



Trees as habitat islands: Temporal variation in alpha and beta diversity in epiphytic laurel forest bryophyte communities

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Abstract

Aim: Trees represent striking examples of habitat islands, with various degrees of spatial isolation and evolving properties during their life cycle. Here, we investigate whether changes in habitat conditions, dispersal limitations or competition cause variation in patterns of epiphytic species richness and turnover.

Location: Madeira island.

Taxon: Bryophytes.

Methods: Using linear mixed effect models, we test whether species richness exhibits a monotonic or hump-shaped relationship with time. Two groups of host-tree species, late- and early-successional, were considered. We further identify the mechanisms explaining the observed variation in species composition by dividing beta diversity into its nestedness (β_{sne}) and turnover (β_{sim}) components and correlating them with tree age and geographical distance among trees.

Results: The best-fit models all included tree age (T), but its quadratic term (T^2) and tree height (H , here a surrogate of area) were not systematically included. β_{sim} , but not β_{sne} , correlated with host-tree age, and both β_{sim} and β_{sne} correlated with geographical distance.

Main conclusions: Tree age was consistently included in all of the best-fit models, reflecting the progressive increase in epiphyte bryophyte species richness through time. The limited contribution of T^2 and H to the best models suggests that competition for space is not a key factor on mature trees. The correlation of β_{sim} , but not β_{sne} , with host-tree age, and of β_{sim} and β_{sne} with distance among trees, suggests that variation in species composition is caused by (1) temporal community shifts due to allogenic drivers and (2) dispersal limitations, which are reflected by the higher similarity of the epiphyte communities on clustered trees rather than by an increasing probability of colonization with tree age. Since actual ancient laurel forests may no longer exist in Madeira, the conservation of clusters of late-successional trees, enhancing connectivity at small spatial scales, is of utmost importance for the conservation and recovery of the unique laurel forest epiphytic flora.

KEYWORDS

beta diversity, dispersal, epiphytes, laurel forest, Macaronesia, nestedness, species turnover

1 | INTRODUCTION

Trees represent striking examples of habitat islands (Adams, Schmitzer, & Yanoviak, 2017; Southwood & Kennedy, 1983; Taylor & Burns, 2015) that host a range of associated plant and animal communities (Mendieta-Leiva & Zotz, 2015; Mondragón, Valverde, & Hernández-Apolinar, 2015). The assembly of epiphyte communities is influenced by their dispersal capacities, geographical isolation and changing characteristics of their host through time (Campos, Vasconcelos, Ribeiro, Neves, & Soares, 2006; Klimes et al., 2012). Building upon Darwin's observations on island ontogeny to describe changes in epiphyte species richness throughout the life span of their host trees, Taylor and Burns (2015) predicted that there are three stages of epiphyte community development. During an initial stage, host trees are devoid of epiphytes because they lack sufficient architectural and physiological characteristics suitable for epiphyte establishment. During a second stage, species richness increases with time due to two main factors: (1) time *per se* and the increasing likelihood of colonization, especially in the case of species with dispersal limitations; and (2) changes in bark texture and chemistry (Fritz & Heilmann-Clausen, 2010; Fritz, Niklasson, & Churski, 2009; Ranius, Johansson, Berg, & Niklasson, 2008; Wagner, Mendieta-Leiva, & Zotz, 2015), canopy structure and stem flow (Patiño & González-Mancebo, 2011; Patiño, Gonzalez-Mancebo, Fernandez-Palacios, Arevalo, & Bermudez, 2009). During the third and final stage, epiphyte communities progress through a period of decline following host-tree mortality.

The peak of diversity during the second phase points to a competition–colonization trade-off (Rees, Condit, Crawley, Pacala, & Tilman, 2001), in which species are either pioneers with a large niche or specialized competitors (Cadotte et al., 2006). Consequently, and in line with the intermediate disturbance hypothesis (Kershaw & Mallik, 2013), the co-existence of both pioneers and species typical of mature tree stages at mid-successional stages accounts for the unimodal distribution of species richness through time (Shea, Roxburgh, & Rauschert, 2004). The subsequent loss of species during a later phase of tree growth demonstrates that the accumulation of species is not a straightforward function of habitat age, but that the number of species is increasingly constrained during community succession.

Bryophytes, which represent an important component of epiphytic floras (Nadkarni, 1984), appear as original models for colonization studies along a chronosequence for two main reasons. First, bryophytes are typically regarded as extremely good dispersers with fat-tailed spore deposition curves (Lönnell, Hylander, Jonsson, & Sundberg, 2012; Sundberg, 2005). In particular, epiphytes colonize temporary habitats at the scale of the host-tree life span, but also at the scale of the entire forest ontogeny, from the youngest colonization stages to old-growth stands. As epiphytes need to track patches of suitable trees in a dynamic landscape for persistence (Snäll, Ehrlén, & Rydin, 2005), they are expected to display high dispersal capacities. In line with this hypothesis, niche preference rather than

dispersal limitation shapes distribution patterns of Amazonian epiphytes (Mota de Oliveira, ter Steege, Cornelissen, & Gradstein, 2009). Using null model analyses based on metacommunity concepts, Mota de Oliveira and ter Steege (2015) concluded that “long-distance dispersal of bryophytes in the Amazon does not lead to geographical structure in species composition.”

Second, the role of competition in shaping bryophyte communities during colonization has been questioned (Wilson, Steel, Newman, & Tangney, 1995). In this context, the unbounded relationship between epiphytic species richness and tree age (Boudreau, Gauthier, & Bergeron, 2000; Fritz, Brunet, & Caldiz, 2009; Johansson, Rydin, & Thor, 2007; Jönsson, Thor, & Johansson, 2011; Kantvilas & Jarman, 2004; Lie, Arup, Grytnes, & Ohlson, 2009; Thor, Johansson, & Jönsson, 2010; but see Ellis & Ellis, 2013; Johansson et al., 2007; Nascimbene, Marini, & Nimis, 2009) has been interpreted in terms of the unrestricted increase in species richness in the absence of competition in unsaturated communities.

The analysis of beta diversity, and more precisely, its nestedness and turnover components, offers an attractive framework to disentangle the contribution of historical (dispersal limitations, competition) and ecological factors to observed patterns of species (Baselga, 2010). Nestedness (β_{sne}) occurs when the poorest assemblages are subsets of the richest assemblages, reflecting the orderly loss of species along, for example a gradient of geographical isolation or competition. Species turnover (β_{sim}), in turn, reflects the shift in species composition along ecological gradients (Baselga, 2010).

Here, we documented the variation in laurel forest bryophyte assemblages depending on host-tree age and size on the island of Madeira. We took advantage of the historical photograph record, which dates back to the middle of the 19th century and has since then accumulated at a very fast rate, offering a unique opportunity to retrace the evolution of the vegetation during one and a half century (Pupo-Correia, Aranha, & Menezes de Sequeira, 2011). In particular, we addressed the following questions:

1. How does species richness vary with host-tree age? We test the hypothesis that species richness is unbounded, and hence, monotonously increases with time in an unsaturated ecological system (H1).
2. To what extent do time and geographical isolation explain variation in epiphyte species composition? Given the intrinsic high dispersal capacities of bryophytes and epiphytes, in particular, we expect that:
 - i. β_{sim} correlates with host-tree age, reflecting changes in species composition due to changes in bark characteristics (H2). We further aim at identifying species shifts during the community succession.
 - ii. β_{sne} does not vary with host-tree age, because there are no colonization delays associated with dispersal constraints or decreasing colonization opportunities through time due to increasing competition (H3).



- iii. Epiphyte communities are not spatially aggregated, so that neither β_{sim} or β_{sne} correlate with geographical distance among trees (H4).

2 | MATERIALS AND METHODS

2.1 | Sampling design

The study sites (Figure 1) were chosen based on historical photographs to include the complete suite of laurel forest stages and tree ages present on Madeira. Following clear-cutting, the first woody stage is represented by a tree-heath forest co-dominated by *Vaccinium padifolium* and *Erica arborea*. The final stage of this dynamical series is the laurel forest, a multi-stratified forest up to 40 m high dominated by *Ocotea foetens*, *Laurus novocanariensis* and *Clethra arborea* (Capelo, 2004). Site selection also involved that all sites had an identical North-facing orientation, an elevation of about 1,000 m, and an identical bedrock. The use of historical documents imposed, however, a strong constraint, as photographs were recurrently taken from the most accessible places (Pupo-Correia et al., 2011), thus limiting the number of areas with a documented photograph record. Each site represents a different dynamical stage along the chronosequence. This allowed us to analyse patterns of epiphytic diversity at

the level of individual trees along the chronosequence but did not allow, in the absence of spatial replication of dynamical stages, to perform analyses at the level of forest sites.

Four sites were selected based on those criteria. Folhadal (site 1, N 32°45'11"/W 17°02'12", 1,021 m) is the oldest stand. Historical documents reveal that the stand was practically inaccessible, and, hence possibly close to the pristine condition, until 50 years ago, when conservation measures also started. *Ocotea foetens*, *L. novocanariensis* and *C. arborea* are the dominant trees. Rabaçal (site 2, N 32°45'54"/W 17°07'49", 1,000 m) is a mature laurel forest. Historical photographs (Figure 1) reveal that site 2 was dominated by an open *Erica* thicket with isolated broadleaved trees 110 years ago. The dominant trees are *L. novocanariensis* and *E. platycodon*, pointing to a mixture of trees typical of mature laurel formations such as *Laurus* and species that are characteristic of younger dynamic stages like *Erica*. The site Levada dos Cedros (site 3, N 32°49'33"/W 17°09'29", 850 m) shows evidence for clear-cutting activities 50 years ago. The canopy encompasses a mixture of tree species that are both characteristic of mature forest stages (e.g. *L. novocanariensis*, *C. arborea*) and younger dynamic stages (e.g. *V. padifolium*, *M. faya* and *E. platycodon*). Finally, another site in Rabaçal (site 4, N 32°45'03.4"/W 17°07'48.3", 955 m) is dominated by an ericaceous ticket clear-cut 110 years ago, and continued to be used by charcoal

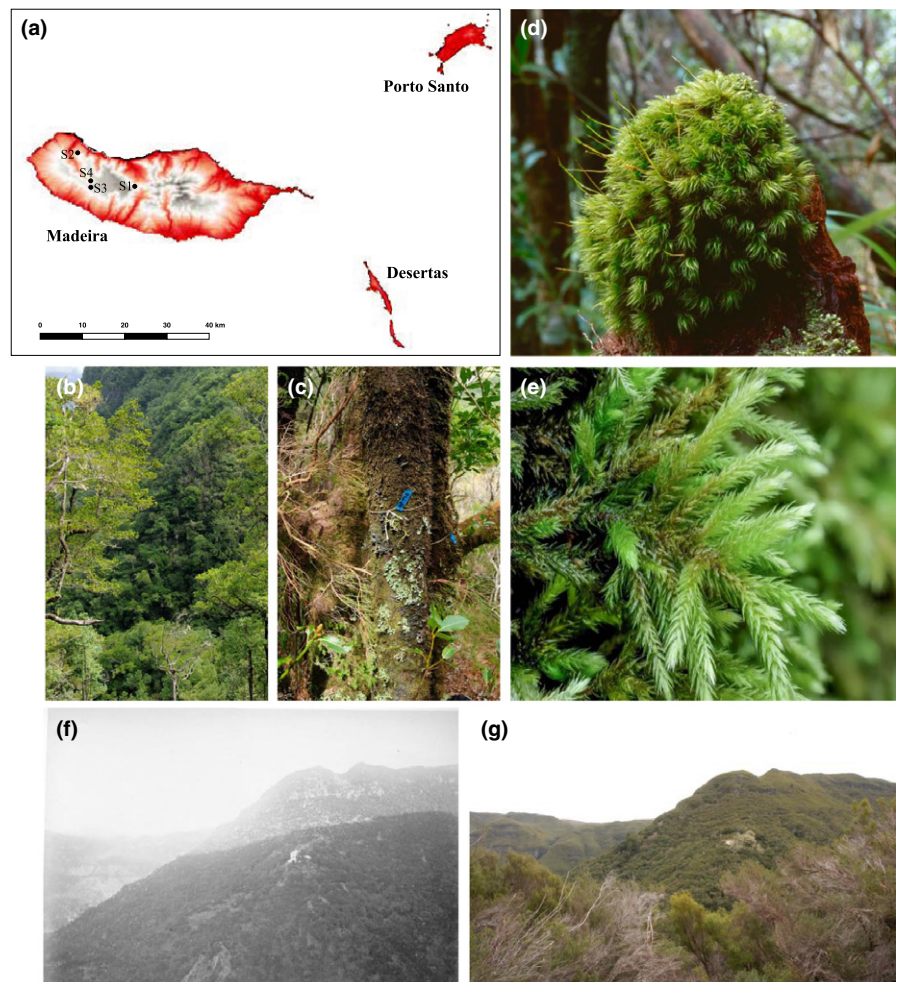


FIGURE 1 (a) Map of the oceanic archipelago of Madeira, with collection sites labelled by site code. (b) Ancient laurel forest (Site 1), with a focus on the general aspect of a typical epiphyte community on *Laurus novocanariensis* (c) and on two representative moss species of the Madeiran laurel forest, *Dicranum scottianum* (d; Photo credit: L. Hedenäs) and the Macaronesian endemic *Isothecium prolixum* (e; Photo credit: Dick Haaksma), which are typical for early- and late-successional trees respectively. (f, g) Evolution of the vegetation at Rabaçal (Site 2), from the ericaceous thicket that prevailed around 1880 (f) to the present intermediate laurel forest (g) [Colour figure can be viewed at wileyonlinelibrary.com]

burners up to the 1960s, as shown by historical documents (such as permits for clear-cutting; see Pupo-Correia et al., 2011). The stand is dominated by trees that are characteristic of young and intermediate successional stages, including *M. faya*, *E. platycodon* and *E. arborea*. The presence of a few isolated trees older than 50 years at sites 3 and 4 indicate that some trees were left during historical clear-cutting episodes, a common harvesting practice in Macaronesia (Bermúdez et al., 2007).

In each site, three plots of 20 m × 20 m were randomly selected. A distance of 10–30 m separated the plots from each other. Each plot was selected at least 10 m away from roads or paths to avoid disturbance. Within each plot, three microplots of 5 m × 5 m were randomly chosen. In each microplot, the diameter at breast height (DBH), height and age of each stem with a DBH larger than 10 cm, excluding dead wood, were measured. The age of each stem was estimated by counting the growth rings from a core extracted with a Presler borer at 50 cm (or 130 cm height, when trees at 50 cm were too wide to reach the pith). In total, the sampling included 395 individual stems belonging to 255 trees (Appendix S1).

Host trees were identified and assigned to one of two categories based on their specific physical properties. Late-successional trees (LST), including *C. arborea*, *L. novocanariensis* and *O. foetens* exhibit higher bark roughness, water-holding capacity, pH, nutrient availability and stem flow than early-successional trees (EST), including *E. arborea*, *E. platycodon*, *M. faya* and *V. padifolium*, resulting in clearly distinct bryophyte communities (Sim-Sim et al., 2011). The assignment of each tree to one of these two groups is hereafter referred to as “host-tree groups.”

2.2 | Data collection

Field work took place in December 2013. In laurel forests, epiphytes are largely restricted to the tree base, trunk and inner canopy. No specialist species occur higher-up in the middle and outer canopy, except on the oldest trees, wherein the young branches of the latter are also colonized (Patiño et al., 2009). Therefore, our sampling strategy was to sample each stem and its lateral branches up to 4 m high to cover the tree base, trunk, inner canopy and pending branches of the upper canopy to capture the entire species richness (alpha diversity) of each stem (Appendix S2). To assess the completeness of sampling in relation to differences in sample size (i.e. number of samples and trees) of each site and host-tree species studied, we compared observed species richness with predicted species richness using bootstrap, Michaelis-Menten, Chao 1, Chao 2, and first- and second-order jackknife (Jackknife 1 and 2), incidence coverage-based (ICE) and abundance coverage-based (ACE) estimators with the program EstimateS version 9.1.0 (Colwell, 2006). Although the results varied slightly among estimators, the overall mean proportion of completeness of all estimators across sites ranged from 0.83 to 0.89 (Appendix S3), suggesting that our sampling captured the bulk of the epiphyte bryophyte diversity.

Specimens of taxonomically critical genera that cannot be readily identified in the field were systematically sampled for subsequent

identification in the laboratory. More than 400 individual specimen vouchers are kept at the herbarium of the University of Liege (LG). Nomenclature follows Sérgio, Sim-Sim, Fontinha, and Figueira (2008). In the liverwort genus *Radula*, our samples included typical, fertile specimens of *Radula carringtonii* and *R. holtii*, but also a large number of depauperate, sterile specimens that cannot be identified with certainty. Specimens from these two species were therefore assigned to *R. carringtonii* in the analyses, due to the higher frequency of this species across the Madeiran laurel forest (Sim-Sim et al., 2011). Similarly, our samples included two *Zygodon* species, namely *Z. conoideus* and *Z. rupestris*, but because some scanty collections do not have gemmae, making identification impossible, all *Zygodon* specimens were assigned to *Z. rupestris*.

2.3 | Statistical analyses

To take the non-independence among observations due to the nested design (plots within sites) into account, we employed linear mixed-effect models with a top-down strategy for model selection (Bunnfeld & Phillimore, 2012; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to analyse the relationship between species richness and host-tree age. We ran these analyses in R 3.3.2 (R Development Core Team 2011) as a function of age (T) and its quadratic term (T^2) to test the fit of monotonic and unimodal models. Tree size was added to the model to disentangle the effects of time per se from the associated increase in colonizable area. Tree height (H) was selected as a proxy for size instead of DBH because of the strong correlation between DBH and tree age, to such an extent, that DBH is used in allometric relationships as a predictor of age (Pupo-Correia, 2016). Log-transformation of these fixed factors (T , T^2 and H) and species richness resulted in poorer fitting than models where variables were not transformed and, therefore, only the latter are presented. We controlled for host-tree group (GROUP) and site-specific factors (i.e. dynamical stage, SITE), which were included in the random structure. The importance of SITE and GROUP in shaping community composition was visualized using a non-metric multidimensional scaling (NMDS) analysis, employing Sørensen's index as a measure of dissimilarity among samples.

The best random effect structures, with all fixed effects considered, were selected using the small-sample corrected Akaike's information criterion (AICc; Burnham & Anderson, 2002). Each configuration of GROUP nested within SITE, SITE singly and GROUP singly was allowed to affect the intercept (random intercept). Having defined the optimal random effects structure, the “dredge” function in the MuMIn package (Bartoń, 2017) was used to find the most parsimonious combination of fixed effects, H , T and T^2 . Different model configurations were ranked according to AICc, and models with a Δ AICc value <2 were considered as having effectively equivalent levels of support (Burnham & Anderson, 2002). We calculated cumulative Akaike weights (ω AICc) using the “importance” function in the MuMIn package (Bartoń, 2017) to measure the contribution of each variable to the best models. To facilitate the comparisons among dynamical stages for each host-tree group (LST vs. EST), we



ran two additional analyses, one for each of the LST and EST groups, respectively, wherein we kept H , T and T^2 as fixed factors and SITE in the random structure.

To investigate the importance of time and geographical isolation in explaining the variation in species composition, and in particular, to disentangle the contribution of the progressive accumulation of species through time from a replacement of communities caused by changing conditions on the host tree, we divided β diversity into its two components, nestedness (β_{sne}) and turnover (β_{sim}). β_{sim} and β_{sne} were computed with the command `beta.pair` in the R package `betapart` (Baselga & Orme, 2012). For each site and host-tree group, we compared β_{sne} and β_{sim} to empirically assess whether they were significantly different. We then tested the hypothesis, within each site and tree type, that β_{sne} and β_{sim} vary as a function of time by computing the correlation of pairwise β_{sne} (and β_{sim} independently) with difference in tree age using Mantel tests. To measure the importance of geographical clustering, we performed Mantel tests between β_{sne} (and β_{sim} independently) and geographical distance among trees, using the following semi-quantitative categories: 0: host trees within the same microplot; (1) host trees in different microplots within the same plot; (2) host trees from different plots. We also used partial Mantel tests between β_{sim} and β_{sne} and host-tree age while controlling for geographical distance with the command `mantel.partial` in the R package `vegan` (Oksanen et al., 2012). Because the sampling was performed along a chronosequence of forest recovery following clear-cutting, the distribution of tree ages per host-tree group was unbalanced among sites (Appendix S4). To avoid comparison biases due to these differences in host-tree numbers per host-tree group and per site, these analyses were computed only when more than 50 trees per site and per host-tree

group were available. Thus, ESTs were considered in analyses at site 4 and LSTs at sites 1, 2 and 3.

We used indicator species analysis (ISA; Dufrene & Legendre, 1997) as implemented by the `multipatt` function of the R package `Indicspecies` (Cáceres & Legendre, 2009) to identify, for each dynamical stage and for each host-tree group, the characteristic suites of epiphyte assemblages that segregate with time on the host trees. ISA is a measure of both species frequency and specificity. Following Patiño et al. (2009), we partitioned the species depending on their occurrence on trees with three age classes (<30, 30–80 and >80 years). Only species with a frequency of >5% per host-tree group and per site were included in the analysis. To determine the significance of the ISA values for each age class, the data were randomized 4999 times.

3 | RESULTS

In the global analysis, host-tree group (GROUP) and site (SITE) were consistently included in the random structure, which included host-tree age (T), its quadratic term (T^2) and host-tree height (H) as fixed factors in all, one and two of the three best-fit models respectively (Table 1). The importance of SITE and, particularly, GROUP in shaping the investigated communities can be visualized along the first two axes of the NMDS (Appendix S5). When the host-tree group LST was analysed separately, the best-fit models consistently included T as a fixed factor and SITE in the random structure, describing a positive species-time relationship (Figure 2). T^2 and H were included in one and none of the two best-fit models respectively. For the host-tree group EST, the best-fit models consistently

TABLE 1 Coefficients of the fixed factors (tree age: T ; quadratic term of time: T^2 ; and tree height: H) included in the best fixed effect models used to predict epiphyte bryophyte species richness, while controlling for host-tree group (GROUP) and dynamical stage (SITE), which were included in the random structure. The random structure, number of parameters in the model (k), AICc, AICc difference (Δ AICc) and Akaike weights (ω AICc) derived from the AICc are given for each model. The best-fit models (Δ AICc < 2) are presented. The contribution of each variable (V.C.) to those models is estimated by summing the ω AICc of the models in which it was included. The proportion of the total variation in epiphyte bryophyte species among trees (R^2) that is accounted for by the selected models is indicated

	Intercept	T	T^2	H	k	AICc	Δ AICc	ω AICc	R^2	Model
Global tree group										
	10.813	0.672	–	0.332	6	2005.3	0	0.348	0.132	$T + H + (1 \text{SITE}) + (1 \text{GROUP})$
	10.822	0.863	–	–	5	2005.8	0.451	0.278	0.068	$T + (1 \text{SITE}) + (1 \text{GROUP})$
	10.813	0.872	–0.221	0.347	7	2007.2	1.886	0.136	0.074	$T + T^2 + H + (1 \text{SITE}) + (1 \text{GROUP})$
V.C.		0.63	0.37	0.24						
Late-successional tree (LST)										
	2.558	0.189	–0.109	–	5	70.6	0	0.372	0.185	$T + T^2 + (1 \text{SITE})$
	2.560	0.085	–	–	4	70.9	0.251	0.328	0.167	$T + (1 \text{SITE})$
V.C.		1	0.53							
Early-successional tree (EST)										
	2.112	0.271	–0.219	–	5	225.7	0	0.388	0.164	$T + T^2 + (1 \text{SITE})$
	2.110	0.058	–	–	4	227.4	1.708	0.165	0.068	$T + (1 \text{SITE})$
	2.112	0.268	–0.219	0.016	6	227.6	1.891	0.151	0.110	$T + T^2 + H + (1 \text{SITE})$
V.C.		1	0.77	0.21						

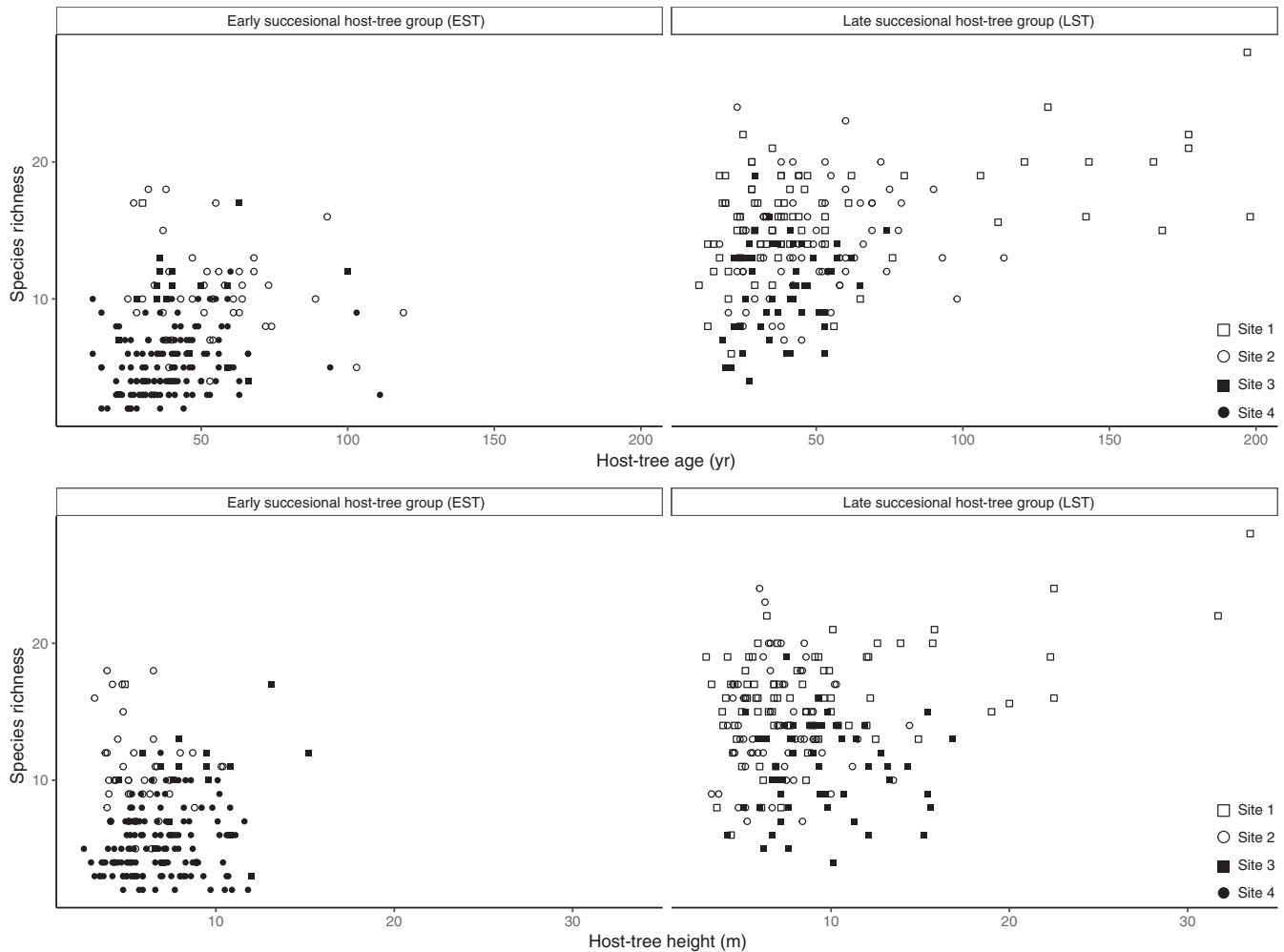


FIGURE 2 Relationships between species richness of epiphyte bryophytes and host-tree age (T ; years), and host-tree height (H ; m) for the four sites studied. The two host-tree groups, early- (EST) and late-successional host trees (LST), are shown separately

included T as a fixed factor and SITE in the random structure. T^2 and H were included in two and one of the three best-fit models respectively.

The relative contribution of each variable to the best-fit models is presented in Table 1. The ratio of the contribution of T^2 and H as compared to T was about 1–1.5:2 and 0–1:3.

The distribution of pairwise dissimilarities (β_{sim} and β_{sne}) for each site and host-tree group is presented in Figure 3. Although β_{sne} was generally lower than β_{sim} , the difference between β_{sne} and β_{sim} was never significant. For the LST group, host-tree age differences significantly correlated with β_{sim} in the oldest stands (sites 1 and 2), but not in the intermediate stand (site 3), even after controlling for spatial distance between trees. In the case of the EST group, analyses could only be conducted for the youngest stand, site 4 (number of trees >50), and also showed a significant correlation between T and β_{sim} , but not β_{sne} . Spatial distance also correlated with β_{sim} in all cases and with β_{sne} in site 4 for the EST group, and site 3 for the LST group (Table 2).

The results of ISA are presented in Table 3. For the host-tree group LST, the number of indicator species and their ISA values

increase with host-tree age and stand age. Macaronesian endemic species were restricted to trees older than 80 and 30 years in the two oldest stands (sites 1 and 2) respectively. The same trend was observed on ESTs, but with a lower number of indicator species and globally lower ISA values.

4 | DISCUSSION

Tree age (T) was systematically included in all of the best-fit species richness models, reflecting the progressive increase in species richness through time, in line with our first hypothesis (H1). The quadratic product of time (T^2), which was expected to significantly contribute to the observed variation in species richness if community assembly is progressively constrained as trees age, was included in some, but not all of the best models ($\Delta AICc < 2$), thus contributing less to explain the observed patterns in epiphyte species richness as compared to T . While a hump-shaped relationship has recurrently been reported in community-level succession studies (for review see Ellis & Ellis, 2013), the lack of a clear signal of community saturation

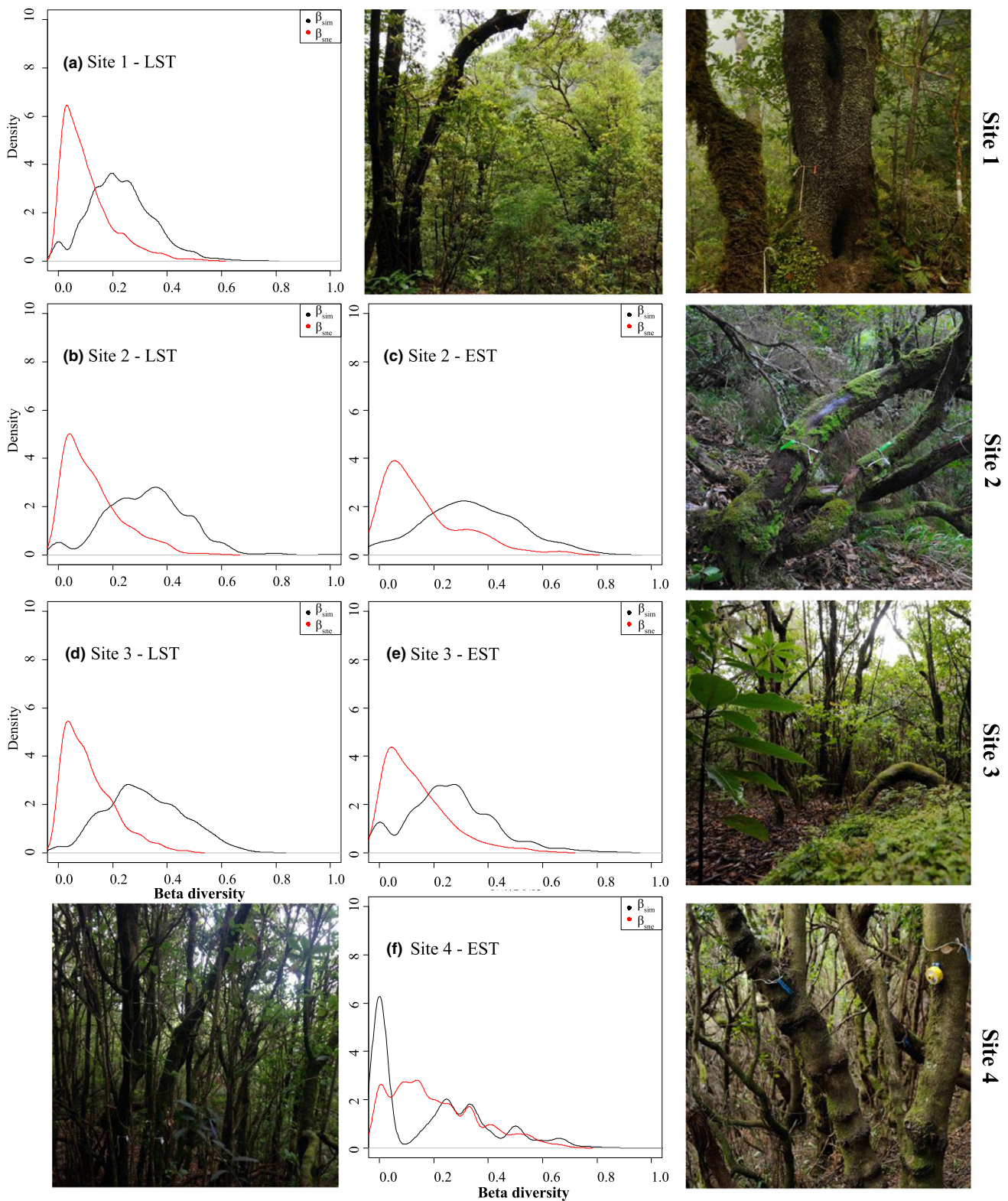


FIGURE 3 Distribution of species turnover (β_{sim}) and nestedness (β_{sne}) pairwise values between epiphyte communities in Madeiran laurel forests of late- (LST: panels a, b, d,) and early-successional host trees (EST: panels c, e, f) at four sites (sites 1–4) characterized by different successional stages [Colour figure can be viewed at wileyonlinelibrary.com]

reflects the contrasting support for monotonic vs. hump-shaped models reported in previous studies for epiphytes (contrast e.g. Johansson et al., 2007; Nascimbene et al., 2009; Ellis & Ellis, 2013).

As tree size, and hence, habitat availability, increases with tree age, a clearer signal might emerge from analyses of species densities at the scale of tens of cm^2 rather than total species richness at the scale of

TABLE 2 Mantel tests between β_{sim} and β_{sne} of epiphytic Madeiran laurel forests communities with host-tree age (with a minimum of 50 host trees per host-tree group per site) and geographical distance and partial Mantel tests between β_{sim} and β_{sne} with host-tree age controlling for the geographical distance among host trees at the four sites (site 1–4) characterized by different recolonization stages for pairs of late- (LST) and early- (EST)-successional trees

	Age		Distance		Age distance	
	β_{sim}	β_{sne}	β_{sim}	β_{sne}	β_{sim}	β_{sne}
Site 1_LST	0.28***	0.08	0.06**	0.01	0.28***	0.08*
Site 2_LST	0.10*	−0.02	0.12***	0.05	0.10*	−0.02
Site 3_LST	0.03	0.01	0.11***	0.08*	0.03	0.01
Site 4_EST	0.12**	0.04	0.09***	0.20***	0.12**	0.04

*** $p < .001$; ** $p < .01$; * $p < .05$.

entire trees (Ellis & Ellis, 2013). Host-tree height, which can be considered as a surrogate for the extent of the colonizable area, was, however, not included in the best-fit models for LSTs, and in only one of the three competing models for ESTs, with a low contribution to this model. This result suggests that area per se does not contribute to epiphytic species richness, as pointed out in former studies (Kiebacher, Keller, Scheidegger, & Bergamini, 2017; Löbel, Snäll, & Rydin, 2006a,b). Altogether, these observations suggest that, despite the inclusion of trees older than 180 years, there was no strong evidence for constraints in community succession and that competition for space does not appear as a key factor on mature trees. In fact, shoot density is associated with both negative and positive effects on fitness and epiphyte species richness, as dense cushions retain higher amounts of water, and hence, are physiologically active for longer periods than isolated shoots. Such a feature is a critical issue for poikilohydric organisms like bryophytes (Rydin, 2009), in particular on such harsh and pioneer environments as tree bark.

In agreement with our second and third hypotheses (H2, H3), β_{sim} , but not β_{sne} , significantly correlated with differences in host-tree age. These results suggest that community composition shifts (turnover of specialized communities) due to allogenic drivers during a tree's development prevail over the progressive accumulation of species through time due to dispersal limitations. For the host-tree group LST, β_{sim} significantly correlated with host-tree age differences in the oldest stands (sites 1 and 2), but not in the intermediate one (site 3). The small difference in number of LST stems among sites ($n = 53, 63$ and 83 at sites 3, 2 and 1 respectively) suggests that the lack of a significant relationship between β_{sim} and host-tree age at site 3 is not due to a lack of statistical power, but rather to the lack of trees older than 65 years in that site (Appendix S4). This finding indicates that, in the youngest stands where the whole range of host-tree ages is not encountered, and until host trees reach about 50–70 years, epiphyte species composition and richness do not substantially vary. Patiño et al. (2009) similarly found no notable increase in both epiphyte bryophyte community abundance and richness 25 years following clear-cutting. In the absence of a significant correlation between β_{sne} and host-tree age, this time-lag points to

the occurrence of major changes on trees in terms of bark roughness, texture, levels of stem flow and, perhaps, chemistry after a period of several decades, before they become suitable for a more specialized flora.

In fact, ISA analyses identified specific suites of indicator species depending on host-tree age. While old trees are characterized by a rich suite of highly specific indicator species (e.g. *Lejeunea eckloniana*, *Saccogyna viticulosa*, *Echinodium spinulosum*, *Isothecium prolixum*), species associated with younger trees (e.g. *Metzgeria violacea*, *Ulota calvescens*, *Cololejeunea minutissima*) are, however, much less numerous and exhibit much lower indicator values because of their ability to shift to terminal branches and twigs on old trees. As a result, both pioneer species of the early colonization stages and species characteristic for the oldest trees can be found on the same tree (Patiño et al., 2009).

The absence of correlation between β_{sne} and host-tree age differences does not point to the progressive colonization by species depending on their dispersal capacities. However, the correlation between β_{sim} and, to a lesser extent, β_{sne} , and the geographical distance among trees, indicates that epiphytic communities are significantly spatially structured. This means that epiphyte species composition is more similar among trees located near to each other than among trees distant from each other. Such a pattern contrasts with our last prediction (H4) because, as a consequence of the fat-tail spore dispersal kernel (Sundberg, 2005), several studies failed to report a significant contribution of connectivity in landscape-scale patterns of bryophyte species richness (Berglund & Jonsson, 2001; Moen & Jonsson, 2003; Sundberg, Hansson, & Rydin, 2006; Tangney, Wilson, & Mark, 1990). Aggregated distribution patterns were, however, consistently reported in epiphytes (Snäll, Ribeiro, & Rydin, 2003; Snäll, Hagström, Rudolphi, & Rydin, 2004; Löbel et al., 2006a, b; Wagner et al., 2015; but see Kiebacher et al., 2017). Such a spatial aggregation could be interpreted in terms of local environmental heterogeneity but, as Löbel et al. (2006b) pointed out, the scale of the observed structured pattern corresponds to the distance of a few metres, at which the density of diaspores from parental sporophytes is the highest (Sundberg, 2005; and references therein). This pattern is further confirmed by strong spatial structure patterns of genetic variation at fine spatial scales consistently reported in bryophytes in general (Hutsemékers, Hardy, & Vanderpoorten, 2013; Korpelainen, von Crautlein, Kostamo, & Virtanen, 2013), and epiphytic bryophytes in particular (Patiño et al., 2013; Snäll, Fogelqvist, Ribeiro, & Lascoux, 2004). Conducting a multiyear demographical census of epiphyllous communities transplanted from continuous forests into a network of fragmented sites, Zartman & Shaw (2006) further evidenced the crucial role of migrations in shaping epiphyllous liverwort distribution and abundance patterns. Altogether, these observations point to the crucial role of dispersal limitations in shaping the structure of epiphyte communities at small spatial scales. In fact, epiphytic mosses typically exhibit peristomial reduction, one of the morphological modifications related to hygromy in mosses (Hedenäs, 2012). The release of spores under wet conditions, which decreases their long-distance dispersal capacities, might be seen as a



TABLE 3 Indicator Species Analysis of epiphytic bryophytes in Madeiran laurel forests for three classes of tree age (<30, 30–80, >80 years), presented for late- (LST) and early-successional (EST) trees, respectively, in four sites (S1–S4) along a chronosequence of forest recolonization. For each species with an ISA >0.10, the ISA value and its significance level (* <0.05, ** <0.01, *** <0.001) are indicated. Macaronesian endemic species are highlighted in bold

	<30 years	30–80 years	>80 years
LST			
S1	<i>Cephaloziella divaricata</i> 0.16 <i>Leucobryum albidum</i> 0.16	<i>Metzgeria violacea</i> 0.41 <i>Sematophyllum substrumulosum</i> 0.33 <i>Ulota calvescens</i> 0.31 <i>Cololejeunea minutissima</i> 0.28 <i>Marchesinia mackaii</i> 0.18	<i>Lejeunea eckloniana</i> 0.82*** <i>Plagiothecium nemorale</i> 0.77*** <i>Saccogyna viticulosa</i> 0.76 *** <i>Echinodium spinosum</i> 0.73*** <i>Isothecium prolixum</i> 0.72** <i>Thamnobryum alopecurum</i> 0.59*** <i>Radula nudicaulis</i> 0.45* <i>Bryum capillare</i> 0.41* <i>Leucodon treleasei</i> 0.41* <i>Plagiomnium affine</i> 0.41* <i>Cololejeunea schaeferi</i> 0.34 <i>Lejeunea flava</i> 0.29 <i>Rhizomnium punctatum</i> 0.25 <i>Scapania gracilis</i> 0.25
S2	<i>Frullania azorica</i> 0.62* <i>Marchesinia mackaii</i> 0.32 <i>Frullania tamarisci</i> 0.26 <i>Scapania gracilis</i> 0.26	<i>Andoa berthelotiana</i> 0.56 <i>Lejeunea eckloniana</i> 0.29 <i>Metzgeria temperata</i> 0.25 <i>Leucodon sciuroides</i> 0.21 <i>Tetrastichium virens</i> 0.21 <i>Cololejeunea minutissima</i> 0.15 <i>Fissidens serrulatus</i> 0.15 <i>Isothecium algarvicum</i> 0.15	<i>Leptodon longisetus</i> 0.79** <i>Plagiochila bifaria</i> 0.765* <i>Pterogonium gracile</i> 0.61 <i>Ulota calvescens</i> 0.52 <i>Echinodium spinosum</i> 0.50 <i>Plagiochila virginica</i> 0.46
S3	<i>Sematophyllum substrumulosum</i> 0.33 <i>Frullania polysticta</i> 0.24 <i>Plagiochila stricta</i> 0.24 <i>Radula nudicaulis</i> 0.24 <i>Rhynchostegium confertum</i> 0.24	<i>Leptodon longisetus</i> 0.17 <i>Pseudoscleropodium purum</i> 0.17	
EST			
S3		<i>Leucobryum albidum</i> 0.49 <i>Dicranum scottianum</i> 0.28	<i>Cololejeunea minutissima</i> 0.97** <i>Neckera cephalonica</i> 0.95* <i>Isothecium prolixum</i> 0.94* <i>Scapania gracilis</i> 0.78
S4	<i>Frullania microphylla</i> 0.49 <i>Lejeunea lamacerina</i> 0.39 <i>Metzgeria furcata</i> 0.38 <i>Lejeunea flava</i> 0.28 <i>Neckera cephalonica</i> 0.21 <i>Sematophyllum substrumulosum</i> 0.20	<i>Frullania azorica</i> 0.23 <i>Radula lindenberiana</i> 0.16 <i>Saccogyna viticulosa</i> 0.16 <i>Isothecium prolixum</i> 0.13 <i>Zygodon rupestris</i> 0.09	<i>Lophocolea heterophylla</i> 0.57* <i>Plagiochila punctata</i> 0.55 <i>Cephaloziella divaricata</i> 0.49 <i>Porella canariensis</i> 0.46

safe-site strategy, forcing spores to land in appropriate, nearby patches where their survival is favoured (Medina & Estébanez, 2014), so that establishment, which occurs at high humidity, is a stronger evolutionary constraint than dispersal distance (Johansson, Lönnell, Rannik, Sundberg, & Hylander, 2016).

The significant correlation between β_{sim} and β_{sne} and geographical distance, but not between β_{sne} and host-tree age, suggests that dispersal limitations are reflected in similar epiphyte communities on clustered trees rather than on trees of the same age. Although host-tree age accounts for community composition shifts (see above), the prevalence of geographical distance may contribute to the poor fit of the ATT² model reported here ($R^2 = .16-.18$ for the best-fit models on the host-tree groups EST and LST respectively) and in other

studies on the relationship between epiphytic species richness and host-tree age and size (0.11; Nascimbene et al., 2009).

In conclusion, our results suggest that there is a time-lag of about 50–70 years before a substantial shift towards species-rich epiphyte communities in Madeiran laurel forests. It is precisely among those indicator species for the oldest trees that we find the highest frequency of Macaronesian endemic species as well as red-listed species considered as Vulnerable (*Cololejeunea schaeferi*, *Echinodium spinosum*, *Leptodon longisetus*) and Near-Threatened (*Andoa berthelotiana*, *Exsertotheca intermedia*, *Frullania polysticta*, *Isothecium algarvicum*, *I. prolixum*, *Leucobryum albidum*, *Plagiothecium nemorale*, *Tetrastichium fontanum*) in Madeira (Sim-Sim et al., 2014). Old trees, even if located in historically harvested forest remnants,

exhibit rich epiphyte communities provided that they are located in climatically suitable areas (Edman, Eriksson, & Villard, 2016; Lindenmayer & Laurance, 2017). Since, in Madeira, even the oldest forest stands such as Folhadal show signs of historical harvesting dating back to about 150 years ago, so that actual ancient forest stands may not exist in the archipelago, the conservation of clusters of late-successional (broadleaved) trees, enhancing connectivity at such small spatial scales as tens of metres, is of utmost importance for the conservation of the unique laurel forest epiphytic flora of Madeira.

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BIOSKETCH

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SUPPORTING INFORMATION

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