Fine-scale population dynamics help to elucidate community assembly patterns of epiphytic lichens in alpine forests

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Fine-scale population dynamics help to elucidate community assembly patterns of epiphytic lichens in alpine forests

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Abstarct

We examined the main and interactive effects of factors related to habitat filtering, dispersal dynamics, and biotic interactions, on tree-level population dynamics of a subset of species composing the epiphytic lichen pool in an alpine forest. We tested these processes evaluating the population size of 14 lichen species on six hundred and sixty-five trees within a 2 ha plot located in a high elevation alpine forest of the eastern Italian Alps. Our results indicate that community assembly patterns at the tree-level are underpinned by the simultaneous effects of habitat filtering, dispersal, and biotic interactions on the fine-scale population dynamics. These processes determine how the single species are sorted into community assemblages, contributing to tree-level community diversity and composition patterns. This corroborates the view that the response of lichen communities to environmental gradients, in terms of compositional and diversity shifts, may reflect differential species responses to different drivers.

Key-words: biotic interactions; dispersal dynamics; facilitation; habitat filtering; host tree; spatial distribution; species distribution modelling

Introduction

Ecological communities are dynamic assemblages of species whose patterns in space and time are regulated by different interacting processes. The relative importance of these processes may depend on environment type, organism traits, and spatial scale of analysis (e.g. Guisan & Thuiller 2005). Habitat filtering, dispersal dynamics, and biotic interactions are the main processes that interact to determine community patterns (Lortie *et al*. 2004). Habitat filtering, invoked in niche-based models, emphasizes the role of environmental factors and habitat quality in determining species distribution patterns, especially at the fine-scale. Among the stochastic processes (i.e., neutral theory of biodiversity; Hubbell 2001), dispersal dynamics play a crucial role in promoting and maintaining diversity, acting mainly at broad spatial scale (Wiszt *et al*. 2013). However, according to the metapopulation theory (Hanski 1999), dispersal processes could be also influential at the fine-scale. Habitat connectivity and dispersal traits may influence species patterns due to the dynamics of their patches (Snäll *et al*. 2004; Snäll, Ehrlén, & Rydin 2005). For instance, poorly dispersed species may be negatively affected by scarce connectivity among habitat patches. Biotic interactions are recognized to contribute to community structure, both at fine and broad spatial scale (Wiszt *et al*. 2013), based on the concept that species are not stand-alone entities and interact positively (e.g., facilitation) and/or negatively (e.g., competitive exclusion) with other species. Interactions influence the patterns of each species and, in turn, influence community patterns (Wiszt *et al*. 2013). The relative effects of these three processes could also depend on the species, or on the successional stage of the habitat. For instance, stochastic processes such as dispersal can initially determine which species arrive at a particular site, while non-random processes, such as habitat filtering or biotic interactions, can determine the persisting of the species (Lortie *et al*. 2004). Fine resolution studies, which simultaneously investigated the role of habitat filtering, dispersal dynamics, and biotic interactions are almost lacking for epiphytic lichens (Ellis 2012), one of the most diverse and functionally important forest organisms. The evaluation of the processes determining their distribution patterns may provide information to prevent loss of forest diversity

and ecosystem functions. There is evidence that in forest ecosystems lichen patterns are influenced by host tree features, such as tree species, size, age, crown dimension (e.g. Nascimbene *et al*. 2009; Nascimbene, Marini, Nimis, 2009) and microclimatic conditions (Nascimbene, Marini, Ódor 2012). However, dispersal dynamics may also play a key role resulting in patterns that could differ between spore- and vegetatively-dispersed species (Löbel, Snäll & Rydin 2006a). The former are considered good dispersers due to the small size of the spores, while vegetatively-dispersed species have lower dispersal capacity due to the larger size of vegetative propagules (e.g. Werth *et al*. 2006). For these species, patch connectivity could be important even at a fine spatial scale, since the establishment and development of a population are density-dependent processes affected by distance and size of propagule sources. The role of biotic interactions in structuring lichen communities is scarcely explored (Ellis 2012), although autogenic processes such as competition and facilitation are likely to contribute in determining lichen patterns. For example, along a chronosequence small and slow growing crustose lichens could be outcompeted by large and fast growing macrolichens, favoring an ecological succession. Facilitation was never demonstrated for epiphytic lichen communities (e.g., Belinchón *et al*. 2012), though biotic interactions are considered to be important drivers of lichen structure (Maestre *et al*. 2008). For instance, in soil lichen communities facilitation would be dominant under stressful conditions (Maestre *et al*. 2008, 2009), or moss carpets are known to improve the performance of high humidity demanding species (Öckinger, Niklasson & Nilsson 2005), or photobiont sharing (Rikkinen, Oksanen, & Lohtander 2002) is a plausible mechanism contributing to the success of the species in forest ecosystems.
This research aims at reacting to a scarcity of studies simultaneously incorporating the analysis of different processes (namely habitat filtering, dispersal dynamics, and biotic interactions) in shaping lichen distribution, explicitly dealing with spatial patterns (see e.g. Schei *et al*. 2012). Our study focuses on fine-scale patterns of selected species in a high elevation Alpine forest, using a fine resolution analysis that is expected to be highly predictive for fixed epiphytic organisms (Guisan & Thuiller 2005). After a preliminary analysis describing the main spatial patterns of the species

(clumped vs random) we explicitly tested the influence of factors indicative of different processes and evaluated their relative importance in determining species patterns. Specifically, we hypothesized that: (i) Habitat filtering is the main process determining fine-scale lichen distribution due to the influence of multiple drivers related to tree features and microclimate. We expected that habitat filtering influences all the species, even if associated with different drivers. (ii) The relevance of dispersal dynamics and biotic interactions should be species-specific. Specifically, we expected that the dispersal dynamics depended on the dispersal traits of the species. For example, vegetatively-dispersed species, having lower dispersal capacity, should be positively affected by patch connectivity. Considering biotic interactions, positive interactions (i.e. facilitation) may explain the pattern of the most abundant species that usually co-occur on the same tree. Conversely, negative interactions (i.e. competition) may explain the pattern of ecologically more demanding species that are likely to be outcompeted by more plastic lichens, especially in benign environments (Bertness & Callaway, 1994). (iii) The spatial distribution of lichens (clumped vs random) may correspond to a different response of the species to habitat filtering, dispersal dynamics, and biotic interactions.

Materials and methods

Study site

The study site is a 2-ha plot located in the Italian Eastern Alps at an elevation of 1900 m a.s.l (Latitude: 46.23 N; Longitude: 11.32 E; Figure 1). The climate is temperate-cold to continental, characterized by strong daily and annual temperature fluctuations. Mean annual temperature is 4.6°C, while mean annual precipitation is c. 950 mm, with a peak during summer and a dip between December and February. On average, a solid precipitation of 260 cm per winter period has been recorded at the nearest nivological station of Obereggen (1872 m a.s.l.), forming a permanent snow cover during 110-131 days per year.

Vegetation belongs to Vaccinio-Piceetea (Larici-Cembretum), with Norway spruce (*Picea abies (L.) Karst.*), stone pine (*Pinus cembra L.*), and European larch (*Larix decidua Mill.*) as main tree species. The shrub layer is mainly composed of *Daphne striata*, *Juniperus communis* subsp. *alpina*, *Rhododendron hirsutum* and *R. ferrugineum*, *Ribes alpinum*, *Vaccinium myrtillus* and *V. vitis-idaea* and the herbal layer of *Adenostyles alliariae*, *Calamagrostis villosa*, *Luzula sylvatica*, *Maianthemum bifolium*, *Melampyrum sylvaticum*, *Petasites albus*, *Saxifraga* sp.

The area is subject to the typical dynamics of many high-elevation forests in the Alps, where the significant reduction of livestock activities and the decreased intensity of silvicultural practices during the last centuries triggered a change in forest composition where larch, the initial dominant species, is decreasing its presence respect to stone pine and spruce (Carrer & Urbinati 2001). These dynamics couple with increasing tree density and canopy closure. Management activities ceased in the 90s and currently the area is completely left to natural evolution and used for long-term ecological studies.

Sampling design and data collection

All the trees taller than 130 cm were mapped with a total station and georeferenced using an electro-optical distance meter and their species (Figure 1), DBH and crown dimension recorded. Tree age has been also determined through increment coring. Further details on the sampling protocol for forest structure can be found in Carrer & Urbinati (2001) and in Carrer, Soraruf. & Lingua (2013). After an exhaustive floristic survey that yielded 84 species (Nascimbene 2013), we selected a subset of 14 species (Table 1). Precondition to be included in our sampling design was that the lichen species could be readily identified in the field with naked eye or the help of a magnifier. The species were also selected as to represent different dispersal strategies, including both sexually (i.e. by spores) and vegetatively (i.e. by lichenized propagules) dispersed species.

On each tree with a DBH >15cm, the abundance of each species was estimated as value of total coverage (in cm^2) on the stem surface up to a height of 1.80 m. Six hundred-sixty-five trees were surveyed, including 311 spruce, 239 stone pine, and 115 larch. The lichen survey was carried out in summer 2012.

Explanatory variables

We quantified 7 explanatory variables indicative of three different processes: environmental filtering, dispersal dynamics, and biotic interactions (see Appendix S1 in Supporting Information). To account for the environmental filtering process we selected four tree-level variables that are known to be among the most meaningful descriptors of forest lichen patterns: tree species, tree size (DBH), tree age, and crown volume. As a proxy for micro-topographic conditions, we calculated a curvature index in a GIS environment. A fine resolution (1-m) DEM was computed by using geographic position (x, y) and elevation (z) of each mapped tree. In this way, we were able to assess if a given tree was located on a linear, concave or convex surface.

For each lichen species on each tree we quantified the Incidence Function Model (IFM; Hanski 1994) to account for dispersal dynamics. The IFM is a typical connectivity measure used in metapopulation ecology (Moilanen & Nieminen 2002). Connectivity (S_i) was calculated for each tree by

$$S_i = \Sigma_{j \neq i} \exp(-\alpha\, d_{ij})\, A_j$$

where d_{ij} is the Euclidean distance between the tree i and each neighbor j and A the surface area occupied by a lichen species on a tree trunk. The parameter α was estimated separately for each species based on tree occupancy data, by testing different α values and selecting the value that gave the best model fit in a logistic regression model (Oksanen 2004; Jönssonn, Edman & Jonsson 2008). The value of S_i was computed using the software R version 2.15.2 (R Core Team 2012) with the add-on package 'metapop' (Oksanen 2004).

For each species at tree level we quantified the cover of the co-occuring species assuming lichen cover to be a reasonable proxy for biotic interactions (Roux et al. 2014).

Statistical analyses

To disentangle the different distribution behavior of the lichens we performed a preliminary analysis to test the spatial autocorrelation of the distribution patterns. We used the Moran's I index, a global index which computes the degree of correlation between the values of a variable (in our case, the abundance) as a function of spatial lags (Fortin, Dale & ver Hoef 2002). The analyses were computed with a lag distance of 10 m, up to 100 m that corresponds to the shortest size of the plot. We considered values of $|z(I)| > 1.96$ ($p < 0.05$).

Depending on the occurrence of the lichen species, two different approaches were used to test the effect of environmental filtering, dispersal dynamics, and biotic interactions on lichen cover. The following covariates were included in the models: tree species, age, DBH, crown volume, curvature, connectivity, and lichen cover. We also tested the interaction between age and DBH. Given the structure of our data (skew distribution), we opted to use generalized linear models (GLM). For common species ($n = 5$; frequency > 44%), lichen cover was analyzed using GLM with a negative binomial distribution to account for the overdispersion of the data (Zuur *et al*. 2009) (see Appendix S2). For relatively rare species ($n = 9$; frequency < 43%) with an excess of zero cases in the dataset, a hurdle regression model was performed (also called zero-altered or two-part models; Zuur *et al*. 2009). Ignoring zero inflation can create problems in model inference by biasing the estimated parameters and standard errors, as well as overdispersion (Martin *et al*. 2005; Zuur *et al.* 2009). In our case, the zero inflation was the result of a large number of 'true zero' observations caused by the real ecological effect of interest (i.e., unsuitable habitat; Martin *et al.* 2005) Specifically, we applied a zero-truncated negative binomial (ZANB) to account for the overdispersion of the data (for more details of the models specification see Appendix S2). In both the models (GLM and ZANB), all predictors were standardized by mean-centering and dividing by two standard deviations to improve interpretability of parameter estimates, particularly when interactions were fitted, and continuous and categorical factors are combined in the same model (Gelman 2008). Negative binomial GLM was analyzed using the 'MASS' package (Venables & Ripley 2002) in R, while the hurdle model using the 'pscl' package (Zeileis, Kleiber & Jackman 2008; Jackman 2012) in R.

We used an information-theoretic model selection procedure to evaluate alternative competing models (Burnham & Anderson 2002). We compared the fit of all possible candidate models obtained by the combination of the predictors using second-order Akaike's information criterion (AICc). Models were chose that differed from the AICc of the best fitting model by < 4. We used the Akaike weights (w_i) to measure the relative importance of each predictor, summing the w_i across the models ($\sum w_i$) in which the predictor occurred. For each parameter, we used model averaging in order to incorporate model selection uncertainty into our parameter estimates (Burnham & Anderson 2002; Grueber *et al*. 2011). Individual predictor variables that had an Akaike weight > 0.75 or model averaged confidence intervals that did not include 0 were considered as most important predictors. Model comparison was implemented using the 'MuMIn' package (Barton 2013) in R.

Finally, the variation in lichen cover was decomposed for each species using a series of (partial) regression analyses implemented in the 'vegan' package for R (Oksanen *et al*. 2013). The total explained variation (TVE) in lichen cover was partitioned into seven components (adjusted R^2; Peres-Neto *et al*. 2006): the pure effect of environmental filtering (E), dispersal dynamics (D), and biotic interactions (B); three first-order joint components (E∩D, E∩B, D∩B); and the joint component among the three groups (E∩D∩B). In the environmental filtering component (E) we included tree species, tree size (DBH), tree age, canopy volume, and curvature. In the dispersal dynamics components (D) we included the connectivity index, while in the biotic interactions component (B) the cover of the other lichen species.

All the statistical analyses were performed separately for each species.

Results

Lichen species and spatial patterns

The 14 species widely differed in frequency (Table 1), ranging from a minimum of 3% of colonized trees for *Letharia vulpina* up to a maximum value of 97,6 % for *Parmeliopsis ambigua*. Three species were extremely common, since they were recorded on more than 90% of the trees, while five species were relatively rare, being recorded on less than 20% of the trees.

After the spatial autocorrelation analysis the species were equally distributed in two groups (Table 1; Appendix S2): i) lichens with a clumped spatial pattern and ii) lichens with a random spatial pattern. Both groups included vegetatively- and spore-dispersed species.

Drivers of fine-scale lichen patterns

Among the variables related with habitat filtering, tree species was by far the most important for both clumped and randomly distributed groups (Figures 2, 3; Appendix S4, S5), only the extremely generalist species *Hypogymnia physodes* being not significantly influenced by this factor. Age and DBH mainly influenced clumped distributed species also by a significant interaction (Figure 4; Appendix S6). While DBH had in general a positive effect (except for one species), Age had contrasting effects with species preferring either young or old trees. Crown dimension had a significant influence on only two species with clumped distribution, with contrasting effects.

For the remaining exploratory variables: i) microclimatic conditions, as inferred by the effect of microtopography, influenced the distribution of five species, two of them preferring trees located on exposed sites (i.e. relatively sun exposed and dry conditions) and three of them preferring trees in small depressions, i.e. sheltered and humid conditions (Figures 2, 3; Appendix S4, S5); ii) dispersal dynamics, as inferred by the role of connectivity, influenced the distribution of five species, mainly reproducing by vegetative propagules (4 species), including two randomly distributed lichens (Figures 2, 3; Appendix S4, S5).

Biotic interactions, as inferred by the role of lichen cover, positively influenced four common species with clumped distribution, while had a negative effect on one relatively rare species with random distribution (Figures 2, 3; Appendix S4, S5).

The relative role of environmental filtering, dispersal dynamics and biotic interactions

The variation partitioning analysis indicated that the total variation in species abundance patterns explained by the models was higher for clumped species (explained variation range between 6 and 37%) than for randomly distributed species (explained variation range between 3 and 12%) (Table 2). Habitat filtering was the most important process for almost all the species, except for *Hypogymnia physodes* and *Pseudevernia furfuracea* for which biotic interaction was the main process determining their patterns (explained variation 15% and 17%, respectively) with an additional impact of the shared component between biotic interaction and environmental filtering, summing up to 12% of the total variance. Dispersal dynamics seemed to have a negligible influence in shaping lichen distribution in our study system (explained variation range between 1 and 3%).

Discussion

Our results reveal that habitat filtering is the main process accounting for the fine-scale patterns of our selected species, indicating that habitat features are the main drivers of lichen distribution for both clumped and randomly distributed species. Dispersal dynamics and biotic interactions play a significant role mainly for clumped species.

Habitat filtering

Tree species is the most important environmental factor whose effect is mainly related with species-specific differences in the chemical and physical traits of the bark, chiefly pH and texture (e.g. Fritz & Heilmann-Clausen 2010; Király *et al.*, 2013). These differences may be relevant even among relatively similar host trees, such in the case of our three coniferous species. Besides tree species, tree size and age are also important drivers of local lichen patterns (Nascimbene *et al*. 2009), with both direct and interactive effects. According to an ‘area effect’, tree size positively influences abundance patterns fostering the population size. Tee age seems to have species-specific effects with some lichens alternatively preferring young or old trees, according with either a pioneer or a late-successional behavior. The interaction between tree size and tree age indicates a decrease of the positive effect of tree size on lichen cover with increasing tree age, even to become neutral on older trees (> 180 years). On these old trees, lichen dynamic are more influenced by a 'time per se' effect (i.e. time available for colonization and increase of population size) than by an 'area effect'. In addition, tree size gains importance on large trees, while age gains importance on small ones, corroborating the hypothesis that the 'area effect' and "time per se" effect are two complementary mechanisms influencing lichen patterns in forest ecosystems. Crown dimension influenced the distribution of only two species, with contrasting effects. *Chaenotheca chrysocephala*, preferring environmental conditions protected from rain, was positively affected by crown dimension, while *Hypogymnia physodes*, which prefers well-lit conditions, was negatively affected by this driver. In general, the effect of this tree level factor is poorly explored in the lichen literature (e.g. Nascimbene *et al*. 2008), although it is likely to interact with dispersal dynamics and to influence microclimatic conditions (e.g. Nascimbene *et al*. 2008, 2009). Further evidence for the importance of microclimatic conditions (Nascimbene, Marini & Ódor 2012) is provided by the significant contribution of microtopography to the abundance pattern of five species, discriminating between those preferring very humid-shaded (e.g. *Schismatomma pericleum*) or relatively dry and well-lit conditions (i.e. *Pseudevernia furfuracea*).

Dispersal dynamics and biotic interactions

Dispersal dynamics scarcely affect the abundance patterns of our selected species. This confirms the hypothesis that dispersal plays a minor role in determining fine-scale patterns (Schei *et al*. 2012). However, the positive effect of habitat connectivity on several vegetatively-dispersed species suggests a trait-mediated response predicting that at fine-scale dispersal dynamics are influential for poor dispersers (Löbel, Snäll & Rydin 2006b). For these species, an excessive distance from propagule sources may hinder the density-dependent processes of establishment and population growth.

A positive effect of biotic interactions was found for the most common species, indicating that their success may depend on some kind of facilitation. To the best of our knowledge, this is the first time that this processes is detected for epiphytic lichens, although, our data did not allow a direct evaluation of the mechanisms behind this effect (e.g., Belinchón *et al*. 2012). Anyway, the high relative importance of biotic interactions in explaining the abundance patterns of *Hypogymnia physodes* and *Pseudevernia furfuracea* suggests that photobiont sharing could be a plausible mechanism. Indeed, these two species host phylogenetically close-related photobionts (Hauck, Helms & Friedl 2007) that could be alternatively used to promote their occurrence along wide ecological gradients (Blaha, Baloch & Grube 2006). Contrary to our expectations, we found low support to competition hypothesis. We found indeed that only one species, such as *Tuckermannopsis chlorophylla*, showed a negative effect of biotic interactions. Also, the effect of biotic interactions seems to play a minor role in determining fine-scale patterns. This could be due to a presence of moderate stress levels in the study area that determine a neutral effect of biotic interactions, as suggested by Maestre *et al*. (2009a, b).

Clumped vs randomly distributed species

The two different patterns of abundance distribution (clumped vs random) correspond to a different response of the species to the drivers indicative of the three processes. The group of clumped species includes lichens that are very common in different types of alpine forests (Nascimbene, Nimis & Dainese 2014) where they constitute the keystones of epiphytic lichen communities. Our results indicate that their patterns are determined by a multiple and complex (i.e. interactive effects) response to several drivers indicative of habitat filtering, dispersal and biotic interactions. This complex behavior may ensure a high degree of adaptation enhancing the resistance and resilience of their populations to forest dynamics induced by natural and anthropogenic disturbances. On the contrary, the group of randomly-distributed species mainly includes relatively rare lichens that have more specific ecological requirements (Nascimbene, Nimis & Dainese 2014). Their abundance patterns are ruled by more simple dynamics, mainly related to habitat filtering. In particular, their strict dependence on the host tree species suggests that they are strongly influenced by tree dynamics. In our dynamic forest, species related with open, larch-dominated stands (e.g. *Letharia vulpina*; Nascimbene, Nimis & Dainese 2014) could be relicts restricted to remnant patches whose connectivity is fundamental for their maintenance, such in the case of *Tuckneraria laureri* and *Tuckermannopsis chlorophylla*. On the other hand, spruce-related species (e.g. *Schismatomma pericleum*; Nascimbene, Nimis & Dainese 2014) may be in an expansion phase enhanced by the increasingly available substrate.

Conclusions

The insights provided by this study on the processes determining fine-scale spatial patterns of epiphytic lichens may contribute to a more conservation-oriented forest management. The high dependence of lichen patterns on habitat filtering highlights the importance of forest management in shaping the dynamics of these organisms at the local level. Indeed, most of the main factors affecting habitat conditions relevant for lichens are controlled by management practices (Nascimbene, Thor & Nimis 2013). On this basis, conservation-oriented management should improve local habitat heterogeneity favouring the coexistence of various tree species with different size and age (i.e., mixed multi-layered and uneven-aged stands). Microtopography could further contribute to habitat heterogeneity, providing fine-scale variability of microclimatic conditions that determine the local occurrence of species with different ecological requirements. Forest management is also responsible for connectivity between trees, that favours the dispersal dynamics of several, mainly vegetatively dispersed, lichens. Yet, the relationships of many species with tree dynamics suggest that habitat heterogeneity should be maintained also at the landscape level enhancing the presence of forest patches at different successional stages.

Besides external processes, our study also highlights the importance of autogenic processes related with biotic interactions for few species. Research in this field is still in its infancy but promising results are expected from specific investigations aimed to reveal the biological mechanisms driving biotic interactions. The case of the photobiont sharing (Rikkinen, Oksanen & Lohtander 2002) that could explain the ecological plasticity of keystone species is just a first example.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1. Descriptive statistics of the covariates.

Appendix S2. Description of the species distribution modeling.

Appendix S3. Moran´s I correlograms.

Appendix S4. Model averaged coefficients for variables predicting species with clumped distribution.

Appendix S5. Model averaged coefficients for variables predicting species with random distribution.

Appendix S6. The effect of tree age on the response of *Parmeliopsis ambigua* and *Vulpicida pinastri* cover to tree size (DBH).

Table 1. Study species. Nomenclature and information on growth form and dispersal strategy were retrieved from Nimis & Martellos (2008). In the last two columns the frequency (F) of the species (expressed as percentage of trees on which they occurred) and the type of spatial pattern (SP; C = clumped, R = random) are reported.

Species name	Dispersal strategy	F (%)	SP
Calicium viride Pers.	Sexual/spores	44.2	C
Chaenotheca chrysocephala (Ach.) Th.Fr.	Sexual/spores	68.1	C
Chaenotheca trichialis (Ach.) Th.Fr.	Sexual/spores	42.1	C
Evernia divaricata (L.) Ach.	Asexual/fragmentation	28	R
Hypogymnia physodes (L.) Nyl.	Asexual/soredia	97	C
Letharia vulpina (L.) Hue	Asexual/soredia	3.4	R
Parmeliopsis ambigua (Wulfen) Nyl.	Asexual/soredia	97.6	C
Platismatia glauca (L.) W. L. Culb. & C. F. Culb.	Asexual/isidia	12.6	R
Pseudevernia furfuracea (L.) Zopf	Asexual/isidia	90.1	C
Ramalina obtusata (Arnold) Bitter	Asexual/soredia	17.4	R
Schismatomma pericleum (Ach.) Branth & Rostr.	Sexual/spores	28.7	R
Tuckermannopsis chlorophylla (Willd.) Hale	Asexual/soredia	17.8	R
Tuckneraria laureri (Kremp.) Randlane & Thell	Asexual/soredia	18.6	R
Vulpicida pinastri (Scop.) J.E.Mattsson & M.J.Lai	Asexual/soredia	35.3	C

Table 2. Variation partitioning of (a) species with clumped distribution and (b) species with random distribution. The total variation explained was partitioned among environmental filtering (E), dispersal dynamics (D), and biotic interactions (B). Values are adjusted R^2 in %. Adjusted fractions of total variation explained (TVE, in %) were estimated following the procedure of Peres-Neto et al. (2006).

	Pure components			Shared components				
	E	D	B	E∩D	E∩B	D∩B	E∩D∩B	**TVE**
(a) Species with clumped distribution								
Calicium viride	3	-	-	-	-	3	-	**6**
Chaenotheca chrysocephala	4	2	-	0	0	-	-	**6**
Chaenotheca trichialis	16	1	1	0	0	-	0	**18**
Hypogymnia physodes	4	-	15	0	12	-	0	**31**
Parmeliopsis ambigua	17	1	6	-	7	1	-	**32**
Pseudevernia furfuracea	8	-	17	-	12	-	-	**37**
Vulpicida pinastri	9	3	1	1	1	0	-	**15**
(b) Species with random distribution								
Evernia divaricata	3	-	1	-	2	-	-	**6**
Letharia vulpina	1	-	1	-	2	-	-	**4**
Platismatia glauca	4	-	0	-		-	0	**4**
Ramalina obtusata	12	-	-	0	0	0	-	**12**
Schismatomma pericleum	6	-	-	-		0	-	**6**
Tuckermannopsis chlorophylla	3	-	-	-	0	-	0	**3**
Tuckneraria laureri	3	-	-	-	0	-	0	**3**

Figure captions:

Figure 1. (a) Study area, (b) study site: a 2-ha plot located in the Italian Eastern Alps at an elevation of 1900 m a.s.l (Latitude: 46.23 N; Longitude: 11.32 E).

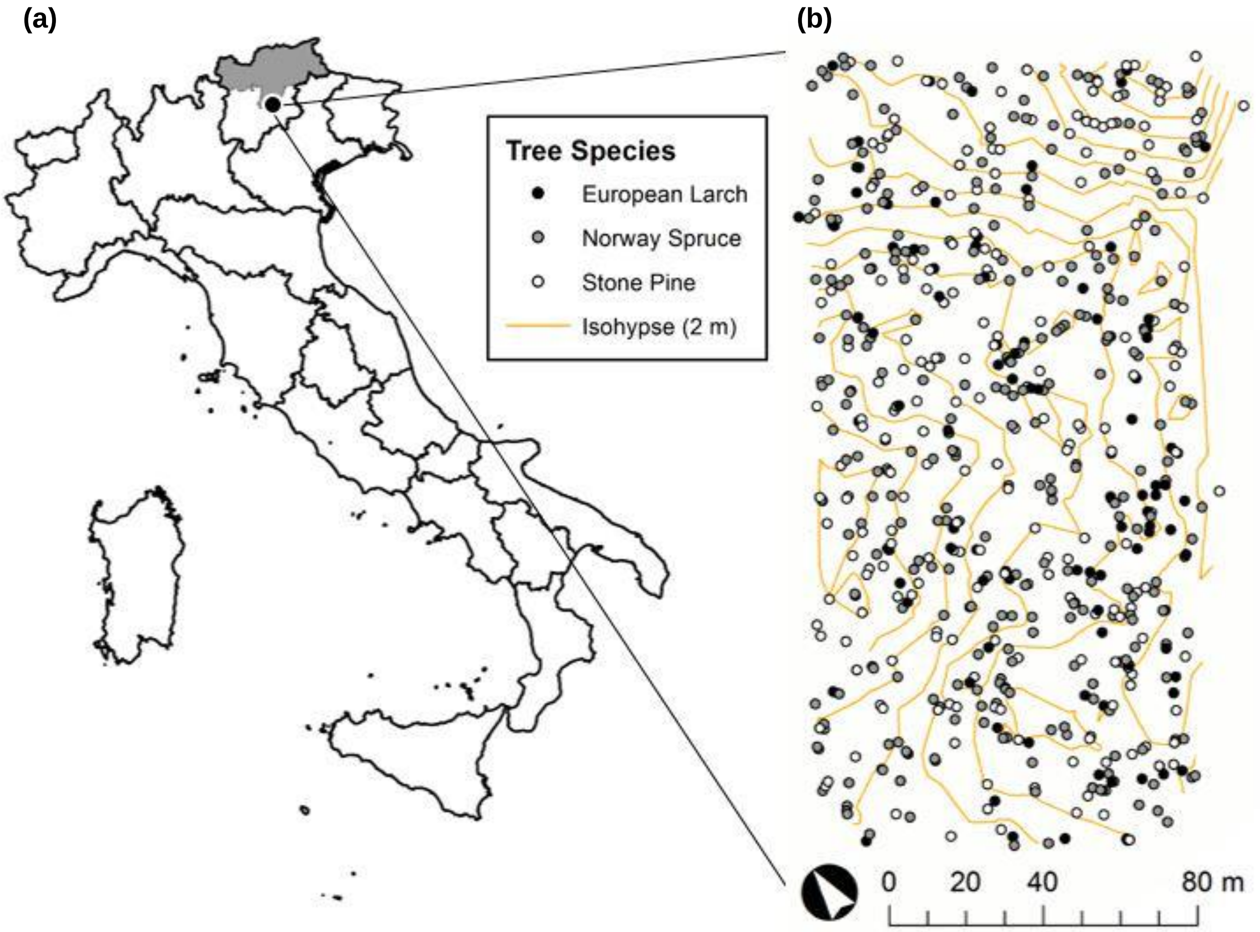


Figure 2. Sum of model weights ($\sum w_i$) for each variable estimated by the multi-model inference procedure for species with clumped distribution. Predictors that consistently occurred in the most likely models ($\sum w_i > 0.75$) or model averaged confidence intervals that did not include 0 were considered well supported by our data and considered as most important predictors (in grey). The distribution of lichen species was modeled using hurdle regression (a-c) or GLM (d-g). The direction of the relationship is indicated by (+) or (-) for continuous variables. For tree species, the main host species, resulting from Tukey contrasts, is indicated: (L) larch, (P) stone pine, (S) spruce, and (n.s.) not significant.

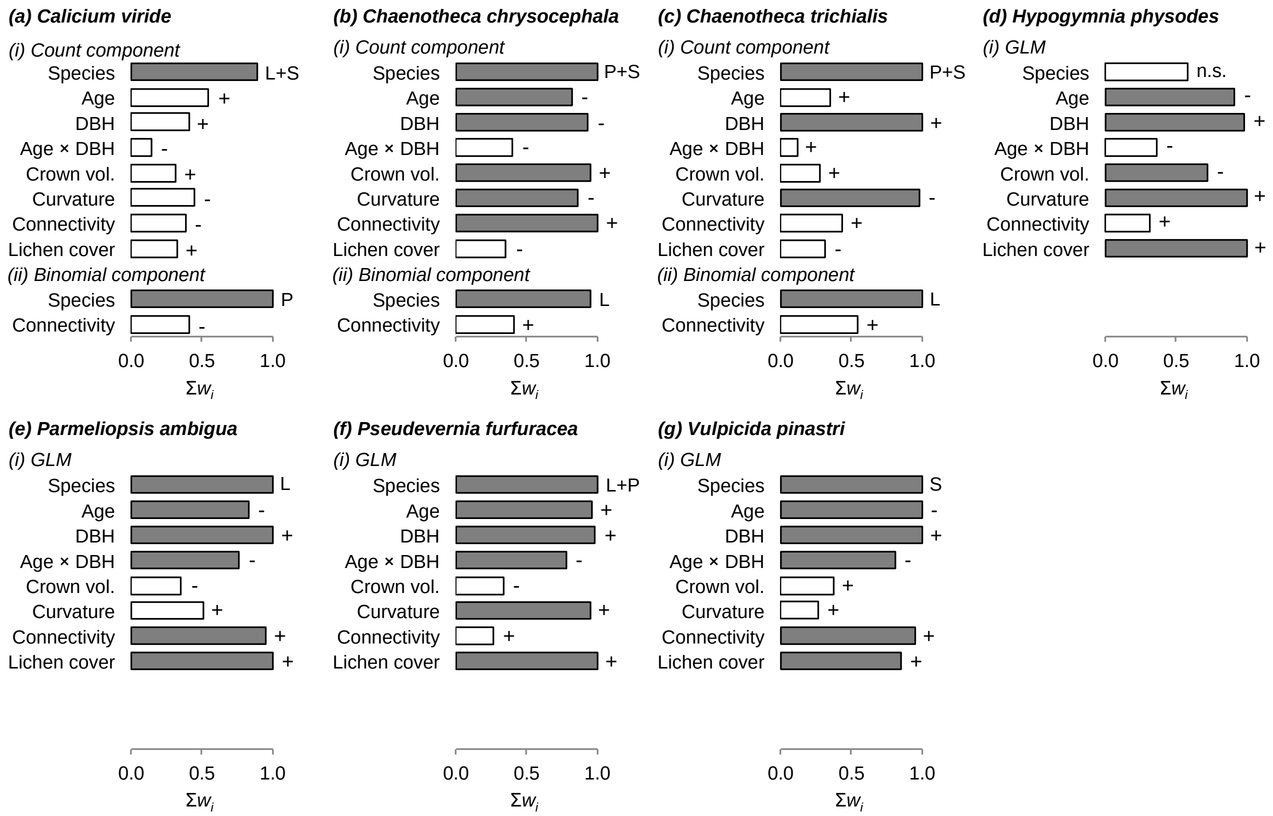


Figure 3. Sum of model weights ($\sum w_i$) for each variable estimated by the multi-model inference procedure for species with random distribution. Predictors that consistently occurred in the most likely models ($\sum w_i > 0.75$) or model averaged confidence intervals that did not include 0 were considered well supported by our data and considered as most important predictors (in grey). The distribution of lichen species was modeled using hurdle regression (a-c and e-g) or GLM (d). The direction of the relationship is indicated by (+) or (-) for continuous variables. For tree species is indicated the main host species resulting from Tukey contrasts: (L) larch, (P) stone pine, (S) spruce, and (n.s.) not significant.

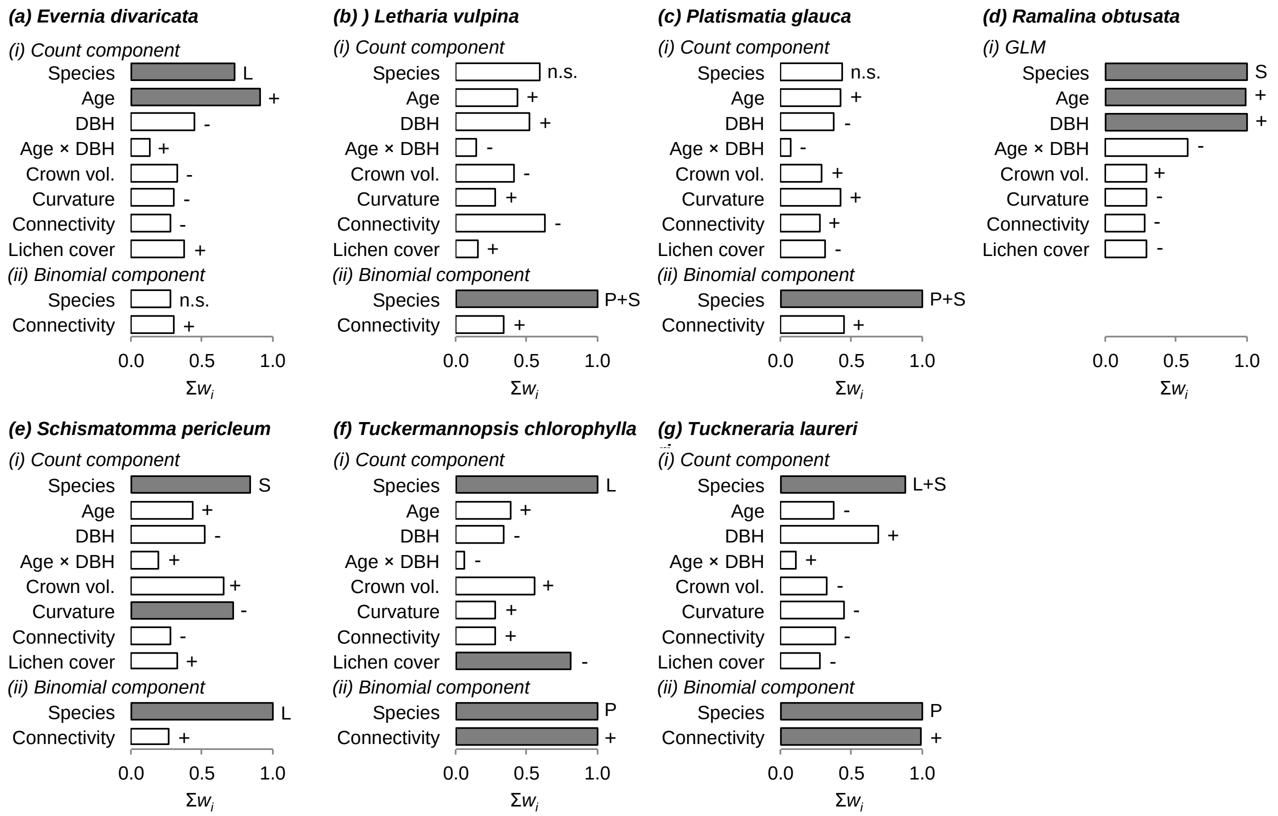
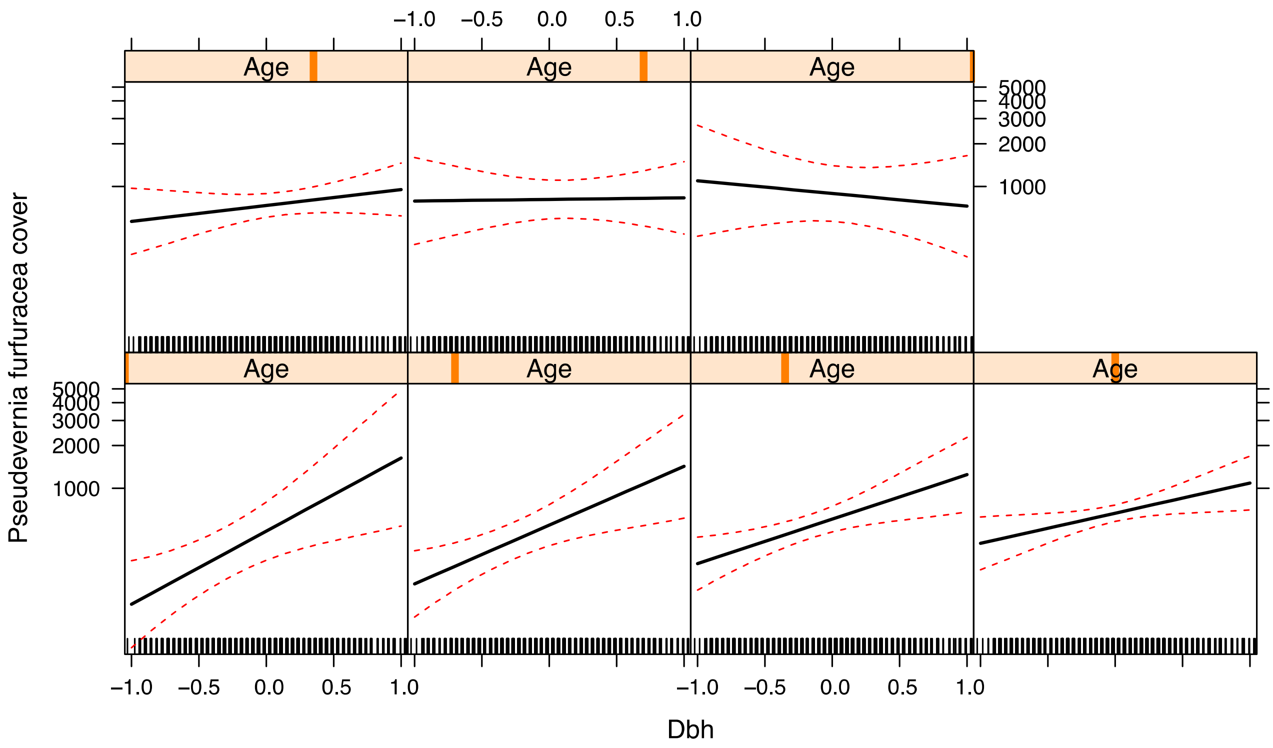


Figure 4. The effect of tree age on the response of *Pseudevernia furfuracea* cover to tree size (DBH). DBH have been standardized on two standard deviation (SD) following Gelman (2008).



SUPPORTING INFORMATION

Appendix S1. Descriptive statistics of the continuous factors used in the models.

	Mean ± SD	Min	Max
(a) Environmental variables			
DBH (cm)	35.4 ± 11.9	6	70
Tree age (years)	149.1 ± 28.4	51	260
Crown volume (m^3)	63.6 ± 53.5	0.7	449.1
Curvature index	-1.3 ± 93.0	-541.8	487.8
(b) Dispersal dynamics (IFM)			
Calicium viride	0.4 ± 2.0	0.0	29.0
Chaenotheca chrysocephala	122.9 ± 389.1	0.0	6778.0
Chaenotheca trichialis	0.9 ± 3.9	0.0	51.2
Evernia divaricata	0.2 ± 1.0	0.0	13.0
Hypogymnia physodes	441.4 ± 1465.3	0.0	33399.2
Letharia vulpina	0.1 ± 0.5	0.0	7.1
Parmeliopsis ambigua	719.5 ± 1098.6	0.0	9679.3
Platismatia glauca	0.2 ± 0.8	0.0	9.3
Pseudevernia furfuracea	4.5 ± 8.1	0.0	62.3
Ramalina obtusata	0.1 ± 0.3	0.0	4.8
Schismatomma pericleum	0.2 ± 1.2	0.0	16.2
Tuckermannopsis chlorophylla	0.3 ± 1.1	0.0	10.8
Tuckneraria laureri	1.8 ± 8.2	0.0	95.9
Vulpicida pinastri	0.9 ± 4.1	0.0	90.7
(c) Biotic interaction (cover co-occuring species in cm^2)			
Calicium viride	5772.3 ± 5362.3	15	45520
Chaenotheca chrysocephala	5694.0 ± 5370.9	20	45515
Chaenotheca trichialis	5285.5 ± 5149.6	0	45520
Evernia divaricata	5994.9 ± 5392.0	20	45520
Hypogymnia physodes	3415.7 ± 3493.5	0	21250
Letharia vulpina	5996.7 ± 5388.4	20	45515
Parmeliopsis ambigua	3773.7 ± 4045.0	0	41505
Platismatia glauca	5984.2 ± 5387.8	20	45520
Pseudevernia furfuracea	5052.3 ± 4444.4	20	44020
Ramalina obtusata	6039.1 ± 5417.2	20	45520
Schismatomma pericleum	5647.8 ± 5259.6	20	45520
Tuckermannopsis chlorophylla	5992.2 ± 5388.4	20	45515
Tuckneraria laureri	5992.4 ± 5387.2	20	45520
Vulpicida pinastri	5994.6 ± 5388.5	20	45515

Appendix S2. Description of the species distribution modeling.

Three steps were considered in defining the GLM models (see Zuur et al. 2009): (i) the choice of the distribution for the response variable (Y_i) and the definition of its mean and variance; (ii) the definition of a predictor function specifying the covariates; and (iii) the link between the predictor function and the mean of the distribution (Zuur et al. 2009). In our case, the following GLM was applied:

1. Y_i, the lichen cover at tree $_i$, was negative binomial distributed (NB) with mean μ_i and a dispersion parameter k.
2. The predictor function (η_1) included the following covariates: tree species, age, DBH, crown volume, curvature, connectivity, and lichen cover. We also tested the interaction between age and DBH.
3. There was a logarithm link between the mean of Y_i and the predictor function

The mathematical formulation was:

$$Lichen\ cover_i \sim NB(\mu_i, k)$$

$$E(Lichen\ cover_i) = \mu_i \quad \text{and} \quad var(Lichen\ cover_i) = \mu_i + \frac{\mu_i^2}{k} = \mu_i + \alpha \times \mu_i^2$$

$$\log(\mu_i) = \eta_i$$

$$\eta_i = \alpha + fTree\ species_i + Age_i \times DBH_i + Crown\ volume_i + Curvature_i + Connectivity_i + Lichen\ cover_i$$

Hurdle model includes two components: (1) a count model for the positive values and (2) a binomial probability model for the distribution of zero values. The count component was modeled using a truncated negative binomial (ZANB) model with a logarithmic link function $log(\mu_i)$ to account for the overdispersion of the data. The binomial component was instead modeled using a binomial error distribution and a logit link function $logit(\mu_i)$. Applying the hurdle model we assumed that a species absence or zero abundance was due to changes in host trees and dispersal dynamics. Thus, the predictor function of binomial component (η_{bi}) included tree species and connectivity as covariates, while the predictor function of count component (η_{ci}) included all covariates (as for GLM).

The mathematical formulation was:

$$Lichen\ cover_i \sim ZANB(\mu_i, \pi_i, k)$$

$$E(Lichen\ cover_i) = \frac{1-\pi_i}{1-P_0} \times \mu_i \quad where \quad P_0 = \left(\frac{k}{\mu_i + k}\right)^k$$

$$var(Lichen\ cover_i) = \frac{1-\pi_i}{1-P_0} \times \left(\mu_i^2 + \mu_i + \frac{\mu_i^2}{k}\right) - \left(\frac{1-\pi_i}{1-P_0} \times \mu_i\right)^2$$

$$log(\mu_i) = \eta_{c_i}$$

$$logit(\mu_i) = \eta_{b_i}$$

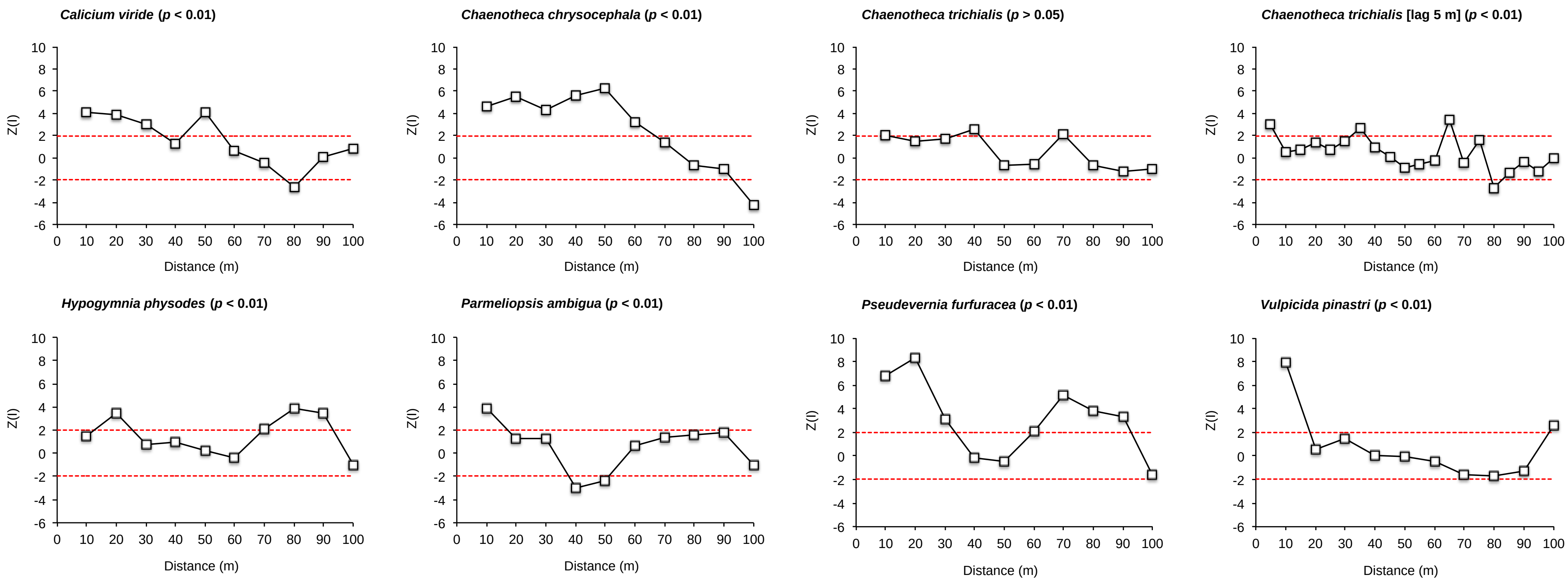
$$\eta_{c_i} = \alpha_1 + fTree\ species_i + Age_i \times DBH_i + Crown\ volume_i + Curvature_i + Connectivity_i + Lichen\ cover_i$$

$$\eta_{b_i} = \alpha_2 + fTree\ species_i + Connectivity_i$$

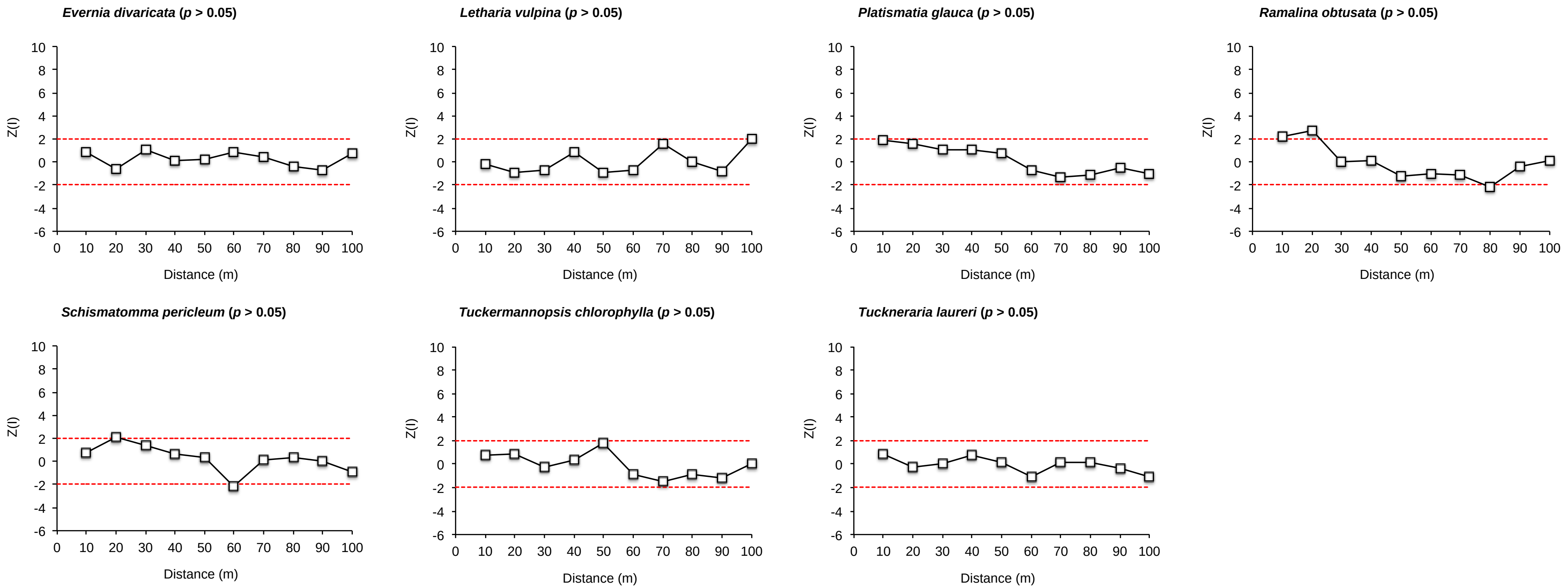
where π_i is the probability that $Y_i = 0$ (*Lichen cover*$_i = 0$).

Appendix S3. Moran´s I correlograms for the 14 studied species, using a lag distance of 10 m. For *Chaenotheca trichialis* the graph based on a lag distance 5m is also given. Global significance, after applying Bonferonni correction, is reported. Species are grouped according to spatial distribution in (a) clumped and (b) random.

(a) Species with clumped distribution



(b) Species with random distribution



Appendix S4. Model averaged coefficients, standard errors (SE), confidence intervals (CI) and relative importance (cumulative Akaike weight) for variables predicting species with clumped distribution: (a) *Calicium viride*, (b) *Chaenotheca chrysocephala*, (c) *Chaenotheca trichialis,* (d) *Hypogymnia physodes,* (e) *Parmeliopsis ambigua*, (f) *Pseudevernia furfuracea,* and (g) *Vulpicida pinastri*.

(a) *Calicium viride*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	6.214	0.190	5.841	6.586	
Pine [3]	-0.409	0.240	-0.878	0.061	0.89
Spruce	0.143	0.221	-0.291	0.576	"
Age	0.267	0.210	-0.145	0.679	0.54
DBH	0.136	0.166	-0.190	0.461	0.41
Age × DBH	-0.571	0.352	-1.261	0.119	0.14
Canopy	0.123	0.186	-0.242	0.487	0.31
Curvature	-0.175	0.141	-0.451	0.102	0.44
Connectivity	-0.275	0.244	-0.753	0.202	0.38
Lichen cover	0.147	0.179	-0.203	0.498	0.32
(a) Binomial component					
(Intercept)	-0.079	0.200	-0.471	0.314	
Pine [3]	-0.762	0.248	-1.247	-0.277	1.00
Spruce	0.303	0.233	-0.153	0.758	"
Connectivity	-0.194	0.178	-0.542	0.154	0.41

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(b) ***Chaenotheca chrysocephala***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	5.985	0.161	5.670	6.300	
Pine [3]	0.432	0.198	0.044	0.819	1.00
Spruce	-0.582	0.195	-0.964	-0.199	"
Age	-0.298	0.145	-0.581	-0.015	0.83
DBH	-0.505	0.192	-0.881	-0.129	0.93
Age × DBH	-0.312	0.202	-0.707	0.083	0.40
Canopy	0.609	0.200	0.216	1.001	0.95
Curvature	-0.264	0.108	-0.476	-0.052	0.85
Connectivity	1.005	0.221	0.572	1.439	1.00
Lichen cover	-0.146	0.170	-0.478	0.187	0.35
(a) Binomial component					
(Intercept)	1.381	0.250	0.890	1.871	
Pine [3]	-0.562	0.289	-1.129	0.005	0.95
Spruce	-0.832	0.278	-1.377	-0.286	"
Connectivity	0.242	0.240	-0.229	0.712	0.41

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(c) ***Chaenotheca trichialis***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	5.590	0.334	4.935	6.244	
Pine [3]	0.335	0.387	-0.424	1.094	1.00
Spruce	1.726	0.349	1.041	2.410	"
Age	0.008	0.224	-0.431	0.446	0.35
DBH	1.060	0.184	0.700	1.420	1.00
Age × DBH	0.277	0.319	-0.349	0.903	0.12
Canopy	0.114	0.245	-0.365	0.594	0.28
Curvature	-0.496	0.157	-0.803	-0.188	0.98
Connectivity	0.151	0.132	-0.107	0.409	0.44
Lichen cover	-0.136	0.193	-0.515	0.243	0.31
(a) Binomial component	-1.744	0.281	-2.295	-1.193	
(Intercept)	0.368	0.268	-0.157	0.894	
Pine [3]					1.00
Spruce	0.196	0.333	-0.456	0.849	"
Connectivity	2.768	0.311	2.159	3.378	0.54

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(d) ***Hypogymnia physodes***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(Intercept)	6.931	0.141	6.655	7.207	
Pine [3]	-0.284	0.139	-0.556	-0.011	0.58
Spruce	-0.247	0.139	-0.520	0.026	"
Age	-0.246	0.098	-0.439	-0.054	0.91
DBH	0.467	0.147	0.179	0.755	0.98
Age × DBH	-0.167	0.143	-0.448	0.114	0.36
Canopy	-0.246	0.123	-0.488	-0.004	0.72
Curvature	0.349	0.088	0.177	0.522	1.00
Connectivity	0.073	0.087	-0.097	0.243	0.31
Lichen cover	1.360	0.100	1.163	1.556	1.00

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(e) ***Parmeliopsis ambigua***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(Intercept)	8.058	0.109	7.844	8.273	
Pine [3]	-0.304	0.131	-0.562	-0.046	1.00
Spruce	-0.787	0.126	-1.034	-0.540	"
Age	-0.115	0.094	-0.301	0.071	0.83
DBH	0.651	0.119	0.417	0.886	1.00
Age × DBH	-0.441	0.140	-0.716	-0.167	0.76
Canopy	-0.113	0.123	-0.355	0.128	0.35
Curvature	0.132	0.084	-0.034	0.297	0.51
Connectivity	0.217	0.084	0.053	0.381	0.94
Lichen cover	0.473	0.091	0.294	0.652	1.00

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(f) ***Pseudevernia furfuracea***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(Intercept)	6.837	0.153	6.538	7.137	
Pine [3]	-0.089	0.184	-0.451	0.273	1.00
Spruce	-0.642	0.177	-0.989	-0.295	"
Age	0.217	0.133	-0.046	0.479	0.96
DBH	0.417	0.162	0.098	0.735	0.98
Age × DBH	-0.467	0.195	-0.850	-0.084	0.78
Canopy	-0.145	0.171	-0.480	0.191	0.34
Curvature	0.336	0.118	0.105	0.567	0.95
Connectivity	0.032	0.116	-0.196	0.261	0.27
Lichen cover	1.321	0.129	1.069	1.573	1.00

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(g) *Vulpicida pinastri*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(Intercept)	-0.459	0.254	-0.958	0.040	
Pine [3]	-0.077	0.310	-0.686	0.533	1.00
Spruce	1.577	0.288	1.012	2.142	"
Age	-0.762	0.218	-1.190	-0.335	1.00
DBH	1.049	0.260	0.538	1.560	1.00
Age × DBH	-0.858	0.338	-1.521	-0.195	0.81
Canopy	0.226	0.257	-0.279	0.730	0.36
Curvature	0.014	0.184	-0.348	0.376	0.26
Connectivity	0.754	0.168	0.426	1.083	0.95
Lichen cover	0.476	0.197	0.089	0.863	0.85

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

Appendix S5. Model averaged coefficients, standard errors (SE), confidence intervals (CI) and relative importance (cumulative Akaike weight) for variables predicting species with random distribution: (a) *Evernia divaricata*, (b) *Letharia vulpina*, (c) *Platismatia glauca*, (d) *Ramalina obtusata*, (e) *Schismatomma pericleum*, (f) *Tuckermannopsis chlorophylla*, and (g) *Tuckneraria laureri*.

(a) *Evernia divaricata*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	1.871	0.405	1.076	2.665	
Pine [3]	-0.383	0.386	-1.140	0.374	0.73
Spruce	-0.820	0.347	-1.501	-0.140	"
Age	0.781	0.299	0.195	1.367	0.91
DBH	-0.325	0.287	-0.888	0.238	0.45
Age × DBH	0.276	0.421	-0.549	1.102	0.13
Canopy	-0.237	0.295	-0.815	0.341	0.32
Curvature	-0.231	0.335	-0.889	0.427	0.29
Connectivity	-0.028	0.242	-0.502	0.446	0.27
Lichen cover	0.245	0.301	-0.345	0.835	0.37
(a) Binomial component					
(Intercept)	-0.877	0.146	-1.163	-0.591	
Pine [3]	-0.389	0.261	-0.900	0.121	0.28
Spruce	-0.239	0.248	-0.724	0.247	"
Connectivity	0.096	0.168	-0.233	0.426	0.30

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(b) *Letharia vulpina*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	0.232	18.270	-35.576	36.040	
Pine [3]	-2.155	1.667	-5.421	1.112	0.58
Spruce	2.295	1.945	-1.518	6.108	"
Age	0.261	3.596	-6.787	7.309	0.44
DBH	1.422	1.650	-1.812	4.657	0.52
Age × DBH	4.752	4.193	-3.466	12.970	0.14
Canopy	-0.302	1.852	-3.931	3.328	0.41
Curvature	0.059	0.879	-1.664	1.781	0.28
Connectivity	-7.508	7.336	-21.886	6.870	0.63
Lichen cover	0.152	0.458	-0.745	1.050	0.17
(a) Binomial component					
(Intercept)	-1.900	0.297	-2.483	-1.317	
Pine [3]	-2.121	0.588	-3.273	-0.969	1.00
Spruce	-3.082	0.770	-4.591	-1.573	"
Connectivity	0.323	0.315	-0.295	0.941	0.34

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(c) *Platismatia glauca*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	4.099	0.421	3.274	4.925	
Pine [3]	-1.745	0.727	-3.170	-0.320	0.43
Spruce	-0.092	0.625	-1.317	1.134	"
Age	0.894	0.827	-0.727	2.516	0.42
DBH	-0.448	0.610	-1.643	0.747	0.38
Age × DBH	-1.165	0.813	-2.759	0.430	0.07
Canopy	0.055	0.546	-1.014	1.124	0.29
Curvature	0.726	0.621	-0.490	1.943	0.42
Connectivity	0.029	0.364	-0.684	0.742	0.27
Lichen cover	-0.276	0.373	-1.007	0.455	0.31
(a) Binomial component					
(Intercept)	-0.182	0.202	-0.578	0.214	
Pine [3]	-2.996	0.396	-3.772	-2.221	1.00
Spruce	-2.385	0.305	-2.981	-1.788	"
Connectivity	0.291	0.212	-0.125	0.707	0.44

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(d) ***Ramalina obtusata***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(Intercept)	-3.044	0.431	-3.891	-2.197	
Pine [3]	1.838	1.510	-1.128	4.804	1.00
Spruce	6.986	1.397	4.245	9.728	"
Age	1.235	0.408	0.435	2.036	0.99
DBH	2.173	0.337	1.512	2.834	1.00
Age × DBH	-1.165	0.638	-2.417	0.087	0.58
Canopy	0.125	0.352	-0.567	0.817	0.29
Curvature	-0.128	0.270	-0.659	0.402	0.29
Connectivity	-0.235	0.523	-1.261	0.791	0.28
Lichen cover	-0.145	0.303	-0.740	0.451	0.29

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(e) ***Schismatomma pericleum***

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	4.873	0.914	3.082	6.664	
Pine [3]	1.231	0.876	-0.487	2.949	0.84
Spruce	2.120	0.810	0.532	3.708	"
Age	0.343	0.454	-0.547	1.233	0.43
DBH	-0.490	0.433	-1.339	0.358	0.52
Age × DBH	1.142	0.628	-0.090	2.374	0.19
Canopy	0.584	0.376	-0.153	1.322	0.65
Curvature	-0.633	0.313	-1.245	-0.020	0.72
Connectivity	-0.027	0.388	-0.787	0.734	0.27
Lichen cover	0.296	0.366	-0.420	1.013	0.33
(a) Binomial component					
(Intercept)	-3.168	0.510	-4.168	-2.167	
Pine [3]	0.909	0.560	-0.188	2.006	1.00
Spruce	3.334	0.524	2.307	4.360	"
Connectivity	0.025	0.187	-0.342	0.392	0.26

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(f) *Tuckermannopsis chlorophylla*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	3.540	0.549	2.465	4.615	
Pine [3]	-4.436	0.654	-5.717	-3.154	1.00
Spruce	-3.011	0.485	-3.961	-2.061	"
Age	0.363	0.439	-0.498	1.224	0.38
DBH	-0.113	0.448	-0.992	0.766	0.34
Canopy	0.460	0.315	-0.158	1.077	0.55
Curvature	0.082	0.328	-0.561	0.725	0.28
Connectivity	0.053	0.219	-0.376	0.483	0.28
Lichen cover	-0.765	0.301	-1.355	-0.175	0.81
(a) Binomial component					
(Intercept)	-0.704	0.218	-1.130	-0.277	
Pine [3]	-2.039	0.358	-2.741	-1.337	1.00
Spruce	-0.701	0.264	-1.219	-0.183	"
Connectivity	0.923	0.214	0.503	1.343	1.00

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

(g) *Tuckneraria laureri*

Predictor	Estimate [1]	SE [2]	Lower CI	Upper CI	Relative importance
(a) Count component					
(Intercept)	0.564	0.452	0.279	0.865	
Pine [3]	-1.579	0.558	-2.672	-0.486	0.88
Spruce	0.140	0.577	-0.991	1.271	"
Age	-0.287	0.652	-1.564	0.991	0.37
DBH	0.942	0.552	-0.139	2.023	0.69
Age × DBH	1.066	0.961	-0.816	2.949	0.11
Canopy	-0.346	0.442	-1.212	0.520	0.33
Curvature	-0.938	0.696	-2.301	0.426	0.44
Connectivity	-0.353	0.263	-0.867	0.162	0.38
Lichen cover	-0.012	0.397	-0.790	0.766	0.27
(a) Binomial component					
(Intercept)	-0.274	0.203	-0.671	0.123	
Pine [3]	-1.708	0.289	-2.274	-1.141	1.00
Spruce	-1.514	0.263	-2.030	-0.998	"
Connectivity	0.598	0.185	0.234	0.961	0.99

[1] Effect sizes have been standardized on two standard deviation (SD) following Gelman (2008).
[2] Unconditional standard errors (SE)
[3] Larch was the reference category.

Appendix S6. The effect of tree age on the response of (a) *Parmeliopsis ambigua* and (b) *Vulpicida pinastri* cover to tree size (DBH). DBH have