Nuanced qualitative trait approaches reveal environmental filtering and phylogenetic constraints on lichen communities

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Abstract

We propose that a qualitative trait approach based on more detailed nuanced traits may reveal previously overlooked patterns, especially when combined with phylogenetic perspectives. By sampling epiphytic lichens and using a functional approach based on nuanced qualitative traits, such as a much greater resolution over photobiont identity, type of cortex, and chemical compounds, we evaluated the effects of environmental filtering and phylogenetic constraints on community assembly along a natural succession of Atlantic rainforest. We found changes in taxonomic, functional, and phylogenetic composition, structure, and diversity. Functional traits such as photobiont genera, type of cortex, reproductive structures, propagule size, and protection strategies showed strong responses to succession. Mature forests with a closed canopy impose strong environment filtering that is reflected in lichen species turnover, limiting diversity, but also holding different functional and phylogenetic composition. The use of a nuanced qualitative trait approach may overcome some of the limitations of using this type of traits and shows the importance of often-overlooked key lichen functional traits, including the presence of carbon-concentrating mechanisms in photobionts and cortex properties. Furthermore, this is the first study showing how patterns of phylogenetic assembly along forest succession structure lichen communities.

KEYWORDS
Atlantic rainforest, community assembly, functional diversity, lichenized fungi, photobiont, phylogenetic composition, turnover

INTRODUCTION

Functional trait approaches have proven to be very powerful when there is a well-established framework of trade-offs (Pérez-Harguindeguy et al., 2013). Quantitative traits are correlated or ideally directly related to the function of interest (i.e., water-holding capacity—moisture availability), while qualitative traits are surrogates of a certain function (i.e., type of photobiont—light, humidity, and temperature conditions), usually simpler, and/or

less expensive to obtain (Violle et al., 2007). A quantitative framework is still in development in many groups of organisms, such as lichens, and as such, there remains an interest in applying qualitative trait approaches. The great morphological variability of lichens makes identifying universally measurable quantitative traits difficult, and for this reason so far, most quantitative trait studies are confined to macrolichens or otherwise narrowly focused (Gauslaa & Coxson, 2011; Hurtado et al., 2020; Wan & Ellis, 2020). These approaches overlook significant portions of lichen diversity, leading to the question: Can qualitative traits be effectively applied to understanding community assembly and functional turnover in lichen communities?

Qualitative trait approaches to lichen communities have so far had mixed success, sometimes with limited predictive power. This may in part be not only due to the limited correspondence between trait categories and well-characterized functional attributes (Wan & Ellis, 2020) but also due to trait intercorrelation and nonindependence, which obscures qualitative trait functionality. Widely used traits, such as growth form and type of photobiont, provide examples of intercorrelation: All types of macrolichens have either chlorococcoid or cyanobacterial photobionts, but rarely *Trentepohlia* (e.g., filamentous species of the genus *Coenogonium*), while crustose lichens mostly have chlorococcoid alga or *Trentepohlia* as their symbiotic partner. The use of a nuanced (i.e., more detailed) perspective, basing qualitative trait categories on known or putative functional attributes in more detail, could be an alternative that makes the application of lichen functional traits more accurate and is better related to environments and lichen physiology.

Traits reflect not only adaptations but also evolutionary constraints, such as niche conservatism. Phylogenetic patterns are part of the underlying processes assembling species organization, and reflecting historical processes that shape present communities (Webb et al., 2002). Thus, environmental filters, such as those that drive succession, act together with evolutionary constraints in determining patterns of community assembly and functional composition. Besides, understanding how communities recover after disturbance, which can be seen as a "natural experiment" to test community assembly, has great importance with regard to restoration and management actions. Integrating phylogenetic approaches into community succession studies may be a valuable tool to unravel the different mechanisms driving community reassembly after disturbance (Norden et al., 2012) and to provide potential indicators for monitoring restoration and management actions (Alves & Metzger, 2006).

Tropical forests are global hotspots of biodiversity and therefore of great ecological relevance for the maintenance of world diversity and necessary for the sustainability of essential global processes, such as climate regulation (Brockerhoff et al., 2017; Marques & Grelle, 2021; Myers et al., 2000). Lichens are an important element of forest ecosystems (Asplund & Wardle, 2014), and forest structure influences the taxonomic (Dymytrova et al., 2018; Li et al., 2011) and functional composition (Aragón et al., 2019; Benítez et al., 2018; Koch et al., 2013), besides the phylogenetic diversity of epiphytic lichen communities (Nascimento et al., 2021; Hurtado et al., 2019). It has been shown that during succession in evergreen tropical forests, initial stages have higher light incidence in the understory than later stages, due to a progressive increase in tree density, biomass, and structural complexity across forest regeneration (Guariguata & Ostertag, 2001; Poorter et al., 2016; Rozendaal et al., 2019; Zanini et al., 2014). Since most lichens require moderate- to high-light levels combined with variable humidity patterns, initial and intermediate stages of forest succession facilitate the establishment of lichens that are unable to grow in later stages (Koch et al., 2013). Therefore, the understories of later successional forests, with much lower light levels combined with less variable, higher humidity values, will function as environmental filters for many lichens. Apart from reduced light, water suprasaturation inside the lichen thallus may limit photosynthesis, requiring specific adaptations (Lakatos et al., 2006).

We propose that a nuanced qualitative trait approach, grounded in well-known functional traits based on more detailed attributes (or trait states), has the potential to reveal previously overlooked patterns, especially when combined with phylogenetic perspectives. This is also applicable to crustose microlichens, as well as macrolichens. Therefore, the present study aimed to understand how environmental filtering and phylogenetic constraints act on lichen community assembly along a natural forest succession, and to evaluate the use of a functional approach based on nuanced traits. We hypothesize that (1) forest succession creates environmental filters on lichens at early stages, which tend to impose excessive light combined with drought stress, and also at late stages, with limited light combined with excessive water supply, leading to a higher turnover at various taxonomic levels (species, genera, and families) between these two extreme successional stages; (2) functional diversity filtered by these conditions is also phylogenetically structured; as a result, both early and late stages should exhibit phylogenetic clustering, whereas communities representing intermediate stages should be more diverse in functional traits and exhibit higher phylogenetic and taxonomic diversity, both as a response to the more balanced environmental conditions and due to the effect of overlap with conditions in both extreme stages; and (3) some lichen functional traits, such as photobiont and growth form, thallus anatomy (e.g., presence of a cortex), and cortical chemistry, tend to be more phylogenetically

constrained, while others, such as reproductive strategy or medullary chemistry, are less dependent on phylogenetic relationships and so may be homoplasious between different phylogenetic groups, with the expectation that they will have a weaker phylogenetic correlation and be more directly related to environmental conditions (Nelsen et al., 2020).

METHODS

Study site

This study was carried out in forest fragments in the river basin Maquiné, between 51°21′–50°05′ W and 29°20′–29°50′ S, northeastern Rio Grande do Sul state, southern Brazil, where the climate is classified as subtropical humid (Moreno, 1961). The annual mean temperature varies from 13 to 22°C, and the annual precipitation is around 1400 and 1800 mm (Hasenack & Ferraro, 1989). The original vegetation is composed of Atlantic rainforests and corresponds to the southern distribution limit of one of the most important and rich tropical forests in the world (Myers et al., 2000). The demographic density in the region is only 11 inhabitants/km^2 (Instituto Brasileiro de Geografia e Estatística, 2010), and the main economic activity is small-scale agriculture (subsistence farming), which means that we do not expect any important anthropogenic influence on lichen communities.

Sampling design

Lichen communities were sampled in four different sites, each of them located in different valleys and each containing stands of three different stages of forest succession: initial—between 6 and 10 years of natural regeneration; intermediate—between 12 and 20 years; and late—between 40 and 60 years (Koch et al., 2013). The criteria used for selecting the areas were the existence of reliable information about the forest age and the possibility of finding all stages in a similar range of altitude and climatic conditions. We estimated stand ages by interviewing local inhabitants, only those living in the areas for at least 40 years. In each successional stage from each site, two sampling units (SUs) were set (for a total of 24 SUs), where three randomly selected adult trees were sampled, all in a radius of 5 m. These tree individuals had cbh >18 cm (cbh: circumference at breast height—1.30 m from the ground), with a straight stem without branches below 1.50 m, without a smooth or peeling cortex. In total, we sampled 72 trees distributed in 24 SUs in four valley slopes, varying from 30 to 250 m of altitude.

We sampled lichens on the tree stems from 30 to 150 cm from the ground, in regular intervals of 10 cm, which represented 13 height levels, using the rubber band method (Marcelli, 1992). This method consists in placing a rubber band, gradually marked in percent-coverage classes from 0% to 100% of coverage around the stem. The length of the rubber bands varied according to the stem circumference; that is, the percent coverage is always relative to the tree size. Lichen species coverage per tree was the sum of the percent coverage (standardized according to the stem circumference), and the coverage of each species in the SU corresponded to the mean value of the three sampled trees.

Functional traits

We evaluated several qualitative lichen functional traits based on their known ecological responses to a great variety of gradients: air pollution/habitat quality (e.g., Koch et al., 2019; Lucheta et al., 2019); climate change (e.g., Hurtado et al., 2020; Matos et al., 2015); and forest changes/land use intensity (e.g., Benítez et al., 2018; Giordani et al., 2019; Koch et al., 2013), and also broke down some of them to a more nuanced classification. In total, we considered 13 categorical functional traits: (1) type of photobiont; (2) photobiont genus; (3) growth form; (4) upper cortex type; (5) main mode of reproduction; (6) main reproduction strategy; (7) type of ascoma disc; (8) size/type of propagules; (9) form of ascospores; (10) cortex substances; (11) medullary substances; (12) ascoma chemistry; and (13) pruina (the known relation of each trait to environmental gradients and the attributes or trait states are detailed in Table 1).

Environmental and structural forest variables

We assessed canopy openness by taking hemispherical pictures with fisheye lens (average of four pictures taken around 1 m from each tree and in the center of the SU). Pictures were analyzed through gap light analyzer (Frazer et al., 1999). The surrounding vegetation structure was assessed through the sum of total basal area estimated from the diameter measured at the breast height of trees with at least 5 cm in each SU. These environmental and structural forest variables were measured in an area of approximately 5 m from the center of the SU.

Data analysis

Based on the list of sampled lichen species, we generated a phylogenetic supertree, following Lücking et al. (2017)

TABLE 1   Functional traits with their known or expected relation to environmental gradients and the attributes of each trait (states) evaluated for this study

Trait	Known relation to	Attribute (trait state)
Type of photobiont	Light, temperature, air humidity, environmental quality[1,2]	Green chlorococcoid, green Trentepohlia, cyanobacteria
Photobiont genus	Light, temperature, air humidity (expected)[1,3]	*Auxenochlorella, Heveochlorella, Symbiochloris, Trebouxia* (green chlorococcoid), *Trentepohlia* (green Trentepohlia), *Nostoc, Rhizonema* (cyanobacteria)
Growth form	Light, air humidity, environmental quality[2]	Crustose attached, crustose loosely attached, squamulose, microfoliose adpressed, foliose narrow lobes = lobes <1 cm wide, foliose wide lobes = lobes >1 cm wide, fruticose, gelatinose, filamentous
Upper cortex type	Water-holding capacity, light protection (expected)[4,5]	Absent, cartilaginous, cellular, thin prosoplectenchymatous, intermediate prosoplectenchymatous, thick prosoplectenchymatous, paraplectenchymatous
Main mode of reproduction	Dispersal ability and establishment[6]	Asexual, sexual
Main reproduction strategy	Dispersal ability and establishment[6]	Apothecia, perithecia, lirellae (sexual), soredia, isidia, pseudoisidia, fragmentation, phyllidia/lobules (asexual)
Type of ascoma disc	Ascospore protection[7]	Concealed, fully exposed, partially exposed
Size/Type of propagules	Dispersal[8,9]	Ascospore volume—width × length: micro = 200 – 1000 μm; very small = 1.001–5.000 μm; small = 5.001–20.000 μm; medium = 20.001–100.000 μm; large = 100.001–500.000 μm; very large = <500.001 μm; vegetative propagules: soredia, pseudoisidia, isidia, phyllidia/lobules, thallus fragments
Form of ascospores	Dispersal[10]	Filiform-elongate = >10 times as long as wide, ellipsoid-oblong = 2–10 times as long as wide, short-rounded = one to two times as long as wide
Cortex substances	Light and herbivory protection[11,12]	Absent, lichexanthone, atranorin, usnic acid, pigments
Medullary substances	Herbivory and pathogen protection[11]	Absent/others, depsidones (1′-6′-OH)—such as stictic, norstictic, and salazinic acids; depsidones (1′-COOH-6-ME)—such as protocetraric acid; depsidones (6′- COOH)—such as psoromic acid; depsides—such as usnic and lecanoric acids; depsidones with different chemical structures; terpenes
Ascoma chemistry	Ascospore protection[11]	Absent, melanization, carbonization, pigmentation, pigmentation/melanization
Pruina	Thallus and ascospore protection[13]	Absent, presence on ascomata, presence on thallus

Note: References shown as superscripts in the "Known relation to" column: 1, Palmqvist (2000); 2, Hurtado et al. (2020); 3, Singh et al. (2019); 4, Lakatos et al. (2006); 5, Pardow et al. (2010); 6, Nelson et al. (2015); 7, Rivas Plata and Lumbsch (2011); 8, Dawson et al. (2020); 9, Deveautour et al. (2020); 10, Pringle et al. (2015); 11, Asplund and Wardle (2017); 12, Solhaug et al. (2010); and 13, Modenesi et al. (2000).

and Nascimento et al. (2021) for higher levels of classification and family-level treatments for lower levels (see Appendix S1: Figure S1 for more details and references). The tree was fully resolved to genus level and partially to species level, depending on published phylogenies, a reliable method for this type of study (Li et al., 2019). Given that the included lichen species (lichenized fungi) represent widely spaced fungal clades across the Ascomycota (four classes in total) and their actual distance in terms of branch lengths can only be assessed through a complete tree of the Ascomycota, including also all known

nonlichenized clades, we opted to express phylogenetic relatedness by the number of nodes between terminals in the subtree including only the target species. As a consequence, real branch lengths cannot be used with such an approach and all branch lengths are to be set to 1, resulting in a relative measure of phylogenetic relatedness specific to our underlying tree. In terms of interpreting phylogenetic structure, the null hypothesis of this approach equals randomization among the relative relationships of the target taxa, which is sufficient for the underlying purpose.

The phylogenetic structure of each SU of each succession stage was characterized by using the net relatedness index (NRI) and the nearest taxon index (NTI) (Webb, 2000). The positive values of NRI and NTI indicate that the community is phylogenetically clustered relative to the underlying tree, while negative values indicate phylogenetic overdispersion ($0.95 \leq p \leq 0.05$). The values of NRI and NTI at each stage were compared through the Mann–Whitney pairwise tests.

Relative percentages were calculated for each lichen family in each sampling unit and plotted for visualization of changes in composition to the three stages of forest succession. Furthermore, we performed a nonmetric multidimensional scaling (NMDS) ordination to visualize how lichen species were organized along the forest successional gradient, and a multi-response permutation procedure (MRPP) was used to test whether the three successional stages were significantly different in their species composition. The NMDS analysis used Bray–Curtis distances on a matrix of sampling units structured by lichen species cover. This matrix was previously relativized by SU to minimize the effects of local site characteristics (Matos et al., 2015). We used 500 iterations per run and Monte Carlo tests to evaluate the significance of the ordination and chose the one with the lowest stress. The analyses were performed starting with three axes, reducing dimensionality at each cycle, with a step length of 0.2 and 0.000001 as the stability criterion.

Environmental and structural forest variables (canopy openness, forest age, and sum of total basal area) were overlaid in the ordination diagram. Both analyses were computed in PC-ORD v.6 (McCune & Mefford, 2011).

We explored community functional composition by calculating CWM (community-weighted mean) of traits taking lichen cover into account (FD package) (Laliberté & Legendre, 2010) based on the 13 categorical functional traits, as previously described. We used a matrix of species cover (sampling sites × species cover) and a matrix of species traits (species × species traits). For qualitative traits, CWM represents the mean trait value in the community weighted by the cover of all species with those traits (Lavorel et al., 2008).

To analyze not only the relationship of each trait with the forest structure during succession but also the control for phylogenetic constraints, we applied two types of the partial Mantel tests: one based on community and the other based on species distance matrices. For the first, we used the following: (1) a functional matrix—based on CWMs described by SUs; (2) an environmental matrix—based on the forest structure variables (canopy openness, sum of trunk basal area, and estimated age of the forest) by SUs; and (3) a phylogenetic matrix—generated through the function "matrix.p" from "SYNCSA" R package (Debastiani & Pillar, 2012), based on the generated phylogenetic tree and a matrix of species composition. The environmental matrix

(2) was log-transformed, and the dissimilarity matrix was based on Euclidean distance. For the other two matrices (1 and 3), the dissimilarity index used was Bray–Curtis. For the partial Mantel test based on species distance, we used (1) a matrix of species coverage at each site, (2) a matrix of functional traits of each species, and (3) a matrix of phylogenetic distance between pairs of species (sum of nodes). For those matrices, the Bray–Curtis dissimilarity was used and the function "mantel.Partial" from "vegan" R package (Oksanen et al., 2020) was used for all the Mantel analyses.

Taxonomic diversity for each community along the successional gradient was calculated based on the Gini-Simpson index. Functional diversity and phylogenetic diversity were assessed for the same communities based on Rao's quadratic entropy (Debastiani & Pillar, 2012; Rao, 1982). Functional diversity was calculated using the "FD" R package, and we excluded nested traits in this analysis (type of photobiont—nested into photobiont genus; and main mode of reproduction—nested into main reproduction strategy), while phylogenetic diversity and taxonomic diversity were calculated with Phylocom 4.2 (Webb et al., 2008). Also, in order to better comprehend community changes along the gradient, we tested for species turnover by calculating beta diversity within and among stages, through the function "betadiver" from "vegan," choosing the option "sim" (Simpson beta diversity) to exclude the influence of species richness (Baselga, 2010; Simpson, 1943). We compared the diversity indexes among forest succession stages through the Mann–Whitney pairwise tests.

The complete dataset of lichen species cover, functional traits, and the phylogenetic tree is available here: https://doi.org/10.5061/dryad.51c59zw9d.

RESULTS

A total of 122 species of corticolous lichen species were sampled in the understory of the forest stands, distributed among seven orders and 24 families (Figure 1; Appendix S1: Figure S1). Some lichen families showed relatively higher abundance in initial stages of forest succession (younger stands with higher canopy openness—Figure 2a–c), while others had higher relative abundance in later stages (older forests with lower canopy openness—Figure 2a–c). There were orders represented by families with high relative abundance at both extremes of the successional gradient (such as Ostropales—Graphidaceae in initial stages, and Coenogoniaceae and Porinaceae in later stages; and Lecanorales—Parmeliaceae in initial stages and Ramalinaceae and Malmideaceae in later stages). In contrast, some orders were represented by families in one successional stage only, such as Pertusariales and Caliciales in initial stages and Arthoniales in later stages (Figure 1).
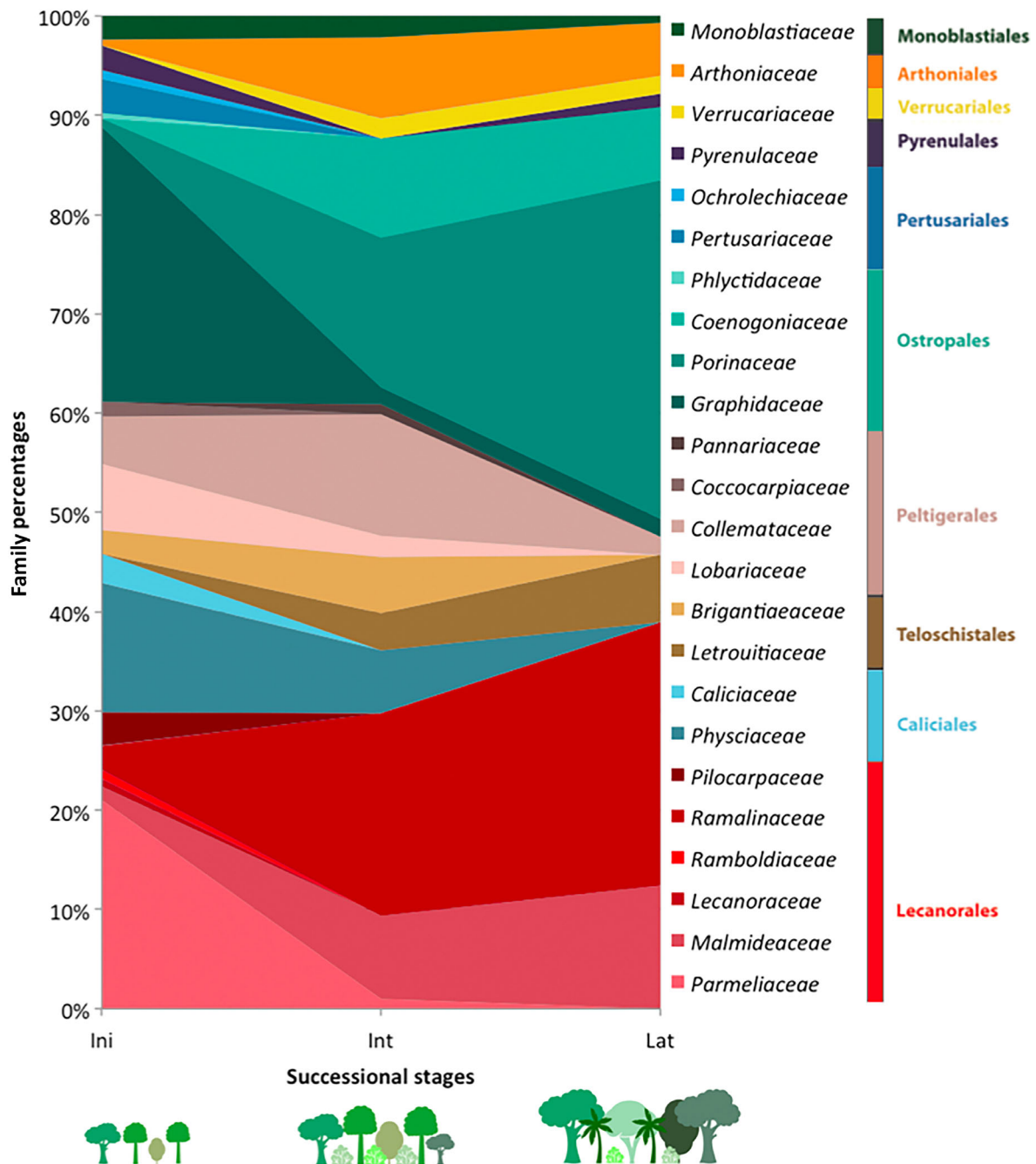
FIGURE 1 Turnover of lichen families along the three successional stages in Atlantic Forest areas. Relative percentages of lichen families' abundance in the eight sampling units in each of the successional stages, and the respective orders are shown. Families color-coded as in the phylogenetic tree (Appendix S1: Figure S1). Ini, initial (6–10 years); Int, intermediate (12–20 years); Lat, late stage (40–60 years)

The MRPP analysis showed significant differences when we compared species composition between the three stages ($T = -9.91$; $A = 0.42$; $p < 0.001$). The NMDS ordination also illustrates the variation in species composition along the gradient of forest succession (Figure 2d; Appendix S1: Figure S2). The NMDS analysis had a final stress of 13.9%, lower than expected by chance ($p = 0.001$). The first axis explained 50.2% of the lichen community composition variation, while the second axis explained 2.2%, so we used the NMDS axis 1 to summarize changes in species composition. All three stages differed significantly based on their distribution in the ordination space (Figure 2d). Regarding the phylogenetic organization of the lichen communities, NRI and NTI values showed clustered patterns (positive values) for all stages, with no significant differences among them. There was a slight tendency for NRI to be lower in the intermediate stage, and NTI to be higher in the later stage (Figure 2e,f).
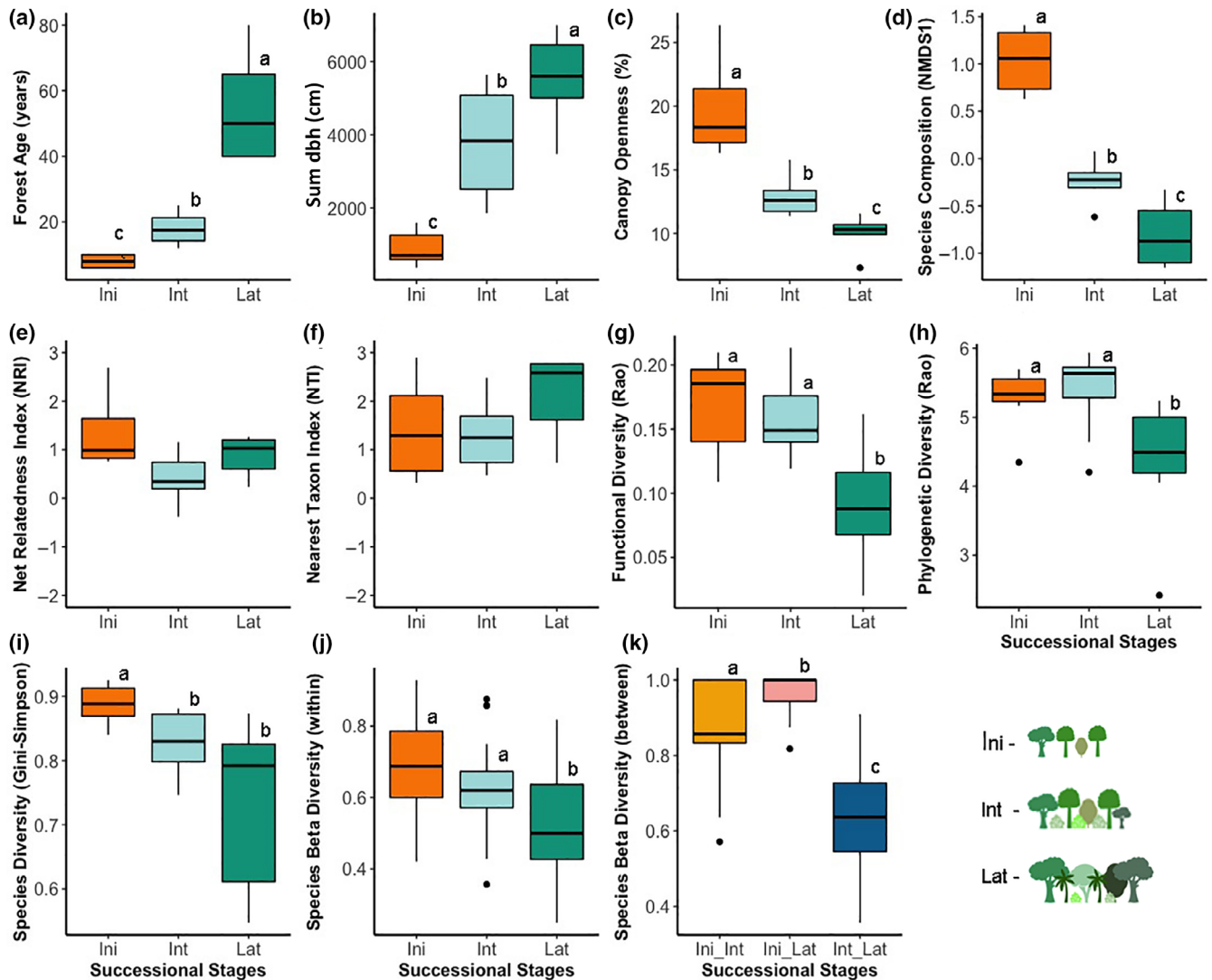
FIGURE 2 (a–c) Variation in the environmental and structural forest variables at each successional stage: (a) Forest estimated age, (b) canopy openness, and (c) sum dbh (trunk basal area); (d) changes in lichen species composition and first axis of a nonmetric multidimensional scaling ordination (Appendix S1: Figure S2); (e, f) clustered phylogenetic patterns (positive values) of (e) net relatedness index (NRI) and (f) nearest taxon index (positive values, clustered; negative, overdispersed); (g–k) decrease in the (g) functional diversity (Rao), (h) phylogenetic diversity (Rao), (i) Gini-Simpson species diversity, Simpson's beta diversity (j) within and (k) between stages of forest succession in an area of Atlantic Forest. The boxes represent the median, the first, and the third quartiles. Vertical bars show minimum and maximum values. Different letters indicate statistical differences among the successional stages. Ini, initial (6–10 years); Int, intermediate (12–20 years); and Lat, late stage (40–60 years)

Species, functional, and phylogenetic diversity showed similar patterns when related to the successional gradient. All these indices decreased in later stages of Atlantic Forest succession (Figure 2g–i). Species beta diversity within stages also decreased along the gradient, while beta diversity among stages was greater between initial and later stages, followed by a high difference between initial and intermediate stages (Figure 2j,k).

Lichen functional traits responded to changes with respect to forest succession, varying in relative abundance among initial, intermediate, and later stages. The main shifts were observed in photobiont groups and genera, growth form, type of upper cortex, reproduction strategies, propagules size, type of ascoma disc, chemical composition, and pruina (Figure 3; Appendix S1: Table S1). Some genera of lichen photobionts had higher percentages in initial stages (*Heveochlorella* and *Trebouxia*—chlorococcoid algae; and *Rhizonema*—cyanobacteria), while others had the opposite pattern, with higher percentages in later stages (*Auxenochlorella* and *Symbiochloris*—chlorococcoid algae; and *Trentepohlia*). The genus *Nostoc* (cyanobacteria) had higher percentages in intermediate stages. Regarding growth forms, foliose and fruticose species showed higher abundance in initial stages of forest succession, while
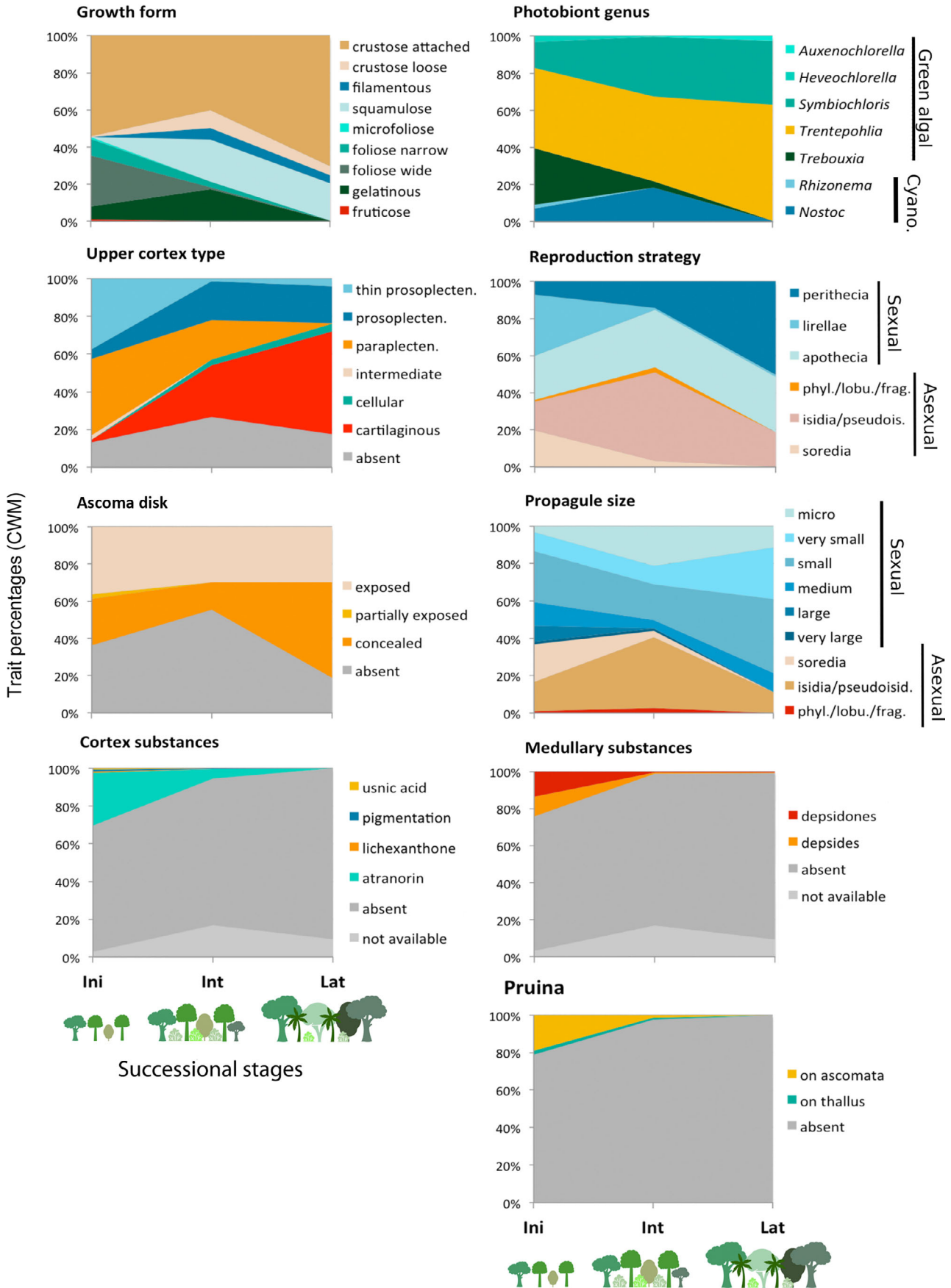
FIGURE 3 Legend on next page.

crustose, filamentous, and squamulose lichens were more frequent in later stages. Distinct types of upper cortex, such as thin prosoplectenchymatous, paraplectenchymatous, and intermediate cortex, had higher percentages of abundance in initial stages, and prosoplectenchymatous, cellular, and cartilaginous cortices were more frequent in later successional stages. Reproduction strategies such as soredia, lirellae, and thallus fragmentation were more common in younger forests, with perithecia, in older forests. Isidia and pseudoisidia showed higher percentages in both intermediate and later stages. Exposed ascoma discs were frequent along the gradient, while partially exposed discs had higher percentages in initial stages and concealed discs were more frequent in later stages. Regarding the size of lichen propagules, ascospores were bigger in older forests, and vegetative propagules were bigger in initial stages. All forms of thallus protection, such as cortex and medullary substances and pruina, showed higher percentages in initial and intermediate stages (Figure 3).

Taking into account phylogenetic constraints on the relationship between forest succession and lichen functional traits, we found that important relationships were significant even when controlling for phylogeny (following Swenson, 2019), showing high correlation values ($r > 0.3$): type of cortex, main reproduction mode, ascoma chemistry, and pruina. In the meanwhile, others were significant but had low correlation ($r < 0.2$) such as the photobiont genus, size of propagules, and medullary chemistry, and some traits had nonsignificant or extremely low phylogenetic signal, such as the type of photobiont, growth form, main type of reproduction, and cortical substances (Table 2).

DISCUSSION

Lichen community organization changed along the forest succession, partly responding to environmental conditions and partly reflecting phylogenetic constraints. Species turnover was accompanied by functional shifts from initial to late stages, and the nuanced qualitative trait perspective allowed a better understanding of such changes, revealing shifts in traits associated with light protection, hydration, and reproduction. Phylogenetic constraints are present, but weak in most of the traits.

All successional stages showed clustered phylogenetic structure. Both NRI and NTI follow this same pattern, indicating high trait conservatism both at deeper and at shallower levels in the phylogenetic tree (Webb et al., 2002). A clustered phylogenetic pattern in initial stages was also observed in plant communities (Letcher, 2010, Duarte, 2011, Norden et al., 2012. Marcilio-Silva et al., 2016). In younger forests, there is a lot of sunlight and plenty of new stems to be colonized by lichens. Nevertheless, communities are phylogenetically grouped, which could mean that only some clades are able to arrive and establish in this high-light and drier environment, usually with smoother stems. Lücking et al. (2016) compared different biomes in Mexico focusing on lichens of the family *Parmeliaceae* and detected phylogenetic clustering related to water stress. Studies in the Iberian Peninsula have also found correlation between water stress and phylogenetic clustering of lichen communities (Geedicke et al., 2016; Prieto et al., 2017). Furthermore, Sillett et al. (2000) have reported that many old-growth-associated lichens from temperate forests have dispersal limitations, while some others have microhabitat-specific requirements. In our study, species arriving and establishing first seem to have traits that ensure high dispersal/establishment ability and shorter generation times (i.e., soredia and thallus fragmentation), as also reported for plants in tropical forests (Norden et al., 2012). Therefore, strategies for efficient dispersal of lichen propagules in tropical rainforests are restricted to few groups. Intermediate and later stages were also phylogenetically clustered, showing that the decrease in canopy openness also constrains community assembly based on phylogenetic relationships corresponding to favorable traits, such as type of photobiont and photobiont genus. Lichens inside closed forest, where humidity is usually high throughout the year, need to have strategies to deal with these constraints, such as water-repellant surface structures (e.g., crustose closely attached thallus) or water-draining surfaces (e.g., crustose loosely attached thallus, absence of an upper cortex) (Hauck et al., 2008; Lakatos et al., 2006).

The changes in community assembly along a gradient is a known common pattern in community ecology, with some traits lacking phylogenetic structure closely following environmental variation (e.g., pruina, medullary chemistry), others reflecting clade-based filtering due to underlying phylogenetic constraints (e.g., type of photobiont), and

FIGURE 3 Turnover of lichen nuanced qualitative traits along the three stages of Atlantic Forest succession represented by the relative percentages of community-weighted mean (CWM) values for each trait. cyano., cyanobacteria; foliose narrow, lobes <1 cm; foliose wide, lobes >1 cm; frag., fragmentation; Ini, initial (6–10 years); Int, intermediate (12–20 years); Lat, late stage (40–60 years); lobu., lobules; paraplecten., paraplectenchymatous; phyl., phyllidia; prosoplecten., prosoplectenchymatous; pseudoisid., pseudoisidia. Ascospore size represents volume (width × length), micro (200–1000 μm), very small (1.001–5.000 μm), small (5.001–20.000 μm), medium (20.001–100.000 μm), large (100.001–500.000 μm), and very large (>500.001 μm)

TABLE 2　Forest succession influence on lichen functional traits excluding the effect of phylogeny

Functional trait (CWM)	Forest succession (community distance)		Forest succession (species distance)	
	r	**p**	**r**	**p**
Type of photobiont	−0.24	ns	**0.04**	**0.02**
Photobiont genus	**0.15**	**0.04**	**0.08**	**0.001**
Growth form	0.10	ns	**0.05**	**0.02**
Type of cortex	**0.68**	**0.001**	**0.11**	**0.001**
Main type of reproduction	−0.10	ns	0.02	ns
Main reproduction strategy	**0.45**	**0.001**	**0.08**	**0.001**
Type of ascoma disc	0.02	ns	**0.04**	**0.01**
Size of propagules	**0.12**	**0.05**	**0.06**	**0.001**
Ascospore form	0.02	ns	**0.04**	**0.02**
Cortex chemistry	0.14	ns	0.01	ns
Medullary chemistry	**0.16**	**0.03**	0.02	ns
Ascoma chemistry	**0.62**	**0.001**	0.04	0.06
Pruina	**0.35**	**0.001**	−0.02	ns

Note: The community distance column shows the results of the partial Mantel tests based on (1) a matrix of environmental and structural forest variables (forest estimated age, canopy openness, and sum dbh—trunk basal area) at each site, and (2) matrices of community-weighted mean (CWM) values for each trait at each site, excluding the effect of (3) a matrix of phylogenetic abundance-weighted distances at each site. The species distance column shows the results of the partial Mantel tests based on (1) a matrix of lichen species cover at each site, and (2) a matrix of functional traits of each species, excluding the effect of (3) a matrix of phylogenetic distance between pairs of species (sum of nodes).

Abbreviations: ns, not significant considering a $p > 0.05$; r = Mantel's statistics.

again others with either a lack of apparent correlation or with noncausal, phylogenetic correlation (e.g., main type of reproduction). Phylogenetic constraints acted on functional traits related to photobiont type, growth form, and main reproduction strategy, as well as on other traits. Some of these have been reported as phylogenetically conserved, including growth form, photobiont type (Hurtado et al., 2020; Prieto et al., 2017), and some types of cortex (Lücking, 1999), while others are relatively conserved and/or only to a small degree, such as the secondary metabolites (Lumbsch et al., 2014). Cortex anatomy (including the absence of cortex) has been associated with water relations and photoprotection in ecophysiological studies (e.g., Pardow et al., 2010). Foliicolous lichen species found at higher light intensity tend to be those with better-developed cortices (Grube & Lücking, 2002; Lücking, 1999); however, to our knowledge, this trait has not been considered at community scales for corticolous lichens. The cortex can affect liquid water repellence, with consequences for hydration and metabolic activation from liquid or vapor forms of water (Gauslaa & Coxson, 2011; Lakatos et al., 2006). While the specific surface properties of different cortex anatomies need empirical study, this is a promising and overlooked functional trait for lichen ecology. Similarly, the more frequent presence of cortical secondary metabolites and pruina in early-successional stages may be associated with increased light stress or, conversely, light

limitation in later stages. However, for both cortical anatomy and chemistry, many of these characteristics also affect herbivory (Asplund & Wardle, 2017), and so attributing their occurrence to abiotic factors alone can be misleading.

Later stage communities were characterized by small ascospores and isidia, whereas early-successional stages tended to have larger-spored species and a wider range of vegetative propagules. Conditions for spore dispersal change considerably with forest succession (decreasing airflow). Spore size has been identified as a promising functional trait in nonlichenized fungi as well (Zanne et al., 2020), and the relationships between spore size, fruiting body type, dispersal mode, and environment are important areas for further study. However, this functional trait is also phylogenetically constrained, so both environment and phylogeny may be acting to determine the observed pattern.

Taxonomic, functional, and phylogenetic diversity all showed the same pattern of decrease across forest succession. Species beta diversity within stages (between sampling units of the same stage) or heterogeneity of species composition also followed the same trend. Similar patterns have been reported in other taxonomic groups, including plants and bacteria in constraining gradients (Bryant et al., 2008, altitude in this case). In our study, they are likely decreasing due to the environmental filters of low light and high constant humidity inside closed older forests, which are constraints that require specific adaptations

for lichens to maintain positive carbon balance (Lakatos et al., 2006). Species turnover (beta diversity between stages) showed that species are being replaced along the successional gradient. It is important to note that this pattern is specific to the lower trunk communities; in tropical forests, later stages of succession tend to show an overall higher epiphyte species diversity when the middle and upper strata (canopy) are considered (e.g., Woods, 2017).

Species beta diversity was also reflected in functional changes as seen for some of the traits. The near-complete turnover in photobiont types and genera during succession would appear to be due to changing humidity and light conditions. Cyanobacterial symbionts represented an important community component in the initial and intermediate stages, but were completely absent from late-stage plots. Green algal photobionts showed a similar transition, with near-complete turnover of dominant genera. The changing photobiont identity aligns with algal physiology: The dominant taxa in initial stages (*Heveochlorella*, *Trebouxia*, *Rhizonema*, and *Nostoc*) all present carbon-concentrating mechanisms (pyrenoids or carboxysomes), thus balancing additional carbon demand under high-light incidence, whereas the photobionts in late stages (*Auxenochlorella*, *Symbiochloris*, and *Trentepohlia*) do not (Ettl & Gärtner, 2014). Carbon-concentrating mechanisms are found in most algal and cyanobacterial lineages, and reduce carbon limitation under saturating conditions (Kroth, 2015). However, leakage from pyrenoids is thought to make them disadvantageous under low-light conditions (Raven et al., 2011). The turnover in photobiont types and genera corresponds to a shift from adaptation to liquid water inputs and intermediate–high light, to adaptation to low light and water vapor activation. Reduced tolerance to wetting may seem counterintuitive in a wet forest interior; however, dense canopies and interception by epiphytes actually reduce direct wetting of lower trunks, while inputs from humid air and dew are more important (Lakatos et al., 2012). This finding emphasizes the importance of considering photobiont functional attributes in finer detail than the classic alga–cyanobacterium dichotomy, especially since photobiont identity is often closely correlated with mycobiont phylogeny. The interaction between evolutionary constraints on potential photobiont associations and photobiont physiology may be a key driver of phylogenetic constraints along environmental gradients (Nelsen et al., 2020).

Our results show clear changes in lichen community mean traits with forest succession, reflecting the dramatic changes in microenvironment with canopy closure. Many of these traits are associated with physiological functions (e.g., cortical anatomy and chemistry) or dispersal (e.g., propagule size). However, the specific mechanistic links between traits and function have been underexplored and will require future study. In particular, the physiological importance of cortex anatomy, which has thus far only been studied in Atlantic Forest in northeastern Brazil (Pardow et al., 2010), merits particular attention in other regions. It is also important to remember that some traits may also vary within species in response to environment (e.g., Asplund & Wardle, 2014; Hurtado et al., 2020). That some of these traits show strong phylogenetic constraints is added reason for further examination: Seemingly, adaptive traits may result from phylogenetic conservatism (when community has been driven by a different, correlated trait) but, contrastingly, may also offer insights into habitat change and radiations (e.g., anthraquinones in some species from *Teloschistaceae*; Gaya et al., 2015).

Environmental filtering and phylogenetic constraints drive lichen community assembly and functional organization at both initial and later stages of forest succession. Changes along this gradient reflect a turnover of species and traits from initial to later stages, with intermediate stages showing a mixture in this composition. Lichens that appear in the understory in early and intermediate stages may overlap with those found in the canopy in later stages (Holz & Gradstein, 2005; Kantvilas, 1990).

The use of a nuanced qualitative trait approach revealed strong environmental and phylogenetic filtering acting on lichen communities during tropical forest succession, overcoming some of the limitations of using these types of traits and showing the importance of often-overlooked key lichen functional attributes, including the presence of carbon-concentrating mechanisms in photobionts, cortex anatomy, and chemistry. Furthermore, this is the first study showing patterns of phylogenetic assembly along forest succession on lichen communities, setting a model for comparison with other regions and forest types.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Koch et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.51c59zw9d.

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