

# 1 Tree crowns as meeting points of diversity generating 2 mechanisms – a test with epiphytic lichens in a temperate forest

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## 121 Introduction

13Forest canopies are known as hotspots of biological diversity (Ozanne et al. 2003, Nakamura et  
14al. 2017). Approximately 28.600 vascular plant species inhabit tree crowns as epiphytes, which  
15comprises about 10 % of the total vascular flora (Nadkarni 1994). Extrapolations based on host  
16specificity of arthropods with respect to tree species, resulted in a total number of 6.1 million  
17terrestrial arthropod species harbored in the tropics (Hamilton et al. 2010). This high diversity of  
18arboreal organisms has been attributed to a number of unique features of tree crowns including  
19the richness of substrates (Barkman 1958, Fritz 2009) and the availability of light energy in  
20comparison with the forest floor. Furthermore, pronounced environmental gradients spanning  
21from dark moist habitats in the lower to sunlit dry habitats in the upper canopy layer (Parker and  
22Brown 2000) create a wealth of niches for canopy organisms. Next to a vertical niche gradient,  
23the complex architecture of tree crowns also creates horizontal variation in environmental  
24conditions (McCune et al. 2000). The extent of this variation is expected to change  
25systematically with height (Parker and Brown 2000). In addition, and thus far not considered in  
26the literature, the availability of branch surface area increases with height as the branching  
27process divides a given wood volume into successively thinner branches with a higher surface to  
28volume ratio. Habitat area for bark-dwelling organisms thus increases with height. According to  
29positive species-area relationships (Connor and McCoy 2000) this alone should allow for higher  
30diversity in the top layer of tree canopies. Using a crane facility, we developed a novel sampling  
31design for canopy research with the goal to quantify the relative importance of different diversity  
32generating mechanisms of epiphytic diversity in tree crowns using lichens as model organisms.

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34Epiphytic lichens represent a ubiquitous component of canopy communities. Even in temperate  
35forests the species richness of lichens may exceed that of forest trees by at least an order of  
36magnitude (Ellis 2012). Here we employ arboreal lichen species as model organisms to explore  
37the relative importance of mechanisms shaping patterns of biodiversity in tree crowns of two  
38temperate tree species (*Fraxinus excelsior* L. and *Quercus robur* L.). We sampled lichens species  
39richness ( $\alpha$  diversity) and abundance in subplots positioned in five canopy layers and at the  
40trunk. The number of plots in these layers was proportional to the available bark surface area.  
41The total number of species per layer is referred to as  $\gamma$  diversity, their turnover between plots  
42within a layer as  $\beta$  diversity.

43For autotrophic organisms like lichens, radiation is inarguably a key resource and influences  
44growth rates (Hilmo 2002). During leaf-on, the amount of radiation transmitted into the canopy  
45decreases quickly from a shallow zone of bright light conditions at the top of the canopy to  
46darker regimes in deeper canopy layers. The bottommost zone around the trunk receives only  
47about 5 % of the radiation above the canopy in temperate deciduous forests (Parker 1997).  
48However, in poikilohydric lichens, photosynthesis may also be quickly limited by water  
49availability (Sillett and Antoine 2004). Although lichens are able to endure severe periods of  
50drought, in such periods they are not metabolically active (Palmqvist 2000, Kranner et al. 2014).  
51With increasing height in the canopy, lichens are exposed to drying winds and high temperatures,  
52while lower canopy layers provide more sheltered microhabitats. Hence, optimal conditions for  
53lichen productivity and survival might be found in intermediate crown layers where the joint  
54availability of light and moisture is highest (Figure ). In this region, a higher productivity may  
55sustain higher population densities. This may allow even rarer species to establish and persist

56(Wright 1983) which in turn should lead to a higher lichen diversity in this zone, both across the  
57entire crown layer ( $\gamma$  diversity) and locally at the level of subplots ( $\alpha$  diversity).

58Orthogonal to vertical environmental gradients there is also horizontal variation in environmental  
59conditions. Whereas the topmost layers are fully illuminated and well-coupled with the  
60atmosphere and are thus uniformly bright, dry and exposed to wind (Unterseher and Tal 2006),  
61the bottom layers tend to be uniformly dark and moist. However, in the transition zone the  
62complex architecture of tree crowns with their clustered branches and foliage creates a patchy  
63mosaic of microsites varying in microclimate (light, rain interception, wind exposure) and  
64structure (branch sizes and inclinations, bark roughness) (McCune et al. 2000, Parker and Brown  
652000). The resulting horizontal variation in substrate and microclimate in mid-canopy layers may  
66promote the co-occurrence of specialists each with preferences for particular habitat types  
67(Connor and McCoy 2000). As a result, the  $\gamma$  diversity of mid-canopy layers is expected to be  
68high as a consequence of high species turnover between contrasting microsites ( $\beta$  diversity), but  
69not because of peaking  $\alpha$  diversity.

70Another potentially important factor impacting composition and diversity of epiphytic  
71communities are successional changes brought forth by the emergence of new habitat surface as  
72trees grow in height and produce new branches. Colonization time on young branches in the top  
73canopy is shorter than on old branches further down (Ellis 2012). Furthermore, during growth,  
74lichen themselves change their microenvironment by altering branch surface structure,  
75facilitating further establishment and increasing moisture interception (Pypker et al. 2006) or by  
76producing allelopathic compounds as competitive means (Lawrey 1986). Thus, autogenic  
77successional drivers may relate to branch age (Rogers 1988, Ellis and Coppins 2006, Johansson  
78et al. 2007), although the continuous growth of the host tree coincides with drastic changes in

79microenvironment making allogenic succession more prevalent (Stone 1989). This leads to  
80successional sequences of lichen community composition (Degelius 1964, 1978, Rogers 1988,  
81Hilmo 1994, Wirth et al. 1999). Young top-layer branches may host lichen communities  
82consisting of a limited set of fast colonizing early-successional species (Rogers 1990), while  
83lichen communities on old branches, representing late stages of succession with high cover, may  
84have lost species due to the exclusion by more competitive lichens and/or bryophytes  
85(Armstrong and Welch 2007, Fritz 2009). As a consequence, lichen diversity is expected to  
86increase from the top-layer downwards to regions where species of different successional stages  
87co-occur before it decreases again (Degelius 1964, Hilmo 1994), thus creating a hump-shaped  
88pattern, referred to as mid-succession peak (Johansson et al. 2007).

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90According to the species-area relationship (SAR), a landmark theory in ecology tested for many  
91taxa, habitats and scales (Connor and McCoy 2000), vertical gradients in total available branch  
92surface area may strongly affect vertical patterns of  $\gamma$  diversity. Although wood volume tapers  
93with height to some extent, the power-law increase in surface-to-volume ratio in progressively  
94thinner branches leads to a sharp increase of bark surface towards the top of the canopy. Thus,  
95the major part of surface area available for epiphytes can be found in the upper canopy.  
96According to SAR, this increase in available area towards the treetop should be paralleled by an  
97increase in species richness. While an increase of lichen biomass with height has been reported  
98(Hale 1952, Ellyson and Sillett 2003, Boch et al. 2013), we are not aware of any study  
99considering SAR as potential driver of vertical patterns in lichen diversity in canopies let alone  
100its component processes ‘area per se’, ‘habitat heterogeneity’ and the ‘passive sampling process’

101(Connor & McCoy, 2000). With the SAR mechanism,  $\gamma$  diversity is expected to increase  
102monotonously with height.

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104This study aims to disentangle the effects of mechanisms generating patterns of lichen diversity  
105in tree canopies. With the exception of the SAR mechanism, all other mechanisms introduced  
106above are hypothesized to produce a mid-canopy peak of  $\gamma$  diversity at the level of canopy layers  
107(Figure ) and are thus indistinguishable without additional information. However, each of the  
108four mechanisms is assumed to produce a characteristic fingerprint with respect to patterns of  
109diversity components such as  $\alpha$  and  $\beta$  diversity, gradients of trait expression and relationships to  
110underlying patterns of niche predictors (see Table 1 in the method section for a summary of our  
111predictions). It is important to note that the four mechanisms are not mutually exclusive. Here,  
112we present a sampling design, theoretical framework and analysis scheme that allows us to  
113holistically assess the relative contributions of the four mechanisms generating patterns of lichen  
114diversity on two tree species of a Central European floodplain forest. To this end, we employ a  
115variety of tools such as linear models, variance partitioning, null model comparisons and  
116structural equation models, where processes and their underlying mechanistic hypotheses are  
117represented by specific pathways.

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119We expect to find evidence that the several mechanisms operate in *parallel* and mutually  
120reinforce each other to produce a distinct mid-canopy peak of  $\gamma$  diversity at the level of canopy  
121layers. We further expect that this diversity peak is displaced upwards as a consequence of the  
122SAR ‘passive sampling’ mechanism operating on the increasing availability of substrate area  
123with height. We hope to contribute to an understanding of tree canopies as meetings points of

124diversity shaping mechanisms that could explain why tree canopies are often found to be

125hotspots of biodiversity.

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## 1292 Methods

### 1302.1 Study site and tree selection

131The study was conducted at the Leipzig Canopy Crane facility (LCC). The crane site is located  
132within the nature reserve “Burgau” in the northwestern part of a floodplain forest that traverses  
133the city of Leipzig in Saxony, Germany (51°20’16” N, 12°22’26” E). Leipzig lies in the transient  
134area of maritime to continental climate with mean annual rainfall of 556.9 mm and a mean  
135temperature of 9.8 °C in average (Kaiser 2014). The crane is a LIEBHERR 71 EC tower crane with  
136a height of 40 m and horizontal reach of 45 m, which is mounted on a 120 m railroad track.  
137Thus, it provides easy access to the forest canopy within an area of 1.65 ha. At the time of  
138sampling this area comprised ~800 trees with diameter at breast height (DBH) > 5 cm belonging  
139to 17 species (10/ha), with *Acer pseudoplatanus* L., *Fraxinus excelsior* L. and *Tilia cordata* Mill.  
140being the most dominant tree species. *Fraxinus excelsior* and a few exceptionally large  
141individuals of *Quercus robur* L. represent the individuals with the highest basal area. Of these  
142species, five large individuals each were chosen as sampling targets.

### 1432.2 Sampling design

144To enable us to account for area-specific effects on lichen diversity patterns, each tree was  
145subdivided into five equally spaced crown layers and a sixth trunk layer. The crown base was  
146defined as the point of separation from the main trunk into erect branches having contact to the  
147upper crown region. Lacking such contact, a branch was assigned to the trunk layer. Within each  
148layer, sampling plots were randomly placed with a minimum distance of 1 m to each other. Their  
149number was proportional to the share of total bark surface of the respective specific layer,  
150whereby the minimum number of plots in the lowermost crown layer was set to five. The



151available surface area within each layer was approximated by means of a Dirichlet regression  
152model (Maier 2014), trained on a dataset containing biometric data collected via *random branch*  
153*sampling* (Gaffrey and Saborowski 1999) originating from 385 single broadleaf trees (Riedel and  
154Kändler 2017). Different models were used for modelling surface area proportions for each  
155phorophyte species (S1). The *F. excelsior* model was using diameter at breast height (DBH) as  
156predictor for a second-order polynomial model, the *Q. robur* model used a logarithmic model  
157with DBH as predictor and the ratio crown base height / total tree height as additional predictor.  
158This resulted in a total number of 55 - 99 plots per tree. Each sampling plot consisted of two  
159sampling areas with dimensions of 1.5 x 33.3 cm (100 cm<sup>2</sup> in total) on the upward and downward  
160facing side of a branch. The dimensions have been chosen to accommodate vastly differing  
161branch diameters (range: >1 – 87 cm) without changing the shape of the sampling area. On the  
162trunk and other vertical branches, the sampling areas were placed on opposite cardinal directions  
163alternating between north/south and east/west. Sampling was carried out from October 2016 to  
164July 2017. For each lichen species, cover was estimated from occurrences using a 5 mm grid.  
165Species were identified in the field if possible. Otherwise, voucher specimens were taken for  
166later identification. Identification and naming convention followed Wirth, Hauck, & Schultz  
167(2013). Some individuals of *Physcia adscendens* and *P. tenella* could not be determined at the  
168species level due to insufficiently developed soralia and were thus grouped under *Physcia sp.*  
169Note: this species aggregate does not include other species of the same genus, like *P. stellaris*. In  
170two cases identification completely failed. These species were noted by their description (for  
171example “sterile grey crustose lichen”). As additional parameters for each sampled branch the  
172height above ground, diameter, inclination and distance and azimuth to the trunk was recorded  
173using measuring tapes or calipers, an inclinometer, a laser rangefinder VERTEX VL 5 (HAGLÖF,

174Järfälla, Sweden) and a compass respectively. Branch age was modelled from branch diameter  
175and species using a data set of branch cross sections collected off fallen trees in the area (S2).  
176Bark roughness was estimated categorically according to an ordinal scale ranging from 1  
177(smooth) to 6 (rough). Bark lesions and deadwood were noted. Leaf area index (LAI) was  
178measured at the plot level in August and September 2018 using a Plant Canopy Analyzer LAI-  
1792200C (LI-COR, Lincoln, NE, U.S.A.).

### 1802.3 Tracing the mechanistic pathways

181The following hypothesized mechanisms are tested for their influence on driving epiphytic lichen  
182diversity in the tree crown: (i) *Habitat optimality*, (ii) *Succession*, (iii) *Habitat Heterogeneity* and  
183(iv) *Species Area Relations (SAR)*. We propose that each of the four mechanisms produces a  
184characteristic fingerprint with respect to the height gradients and correlations patterns of its  
185diversity components ( $\alpha$ ,  $\beta$ ,  $\gamma$ ), gradients of trait expression and relationships to underlying  
186patterns of niche predictors, which are summarized in Table 1. These mechanisms are not  
187mutually exclusive, but presumed to interfere and interact with each other.

188For the *Optimality mechanism* to operate, a mid-canopy  $\gamma$  diversity peak has to occur which is  
189driven by a peaking  $\alpha$  diversity, i.e.  $\gamma$  and mean  $\alpha$  diversity are correlated at the canopy-layer  
190level. It is further presumed that  $\alpha$  diversity is related to one or several relevant environmental  
191predictors. The optimal conditions should also be reflected by a higher cover of lichens. Under  
192the *Optimality mechanism* one would not expect a positive relationship between the within-layer  
193variability of environmental variables and  $\gamma$  diversity and no systematic species turnover along  
194the vertical canopy gradient.

195The *Succession mechanism* is expected to produce a mid-canopy  $\gamma$  diversity peak driven by a  
196peaking  $\alpha$  diversity as above. It is an additional necessary condition that that there is a systematic

197species turnover along the gradient of branch age, as a proxy of successional time. There also  
198needs to be systematic species turnover along the vertical canopy gradient, as mean successional  
199time decreases with height, making plots within a layer more similar to each other than plots in  
200other layers. Consistent with the *Succession mechanism* is a positive correlation of within-layer  
201 $\beta$  diversity and the variation in branch age.

202The *Habitat Heterogeneity mechanism* is expected to produce a mid-canopy  $\gamma$  diversity peak that  
203is driven by a peaking  $\beta$  diversity, but not  $\alpha$  diversity as in the first two mechanisms mentioned  
204above. As  $\alpha$  and  $\beta$  diversity are often correlated (Chase et al. 2011), this implies that observed  
205dissimilarities between layers have to exceed the level of dissimilarity expected by a baseline  $\alpha$ - $\beta$   
206correlation. It is a necessary condition that  $\beta$  diversity is positively correlated with variation in  
207habitat variables (inclination and bark roughness, LAI) pointing to niche diversity within layers.

208For the *SAR mechanism* to operate according to the *passive sampling hypothesis sensu* Connor &  
209McCoy (1979), where a higher surface area acts as larger sample for colonists,  $\gamma$  diversity should  
210correlate with available substrate area per layer and thus should peak in the top canopy layer.  
211 $\gamma$  diversity can be independent of either  $\alpha$  or  $\beta$  diversity. If available area is a strong determinant  
212for species diversity, its peak may be skewed towards the top of the crown. In contrast, the  
213*Optimality, Succession and Heterogeneity mechanisms* all may predict a richness peak towards  
214the mid crown, as this region may offer a more balanced mix of sheltered, yet light habitats  
215(McCune et al. 2000, Parker and Brown 2000), a transition zone from early to late successional  
216species (Rogers 1988, Hilmo 1994) and environmentally and architecturally more diverse  
217habitats respectively.

218Those and further assumptions made by each hypothesis are laid out in Table 1 and Figure 2.

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## 2212.4 Analysis

222Data Analysis was carried out in R, version 3.5.1 (R Core Team 2018). In this study, species  
223richness on plot level is referred to as  $\alpha$  diversity while layer-level species richness is referred to  
224as  $\gamma$  diversity. As real abundances in terms of individual counts are hard to estimate in lichen  
225without resorting to molecular methods (Snäll et al. 2004, Walser et al. 2005, Gjerde et al. 2012),  
226within this study abundances are represented as cover. Within-layer  $\beta$  diversity was calculated on  
227incidence data using the Simpson-based multiple-site dissimilarity (Baselga 2010). A  
228composition index was calculated as first axis of a non-metric multidimensional scaling (nMDS)  
229ordination using the function *metaMDS* implemented in the *vegan* package (Oksanen et al.  
2302019). The number of dimensions ( $k$ ) was deliberately set to one to generate a single  
231compositional gradient (variable ‘com’ in Figure 3). Goodness of fit was evaluated using the  
232*stressplot* function from the same package, in which  $R^2$  is defined as  $1 - S^2$ , with  $S$  being the  
233stress value, which is a measure based on the sum of squared residuals of the ordination  
234(Legendre and Legendre 2003 p. 447 ff.). The nMDS ordination was based on a  $\beta$  diversity  
235matrix, which used pairwise between-plot dissimilarities based on the Simpson  $\beta$  diversity index  
236( $\beta_{sim}$ ; Koleff, Gaston, & Lennon, 2003).

### 2372.4.1 Multiple linear regression model

238An important distinction between the hypotheses is whether variation in  $\gamma$  diversity and mean  $\alpha$   
239diversity are closely connected (*Optimality, Succession*) or whether patterns in  $\gamma$  diversity are an  
240emergent property at the layer level either driven by variation in  $\beta$  diversity (*Heterogeneity*) or  
241area (*SAR*). To get insight into this question a multiple linear regression model was created using  
242a z-transformed layer-level data set with  $\gamma$  diversity as response variable and mean  $\alpha$  diversity,  $\beta$

243diversity and available surface area as explanatory variables. Additionally, the interaction terms  
244of area with mean  $\alpha$  and  $\beta$  diversity were included. This allowed us to assign a potential area  
245effect to one of its composite mechanisms *heterogeneity* or *area per se* which make different  
246predictions about their scale of impact (Schoereder et al. 2004).

#### 2472.4.2 Piecewise Structural Equation Model

248To test for the plausibility of aforementioned mechanisms of shaping biodiversity patterns being  
249expressed at the plot level ( $\alpha$  diversity) piecewise structural equation modelling (SEM) was  
250applied. This analysis was performed for the pooled phorophyte species dataset and on datasets  
251containing only a single phorophyte species, separately. The SEM model was constructed using  
252the *piecewiseSEM* package in R (Lefcheck 2016). Numerical data had been either log- or tukey-  
253transformed using the *rcompanion* package (Mangiafico 2019), if the transformation improved  
254residual normal distribution of the models used within the SEM and subsequently standardized  
255(z-score). Exponents used for transformation are provided in the supplement (S3). Global model  
256fit was evaluated using the Fisher's C. The Fisher's C statistic is derived of the combined p-  
257values of each independence claim associated with the hypothesized path diagram of the SEM,  
258known as the *basis set* (Lefcheck 2016). A test of directed separations (Shipley 2013) was  
259performed on the model to test for missing possible paths, which upon inclusion would lead to an  
260improvement of the model. Such improvements of the model were compared against the initial  
261model using the Akaike's information criterion (AIC) as calculated by Shipley (2013).

262

263The piecewise SEM was constructed with  $\alpha$  diversity as main target variable (Figure 3). SEMs  
264feature exogenous variables and endogenous variables, the first of which are variables without  
265incoming causal relations within the model. The latter are defined as being caused by other

266variables. Endogenous variables may also mediate causal relations to further endogenous  
267variables. Exogenous variables on the plot level include branch age as linear and quadratic term,  
268branch inclination and LAI in both a linear and quadratic term. The inclusion of both linear and  
269quadratic terms for branch age and LAI was based on the expectation of a hump-shaped relation  
270of species richness according to the mid-successional diversity peak and a hump-shaped  
271productivity-diversity relationship, respectively. Originally, bark roughness was included as  
272additional exogenous variable to capture small scale local variation in branch surface  
273environment, but it was dismissed due to its high correlation with branch age (Spearman  
274correlation coefficient = 0.83). All endogenous variables within the plot level are dependent on  
275all the aforementioned exogenous variables. These are the composition index, cover and  $\alpha$   
276diversity. Branch inclination and LAI are assumed to have implications for the energy budget of  
277epiphytic lichen and thus are expected to show significant relations towards  $\alpha$  diversity under the  
278*Optimality mechanism* (Figure 2). As under this assumption species richness is regulated via  
279higher population densities a strong link between cover and  $\alpha$  diversity can also be expected.  
280Branch age can be expected to be a strong determinant for the sequential establishment of lichen  
281communities along the successional gradient. The composition of these communities in turn is  
282intended to be captured with the composition index. The *Succession mechanism* hypothesis  
283(Figure ) predicts an overlap of distinct early and late successional communities at the mid  
284successional peak, which is translated into a link of the community indicator towards  $\alpha$  diversity.  
285As the shape of this relationship can expected to be hump-shaped, the quadratic composition  
286index is added as predictor for  $\alpha$  diversity as well. Thus, the piecewise SEM is constructed based  
287on three linear models:

288

$$com \quad a_0 + a_1 \cdot branch \text{ age} + a_2 \cdot inclination + a_3 \cdot LAI \quad (1)$$

$$cover \quad b_0 + b_1 \cdot branch + b_2 \cdot (branch \text{ age})^2 + b_3 \cdot inclination + b_4 \cdot LAI + b_5 \cdot (L \quad (2)$$

$$\alpha \text{ diversity} \quad c_0 + c_1 \cdot branch \text{ age} + c_2 \cdot (branch \text{ age})^2 + c_3 \cdot inclination + c_4 \cdot LA \quad (3)$$

289 With *com* referring to the composition index and *a*, *b* and *c* to the estimated slopes of equation 1,  
290 2 and 3, respectively. In order to highlight potential idiosyncrasies of the phorophyte species, this  
291 SEM is calculated on both the full data set as well as separately for each species.

#### 292 2.4.3 Distance-based redundancy analysis

293 A distance-based redundancy Analysis (dbRDA, Legendre & Anderson, 1999) was applied to the  
294 same pairwise  $\beta_{sim}$ -matrix, which also served as the basis for the nMDS (see above). Categorical  
295 identity properties (phorophyte species, layer) as well as environmental and structural properties  
296 (branch age, inclination, bark roughness, LAI, height and distance to the tree center) were used  
297 to delineate variation in turnover and community composition both spatially and mechanistically.  
298 Variance partitioning (S8) was applied to check for significance and quantify explained variation  
299 of these predictors.

#### 300 2.4.4 Raup-Crick Null model

301 In studies comparing  $\alpha$  and  $\beta$  diversities, both measures are usually expected to be correlated to  
302 some degree, as many  $\beta$  metrics can vary simply due to changes in either  $\alpha$  or  $\gamma$  diversity (Chase  
303 et al. 2011). Null model approaches can be used to disentangle and correct for this correlation.  
304 Furthermore, these null models offer insight into the mechanistic signature of  $\beta$  diversities, as the  
305 correlation between  $\alpha$  diversity and a given  $\beta$  diversity metric offers a null expectation which  
306 observed  $\beta$  diversities may fall below or exceed. In our case,  $\beta$  diversities within layer higher  
307 than expected may hint towards deterministic species sorting processes between communities as  
308 expected with the *Habitat Heterogeneity* mechanism;  $\beta$  diversities within a layer lower than

309expected may hint towards deterministic sorting processes that operate across layers, for example  
310along a successional gradient. The model used in this study was originally devised by Raup &  
311Crick (1979) and modified by Chase et al. (2011) and has been applied in numerous studies  
312(Muñoz et al. 2004, Zhou et al. 2014, Dini-Andreote et al. 2015). It provides an index ranging  
313from -1 (communities are more similar than expected by random chance) to 1 (communities are  
314more dissimilar than expected by random chance) with a value of 0 corresponding to the Null  
315expectation.

#### 3162.4.5 Species trait variance analysis

317Successional series of lichens are often reflected by changes in trait composition (Rogers 1990,  
318Lawrey 1991). Early successional species tend to have smaller thalli and reproduce sexually and  
319with smaller diaspores. Late succession species achieve competitiveness through faster growth  
320rates and are defended against herbivores, pathogens and UV radiation by secondary metabolites  
321(Lawrey 1986, Ellis 2012). For all observed lichen species an average value of the composition  
322index could be computed using the presence/absence data for each plot. If the composition index  
323adequately represents a successional gradient, this would yield the species average position on  
324this gradient. These species averages were modelled in a variance analysis against species traits  
325known to reflect a successional trait gradient (Rogers 1990), such as growth form, dispersal  
326strategy and their reaction to chemical identification tests as a proxy for chemical traits (K-,C-  
327and P-test), to check for significant trait gradients.

328



## 3293 Results

330A total number of 27 lichen species was recorded ( $17 \pm 2.5$  species per individual tree; for a  
331complete list see S4). Out of these, 20 species occurred on both phorophyte species. Four species  
332were exclusive to *F. excelsior* and three species to *Q. robur*.

333Species richness patterns were similar between both phorophyte species, differing more between  
334layers than between tree individuals or tree species (Figure 4). In both  $\alpha$  and  $\gamma$  diversity a general  
335increase with height could be observed with a sharp decrease in the topmost layer. Trunks were  
336almost devoid of any lichen growth with only 7 species found there and 61.3 % empty plots  
337compared to 3.8 % in all crown layers. Layer 4 was the most species-rich layer in all trees,  
338containing all but 5 of the recorded species. On both plot and layer level, species richness was  
339significantly correlated with lichen cover (Spearman;  $\alpha$ : 0.65;  $\gamma$ : 0.68; both  $p < 0.001$ ). Within-  
340layer  $\beta$  diversity was lowest on the trunks and in layer 5. Values for the inner crown layers were  
341not significantly different from each other (Kruskal-Wallis;  $p = 0.66$ ;  $p < 0,001$  for all layers).  
342Correlations between the environmental and structural predictors (age, bark roughness, branch  
343inclination and LAI) were generally high and significant, but most pronounced between branch  
344age and bark roughness (Spearman; *Fraxinus*: 0.90, *Quercus*: 0.91;  $p < 0.001$ ), and branch age  
345and LAI (Spearman; *Fraxinus*: 0.66, *Quercus*: 0.67;  $p < 0.001$ ).

### 3463.1 Multiple linear regression

347In the multiple regression modeling  $\gamma$  diversity as a function of mean  $\alpha$  diversity,  $\beta$  diversity and  
348area (including interactions), mean  $\alpha$  diversity had the strongest effect (0.87,  $p < 0.001$ ), with the  
349only other significant effect being the interaction term of  $\alpha$  diversity and area (0.31,  $p = 0.002$ ).

350 Available surface area (Figure 5) alone only had a small, non-significant effect (0.12,  $p = 0.10$ ).

351 Overall explained variance was 82.4 %.

## 3523.2 Piecewise Structural Equation Model

353 The SEM exploring the determinants of  $\alpha$  diversity using the full data set, including both  
354 phorophyte species, obtained a non-significant Fisher's C (8.52,  $p = 0.384$ ), indicating an  
355 appropriate representation of the data. The tree species-specific models performed similarly well  
356 (*F. excelsior*: 7.726,  $p = 0.461$ ; *Q. robur*: 10.784,  $p = 0.214$ ).

357 Branch age was the exogenous parameter with the strongest significant effect on all plot-level  
358 dependent variables (Figure 6) with concave quadratic relations towards  $\alpha$  diversity ( $-0.20$ ,  $p <$   
359  $0.001$ ; linear term:  $-0.11$ ,  $p = 0.002$ ) and cover ( $-0.50$ ,  $p < 0.001$ ; linear term non-significant) and  
360 linear relations towards community composition ( $-0.67$ ,  $p < 0.001$ ). Yet, cover constituted the  
361 strongest predictor for  $\alpha$  diversity ( $0.63$ ,  $p < 0.001$ ). LAI had significant effects on  $\alpha$  diversity  
362 (linear:  $-0.06$ ,  $p = 0.033$ ), cover (linear:  $-0.23$ ,  $p < 0.001$ , quadratic:  $-0.11$ ,  $p < 0.001$ ) and  
363 community composition (linear:  $-0.08$ ,  $p = 0.026$ ), while branch inclination only affected  
364 community composition significantly ( $0.09$ ,  $p = 0.001$ ). The effect of community composition on  
365  $\alpha$  diversity was non-significant. Variance explained in endogenous variables was 72 % ( $\alpha$   
366 diversity), 40 % (cover) and 52 % (community composition).

367 The species-specific models (S7) confirmed the main patterns of the full model, although they  
368 diverged in a few aspects. While the number of significant paths was slightly reduced in the  
369 model for *F. excelsior*, the model for *Q. robur* included one additional significant path compared  
370 to the full model, a negative linear effect of branch age on cover. As a consequence, both hump-  
371 shaped branch age relations towards  $\alpha$  diversity and cover were shifted slightly towards younger

372 branches in *Q. robur* with a maximum of the species richness-branch age relation at  $41 \pm 6$  years  
373 compared to  $50 \pm 3$  years in *F. excelsior* ( $45 \pm 6$  years in all trees).

### 3743.3 Distance-based Redundancy analysis

375 Pairwise between-plot species turnover (dbRDA, overall 34.9 % explained variance) varied  
376 mainly between layers (26.8 % variance explained, 4.0 % purely attributed to layer with no  
377 overlap to other effects, see Figure 9), with plots of different layers having a significantly higher  
378  $\beta$  diversity than plots within layers of equal height (Wilcoxon;  $p < 0.001$ ). All crown  
379 environmental variables were significant predictors of pairwise  $\beta$  diversity, such as branch  
380 inclination ( $p = 0.003$ ), LAI ( $p = 0.010$ ) and especially branch age ( $p < 0.001$ ), except for bark  
381 roughness, which did not explain additional variation in  $\beta$  diversity and was thus removed from  
382 the model. They generally shared high overlap with layer. This might imply that these factors are  
383 in part responsible for between layer differences. Branch age, for example, explained 25.1 % of  
384 variation in pairwise  $\beta$  diversity, 22.7 % of which was shared with layer (which also includes  
385 13.9 % overlap with LAI), while 2.4 % of variation was purely attributed to branch age.  
386 Phorophyte species explained a comparably small amount of variation (5.5 %) but displayed very  
387 little overlap with other effects.

### 3883.4 Raup-Crick Null Model

389 Within layers, the number of shared species between plots was significantly higher than null  
390 model expectations (t-test,  $p < 0.001$ ) resulting in mostly negative within-layer means of the  
391 Raup-Crick metric ( $-0.36 \pm 0.26$ , Figure 8). This implies within-layer homogeneity and thus  $\gamma$   
392 diversity control by raised levels of  $\alpha$  diversity rather than  $\beta$  diversity. Exceptions could mainly  
393 be found on the trunk, where the observed number of shared species mainly matched null model

394 expectations ( $-0.08 \pm 0.10$ ). Deviations from the null model were highest in layer 5 ( $-0.62 \pm$   
395 0.12). The increase in deviation from the trunk to the uppermost layers diverged in shape  
396 between the tree species with the increase being steeper in *F. excelsior* compared to *Q. robur*.

### 397 3.5 Species composition and Species trait variance analysis

398 Foliose lichens constituted the most common growth form in both species numbers (13) and total  
399 cover. Crustose lichens (10) were less abundant. Leprous species were fewer in number of  
400 species (3) but had amongst them one of the most abundant species *Candelariella xanthostigma*  
401 (Ach.) Lettau. Finally, only three fruticose species could be observed, all of them in small  
402 numbers and restricted to only three tree individuals. The nMDS ( $k=1$ ,  $n=652$ ) conducted in  
403 order to create the composition index produced a stress value of 0.26 (non-metric  $R^2$  of 0.93).  
404 The composition index itself showed negative correlations towards branch age (see fig. 11;  
405 Spearman:  $-0.70$ ;  $p < 0.001$ ) and LAI (Spearman:  $-0.51$ ;  $p < 0.001$ ) but was independent of  
406 branch inclination (Spearman:  $-0.06$ ;  $p = 0.140$ ). Variations in the averages of the composition  
407 index for each species were best explained by growth form (33.3 %, including 16.3 % unshared  
408 explained variation;  $p = 0.002$ ) and presence of Apothecia (30.0 %, including 12.7 % unshared  
409 explained variation;  $p = 0.020$ ). Other traits in regards to dispersal mode or chemistry did not  
410 contribute significant explanation of variance in composition (all  $p > 0.2$ ).

411

## 4124 Discussion

413 Several lines of evidence have been investigated in order to trace the influence of *Optimality*,  
414 *Succession*, *Heterogeneity* and *SAR* as mechanisms shaping patterns in lichen diversity in the tree  
415 crown (Table 3). The emergence of the gradients in richness and composition due to these  
416 mechanisms are not necessarily mutually exclusive, but may have interactions and added effects,  
417 and are discussed in the following subsections. While criteria for the *Optimality* and *Succession*  
418 *mechanisms* were generally met, we could not find any evidence for the *Heterogeneity*  
419 *mechanism*. The *SAR mechanism* was only weakly and indirectly supported: area did not  
420 influence  $\gamma$  diversity directly, but had a significant interaction term with  $\alpha$  diversity.

421

### 4224.1 Optimality

423 Both  $\alpha$  and  $\gamma$  diversity exhibited a mid-canopy peak and were significantly correlated (criterion  
424 1, Table 1). In contrast, a distinct peak in  $\beta$  diversity was not observed and  $\beta$  diversity was not  
425 correlated with  $\gamma$  diversity. An increase in  $\alpha$  diversity was expected to be mediated by an increase  
426 in cover (criterion 3, Table 1). This was supported by the SEM, where cover was the strongest  
427 predictor of  $\alpha$  diversity (Figure 6). Cover itself depended significantly on LAI (criterion 2, Table  
428 1), displaying a hump-shaped relationship. Notably, this includes a decrease of cover on old  
429 branches in the dim lower part of the trunk, on which sufficient time for colonization without  
430 light limitation could have created a high lichen cover (compare 4.2). Lichens, being  
431 photoautotrophic organisms, certainly depend on available light in the canopy. It has been shown  
432 to be a significant predictor for species richness of epiphytic lichens (Gustafsson and Eriksson  
433 1995, Fritz et al. 2009, Moning et al. 2009, Normann et al. 2010, Rosabal et al. 2012). However,

434other microclimatic factors like water limitation can be of overriding importance (Sillett and  
435Antoine 2004, Rambo 2010). While we did not measure humidity, we expected that water  
436limitation is highest in the top crown due to drying winds and higher irradiation leading to  
437suboptimal growing conditions thus creating the observed hump-shape. The strong signal of  
438*Optimality* emphasizes the importance of growing seasons conditions for lichen diversity  
439patterns, because during the leaf-off period neither light nor humidity gradients are particularly  
440pronounced.

#### 4414.2 Succession

442In the piecewise SEM, branch age was not only an important determinant of species richness  
443(Figure 10) but also of species composition (criterion 4, Table 1). It even outperformed LAI as  
444predictor of both cover and richness. After accounting for height layer and phorophyte species,  
445pairwise differences in composition between plots (dbRDA, see 3.3) also were best explained by  
446branch age (criterion 6, Table 1). Moreover, species composition was expected to be more  
447similar within layers than between layers (criterion 7, Table 1), which was supported by both the  
448dbRDA variance partitioning and the Raup-Crick null model deviations. In the first case, the  
449majority of variation was attributed to height layers. In the second case, excluding the trunk,  
450within-layer deviations of the Raup-Crick null model were mostly negative, indicating that plots  
451within layers were more similar than expected by chance.

452Evidence for succession further requires branch age to be connected to a successional sequence  
453of epiphytic lichen (Degelius 1964, Hilmo 1994, Wirth et al. 1999), expressing a systematic trait  
454gradient (criterion 5, Table 1). Most common pioneers comprise of physically smaller crustose or  
455foliose lichen with lower investments in longevity. These typically settle on the first uneven  
456surfaces like bud scars and joints (Degelius 1964, Rogers 1990, Ellis 2012). This could be

457observed in this study and growth form was the trait that best explained the compositional  
458gradient. Common species found in the top canopy layer included small, intricate foliose species  
459(i.e. genus *Physcia* and *Xanthoria*) and crustose species like *Amandinea punctata* (Hoffm.)  
460Coppins & Scheid. Smooth branch surfaces were mainly colonized by small rosettes of crustose  
461species (e.g. genus *Lecanora* and *Caloplaca*). Another typical trait for pioneers is the ability to  
462efficiently disperse propagules in order to colonize new sites (Rogers 1990, Armstrong and  
463Welch 2007). The presence of apothecia did also explain the compositional gradient, with  
464species developing apothecia being more prevalent on younger branches. Apothecia produce  
465sexual spores that are much smaller and hence are dispersed more readily than asexual modes of  
466dispersal (soredia, isidia and thallus fragments). Bigger, more robust foliose species, fruticose  
467and leprous species with predominantly asexual modes of dispersal appeared further down on  
468relatively older branches and the trunk.

469One caveat remained: The hump-shaped relation between branch age and  $\alpha$  diversity (Figure 11)  
470might suggest a mid-succession peak at a branch age of about 45 years. However, the decline in  
471species richness on the peak's descent is assumed to result from competitive exclusions  
472(Purschke et al. 2013), also described as “quorum effect” (Jenkins 2006). Evidence for  
473competitive interactions, such as overgrowth between lichens could not be observed on the lower  
474parts of the crown and the trunk. On the contrary, lichen thalli became more sparsely distributed  
475and the cover decreased (Figure 10b) making competitive exclusion less probable. This is in line  
476with previous studies on epiphytic lichens which concluded that competitive exclusions rarely  
477occurs once thalli are established (Lawrey 1991, Snäll et al. 2003, Pentecost 2014).

478In conclusion, the *Succession* mechanism aptly describes the increase in species richness as  
479environmental filters get alleviated and species accumulate on the surfaces of growing branches

480that are gradually overtopped and sheltered as the tree gains height. Past the species richness  
481maximum, however, a different mechanism than competitive exclusion has to account for the  
482decrease in cover and species richness on the oldest parts of the tree. As possible alternative  
483mechanisms competition by bryophytes, shedding of bark surface (Cáceres et al. 2007) or  
484grazing pressure by gastropods (Asplund et al. 2010) have been suggested. However, the  
485coinciding decrease in environmental *Optimality* and of lichen cover on older branches in lower  
486canopy layers despite the long time for colonization, hinting towards less favorable conditions  
487further below (see 4.1) might be the strongest candidate.

### 4884.3 Heterogeneity

489Heterogeneity is amongst the first and the most commonly documented drivers of diversity  
490(Stein et al. 2014). The horizontal variation of environmental variables has been highlighted as  
491distinct ecological feature of tree crowns (Parker and Brown 2000) and as driver of arboreal  
492diversity patterns. This has been exemplified for tropical vascular epiphytes (Woods et al. 2015).  
493It is thus surprising that in our study heterogeneity showed little to no influence in shaping the  
494diversity gradient within the trees.

495Firstly,  $\beta$  diversity was not related to  $\gamma$  diversity (criterion 8, Table 1) and secondly, deviations  
496from the Raup-Crick null model did not indicate that within-layer differences were higher than  
497expected by chance. Both would have been prerequisites for the *Heterogeneity mechanism*.  
498Although variation in pairwise  $\beta$  diversity was reasonably well explained in the dbRDA, little  
499variation was attributed to within-layer variation of environmental variables (criterion 9, Table  
5001). Out of 34.9 % explained variation, 26.2 % could at least partially ascribed to height layers,  
5014.4 % to phorophyte species, leaving only about 4 % remaining to be explained.



#### 5024.4 Species Area Relationship

503 In the multiple linear regression analysis, only mean  $\alpha$  diversity and its interaction with area had  
504 a significant effect on  $\gamma$  diversity. Available surface area was not significant as a main effect  
505 (criterion 10, Table 1). Thus, area does not have an effect at the layer level, but it amplifies the  
506 effect of  $\alpha$  diversity in layers with a high amount of surface area. This may suggest that area does  
507 have an influence on small scale processes of species richness regulation in line with the *area*  
508 *per se* – hypothesis (Connor and McCoy 2000, Schoereder et al. 2004). However, layers in the  
509 upper crown not only possess greater branch surface area; they also are less shaded and span a  
510 greater extent of projected area. As a result, they are able to collect more photosynthetically  
511 active radiation. The interaction effect of surface area may thus also contain elements of the  
512 *Optimality mechanism*.

#### 5134.5 Conclusion and implications for lichen biodiversity in canopies

514 The results of this study suggest an intricate interplay between the mechanisms of environmental  
515 *Optimality* and *Succession* in controlling vertical diversity patterns of epiphytic lichen in the tree  
516 crown. This includes environmental limitations in the harshly exposed young branches and dim  
517 understory (*Optimality*), as well as the strong vertical species turnover associated with  
518 successional dynamics in the upper height layers. On older branches in height layer four both  
519 mechanisms jointly create a sheltered, yet light habitat where a majority of species of the whole  
520 successional gradient co-occur to create the observed peak in species richness. The strong  
521 increase in surface area with height resulting from the fractal branching process did not translate  
522 into a monotonously increasing diversity signal. While we found horizontal heterogeneity within  
523 height layers to have little effect, vertical heterogeneity in environmental conditions and  
524 successional time appeared to be strong driver of lichen diversity and composition in our study

525(compare Figure 7) and in the literature (Bates 1992, McCune et al. 2000). These gradients may  
526be steeper than elevational gradients by an order of magnitude (Nakamura et al. 2017) and thus  
527have the potential to strongly contribute to the creation of the biodiversity hotspots that are forest  
528canopies (Ozanne et al. 2003, Nakamura et al. 2017).

## 5294.6 Outlook

530It comes as little surprise that the effects of mechanisms such as *Succession* and *Optimality* were  
531hard to disentangle. Not only because they are found to be mechanistically intertwined, but so  
532are the predictors used to describe energetic as well as age relations. LAI and branch age were  
533significantly correlated as the architecture of the tree itself is responsible in shaping the vertical  
534gradients found within the canopy (McCune et al. 2000). Such correlations put limits on the  
535insights that can be gained in observational studies. Experiments which separate both effects, for  
536instance by distributing standardized logs as lichen habitat along the vertical and horizontal  
537gradient (Antoine and McCune 2006), offer a way to separate and quantify the relative  
538importance of mechanisms like *Succession*, *Optimality* as well as surface area relationships and  
539dispersal. Effects of dispersal limitations were not included in the original hypotheses as lichen  
540are considered to have a generally high dispersal ability at the canopy scale we considered  
541(Muñoz et al. 2004, Lenoir et al. 2012). However, evidence for small scale dispersal limitations  
542does exist, in particular in dependence of propagule size (Sillett et al. 2000, Löbel et al. 2006).  
543We propose to install air traps collecting diaspores and use the knowledge of lichen distribution  
544to infer dispersal kernels depending on diaspore size. Finally, lichens are a ubiquitous element of  
545biodiversity in temperate tree crowns but by far only one of many. To date, only limited  
546literature exists on multi-taxa approaches on multi-trophic dynamics (Shorrocks et al. 1991,  
547Nadkarni 1994, Lamit et al. 2015, Asplund et al. 2016). It certainly would be of interest to

548investigate how the patterns of lichen diversity found within this study propagate through the  
549complex ecosystem that is the forest canopy including diversity patterns of lichen-associated  
550organisms as well as processes such as nutrient cycling. Facilities such as the Canopy Crane in  
551Leipzig are promising tools to tackle this challenge.

552

553

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- 735
- 736



## 737 Table 1

738 *Table 1: Evidence matrix: Expected observations according to each hypothesized mechanism.*

739 *The first column details where in the crown a peak in diversity is to be expected and which*

740 *measure or scale of biodiversity will be affected. Here, ‘mid crown’ does not necessarily refer to*

741 *the mathematical midpoint of the crown but rather may be slanted to either top or bottom of the*

742 *canopy. The second and third column feature conditions that have to be observed necessarily or*

743 *are indicative of a mechanism, respectively. Symbols and abbreviations used are:  $\alpha$ ,  $\beta$ ,  $\gamma$  =  $\alpha$ ,  $\beta$*

744 *or  $\gamma$  diversity; com = community composition; A = branch surface area; P = habitat predictors*

745 *(e.g. branch inclination, LAI); age = branch age, ‘traits’ is referring to a successional species*

746 *trait gradient; i = layer marker, j = plot marker ( $j_a$  and  $j_b$  mark different layers). The numbers*

747 *following the conditions in the third and fourth column are for reference in Figure 2.*

<b>Mechanism</b>	<b>Expected <math>\gamma</math> diversity peak and scale of emergence</b>	<b>Necessary conditions</b>	<b>Sufficient conditions</b>
<b><i>Optimality</i></b>	Mid crown ( $\alpha$ , $\gamma$ )	$\gamma_i \sim \alpha_i$ c1 $\alpha_{ij} = f(P_{ij})$ c2	$!(\gamma \sim \text{Var}(P))$ $\alpha_{ij} \sim \text{cover}_{ij}$ c3
<b><i>Succession</i></b>	Mid crown ( $\alpha$ , $\gamma$ )	$\gamma_i \sim \alpha_i$ c1 $\text{com}_{ij} = f(\text{age}_{ij})$ c4 $\text{traits} = f(\text{age}_{ij})$ c5 $\beta(i,i)_j < \beta(ij_a, ij_b)$ c7	$\beta(ij, ij) =$ c6 $f(\Delta \text{age})$
<b><i>Heterogeneity</i></b>	Mid crown ( $\beta$ , $\gamma$ )	$\gamma_i \sim \beta_i$ c8 $\beta_i \sim \text{Var}(P)_i$ c9	$\text{com}_{ij} = f(P_{ij})$
<b><i>SAR</i></b>	Top crown (passive sampling: $\gamma$ area per se: $\alpha$ , $\gamma$ )	$\gamma_i = f(A_i)$ c10 $\alpha_i \sim A_i$ (area per se)	$\gamma_i \neq f(\alpha_i   \beta_i)$ (passive sampling)

748

749 **Table 2**

750 *Table 2: Used statistical methods by reference number (white on black) and criteria from Table*  
751 *7512 to be tested (reference in brackets)*

reference number	model type	Aim
<b>1</b>	multiple linear regression model	test contributions of mean $\alpha$ and $\beta$ diversity and area to $\gamma$ diversity (c1,c8,c10)
<b>2</b>	piecewise structural equation model	contributions to $\alpha$ diversity (c2,c3,c4)
<b>3</b>	distance-based redundancy analysis	contributions of environmental variation to beta diversity (c6, c9)
<b>4</b>	Raup-Crick Null model	delineate $\beta$ diversity characteristics independent of $\alpha$ diversity variation (c7,c8)
<b>5</b>	variance analysis of trait gradients	test for a successional trait gradient (c5)

752  
753

754 **Table 3**

755 *Table 3: Criteria from the evidence matrix (Table 1) with information about their support by the*  
 756 *results. Symbols and abbreviations used are:  $\alpha$ ,  $\beta$ ,  $\gamma = \alpha$ ,  $\beta$  or  $\gamma$  diversity; *com* = community*  
 757 *composition; *A* = branch surface area; *P* = habitat predictors (e.g. branch inclination, LAI);*  
 758 *age = branch age, ‘traits’ is referring to a successional species trait gradient; *i* = layer marker,*  
 759  *$j =$  plot marker ( $j_a$  and  $j_b$  mark different layers). The criterion numbers are for reference in*  
 760 *Figure 2.*

<b>Mechanism</b>	<b>Criterion</b>	<b>Support</b>
<b><i>Optimality</i></b>	c1 $\gamma_i \sim \alpha_i$	<b>Yes</b>
	c2 $\alpha_{ij} = f(P_{ij})$	<b>Yes</b>
	c3 $\alpha_{ij} \sim \text{cover}_{ij}$	<b>Yes</b>
<b><i>Succession</i></b>	c1 $\gamma_i \sim \alpha_i$	<b>Yes</b>
	c4 $\text{com}_{ij} = f(\text{age}_{ij})$	<b>Yes</b>
	c5 $\text{traits} = f(\text{age}_{ij})$	<b>Yes</b>
	c6 $\beta(i_j, i_j) = f(\Delta \text{age})$	<b>Yes</b>
	c7 $\beta(i, i)_j < \beta(i_j, i_j)_b$	<b>Yes</b>
<b><i>Heterogeneity</i></b>	c8 $\gamma_i \sim \beta_i$	No
	c9 $\beta_i \sim \text{Var}(P)_i$	Weak, mainly supported by branch age (see c6)
<b><i>SAR</i></b>	c10 $\gamma_i = f(A_i)$	Weak, significant interaction with $\alpha$ diversity, but no direct effect on $\gamma$ diversity

761

## 762 Figure legends

763 Figure 1: Schematic representation of the interplay between biodiversity shaping mechanisms  
764 (columns) and their expected spatial fingerprints on layer-level species richness ( $\gamma$  diversity,  
765 represented as encircled number in the center). Each smaller square represents a sampling unit  
766 area within a layer (bigger square). Optimality: Concurrence of environmental variables such as  
767 available light and humidity leads to favorable growth conditions in a mid-canopy layer.  
768 Heterogeneity: Differentially adapted species (indicated by different color gradients) coexist in a  
769 more heterogeneous layer in the mid crown. Succession: Early and late successional species  
770 (indicated by different color gradients) coincide on branches of median age opposed to young  
771 branches in the top crown layer and old branches in the bottom layer. Species Area Relation  
772 (SAR): The creation of surface area due to continuous branching along the vertical axis leads to a  
773 species-indiscriminate increase in richness.

774

775 Figure 2: Conceptual scheme of hypothesized mechanisms for the emergence of lichen diversity  
776 in the tree crown. Rounded boxes represent the mechanism itself, square boxes measurable  
777 variables. Numbers in small white boxes refer to expected conditions in the evidence matrix  
778 (Table 1), numbers inside black boxes refer to statistical methods used (detailed in table 2).

779

780 Figure 1: piecewise structural equation model for the plot level. Mechanistic distinctions can be  
781 made according to the path followed (The numbers correspond to conditions mentioned in Table  
782 1 and Figure 2). According to the optimality hypothesis, paths in the lower half (2,3; marked red)  
783 should be more distinguished as species richness is thought to be driven by energetic optimality

784and mediated by abundance, represented by leaf area index (LAI) and cover, respectively. If  $\alpha$   
785diversity is mainly determined by successional mechanisms species richness is expected to  
786depend strongly on branch age, mediated by species composition (respective pathways marked  
787blue). For each branch age, LAI and composition index both the linear and quadratic term are  
788included to account for hump shaped patterns. No mechanistic distinction can be stated for either  
789heterogeneity or Species area relation hypothesis as these are assumed to be emergent at the  
790layer level.

791

792Figure 4: Vertical patterns of lichen diversity in the tree crown. White boxes represent  
793individuals of *Fraxinus excelsior*, grey boxes *Quercus robur*. a)  $\gamma$  diversity (layer level) b)  $\alpha$   
794diversity (plot level) c)  $\beta$  diversity (within layer)

795

796Figure 5: Modelled amount of available surface area within layers in relation to total tree surface.  
797White boxes represent *Fraxinus excelsior*, grey boxes *Quercus robur*. Note the amount of  
798variation in surface area being visibly higher in *Q. robur*.

799

800Figure 6: piecewise SEM of plot level pathways using the full dataset.  $R^2$  in small boxes in top  
801right; arrow width is proportional to parameter estimates, straight lines indicate regressions,  
802double-headed, curved arrows covariance dotted lines  $p < 0.1$ , full lines  $p < 0.05$ , grey lines  $p >$   
8030.1 plot marker (j); layer marker (i). See supplement S7 for species specific models.

804

805Figure 7: Variation partitioning of  $\beta$  diversity (dbRDA). The bars represent total explained  
806variation by respective variables as the sum of its pure effect and overlap shared with other

807variables. Blank portions of the bars represent the pure effect; black portions represent the sum  
808of shared overlaps each explaining less than 1% of variance in  $\beta$  diversity. Overall explained  
809variation: 34.9 % (65.1 % unexplained).

810

811Figure 8: Raup-crick model: mean Raup-Crick metric [-1,1] value by layer and tree species. A  
812value close to 1 represents communities more dissimilar than expected in the null model,  
813indicating community assembly to be highly deterministic (environmental filtering) within  
814layers. Negative values represent communities more similar compared to the null model,  
815indicating assembly processes to be highly deterministic across layers with the communities  
816within the layer being more similar than expected by chance, while values close to zero conform  
817with null expectations and indicate stochastic community assembly.

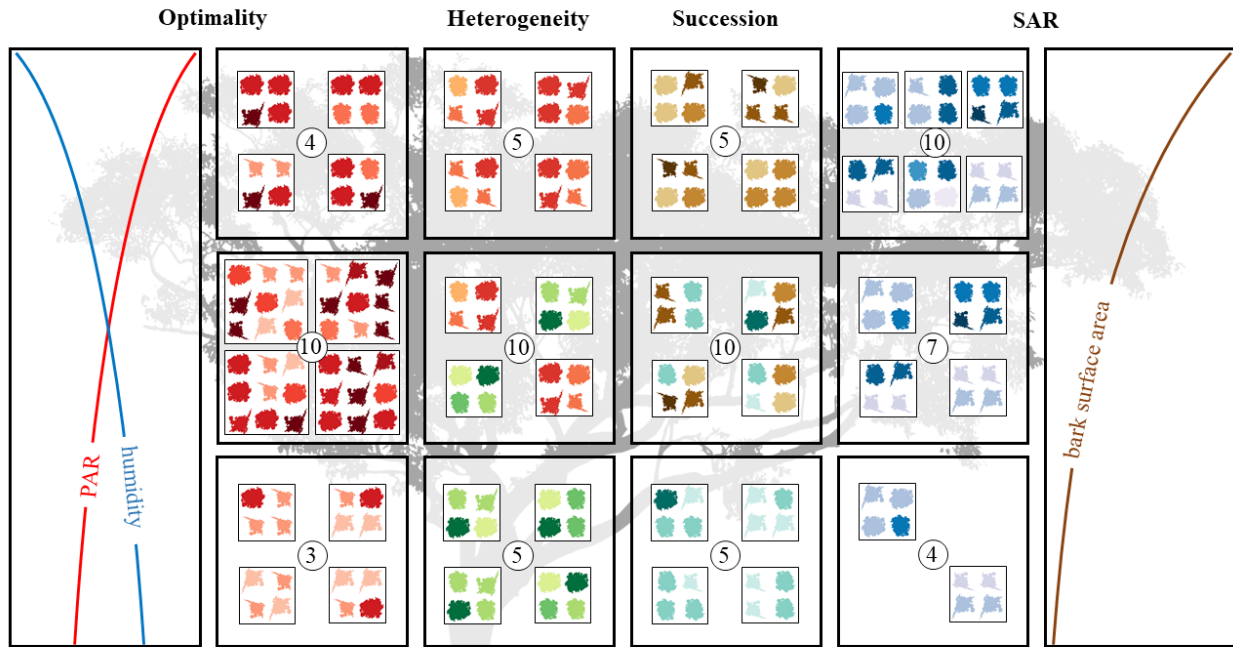
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819Figure 9: Species trait relations towards branch age. Grey triangles (*Fraxinus excelsior*) and  
820empty circles (*Quercus robur*) represent sampling plots in a 2D composition by branch age  
821ordination. The composition index is calculated as first axis of a non-metric multidimensional  
822scaling (nMDS) based on a pairwise  $\beta$  diversity matrix. Species means for both the nMDS axis  
823as well as branch age determine species position in this 2D ordination, represented by the colored  
824symbols. Noteworthy, a trend for spore-dispersed, crustose and small foliose lichens to be  
825aligned to younger branches, whereas species in which vegetative dispersal is more common are  
826increasingly prevalent with increasing branch age.

827

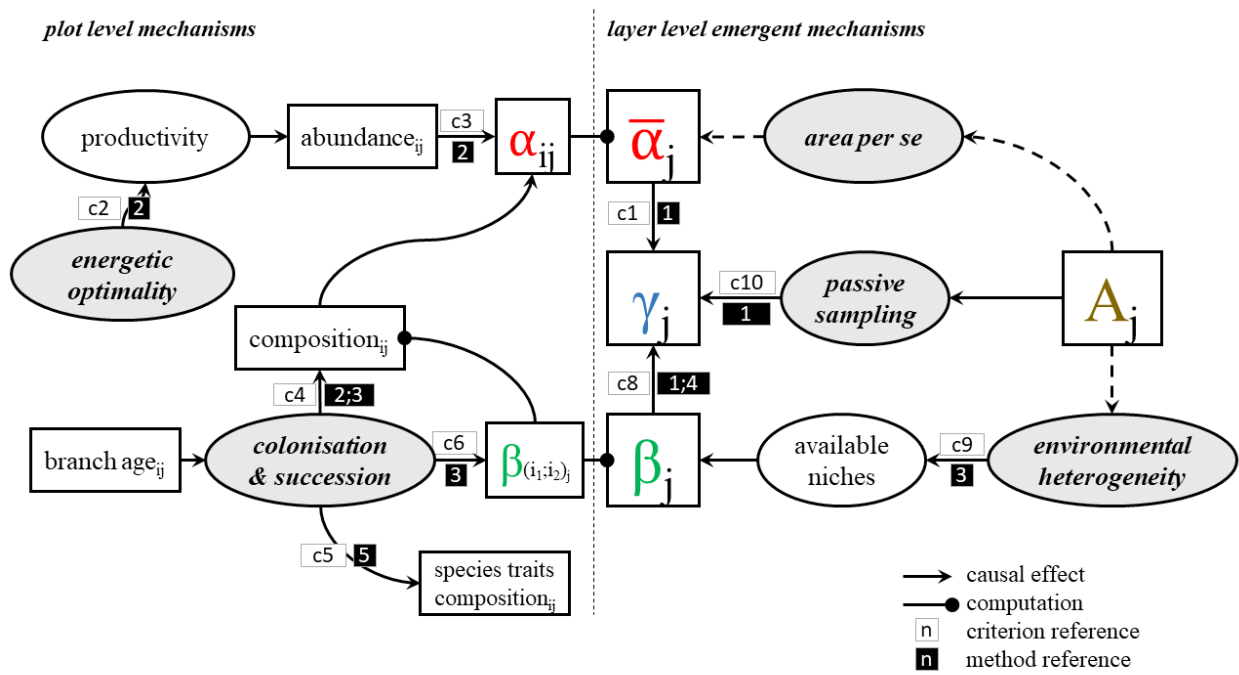
828Figure 10: Both the  $\alpha$  diversity and cover - branch age relationship shows a distinct hump shape

829 **Figure 1**



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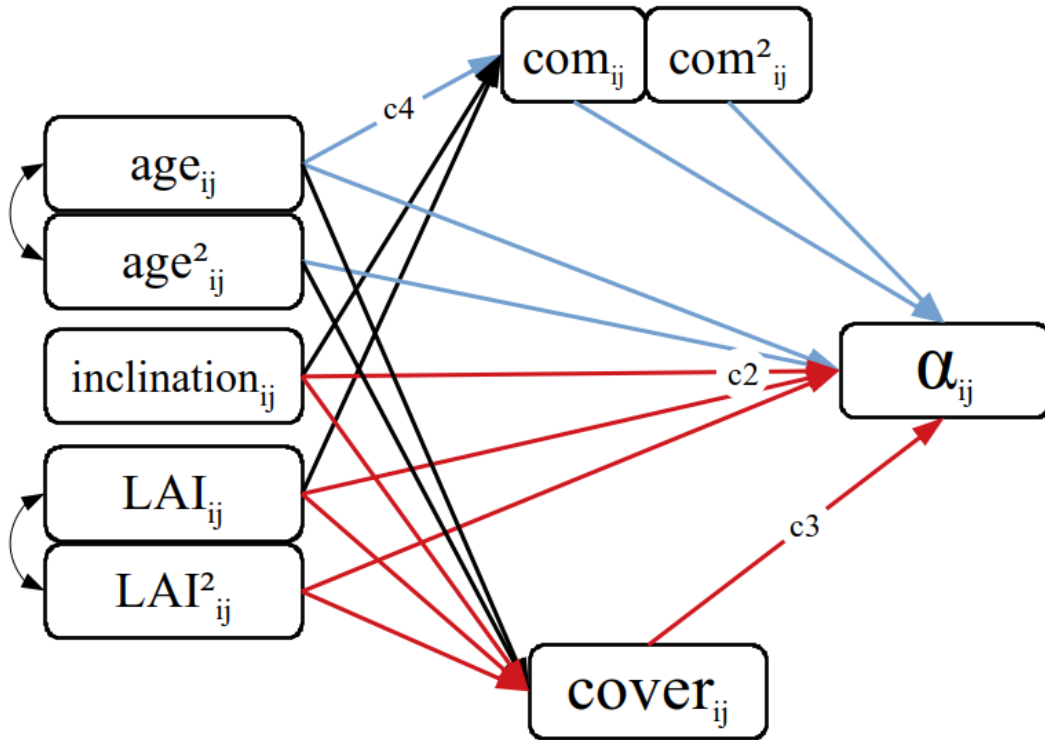
831 **Figure 2**



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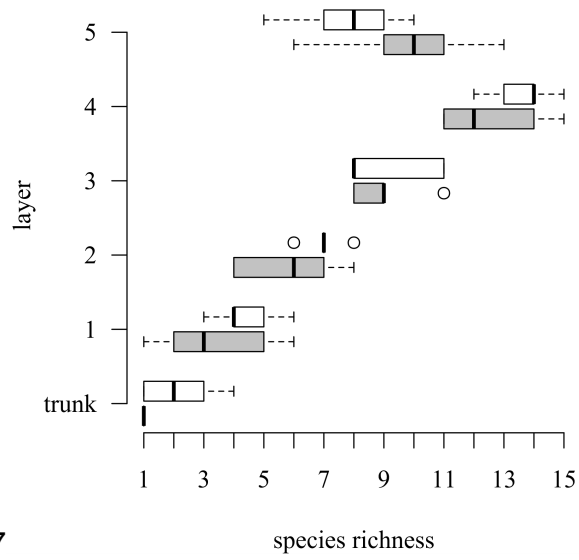
833 Figure 3



834

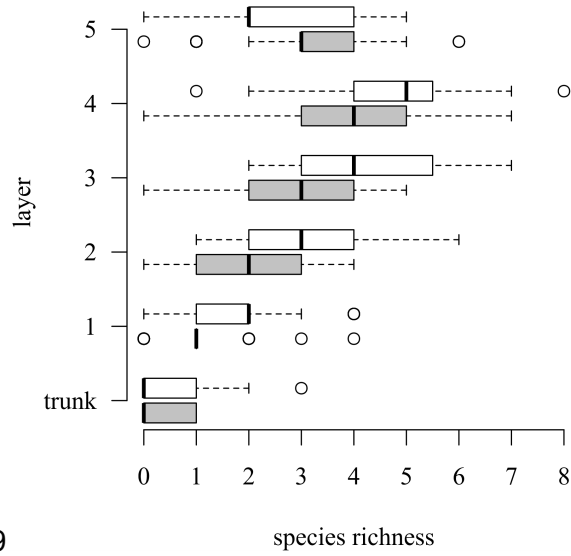
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## 836 Figure 4a



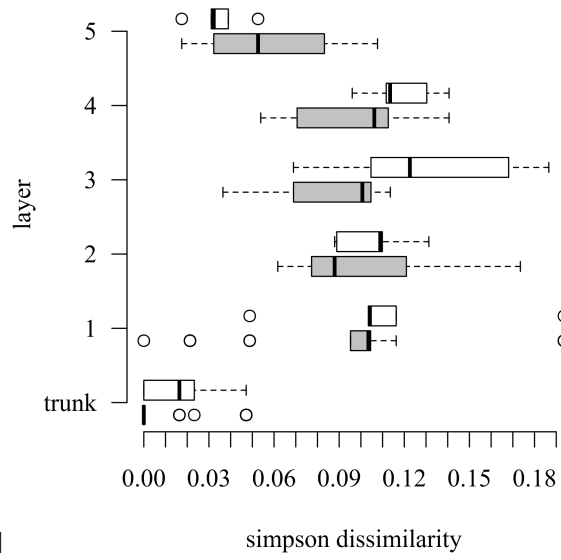
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838 Figure 4b



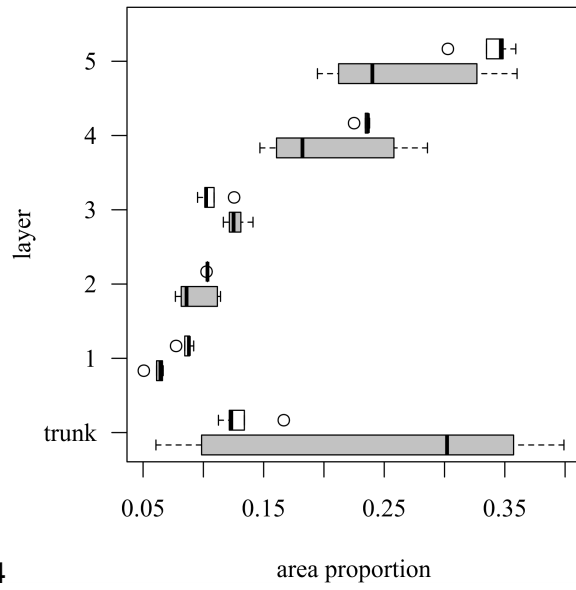
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840 **Figure 4c**



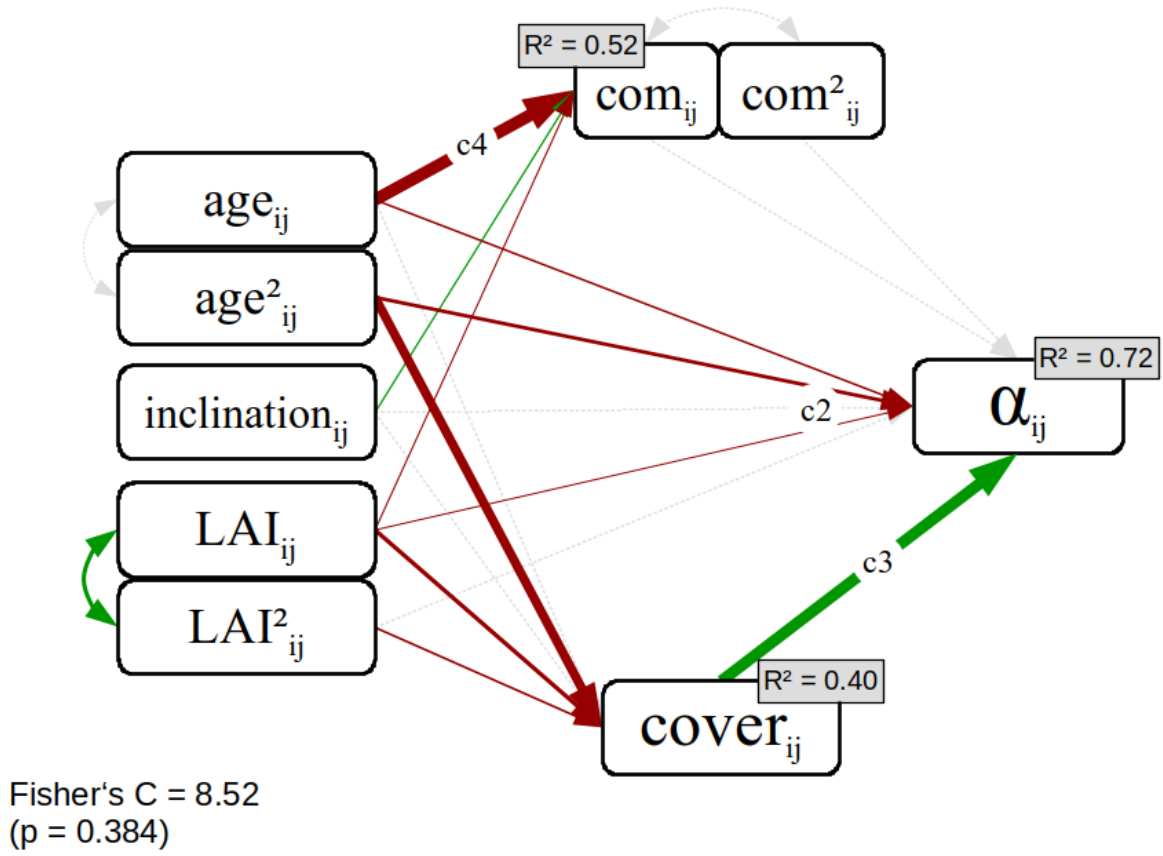
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843 Figure 5



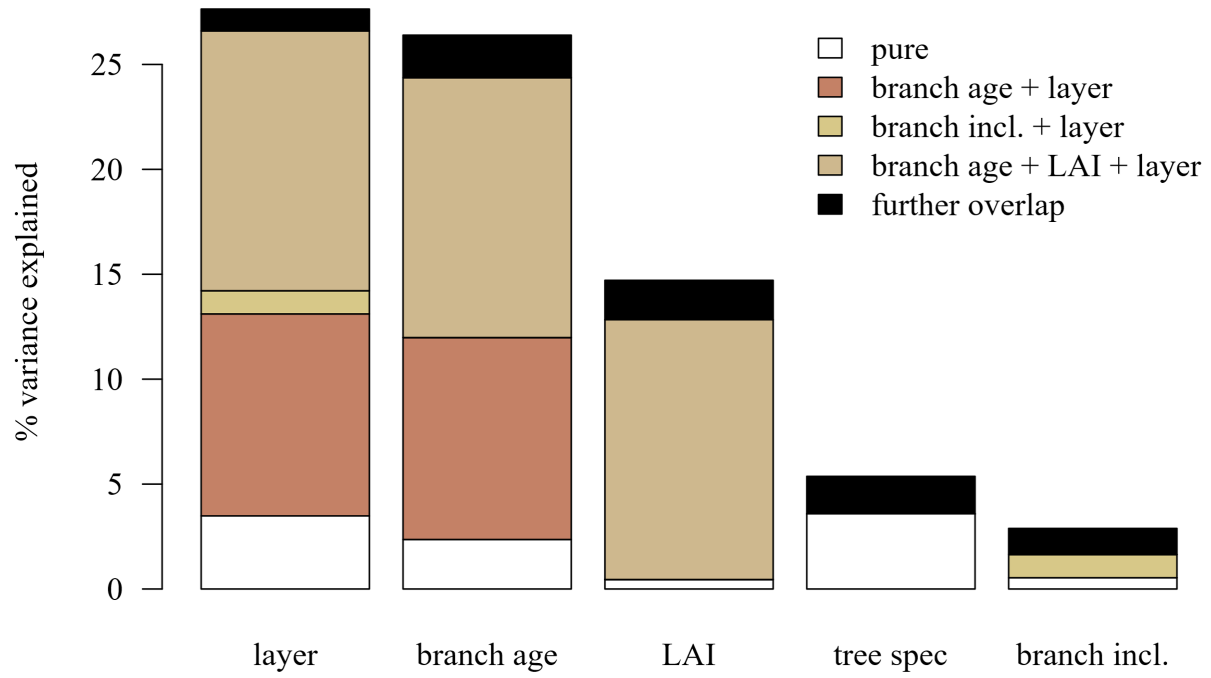
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846 Figure 6



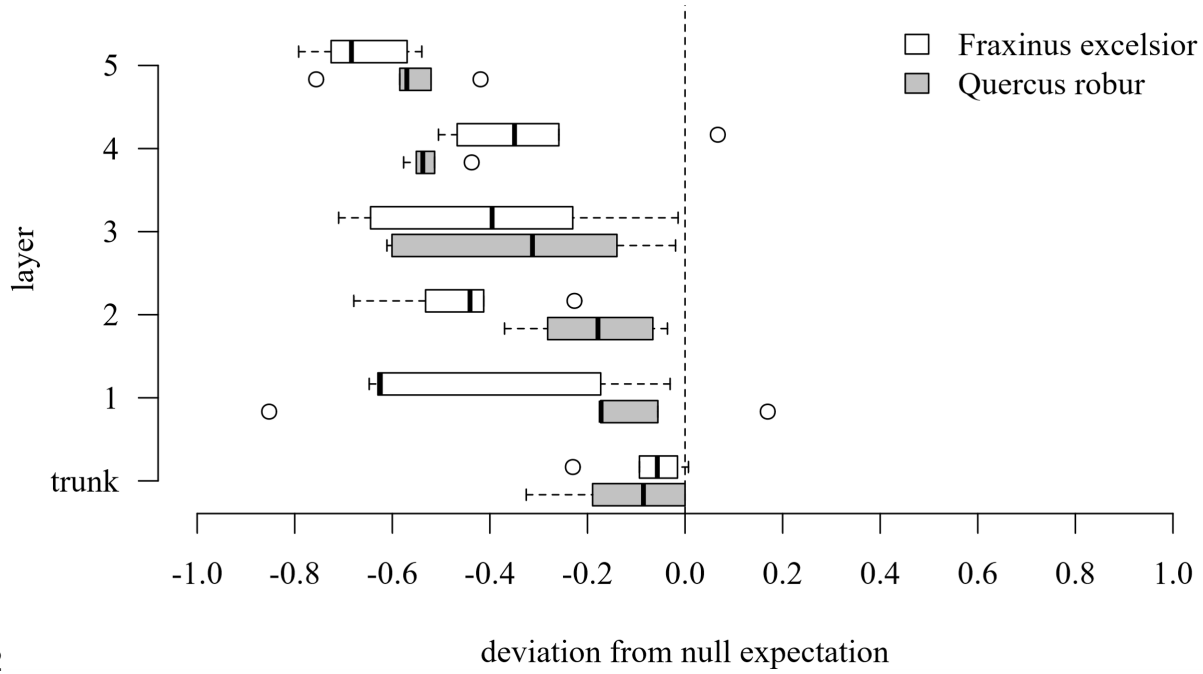
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849 **Figure 7**



850

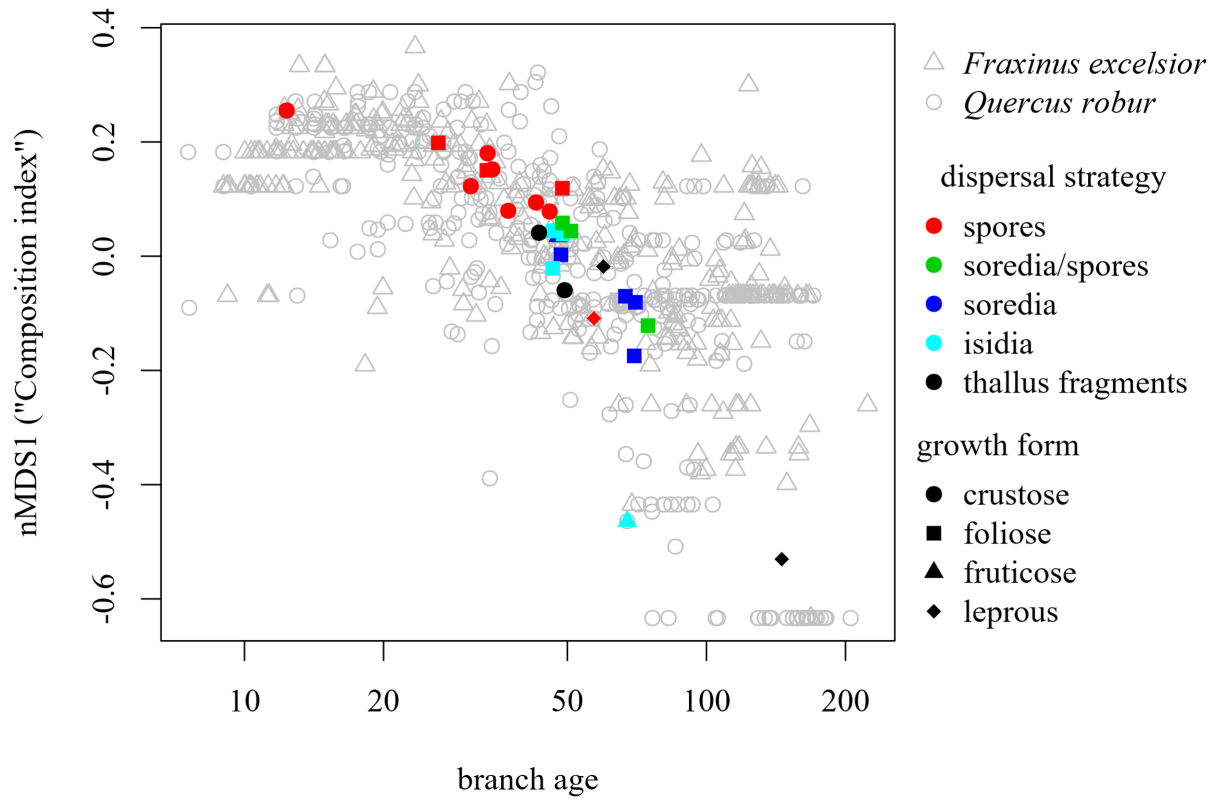
851 Figure 8



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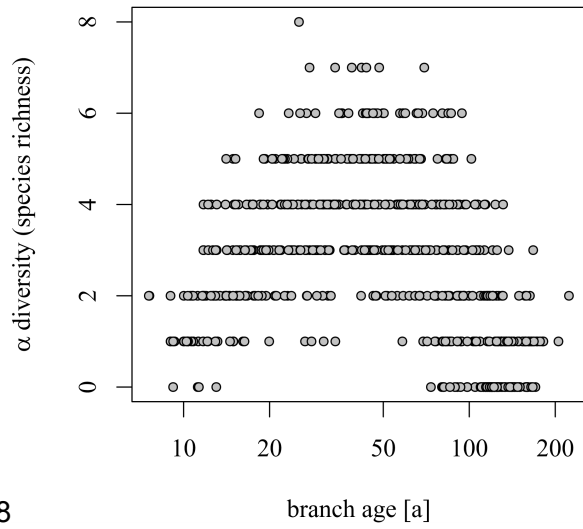


854 Figure 9



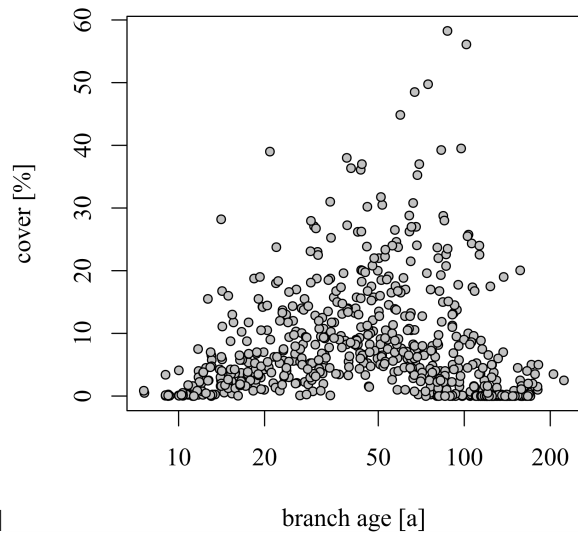
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857 Figure 10a



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860 **Figure 10b**



861  
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