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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.

33

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 (α 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 γ diversity, their turnover between plots
42within a layer as β 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 (γ diversity) and locally at the level of subplots (α 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 γ diversity of mid-canopy layers is expected to be
68high as a consequence of high species turnover between contrasting microsites (β diversity), but
69not because of peaking α 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).

89

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 γ 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, γ diversity is expected to increase
102monotonously with height.

103

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 γ 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 α and β 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.

118

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 γ 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 cm² 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 (α , β , γ), 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 γ diversity peak has to occur which is
189driven by a peaking α diversity, i.e. γ and mean α diversity are correlated at the canopy-layer
190level. It is further presumed that α 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 γ diversity and no systematic species turnover along
194the vertical canopy gradient.

195The *Succession mechanism* is expected to produce a mid-canopy γ diversity peak driven by a
196peaking α 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 β diversity and the variation in branch age.

202The *Habitat Heterogeneity mechanism* is expected to produce a mid-canopy γ diversity peak that
203is driven by a peaking β diversity, but not α diversity as in the first two mechanisms mentioned
204above. As α and β 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 α - β
206correlation. It is a necessary condition that β 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, γ diversity should
210correlate with available substrate area per layer and thus should peak in the top canopy layer.
211 γ diversity can be independent of either α or β 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.

219

220

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 α diversity while layer-level species richness is referred to
224as γ 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 β 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 β diversity
235matrix, which used pairwise between-plot dissimilarities based on the Simpson β diversity index
236(β_{sim} ; Koleff, Gaston, & Lennon, 2003).

2372.4.1 Multiple linear regression model

238An important distinction between the hypotheses is whether variation in γ diversity and mean α
239diversity are closely connected (*Optimality, Succession*) or whether patterns in γ diversity are an
240emergent property at the layer level either driven by variation in β 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 γ diversity as response variable and mean α diversity, β

243diversity and available surface area as explanatory variables. Additionally, the interaction terms
244of area with mean α and β 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 (α 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 α 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 α
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 α 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 α 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 α diversity.
285As the shape of this relationship can expected to be hump-shaped, the quadratic composition
286index is added as predictor for α 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 β_{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 α and β diversities, both measures are usually expected to be correlated to
302 some degree, as many β metrics can vary simply due to changes in either α or γ 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 β diversities, as the
305 correlation between α diversity and a given β diversity metric offers a null expectation which
306 observed β diversities may fall below or exceed. In our case, β diversities within layer higher
307 than expected may hint towards deterministic species sorting processes between communities as
308 expected with the *Habitat Heterogeneity* mechanism; β 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 ± 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 α and γ 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; α : 0.65; γ : 0.68; both $p < 0.001$). Within-
340layer β 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 γ diversity as a function of mean α diversity, β diversity and
348area (including interactions), mean α diversity had the strongest effect (0.87, $p < 0.001$), with the
349only other significant effect being the interaction term of α 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 α 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 α 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 α diversity (0.63, $p < 0.001$). LAI had significant effects on α 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 α diversity was non-significant. Variance explained in endogenous variables was 72 % (α
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 α 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 ± 6 years
373 compared to 50 ± 3 years in *F. excelsior* (45 ± 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 β diversity than plots within layers of equal height (Wilcoxon; $p < 0.001$). All crown
379 environmental variables were significant predictors of pairwise β 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 β 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 β 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 ± 0.26 , Figure 8). This implies within-layer homogeneity and thus γ
392 diversity control by raised levels of α diversity rather than β 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 ± 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 γ diversity directly, but had a significant interaction term with α diversity.

421

4224.1 Optimality

423 Both α and γ diversity exhibited a mid-canopy peak and were significantly correlated (criterion
424 1, Table 1). In contrast, a distinct peak in β diversity was not observed and β diversity was not
425 correlated with γ diversity. An increase in α 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 α 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 α 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, β diversity was not related to γ 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 β 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 α diversity and its interaction with area had
504 a significant effect on γ 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 α 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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562

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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: α , β , γ = α , β*

744 *or γ 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.*

Mechanism	Expected γ diversity peak and scale of emergence	Necessary conditions	Sufficient conditions
<i>Optimality</i>	Mid crown (α , γ)	$\gamma_i \sim \alpha_i$ c1 $\alpha_{ij} = f(P_{ij})$ c2	$!(\gamma \sim \text{Var}(P))$ $\alpha_{ij} \sim \text{cover}_{ij}$ c3
<i>Succession</i>	Mid crown (α , γ)	$\gamma_i \sim \alpha_i$ 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 $f(\Delta \text{age})$
<i>Heterogeneity</i>	Mid crown (β , γ)	$\gamma_i \sim \beta_i$ c8 $\beta_i \sim \text{Var}(P)_i$ c9	$\text{com}_{ij} = f(P_{ij})$
<i>SAR</i>	Top crown (passive sampling: γ area per se: α , γ)	$\gamma_i = f(A_i)$ 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
1	multiple linear regression model	test contributions of mean α and β diversity and area to γ diversity (c1,c8,c10)
2	piecewise structural equation model	contributions to α diversity (c2,c3,c4)
3	distance-based redundancy analysis	contributions of environmental variation to beta diversity (c6, c9)
4	Raup-Crick Null model	delineate β diversity characteristics independent of α diversity variation (c7,c8)
5	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: α , β , $\gamma = \alpha$, β or γ 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.

Mechanism	Criterion	Support
Optimality	c1 $\gamma_i \sim \alpha_i$	Yes
	c2 $\alpha_{ij} = f(P_{ij})$	Yes
	c3 $\alpha_{ij} \sim \text{cover}_{ij}$	Yes
Succession	c1 $\gamma_i \sim \alpha_i$	Yes
	c4 $\text{com}_{ij} = f(\text{age}_{ij})$	Yes
	c5 $\text{traits} = f(\text{age}_{ij})$	Yes
	c6 $\beta(i_j, i_j) = f(\Delta \text{age})$	Yes
	c7 $\beta(i, i)_j < \beta(i_j, i_j)_b$	Yes
Heterogeneity	c8 $\gamma_i \sim \beta_i$	No
	c9 $\beta_i \sim \text{Var}(P)_i$	Weak, mainly supported by branch age (see c6)
SAR	c10 $\gamma_i = f(A_i)$	Weak, significant interaction with α diversity, but no direct effect on γ 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 (γ 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 α
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) γ diversity (layer level) b) α
794diversity (plot level) c) β 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 β 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 β 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.

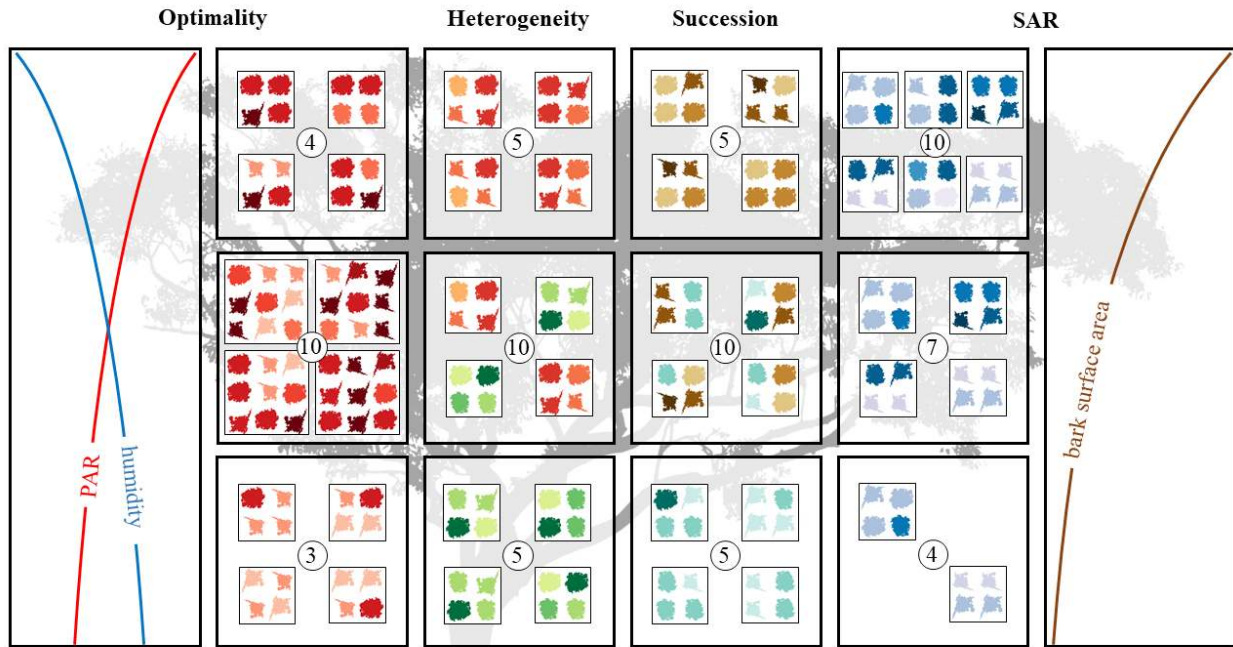
818

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 β 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

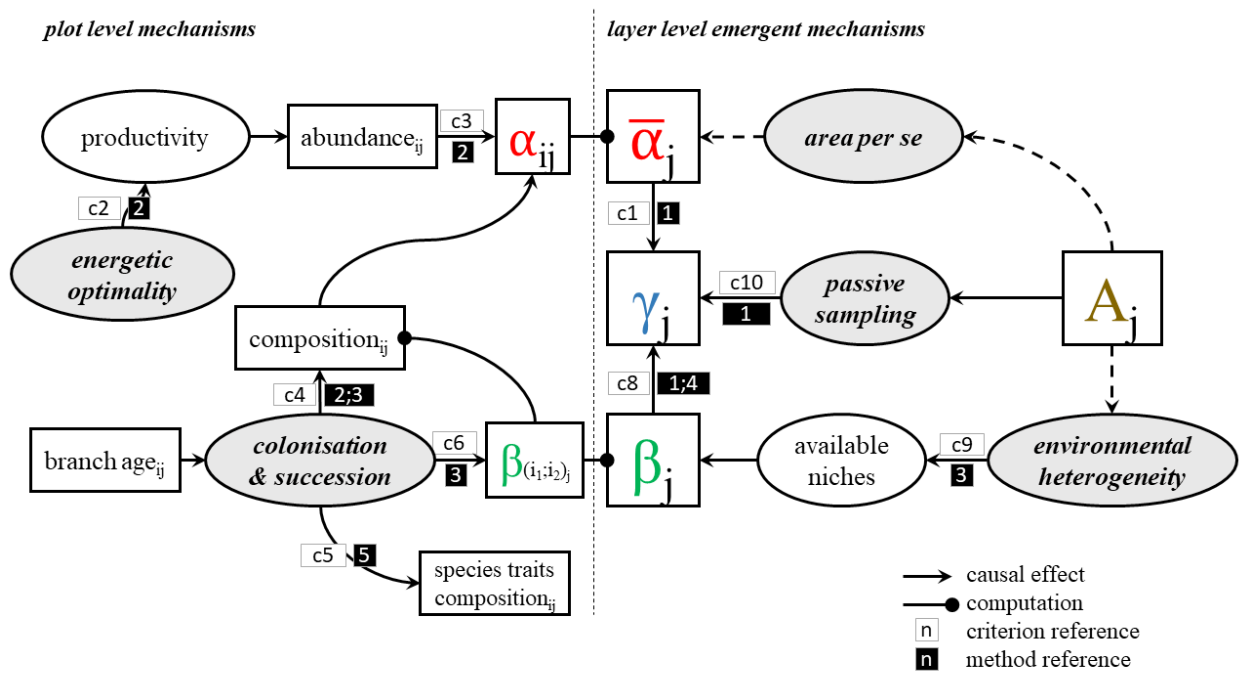
828Figure 10: Both the α diversity and cover - branch age relationship shows a distinct hump shape

829 Figure 1



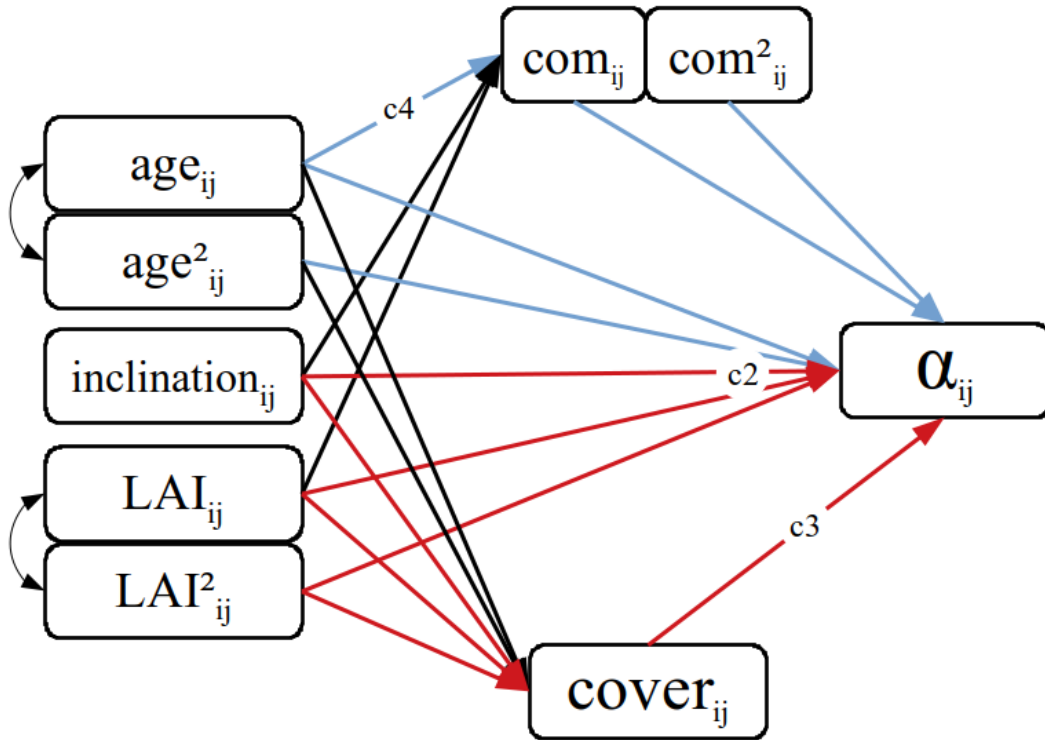
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831 **Figure 2**



832

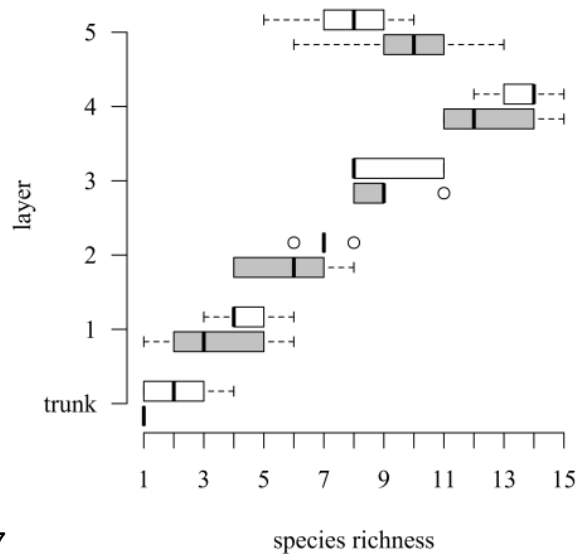
833 Figure 3



834

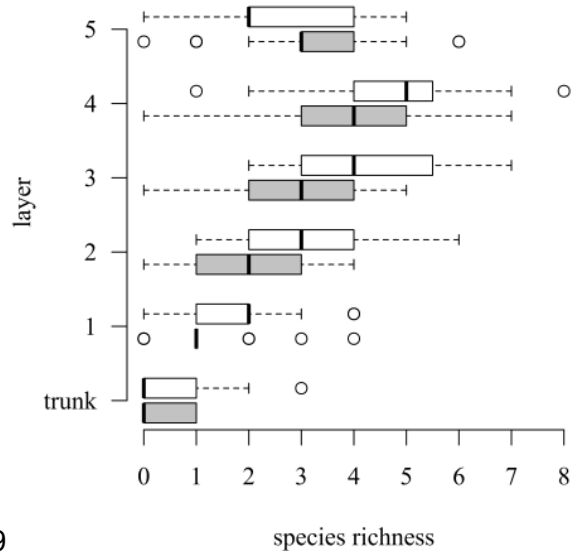
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836 Figure 4a



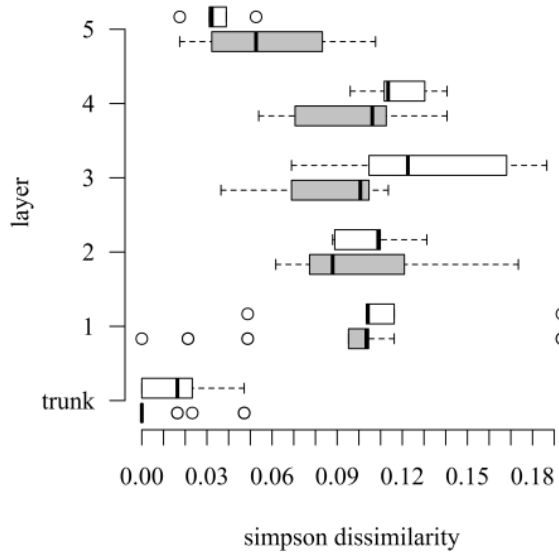
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838 Figure 4b



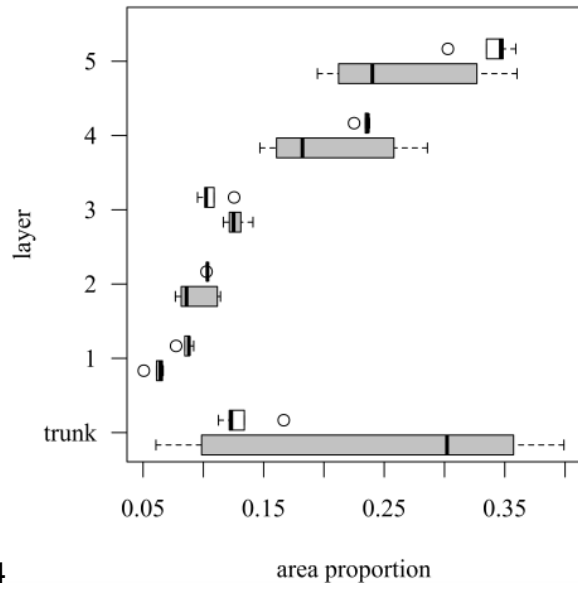
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840 Figure 4c



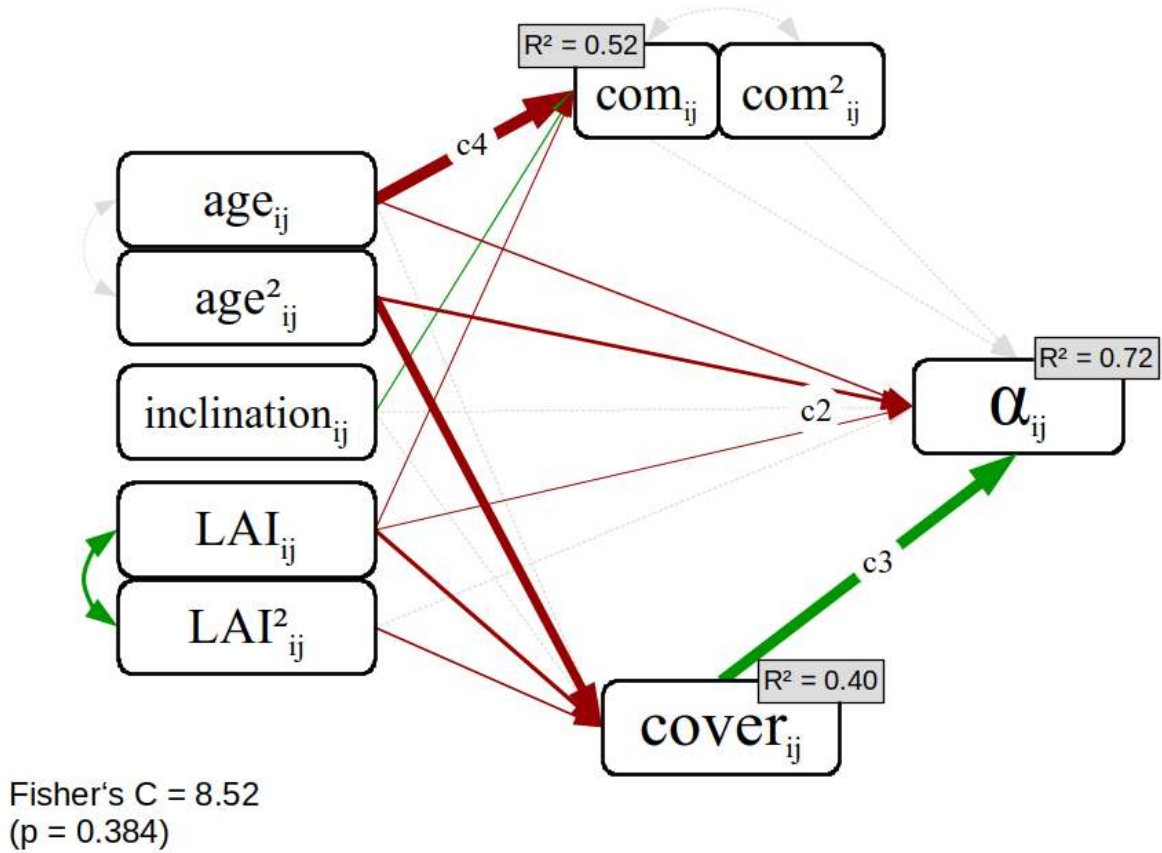
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843 Figure 5



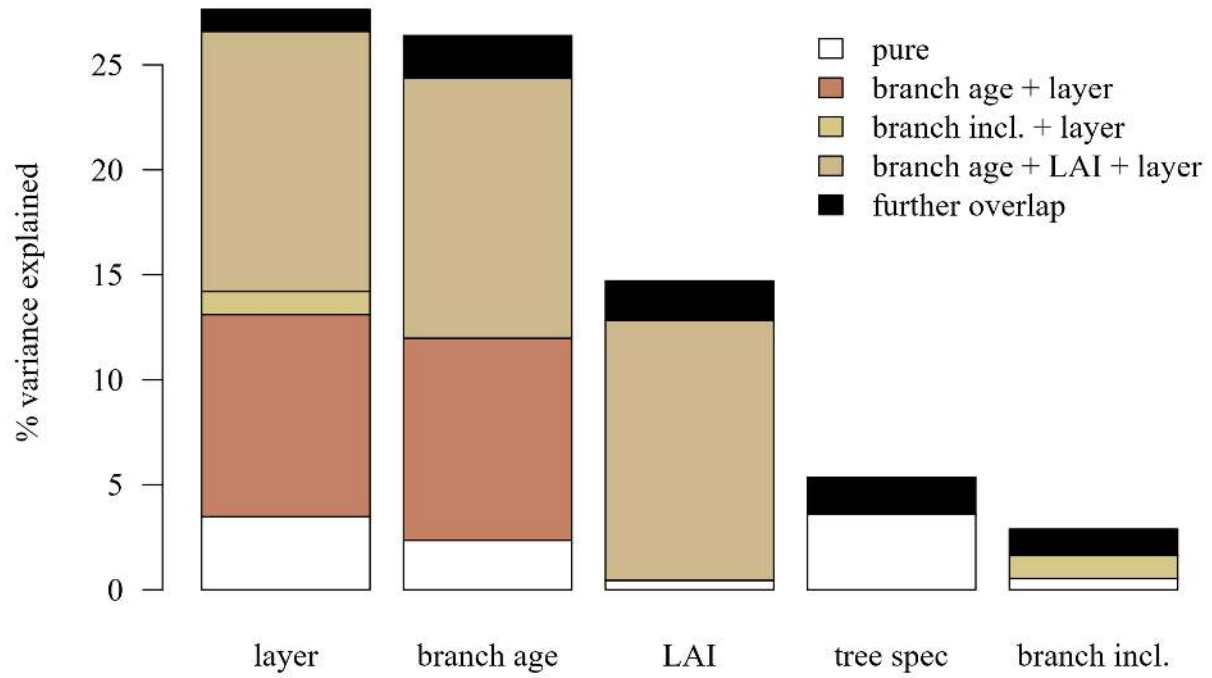
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846 Figure 6



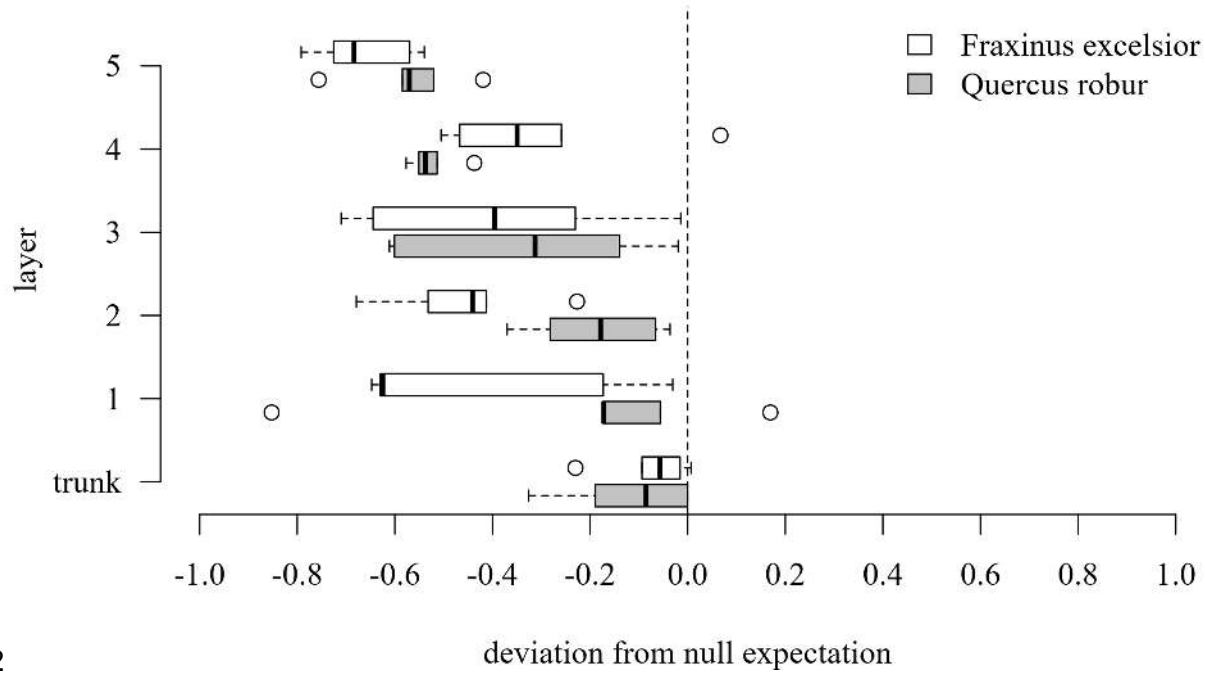
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849 **Figure 7**



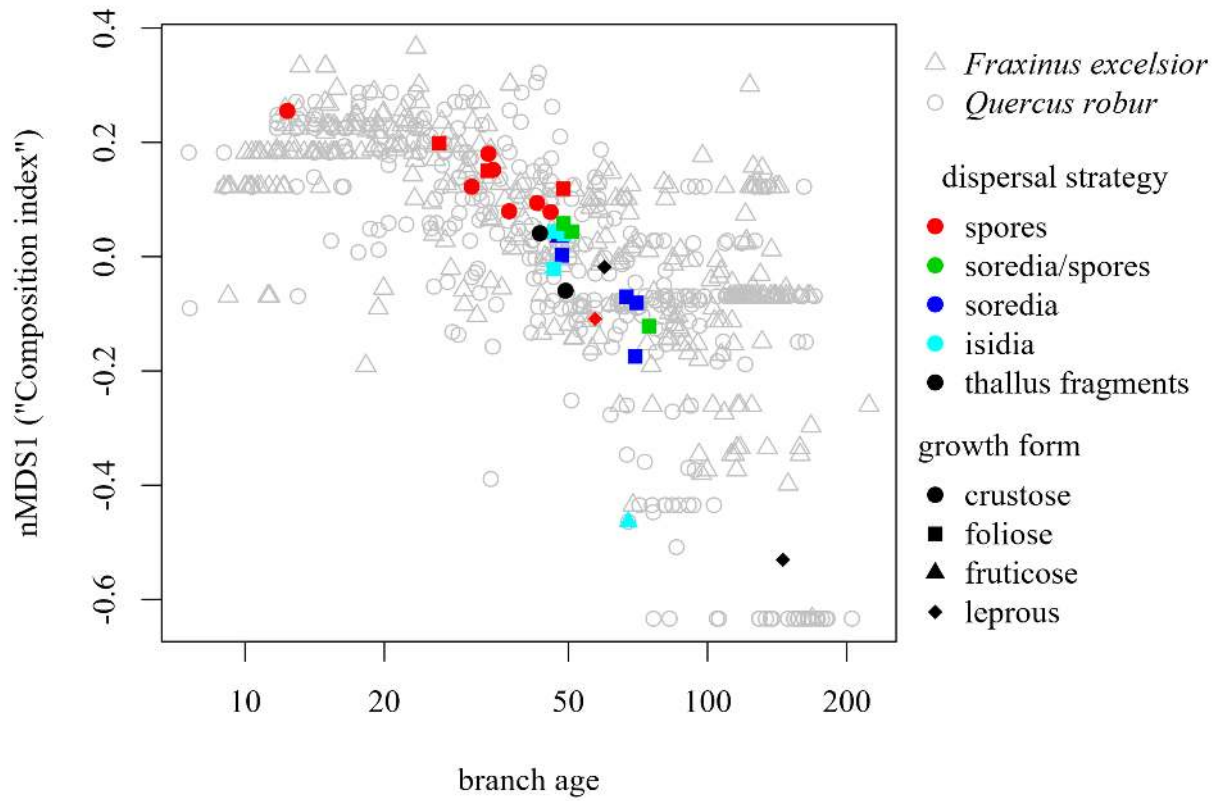
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851 Figure 8



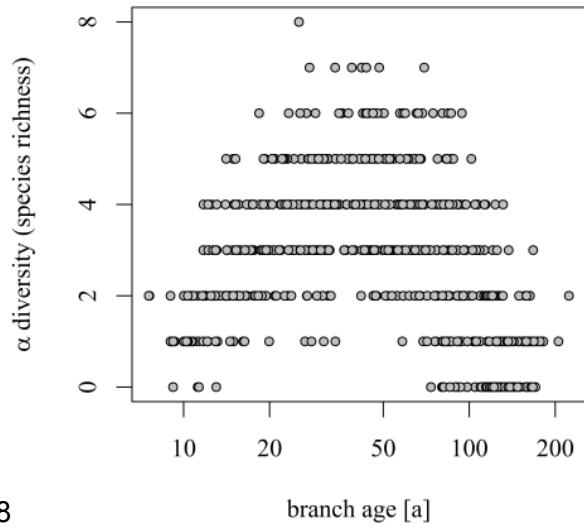
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854 Figure 9



855
856

857 Figure 10a



858
859

860 **Figure 10b**



861
862