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This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1622737> since 2017-01-20T11:42:51Z

Published version:

DOI:10.1016/j.funeco.2016.08.006

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(Article begins on next page)

This is the author's final version of the contribution published as:

[Nascimbene J., Ackermann S., Dainese M. Garbarino M., Carrer M. 2016. Fine-scale population dynamics help to elucidate community assembly patterns of epiphytic lichens in alpine forests. *Fungal Ecology* 24: 21-26. doi: 10.1016/j.funeco.2016.08.006.]

The publisher's version is available at:

[<http://www.sciencedirect.com/science/article/pii/S1754504816300873>]

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Link to this full text:

[<http://hdl.handle.net/2318/1622737>]

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

3

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5

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11

12 **Running title: Fine-scale patterns of lichens**

13

14

15 **Abstract**

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

27

28

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

31 **Introduction**

32 Ecological communities are dynamic assemblages of species whose patterns in space and time are
33 regulated by different interacting processes. The relative importance of these processes may depend
34 on environment type, organism traits, and spatial scale of analysis (e.g. Guisan & Thuiller 2005).
35 Habitat filtering, dispersal dynamics, and biotic interactions are the main processes that interact to
36 determine community patterns (Lortie *et al.* 2004). Habitat filtering, invoked in niche-based models,
37 emphasizes the role of environmental factors and habitat quality in determining species distribution
38 patterns, especially at the fine-scale. Among the stochastic processes (i.e., neutral theory of
39 biodiversity; Hubbell 2001), dispersal dynamics play a crucial role in promoting and maintaining
40 diversity, acting mainly at broad spatial scale (Wiszt *et al.* 2013). However, according to the
41 metapopulation theory (Hanski 1999), dispersal processes could be also influential at the fine-scale.
42 Habitat connectivity and dispersal traits may influence species patterns due to the dynamics of their
43 patches (Snäll *et al.* 2004; Snäll, Ehrlén, & Rydin 2005). For instance, poorly dispersed species may
44 be negatively affected by scarce connectivity among habitat patches. Biotic interactions are
45 recognized to contribute to community structure, both at fine and broad spatial scale (Wiszt *et al.*
46 2013), based on the concept that species are not stand-alone entities and interact positively (e.g.,
47 facilitation) and/or negatively (e.g., competitive exclusion) with other species. Interactions
48 influence the patterns of each species and, in turn, influence community patterns (Wiszt *et al.*
49 2013). The relative effects of these three processes could also depend on the species, or on the
50 successional stage of the habitat. For instance, stochastic processes such as dispersal can initially
51 determine which species arrive at a particular site, while non-random processes, such as habitat
52 filtering or biotic interactions, can determine the persisting of the species (Lortie *et al.* 2004).
53 Fine resolution studies, which simultaneously investigated the role of habitat filtering, dispersal
54 dynamics, and biotic interactions are almost lacking for epiphytic lichens (Ellis 2012), one of the
55 most diverse and functionally important forest organisms. The evaluation of the processes
56 determining their distribution patterns may provide information to prevent loss of forest diversity

57 and ecosystem functions. There is evidence that in forest ecosystems lichen patterns are influenced
58 by host tree features, such as tree species, size, age, crown dimension (e.g. Nascimbene *et al.* 2009;
59 Nascimbene, Marini, Nimis, 2009) and microclimatic conditions (Nascimbene, Marini, Ódor 2012).
60 However, dispersal dynamics may also play a key role resulting in patterns that could differ
61 between spore- and vegetatively-dispersed species (Löbel, Snäll & Rydin 2006a). The former are
62 considered good dispersers due to the small size of the spores, while vegetatively-dispersed species
63 have lower dispersal capacity due to the larger size of vegetative propagules (e.g. Werth *et al.*
64 2006). For these species, patch connectivity could be important even at a fine spatial scale, since the
65 establishment and development of a population are density-dependent processes affected by
66 distance and size of propagule sources. The role of biotic interactions in structuring lichen
67 communities is scarcely explored (Ellis 2012), although autogenic processes such as competition
68 and facilitation are likely to contribute in determining lichen patterns. For example, along a
69 chronosequence small and slow growing crustose lichens could be outcompeted by large and fast
70 growing macrolichens, favoring an ecological succession. Facilitation was never demonstrated for
71 epiphytic lichen communities (e.g., Belinchón *et al.* 2012), though biotic interactions are considered
72 to be important drivers of lichen structure (Maestre *et al.* 2008). For instance, in soil lichen
73 communities facilitation would be dominant under stressful conditions (Maestre *et al.* 2008, 2009),
74 or moss carpets are known to improve the performance of high humidity demanding species
75 (Öckinger, Niklasson & Nilsson 2005), or photobiont sharing (Rikkinen, Oksanen, & Lohtander
76 2002) is a plausible mechanism contributing to the success of the species in forest ecosystems.
77 This research aims at reacting to a scarcity of studies simultaneously incorporating the analysis of
78 different processes (namely habitat filtering, dispersal dynamics, and biotic interactions) in shaping
79 lichen distribution, explicitly dealing with spatial patterns (see e.g. Schei *et al.* 2012). Our study
80 focuses on fine-scale patterns of selected species in a high elevation Alpine forest, using a fine
81 resolution analysis that is expected to be highly predictive for fixed epiphytic organisms (Guisan &
82 Thuiller 2005). After a preliminary analysis describing the main spatial patterns of the species

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

98

99 **Materials and methods**

100 *Study site*

101 The study site is a 2-ha plot located in the Italian Eastern Alps at an elevation of 1900 m a.s.l
102 (Latitude: 46.23 N; Longitude: 11.32 E; Figure 1). The climate is temperate-cold to continental,
103 characterized by strong daily and annual temperature fluctuations. Mean annual temperature is
104 4.6°C, while mean annual precipitation is c. 950 mm, with a peak during summer and a dip between
105 December and February. On average, a solid precipitation of 260 cm per winter period has been
106 recorded at the nearest nivological station of Obereggen (1872 m a.s.l.), forming a permanent snow
107 cover during 110-131 days per year.

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

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

121

122 *Sampling design and data collection*

123 All the trees taller than 130 cm were mapped with a total station and georeferenced using an
124 electro-optical distance meter and their species (Figure 1), DBH and crown dimension recorded.
125 Tree age has been also determined through increment coring. Further details on the sampling
126 protocol for forest structure can be found in Carrer & Urbinati (2001) and in Carrer, Soraruf. &
127 Lingua (2013). After an exhaustive floristic survey that yielded 84 species (Nascimbene 2013), we
128 selected a subset of 14 species (Table 1). Precondition to be included in our sampling design was
129 that the lichen species could be readily identified in the field with naked eye or the help of a
130 magnifier. The species were also selected as to represent different dispersal strategies, including
131 both sexually (i.e. by spores) and vegetatively (i.e. by lichenized propagules) dispersed species.
132 On each tree with a DBH >15cm, the abundance of each species was estimated as value of total
133 coverage (in cm²) on the stem surface up to a height of 1.80 m. Six hundred-sixty-five trees were

134 surveyed, including 311 spruce, 239 stone pine, and 115 larch. The lichen survey was carried out in
135 summer 2012.

136

137 *Explanatory variables*

138 We quantified 7 explanatory variables indicative of three different processes: environmental
139 filtering, dispersal dynamics, and biotic interactions (see Appendix S1 in Supporting Information).

140 To account for the environmental filtering process we selected four tree-level variables that are
141 known to be among the most meaningful descriptors of forest lichen patterns: tree species, tree size
142 (DBH), tree age, and crown volume. As a proxy for micro-topographic conditions, we calculated a
143 curvature index in a GIS environment. A fine resolution (1-m) DEM was computed by using
144 geographic position (x, y) and elevation (z) of each mapped tree. In this way, we were able to assess
145 if a given tree was located on a linear, concave or convex surface.

146 For each lichen species on each tree we quantified the Incidence Function Model (IFM; Hanski
147 1994) to account for dispersal dynamics. The IFM is a typical connectivity measure used in
148 metapopulation ecology (Moilanen & Nieminen 2002). Connectivity (S_i) was calculated for each
149 tree by

$$150 S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j$$

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

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

159

160 *Statistical analyses*

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

167 Depending on the occurrence of the lichen species, two different approaches were used to test the
168 effect of environmental filtering, dispersal dynamics, and biotic interactions on lichen cover. The
169 following covariates were included in the models: tree species, age, DBH, crown volume, curvature,
170 connectivity, and lichen cover. We also tested the interaction between age and DBH. Given the
171 structure of our data (skew distribution), we opted to use generalized linear models (GLM). For
172 common species ($n = 5$; frequency $> 44\%$), lichen cover was analyzed using GLM with a negative
173 binomial distribution to account for the overdispersion of the data (Zuur *et al.* 2009) (see Appendix
174 S2). For relatively rare species ($n = 9$; frequency $< 43\%$) with an excess of zero cases in the dataset,
175 a hurdle regression model was performed (also called zero-altered or two-part models; Zuur *et al.*
176 2009). Ignoring zero inflation can create problems in model inference by biasing the estimated
177 parameters and standard errors, as well as overdispersion (Martin *et al.* 2005; Zuur *et al.* 2009). In
178 our case, the zero inflation was the result of a large number of 'true zero' observations caused by
179 the real ecological effect of interest (i.e., unsuitable habitat; Martin *et al.* 2005) Specifically, we
180 applied a zero-truncated negative binomial (ZANB) to account for the overdispersion of the data
181 (for more details of the models specification see Appendix S2). In both the models (GLM and
182 ZANB), all predictors were standardized by mean-centering and dividing by two standard
183 deviations to improve interpretability of parameter estimates, particularly when interactions were
184 fitted, and continuous and categorical factors are combined in the same model (Gelman 2008).
185 Negative binomial GLM was analyzed using the 'MASS' package (Venables & Ripley 2002) in R,

186 while the hurdle model using the ‘pscl’ package (Zeileis, Kleiber & Jackman 2008; Jackman 2012)
187 in R.

188 We used an information-theoretic model selection procedure to evaluate alternative competing
189 models (Burnham & Anderson 2002). We compared the fit of all possible candidate models
190 obtained by the combination of the predictors using second-order Akaike’s information criterion
191 (AICc). Models were chose that differed from the AICc of the best fitting model by < 4 . We used
192 the Akaike weights (w_i) to measure the relative importance of each predictor, summing the w_i across
193 the models ($\sum w_i$) in which the predictor occurred. For each parameter, we used model averaging in
194 order to incorporate model selection uncertainty into our parameter estimates (Burnham &
195 Anderson 2002; Grueber *et al.* 2011). Individual predictor variables that had an Akaike weight $>$
196 0.75 or model averaged confidence intervals that did not include 0 were considered as most
197 important predictors. Model comparison was implemented using the ‘MuMIn’ package (Barton
198 2013) in R.

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

208 All the statistical analyses were performed separately for each species.

209

210 **Results**

211 *Lichen species and spatial patterns*

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

216 After the spatial autocorrelation analysis the species were equally distributed in two groups (Table
217 1; Appendix S2): i) lichens with a clumped spatial pattern and ii) lichens with a random spatial
218 pattern. Both groups included vegetatively- and spore-dispersed species.

219

220 *Drivers of fine-scale lichen patterns*

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

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

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

238

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

240 The variation partitioning analysis indicated that the total variation in species abundance patterns
241 explained by the models was higher for clumped species (explained variation range between 6 and
242 37%) than for randomly distributed species (explained variation range between 3 and 12%) (Table
243 2). Habitat filtering was the most important process for almost all the species, except for
244 *Hypogymnia physodes* and *Pseudevernia furfuracea* for which biotic interaction was the main
245 process determining their patterns (explained variation 15% and 17%, respectively) with an
246 additional impact of the shared component between biotic interaction and environmental filtering,
247 summing up to 12% of the total variance. Dispersal dynamics seemed to have a negligible influence
248 in shaping lichen distribution in our study system (explained variation range between 1 and 3%).

249

250 **Discussion**

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

255

256 *Habitat filtering*

257 Tree species is the most important environmental factor whose effect is mainly related with species-
258 specific differences in the chemical and physical traits of the bark, chiefly pH and texture (e.g. Fritz
259 & Heilmann-Clausen 2010; Király *et al.*, 2013). These differences may be relevant even among
260 relatively similar host trees, such in the case of our three coniferous species. Besides tree species,
261 tree size and age are also important drivers of local lichen patterns (Nascimbene *et al.* 2009), with
262 both direct and interactive effects. According to an ‘area effect’, tree size positively influences
263 abundance patterns fostering the population size. Tree age seems to have species-specific effects

264 with some lichens alternatively preferring young or old trees, according with either a pioneer or a
265 late-successional behavior. The interaction between tree size and tree age indicates a decrease of the
266 positive effect of tree size on lichen cover with increasing tree age, even to become neutral on older
267 trees (> 180 years). On these old trees, lichen dynamic are more influenced by a ‘time per se’ effect
268 (i.e. time available for colonization and increase of population size) than by an ‘area effect’. In
269 addition, tree size gains importance on large trees, while age gains importance on small ones,
270 corroborating the hypothesis that the ‘area effect’ and “time per se” effect are two complementary
271 mechanisms influencing lichen patterns in forest ecosystems. Crown dimension influenced the
272 distribution of only two species, with contrasting effects. *Chaenotheca chrysocephala*, preferring
273 environmental conditions protected from rain, was positively affected by crown dimension, while
274 *Hypogymnia physodes*, which prefers well-lit conditions, was negatively affected by this driver. In
275 general, the effect of this tree level factor is poorly explored in the lichen literature (e.g.
276 Nascimbene *et al.* 2008), although it is likely to interact with dispersal dynamics and to influence
277 microclimatic conditions (e.g. Nascimbene *et al.* 2008, 2009). Further evidence for the importance
278 of microclimatic conditions (Nascimbene, Marini & Ódor 2012) is provided by the significant
279 contribution of microtopography to the abundance pattern of five species, discriminating between
280 those preferring very humid-shaded (e.g. *Schismatomma pericleum*) or relatively dry and well-lit
281 conditions (i.e. *Pseudevernia furfuracea*).

282

283 *Dispersal dynamics and biotic interactions*

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

289 propagule sources may hinder the density-dependent processes of establishment and population
290 growth.

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

305

306 *Clumped vs randomly distributed species*

307 The two different patterns of abundance distribution (clumped vs random) correspond to a different
308 response of the species to the drivers indicative of the three processes. The group of clumped
309 species includes lichens that are very common in different types of alpine forests (Nascimbene,
310 Nimis & Dainese 2014) where they constitute the keystones of epiphytic lichen communities. Our
311 results indicate that their patterns are determined by a multiple and complex (i.e. interactive effects)
312 response to several drivers indicative of habitat filtering, dispersal and biotic interactions. This
313 complex behavior may ensure a high degree of adaptation enhancing the resistance and resilience of
314 their populations to forest dynamics induced by natural and anthropogenic disturbances. On the

315 contrary, the group of randomly-distributed species mainly includes relatively rare lichens that have
316 more specific ecological requirements (Nascimbene, Nimis & Dainese 2014). Their abundance
317 patterns are ruled by more simple dynamics, mainly related to habitat filtering. In particular, their
318 strict dependence on the host tree species suggests that they are strongly influenced by tree
319 dynamics. In our dynamic forest, species related with open, larch-dominated stands (e.g. *Letharia*
320 *vulpina*; Nascimbene, Nimis & Dainese 2014) could be relicts restricted to remnant patches whose
321 connectivity is fundamental for their maintenance, such in the case of *Tuckneraria laureri* and
322 *Tuckermannopsis chlorophylla*. On the other hand, spruce-related species (e.g. *Schismatomma*
323 *pericleum*; Nascimbene, Nimis & Dainese 2014) may be in an expansion phase enhanced by the
324 increasingly available substrate.

325

326 **Conclusions**

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

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

346

347 **Acknowledgements**

348 The study was conducted in the framework of the project “Biodiversità, biomonitoraggio e
349 conservazione dei licheni epifiti negli ambienti forestali della provincia di Bolzano”, funded by the
350 Autonomous Province of Bolzano (Ripartizione Diritto allo studio, Università e Ricerca scientifica).
351 The Forest planning office of the Autonomous Province of Bolzano (project partner) is thanked for
352 providing logistic and technical support. In particular, we are grateful to Günther Unterthiner, Fabio
353 Maistrelli and their collaborators.

354

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478 SUPPORTING INFORMATION

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

480

481 **Appendix S1.** Descriptive statistics of the covariates.

482 **Appendix S2.** Description of the species distribution modeling.

483 **Appendix S3.** Moran's I correlograms.

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

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

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

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

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

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507 **Table 2.** Variation partitioning of (a) species with clumped distribution and (b) species with random
 508 distribution. The total variation explained was partitioned among environmental filtering (E),
 509 dispersal dynamics (D), and biotic interactions (B). Values are adjusted R^2 in %. Adjusted fractions
 510 of total variation explained (TVE, in %) were estimated following the procedure of Peres-Neto et al.
 511 (2006).

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

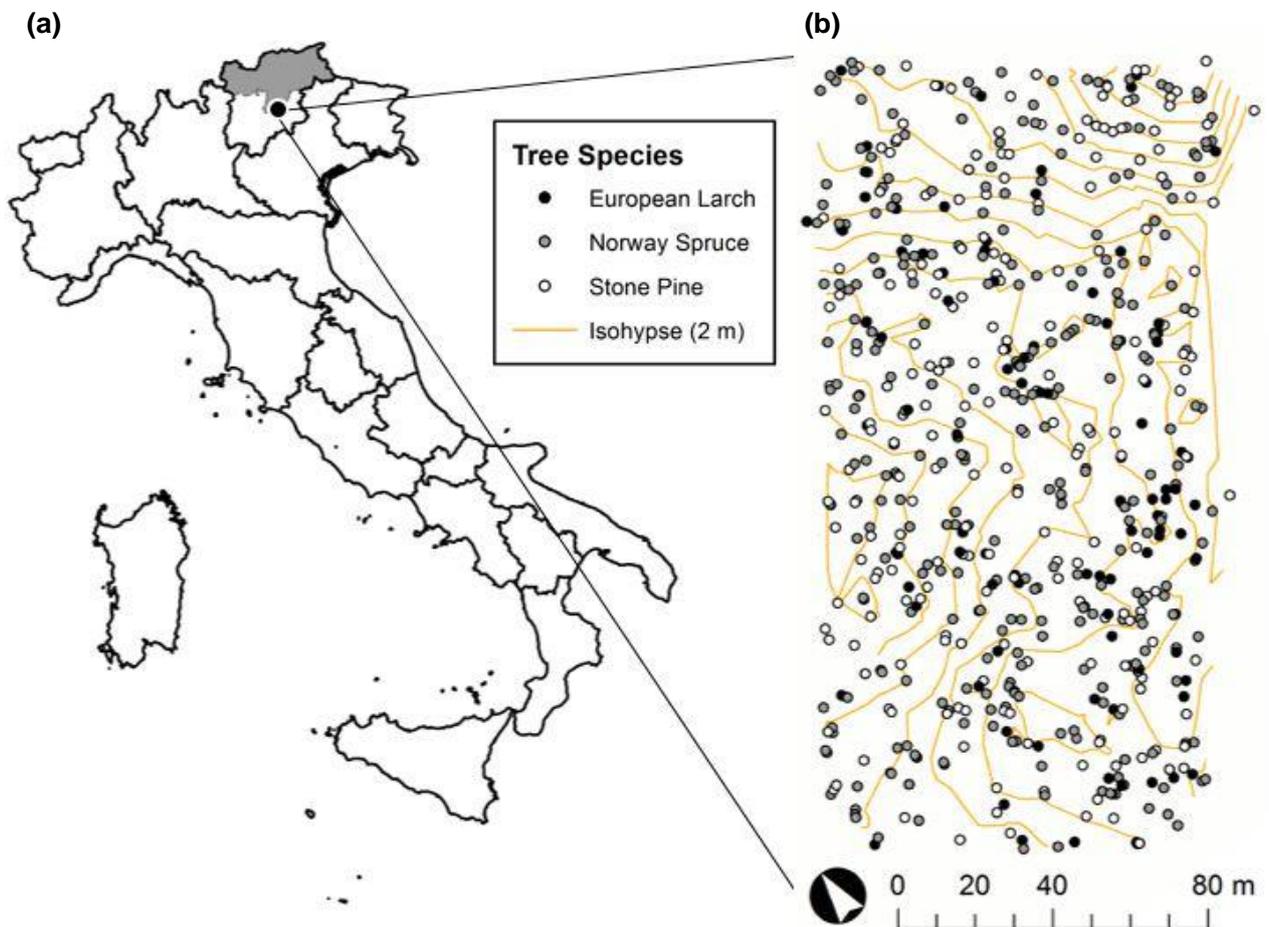
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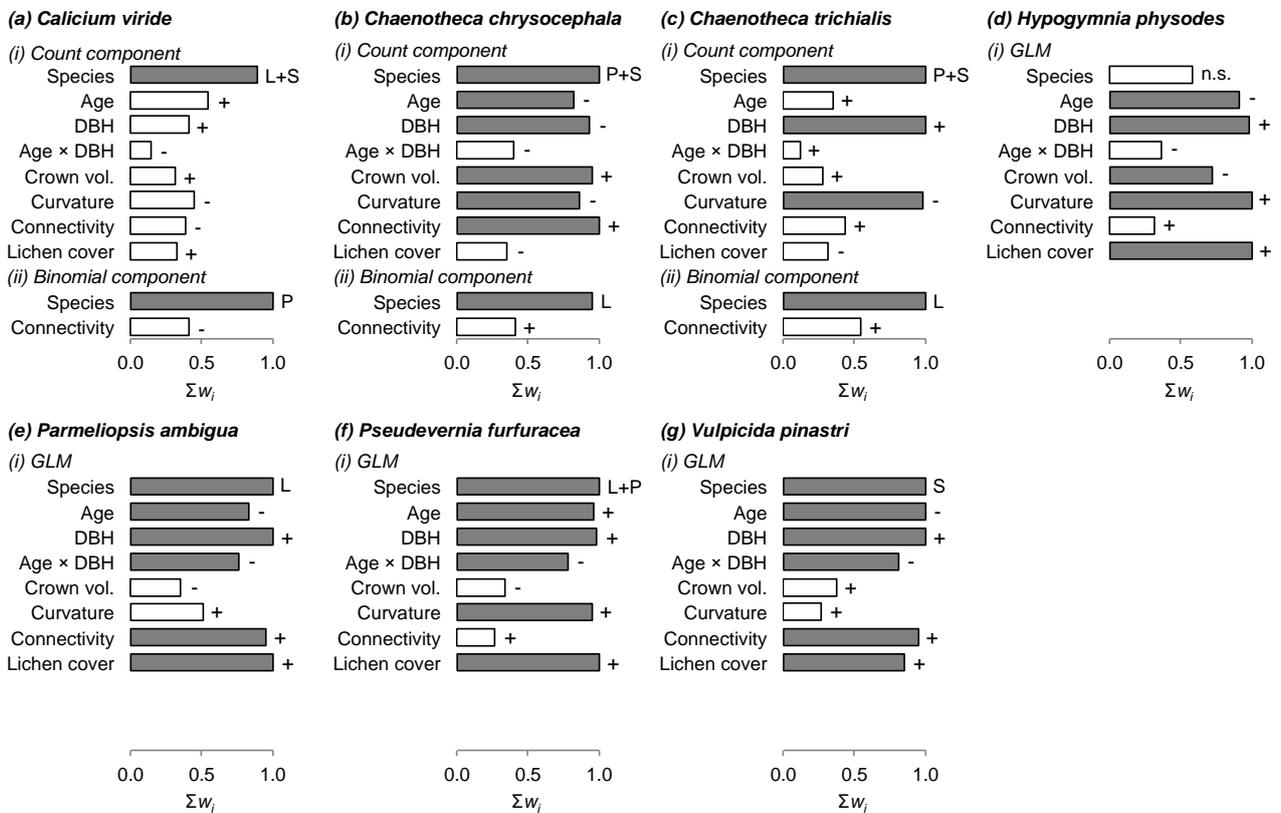
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515 **Figure captions:**

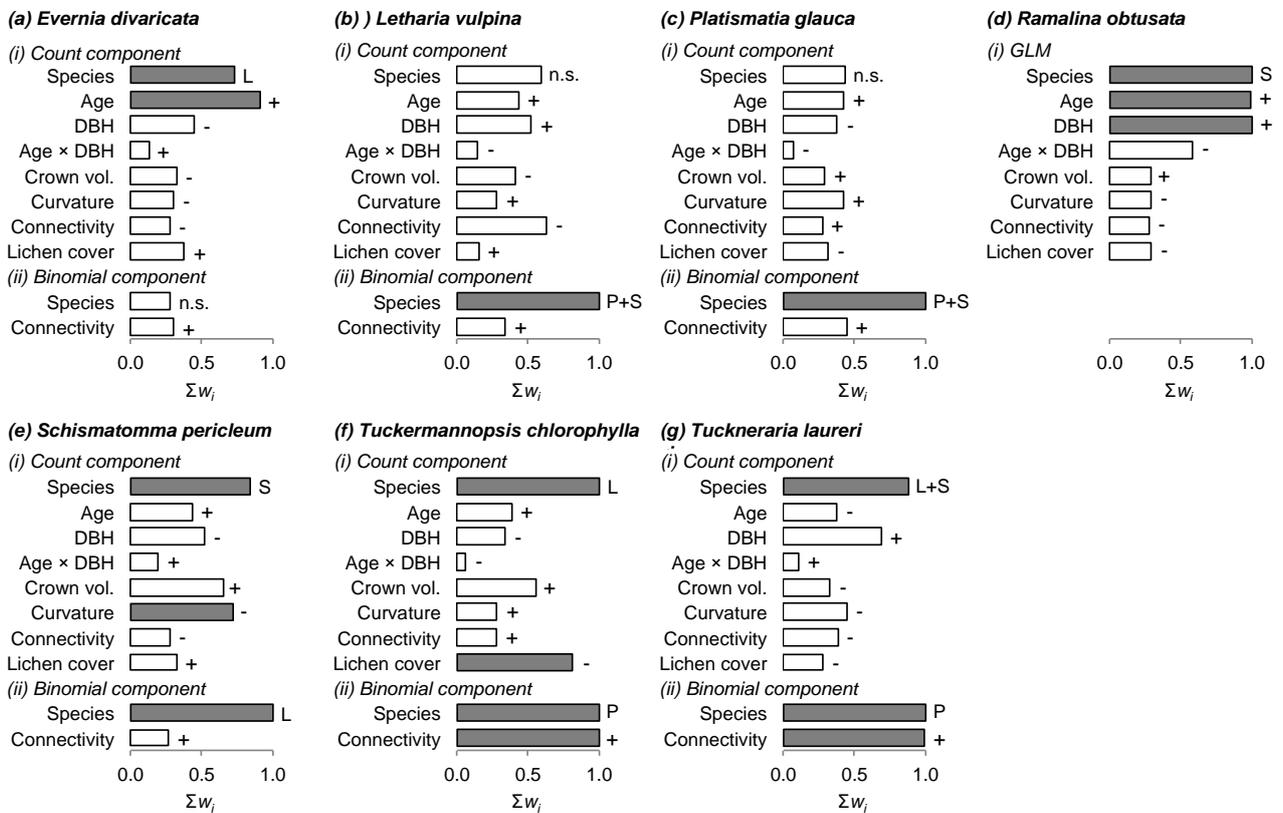
516 **Figure 1.** (a) Study area, (b) study site: a 2-ha plot located in the Italian Eastern Alps at an elevation
517 of 1900 m a.s.l (Latitude: 46.23 N; Longitude: 11.32 E).



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

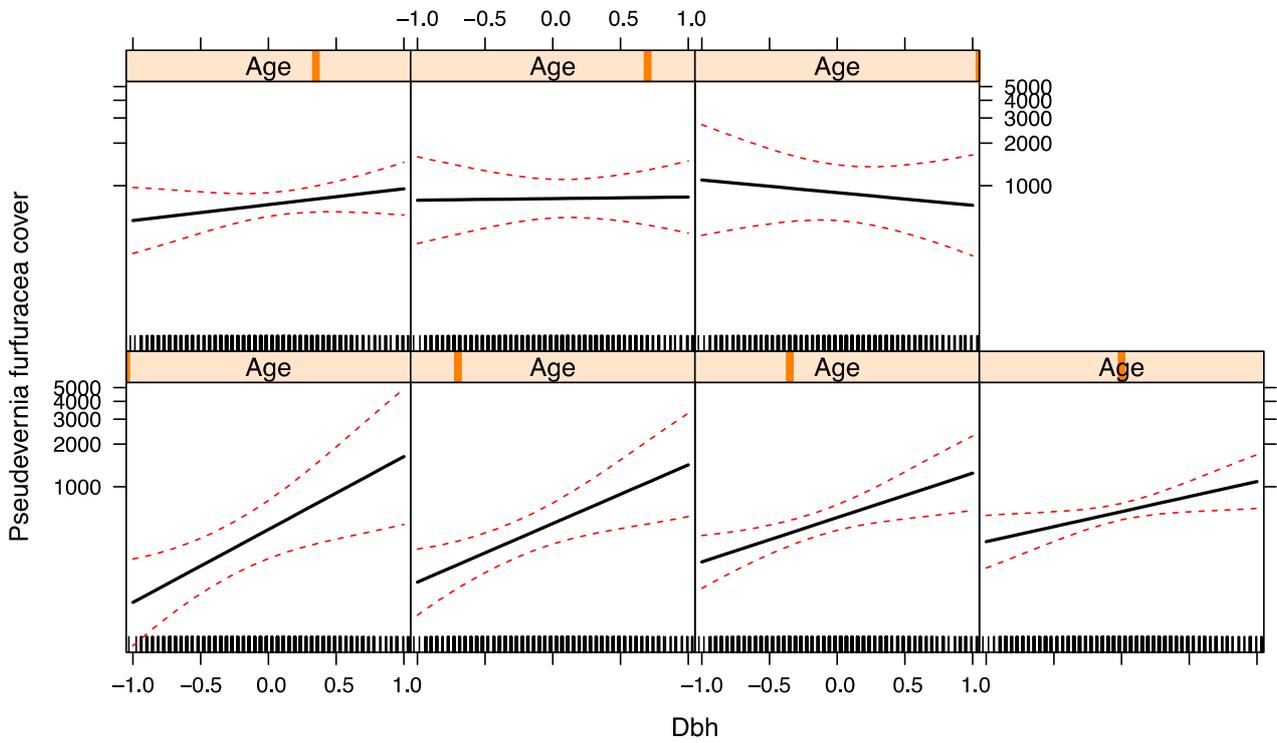


527 **Figure 3.** Sum of model weights ($\sum w_i$) for each variable estimated by the multi-model inference
 528 procedure for species with random distribution. Predictors that consistently occurred in the most
 529 likely models ($\sum w_i > 0.75$) or model averaged confidence intervals that did not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



535 **Figure 4.** The effect of tree age on the response of *Pseudevernia furfuracea* cover to tree size

536 (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 \pm SD	Min	Max
(a) Environmental variables			
DBH (cm)	35.4 \pm 11.9	6	70
Tree age (years)	149.1 \pm 28.4	51	260
Crown volume (m ³)	63.6 \pm 53.5	0.7	449.1
Curvature index	-1.3 \pm 93.0	-541.8	487.8
(b) Dispersal dynamics (IFM)			
<i>Calicium viride</i>	0.4 \pm 2.0	0.0	29.0
<i>Chaenotheca chrysocephala</i>	122.9 \pm 389.1	0.0	6778.0
<i>Chaenotheca trichialis</i>	0.9 \pm 3.9	0.0	51.2
<i>Evernia divaricata</i>	0.2 \pm 1.0	0.0	13.0
<i>Hypogymnia physodes</i>	441.4 \pm 1465.3	0.0	33399.2
<i>Letharia vulpina</i>	0.1 \pm 0.5	0.0	7.1
<i>Parmeliopsis ambigua</i>	719.5 \pm 1098.6	0.0	9679.3
<i>Platismatia glauca</i>	0.2 \pm 0.8	0.0	9.3
<i>Pseudevernia furfuracea</i>	4.5 \pm 8.1	0.0	62.3
<i>Ramalina obtusata</i>	0.1 \pm 0.3	0.0	4.8
<i>Schismatomma pericleum</i>	0.2 \pm 1.2	0.0	16.2
<i>Tuckermannopsis chlorophylla</i>	0.3 \pm 1.1	0.0	10.8
<i>Tuckneraria laureri</i>	1.8 \pm 8.2	0.0	95.9
<i>Vulpicida pinastri</i>	0.9 \pm 4.1	0.0	90.7
(c) Biotic interaction (cover co-occurring species in cm²)			
<i>Calicium viride</i>	5772.3 \pm 5362.3	15	45520
<i>Chaenotheca chrysocephala</i>	5694.0 \pm 5370.9	20	45515
<i>Chaenotheca trichialis</i>	5285.5 \pm 5149.6	0	45520
<i>Evernia divaricata</i>	5994.9 \pm 5392.0	20	45520
<i>Hypogymnia physodes</i>	3415.7 \pm 3493.5	0	21250
<i>Letharia vulpina</i>	5996.7 \pm 5388.4	20	45515
<i>Parmeliopsis ambigua</i>	3773.7 \pm 4045.0	0	41505
<i>Platismatia glauca</i>	5984.2 \pm 5387.8	20	45520
<i>Pseudevernia furfuracea</i>	5052.3 \pm 4444.4	20	44020
<i>Ramalina obtusata</i>	6039.1 \pm 5417.2	20	45520
<i>Schismatomma pericleum</i>	5647.8 \pm 5259.6	20	45520
<i>Tuckermannopsis chlorophylla</i>	5992.2 \pm 5388.4	20	45515
<i>Tuckneraria laureri</i>	5992.4 \pm 5387.2	20	45520
<i>Vulpicida pinastri</i>	5994.6 \pm 5388.5	20	45515

Appendix S2. Description of the species distribution modeling.

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

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

548 The mathematical formulation was:

549 $Lichen\ cover_i \sim NB(\mu_i, k)$

550 $E(Lichen\ cover_i) = \mu_i$ and $var(Lichen\ cover_i) = \mu_i + \frac{\mu_i^2}{k} = \mu_i + \alpha \times \mu_i^2$

551 $\log(\mu_i) = \eta_i$

552 $\eta_i = \alpha + fTree\ species_i + Age_i \times DBH_i + Crown\ volume_i + Curvature_i + Connectivity_i$
 $+ Lichen\ cover_i$

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

560 connectivity as covariates, while the predictor function of count component (η_{ci}) included all
561 covariates (as for GLM).

562 The mathematical formulation was:

563 $Lichen\ cover_i \sim ZANB(\mu_i, \pi_i, k)$

564 $E(Lichen\ cover_i) = \frac{1 - \pi_i}{1 - P_0} \times \mu_i \quad \text{where} \quad P_0 = \left(\frac{k}{\mu_i + k}\right)^k$

565 $var(Lichen\ cover_i) = \frac{1 - \pi_i}{1 - P_0} \times \left(\mu_i^2 + \mu_i + \frac{\mu_i^2}{k}\right) - \left(\frac{1 - \pi_i}{1 - P_0} \times \mu_i\right)^2$

566 $log(\mu_i) = \eta_{c_i}$

567 $logit(\pi_i) = \eta_{b_i}$

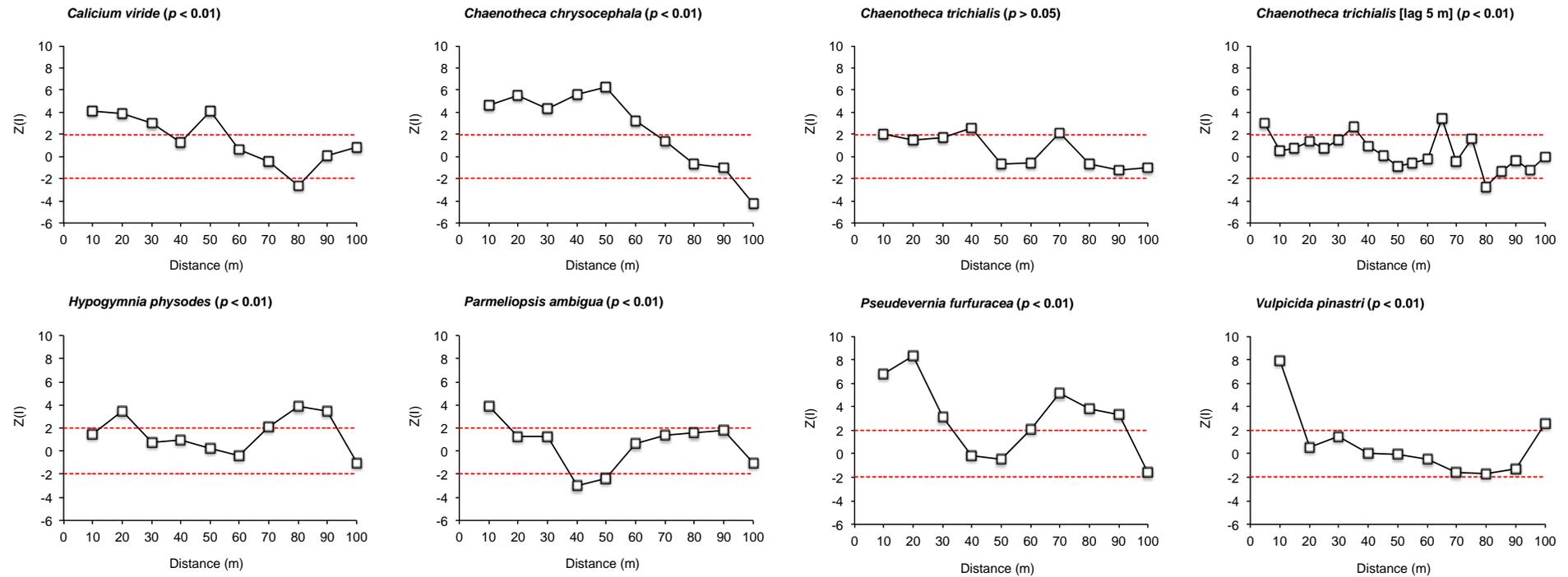
568 $\eta_{c_i} = \alpha_1 + fTree\ species_i + Age_i \times DBH_i + Crown\ volume_i + Curvature_i + Connectivity_i$
 $\quad + Lichen\ cover_i$

569 $\eta_{b_i} = \alpha_2 + fTree\ species_i + Connectivity_i$

570 where π_i is the probability that $Y_i = 0$ ($Lichen\ cover_i = 0$).

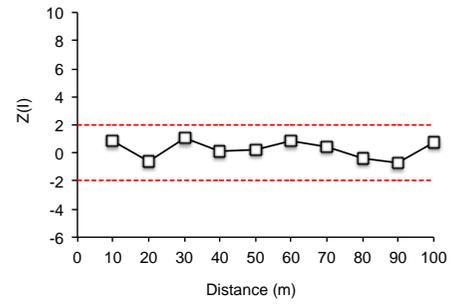
Appendix S3. Moran's I correlograms for the 14 studied species, using a lag distance of 10 m. For *Chaenotheca trichialis* the graph based on a lag distance 5m is also given. Global significance, after applying Bonferonni correction, is reported. Species are grouped according to spatial distribution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

(a) Species with clumped distribution

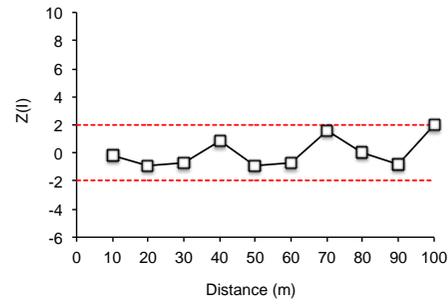


(b) Species with random distribution

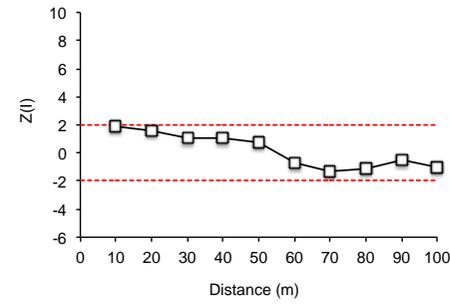
Evernia divaricata ($p > 0.05$)



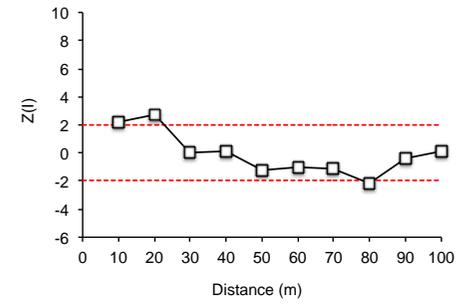
Letharia vulpina ($p > 0.05$)



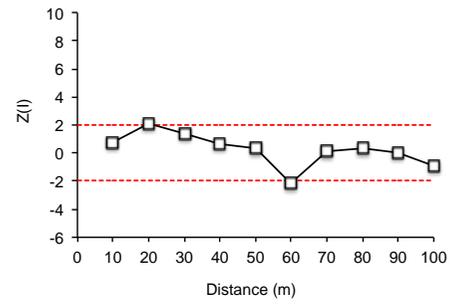
Platismatia glauca ($p > 0.05$)



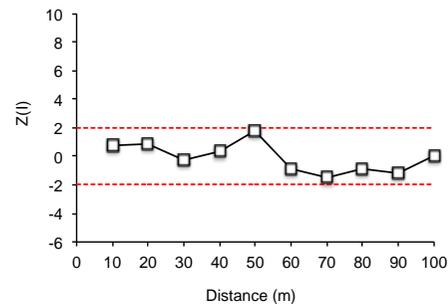
Ramalina obtusata ($p > 0.05$)



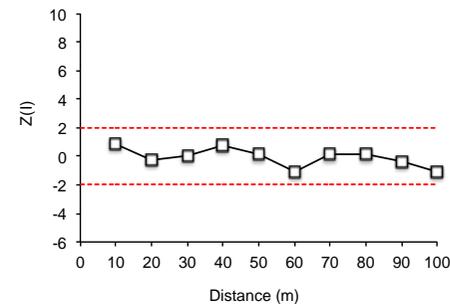
Schismatomma pericleum ($p > 0.05$)



Tuckermannopsis chlorophylla ($p > 0.05$)



Tuckneraria laureri ($p > 0.05$)



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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(Intercept)	-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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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
<i>(a) Count component</i>					
(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
<i>(a) Binomial component</i>					
(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

