the case of cyanobionts) along our elevation gradient (Marini et al., 2011). In general, system-level approaches such as networks allow the identification of key ecosystem components taking into account all the species in the community simultaneously. This species can then be used to improve the management of lichen communities, using them as biological indicators or priority targets for ecosystem conservation and restoration.

5 | CONCLUSIONS

In the present study, we characterized the structure of lichen–tree communities using a network approach, and evaluated how environmental drivers and lichen traits determined community assembly. Our results highlight the value of lichen–tree networks to inform about assemblage processes acting at different organizational levels. Specifically, forests epiphytic lichen communities in Southern Alps are characterized by microhabitat specialization, showing a strong segregation between the species. In these communities, coexistence is enhanced by the existence of contrasted traits between species and the presence of habitat generalists, foliose lichens characterized by asexual reproduction. Finally, environmental stress associated with water scarcity strongly reduced community diversity, principally by excluding those generalist species. Considering the upcoming decrease in precipitation and habitat diversity loss expected under global change scenarios, lichens might become one of the most threatened groups (Aragón et al., 2012; Nascimbene, Casazza, et al., 2016). The identification of species and traits contributing most to community assembly can be a key step to develop improved management actions to preserve lichen diversity in alpine environments.

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AUTHORS’ CONTRIBUTIONS

H.S., M.D., A.C. and J.N. conceived the ideas and designed the methodology; J.N. collected the data; H.S. analysed the data; H.S. and...
J.N. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data of this paper are available on Dryad Digital Repository: https://doi.org/10.5061/dryad.7sqv9s9 (Nascimbene et al., 2020).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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