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# 1 Simple attributes predict the importance 2 of plants as hosts to the richness of fungi 3 and arthropods

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20

## 21 Abstract

22 Consumers constitute the vast majority of global terrestrial biodiversity. Yet, local consumer  
23 richness is poorly understood. Plant species richness offers a simple hypothesis to how the  
24 diversification of carbon substrates may promote the diversity of arthropods and fungi. We took  
25 this one step further and used databases on plant-consumer interaction links to derive the  
26 richness of associated biota per plant species (link score). Using a species inventory of 130 sites  
27 we investigated 1) how well the link score could be predicted by plant attributes and 2) if the  
28 sum of plant species' observed or predicted link scores could predict site richness of arthropods  
29 and macrofungi better than plant species richness alone. We found plant link scores to be  
30 positively related to plant size, abundance, nativeness and ectomycorrhizal status. Link based  
31 indices generally improved prediction of richness, stressing the importance of plants as niche  
32 space for the megadiverse groups of insects and fungi.

33

34 *Keywords:* trophic interactions, plant traits, mycorrhizal fungi, phytophagous arthropods,  
35 consumer diversity, ecospace, multi-taxon species richness

## 36 Introduction

37 Plants constitute an important part of biodiversity in their own right, but in addition provide  
38 resource and habitat to all terrestrial heterotrophic biodiversity, including the megadiverse  
39 groups of arthropods and fungi. The link from plant diversity to consumer diversity is modulated  
40 by the degree of host specialism among consumers. Most species of insects, mites and fungi  
41 associated with living plants are strongly specialised, i.e. dependent on a single or a few plant  
42 species as both resource and habitat (Strong, Lawton & Southwood 1984; Hawksworth 2001).  
43 Even many decomposers show a high degree of specialism, due to after-life effects of plant  
44 structure and chemical composition (Heilmann-Clausen *et al.* 2016). Generalist arthropod and  
45 fungal species are relatively few in number. Cascading effects from plants to the third and fourth  
46 trophic levels have been demonstrated and may be particularly important to specialist parasitoids  
47 (Godfray 1995).

48 The direct effect of plants on the trophic levels above is encapsulated in the *ecospace*  
49 dimension coined *expansion* signifying the build-up and diversification of organic carbon in the  
50 ecosystem (Brunbjerg *et al.* 2017b). However, empirical predictive power of plants on consumer  
51 richness may result from both direct effects of plant diversity or from indirect effects of  
52 consumers and producers responding in similar ways to extrinsic factors (Kemp & Ellis 2017), in  
53 particular abiotic properties such as microclimate, soil moisture, soil nutrients and inorganic  
54 substrates, i.e. the position component of *ecospace* (Brunbjerg *et al.* 2017b). Thus, testing the  
55 effect of plant diversity on consumer diversity must account also for the effects of the abiotic  
56 environment.

57 Prediction of local site biodiversity provides essential knowledge to prioritization of  
58 conservation efforts, apart from being an intriguing task in itself. While biodiversity surrogacy

59 has been questioned in general (Larsen, Bladt & Rahbek 2009; Lindenmayer *et al.* 2015), plant  
60 species richness has proven to promote multi-taxon diversity, provided that - on top of plant  
61 species richness - plant species identities are used for bioindication of key habitat conditions  
62 (Brunbjerg *et al.* 2018). However, it remains to be tested if higher predictive power may be  
63 attained after including plant species' value as food and habitat to consumer species.

64 The question goes deeper than surrogacy, however. Some plant species support a much  
65 greater diversity of associated consumers than others. So plant identity may be more important  
66 than plant species number to local consumer diversity. There are however only few regions in the  
67 world where the consumer to host links have been mapped adequately, and it is therefore  
68 interesting to know if host attractiveness can be predicted.

69 A number of key plant attributes are known to be related to the richness of associated  
70 arthropod and fungal species. In particular properties revolving around plant apparency and  
71 predictability as a resource have been found important (Feeny 1976), i.e. species range size and  
72 local abundance, body size and life span, time since immigration and nativeness (Southwood  
73 1961; Lawton & Schröder 1977; Kennedy & Southwood 1984; Brändle & Brandl 2001; Miller  
74 2012). In addition, chemical defences and phylogenetic isolation are among the proposed plant  
75 determinants of arthropod richness (Tahvanainen & Niemelä 1987; Brändle & Brandl 2006) and,  
76 for symbiotic fungi, plant species' ability to form mycorrhiza of different types (Tedersoo *et al.*  
77 2015). The literature regarding arthropods is much bigger than for fungi; few analyses have  
78 combined the two (Strong & Levin 1979; Brändle & Brandl 2003), and even fewer have taken  
79 investigations from the level of whole biotas to the level of local communities.

80 Here we use species richness of vascular plants, arthropods and macrofungi surveyed at 130  
81 sites representing all terrestrial ecosystems in a region as a study case. We used independently

82 recorded plant-consumer interaction links to derive the size of the associated consumer biota per  
83 plant species (observed link score). This observed link score was modelled from plant attributes,  
84 such as range size and growth form (predicted link score). Link scores were summed over the  
85 plant species occurring in each site to obtain an observed and predicted link sum per site. In  
86 addition to modelling total fungal and arthropod richness over study sites, the fungi and  
87 arthropod fauna were divided into functional response groups, which we expected were controlled  
88 by different abiotic and biotic drivers.

89 Specifically we asked: 1) Which plant attributes can predict the potential number of  
90 interaction links between plants and associated arthropods and fungi, 2) Can link sum predict the  
91 observed species richness of fungi and arthropods (and functional subgroups thereof) on the  
92 scale of communities, better than raw plant species richness? 3) Can the observed link score be  
93 substituted by a trait-predicted link sum in the prediction of insect and fungi richness?

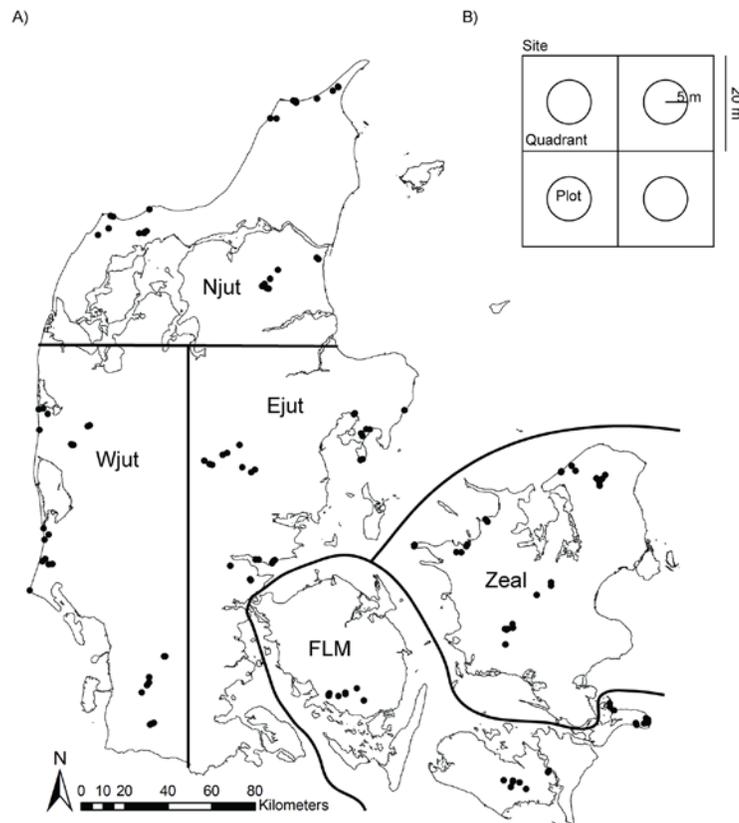
## 94 **Methods**

### 95 **Study area and collection of biodiversity data**

96 The study area was Denmark (Fig. 1). In the field, we collected data from 130 sites, each with an  
97 area of 40 × 40 m, deemed to be homogenous with respect to topography and vegetation  
98 structure, but accepting the inherent heterogeneity of some habitat types. The study design aimed  
99 at coverage of the major environmental gradients, including naturalness of habitat (i.e. the  
100 intensity of silviculture and agriculture). Thirty sites were allocated to cultivated habitats and 100  
101 sites to natural habitats. The cultivated subset was stratified according to major land use classes  
102 and the natural subset was stratified across gradients in soil fertility, soil moisture and vegetation  
103 openness. The design has been described in detail by Brunbjerg et al. (2017a).

104 We collected data on the occurrence of vascular plants, macrofungi and arthropods, aiming  
105 for an unbiased and representative assessment of the multi-taxon species diversity in each of the  
106 130 sites. For vascular plants, the sampling included abundance assessment on a coarse scale.  
107 Each site was divided into four quadrants and, at the centre of each quadrant, a 50 × 50 cm inner  
108 quadrat embedded in circular plot (5 m radius) was situated. Presence of species was recorded in  
109 inner quadrats and 5 m plots separately, in addition to records for the whole site. Plant species  
110 judged by visual inspection to be dominant at site-level were noted. For the present analysis, we  
111 assigned an ordinal abundance of 3 to plants species either judged as dominants or recorded in all  
112 four inner quadrats. Plant species recorded in at least one inner quadrat and at least one 5 m plot  
113 were assigned an ordinal abundance of 2. The remaining species were assigned a weight of 1.  
114 Proxy variables for site environmental conditions were derived from site plant lists by  
115 bioindication using Ellenberg Indicator Values for light, soil nutrients, soil moisture and soil pH  
116 (Ellenberg *et al.* 1991; Brunbjerg *et al.* 2018).  
117 The data for vascular plants may be considered as good as exhaustive, while for the remaining  
118 species groups, which are more demanding to find or catch and to identify, the data represent a  
119 reproducible and unbiased sampling effort across the 130 sites. For arthropods, we operated a  
120 standard set of pitfall traps, yellow pan traps and Malaise traps during two set periods in 2014.  
121 Furthermore, two active-search approaches were used to retrieve externally and internally plant-  
122 feeding arthropods, respectively: 1) Sweep netting and beating with a focus on bugs, cicadas and  
123 leaf beetles, 2) strategic search for plant galling and mining arthropods, including non-galling  
124 Cecidomyiinae. Metabarcoding was applied to soil samples from all 130 sites in order to obtain  
125 OTU-richness estimates for cryptic soil biota (see Brunbjerg *et al.* 2017a for details). OTUs were  
126 derived using the nuclear ribosomal ITS2 marker for fungi and the nuclear 16S rRNA marker for

127 arthropods. The fungal OTU data were split into Agaricomycetes, which largely overlap with the  
128 macrofungi surveyed, and non-Agaricomycetes, which is a large and phylogenetically  
129 heterogeneous group that mostly goes undetected in traditional surveys, using the UNITE  
130 database (Nilsson *et al.* 2019). For full details on data collection, see Brunbjerg *et al.* (2017a).



131

132 *Fig. 1. Map of Denmark showing the location of the 130 sites grouped into 15 clusters within five regions (Njut: Northern*  
133 *Jutland, Wjut: Western Jutland, Ejut: Eastern Jutland, FLM: Funen, Lolland, Møn, Zeal: Zealand). B) Site layout with four 20 × 20*  
134 *m quadrants each containing a central 5 m radius circular plot.*

### 135 **Interaction data and link score calculation**

136 We extracted data for interaction links from existing databases for each plant species found at the  
137 130 field sites. For both fungi and arthropods, the estimation had to take into account that many  
138 interaction links have been recorded at the level of plant genus, either because consumers do not

139 discriminate between different species of the same plant genus (Savile 1979) or because of  
140 incomplete identification of the host by the human observer.

141 We mined a Danish fungal database (<https://svampe.databasen.org>) for fungi and the  
142 Biological Records Centre's host plant database for arthropods  
143 (<http://www.brc.ac.uk/dbif/hosts.aspx>) for reported links to the list of vascular plants found in the  
144 studied sites, including common plant name synonyms. We included interaction links reported at  
145 plant subspecies, species or genus levels.

146 The fungal database is based on repeated field observations of fungi and the arthropod  
147 databases is based on unique reported links and we thus had to be handle them in slightly  
148 different ways in order to obtain comparable data for analysis. A particular challenging task was  
149 to distribute fungal and arthropod links reported at the plant genus level onto the plant species  
150 belonging to that genus. The procedure is detailed below.

151 The Danish fungal database consists of observations of fungi made by citizens and  
152 professionals, with records accompanied by observational data on substratum, i.e. live plants or  
153 dead plant parts, or – for ectomycorrhizal fungi – close association with plants, identified at least  
154 to plant genus.

155 The British BRC host plant database is a meta-database, compiling arthropod-plant  
156 associations reported in the scientific literature. The geographic focus is Great Britain and  
157 adjacent continental Europe. The database is regularly updated, but curation of arthropod  
158 taxonomy and nomenclature is not better than the most recent source for each arthropod group,  
159 which for many little studied groups may be quite old. Because of the vast number of literature  
160 sources, cleaning the arthropod names for synonyms was considered intractable. However,  
161 despite fair criticisms of biases towards common plant species, the reliability of published host

162 records is very well supported (Brändle & Brandl 2001). We retrieved arthropod links for all  
163 vascular plant species found across the 130 field sites, under the assumption that the BRC  
164 database would give a fair picture of the size of the total coterie of associated arthropods on  
165 Danish plants.

### 166 *Plant-associated fungi*

167 We retrieved all records of fungi having at least one reported association with a vascular plant at  
168 the species or genus level ( $n = 255\,700$ ). Removing duplicate links and filtering to the total list of  
169 vascular plant species found at the 130 study sites led to a reduction of data entries to 20\,309  
170 links between 4\,549 fungal and 538 vascular plant taxa (at species or genus level). For each  
171 fungal species, each of its plant links were given a weight corresponding to 1 divided by the  
172 number of linked plant genera for that fungus. Thus, all fungal species would contribute identical  
173 total weights to the final index, but a specialist fungus would contribute more to the link score of  
174 its host plant than would a generalist fungus. These link weights were summed for each vascular  
175 plant species over all fungal taxa at both species and genus level, accepting that some fungal  
176 species had links reported at both levels. When calculating the final link score for a plant species,  
177 we allocated the plant genus score to the species belonging to a given genus in the following  
178 way:

179 1) Plant species having link records at both the species and genus levels were allocated a  
180 percentage of the genus link score proportional to their species-level link score relative to  
181 the link score of the species within the genus with the highest species-level link score.

182 This rule applied to 265 plant species.

- 183        2) Plant species belonging to a genus with link records at the genus level only (no species-  
184        level records for any constituent species) were allocated an arbitrary 90% of the genus  
185        link score, equal for all species in the genus. This rule applied to 104 plant species.
- 186        3) Plant species having link records at the genus level only, but belonging to a genus  
187        containing other species with species-level records, were scored as “NA”, based on the  
188        argument that neither zero nor a positive link score would be correct. This applied to 245  
189        plant species.
- 190        4) Plant species without reported fungal links at neither genus nor species level were given a  
191        zero link score. This applied to 293 plant species.

192        We calculated the final fungal link score for each plant as the sum of the species score and the  
193        share of the genus score.

#### 194        *Phytophagous arthropods*

195        For the total list of plant species encountered at the 130 sites, we retrieved all reported  
196        interactions involving insects and mites from the BRC host plant database. Interactions reported  
197        on plant subspecies level were merged on the parent species level. We found 30 895 interaction  
198        links, involving 6 870 arthropod species and 1427 vascular plant taxa (at species or genus level),  
199        of which 37 % were reported at the plant genus level. Similarly to the procedure for fungi, each  
200        plant link of an arthropod species were given a weight corresponding to 1 divided by the number  
201        of linked plant genera. For arthropods, however, we gave priority to plant genus links and only  
202        used species-level links in case no links were reported at genus level. The link score at plant  
203        genus level was allocated to all constituent species equally. While this may often be correct, it  
204        may also sometimes imply unwarranted link points to exotic or biologically deviating members  
205        of a plant genus. In order to compensate for this possible bias and give some priority to species-

206 specific links, we decided to assign triple weight to link points reported at species level. The final  
207 link score for a plant was calculated as the sum of genus-level link weights and three times the  
208 sum of species level link weights.

## 209 **Plant attributes**

210 In order to re-cast the interaction link score of plants species in terms of their traits, we compiled  
211 plant attributes for the plant species found across the 130 field sites. Information on  
212 ectomycorrhiza was extracted from the MycoFlor database (Hempel *et al.* 2013). Information on  
213 nativeness of plant species at 1) national scale, 2) at the European scale and 3) nativeness of the  
214 genus, were taken from Buchwald *et al.* (2013). Plant species were assigned to one of the  
215 following taxonomic groups: Angiosperm, Gymnosperm and Pteridophyte, based on standard  
216 plant classification. Lifespan was scored as 1) annuals + short-lived perennials, 2) medium-lived  
217 perennials, 3) long-lived perennials. Lifeform was scored as 1) tree = macrophanerophyte, 2)  
218 shrub+liana = nanophanerophyte, 3) dwarf-shrub = hemiphanerophyte, 4) herb =  
219 hemicryptophyte + geophyte + chamaephyte + therophyte + hydrophyte + pseudophanerophyte  
220 (Klotz, Kühn & Durka 2002). Plant body size was based on maximum canopy height and re-  
221 classified as 1) huge, 2) large, 3) medium-sized, 4) small and 5) tiny, following the LEDA trait  
222 data base (Kleyer *et al.* 2008). These attributes were extracted using the R-package TR8 (Bocci  
223 2015). We used family, genus and species descriptions in Hansen (2004) for filling gaps in  
224 height information. Plant species regional occupancy was extracted from a national plant survey  
225 (Atlas Flora Danica), carried out in  $5 \times 5$  km grid cells, of which 1300 were thoroughly  
226 surveyed, resulting in reliable presence-absence data (Hartvig & Vestergaard 2015). Species  
227 incidence frequency across reference grid cells was re-coded as High ( $> 0.75$ ), Moderate (0.26 –

228 0.75) and Low ( $< 0.25$ ) occupancy. Because of a bimodal frequency distribution, there were  
229 approximately equal numbers of species in the three occupancy classes.

230 We modelled plant species link score, for fungi and arthropods separately, in response to  
231 plant attributes using a linear modelling approach with ectomycorrhizal status, national  
232 nativeness, European nativeness, nativeness on the genus level, taxonomic group, life form,  
233 lifespan, body size and regional occupancy as explanatory variables. All explanatory variables  
234 were coded as factor variables (nominal), fungi link score was log-transformed and insect link  
235 score was square-root transformed. Model performance was assessed with type III sum of  
236 squares based on reducing a full model with the least significant variable until all variables were  
237 significant. The resulting regression models were used to predict the expected number of fungal  
238 and arthropod links per plant species based on species traits. The resulting metric is, henceforth,  
239 called ‘predicted link score’ as opposed to the ‘observed link score’ based on databases. The  
240 correlation between observed and predicted links scores across species was assessed with  
241 Spearman rank correlation.

#### 242 **Link sum per site**

243 For each of the 130 sites, we calculated a simple sum of link scores as well as a weighted link  
244 sum, the latter using plant species abundance as weight. The use of plant abundance as weight  
245 was based on the reasoning that the local abundance of a plant species would increase the chance  
246 that the plant was used as host by fungal or insect species. Simple and weighted link sums were  
247 calculated for both observed and predicted link scores. These link sums for a given site would  
248 increase with local plant species richness and with the value of the plant species present to fungal  
249 and arthropod associates, and thus could also be seen as a link-weighted plant species richness of  
250 the site.

## 251 **Testing the prediction of biodiversity by interaction scores**

252 We tested the predictive power of interaction link scores on observed multi-taxon species  
253 richness data from the 130 field sites. We used total observed species richness of fungi and  
254 arthropods as response variable, but also investigated models for functional subgroups of fungi  
255 and arthropods, divided according to their relation to plants as resources and ecospace at large.  
256 Fungi were divided into symbionts (mainly ectomycorrhizal fungi, but also including biotrophic  
257 parasites) and decomposers (saprotrophs). Arthropods were divided into 1) predators, 2) flyers,  
258 3) externally feeding herbivores and 4) internally feeding arthropods, i.e. gallers and miners. The  
259 group ‘flyers’ differ from the trophically defined subgroups and was defined by mode of  
260 movement and dispersal, reflecting an assumed decoupling of adult and juvenile life stages.  
261 We modelled species richness with GLM, using negative binomial error structure to account for  
262 frequent overdispersion of Poisson models. For each taxonomic response group we made a  
263 bivariate GLM in response to the link sum. In order to avoid confounding effects from variation  
264 in the abiotic environment potentially co-varying with plant link scores, we subsequently ran  
265 parallel GLM modelling, in which community mean Ellenberg Indicator Values for light, soil  
266 nutrients, soil moisture and soil pH were added to the models as co-variables. We applied  
267 multiple regression to test if link sum remained important after fitting a general environmental  
268 calibration of the habitat. Both types of model were made for three different sets of plant host  
269 richness variables: 1) simple plant richness (corresponding to a null hypothesis of all plant  
270 species having equal abundance and equal value as consumer species’ resource), 2) the observed  
271 link sum and 3) the predicted link sum. We log-transformed these plant ecospace variables, as  
272 this led to decreasing model AIC in most cases – particularly for response groups with strong

273 dependence on host richness. We also modelled abundance-weighted plant richness, but results  
274 were almost identical to the simple richness models, so only the latter will be reported here.

## 275 Results

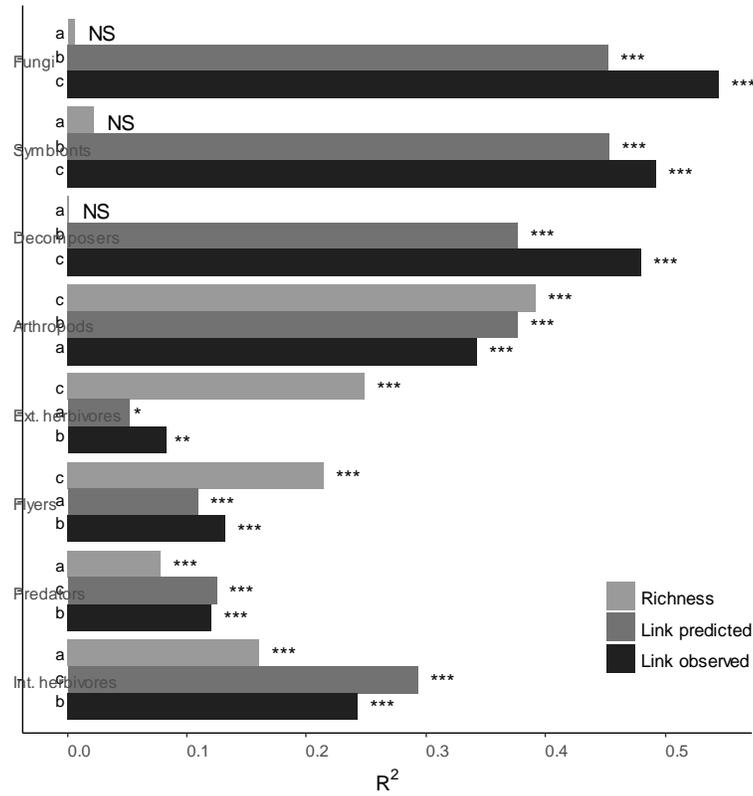
276 The plant taxa with most fungal interaction links from our database were *Fagus sylvatica*,  
277 *Quercus robur*, *Picea abies*, *Pinus sylvestris* and *Salix cinerea*, i.e. all woody plant, and well  
278 aligned with previous syntheses (Heilmann-Clausen *et al.* 2016). The herbaceous plants with  
279 most fungal links were *Phragmites australis* and *Carex paniculata*. For arthropods, the plant taxa  
280 with most interaction links were *Salix* (e.g. *S. cinerea* and *S. repens*), *Quercus* (*Q. robur*), *Pinus*  
281 *sylvestris*, *Betula* and *Populus* (*P. tremula*), again woody plants and similarly in agreement with  
282 previously published evidence (Kelly & Southwood 1999; Brändle & Brandl 2003). The  
283 herbaceous plants with most fungal links were *Achillea millefolium* and *Medicago sativa*.

284 The trait based model of fungal link scores across plant species revealed that capacity to form  
285 ectomycorrhiza, high regional occupancy, nativeness to Europe and intermediate to long lifespan  
286 all had strong positive effects on the fungal link score, while small body size and herbaceous life  
287 form had negative effects (Table 1). The adjusted model  $R^2$  was 0.65. The parallel model of  
288 arthropod link score showed that ectomycorrhizal capacity, high regional occupancy, dwarf  
289 shrub lifeform (as opposed to tree, herb or shrub+liana) had significantly positive effects on the  
290 arthropod link score, while small body size, short life span and fern phylogenetic placement had  
291 significantly negative effects (Table 2). The adjusted model  $R^2$  was 0.45, i.e. somewhat lower  
292 than for the fungal model. Link scores for fungi and insects were significantly positively  
293 correlated ( $Rho = 0.66$ ,  $p < 0.0001$ ).

294 The bivariate models showed in general that observed and predicted link sum were roughly  
295 equally good predictors, with the observed link sum working slightly better in most cases. Only

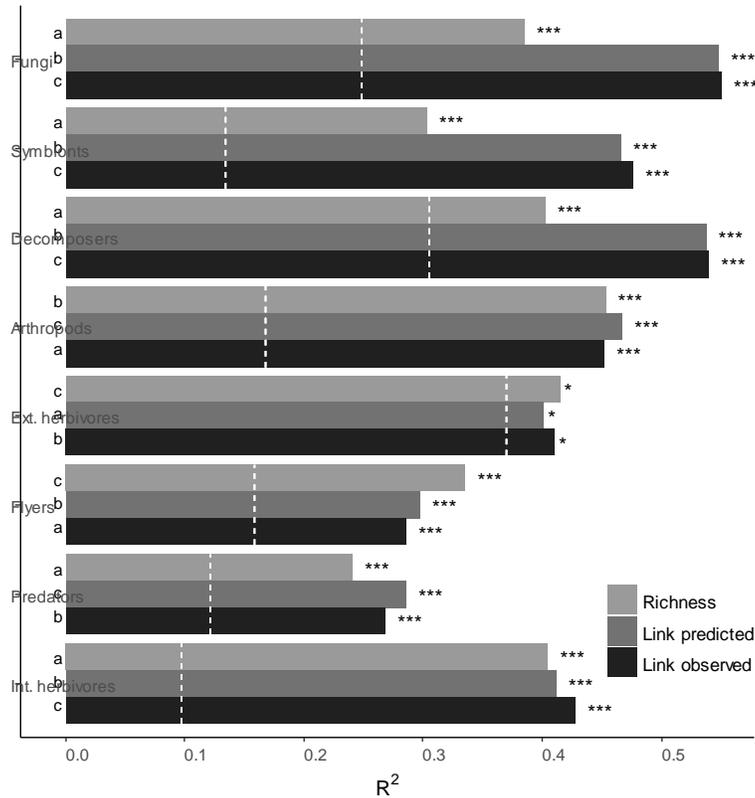
296 for internally feeding phytophagous arthropods, the predicted link sum yielded much better than  
297 the observed link sum (Fig. 2).

298 Comparing the predictive power of link sum (link-weighted plant species richness) to simple  
299 plant richness gave somewhat contrasting results for fungi and arthropods. For fungal richness,  
300 simple plant species richness was a very poor predictor. In contrast, both observed and predicted  
301 link sum were quite strong and significant predictors of fungal richness, and with observed link  
302 sum providing consistently better modelling results than predicted link sum, accounting for more  
303 than 50% of the variation in fungal richness (Fig. 2). Moreover, this result was almost equally  
304 attributable to decomposer and symbiotic fungi. For genetic richness of soil fungi (OTU Fungi),  
305 in contrast, simple plant species richness outperformed link sum. The modelling outcome of the  
306 bivariate models was very different for total arthropod richness and most arthropod subgroups,  
307 for which plant richness was a superior predictor. However, for internally feeding phytophagous  
308 arthropods (gallers and miners), link sum performed markedly better than simple plant richness,  
309 while for predatory arthropods, only somewhat better. The best models reached 39% explained  
310 variation for total arthropod richness (simple plant richness) and 29% explained variation for  
311 internal feeders (predicted link score).



312

313 *Fig. 2. Bivariate models. Bars represent pseudo- $R^2$  for regression models of consumer species richness in response to simple*  
 314 *vascular plant species richness and plant richness weighted link scores for consumer associations. Significance of plant richness*  
 315 *or link effects*



316

317 *Fig. 3. Multiple regression. Bars represent pseudo-R<sup>2</sup> for regression models of consumer species richness in response to simple*  
 318 *vascular plant species richness and plant richness weighted link scores for consumer associations, and with environmental*  
 319 *calibration by mean Ellenberg Indicator Values as co-variables. The R<sup>2</sup> for a model on environmental calibration alone is*  
 320 *indicated by white lines.*

321 After fitting environmental proxies (community mean Ellenberg Indicator Values) as  
 322 covariates in a multiple regression model, plant species richness became a significant predictor  
 323 of all three measures of fungal richness. However, link sum, observed and predicted alike,  
 324 remained stronger predictors of fungi richness and richness of most arthropod response groups  
 325 than simple species richness. Observed link score was generally stronger than predicted link  
 326 score, although the difference was modest. The multiple regression model for total fungi richness  
 327 using observed link score reached 55% explained variation. Multiple regression including  
 328 environmental proxies only contributed with a minor improvement of predictions compared to  
 329 the best bivariate model (54.5% explained variation). Environmental proxies alone explained less

330 than half of the variation of fungi richness, a little more than half of the variation for  
331 decomposers and one third of the variation in fungal symbiont richness (Fig. 3).

332 Arthropod models improved markedly after fitting Ellenberg variables, with 47% explained  
333 variation for total arthropod richness (predicted link sum), 43% for internal feeders (observed  
334 link sum) and 42% for external feeders (simple plant richness). The difference between  
335 performance of plant richness and link scores was reduced compared to the bivariate models.  
336 The amount of variation explained by environmental proxies alone was low for internal feeders  
337 and total arthropod richness (23 and 36%, respectively), moderate for predators and flyers (43%  
338 and 47%, respectively) and high for external feeders (89%).

## 339 Discussion

340 An overarching question of this study was whether plant species community composition may  
341 work as a predictor of consumer species richness. In a previous study in the same system of 130  
342 sites, we showed that plants predict general species richness across taxonomic and functional  
343 groups, given that predictions are based on plant species richness amended with plant-based  
344 bioindication of habitat properties (Brunbjerg *et al.* 2018). In the present study, we have  
345 demonstrated that plant surrogacy of multi-taxon biodiversity can be taken a step further by  
346 including the value to consumer biodiversity of individual plant species.

347 The coterie of plant-associated arthropods and fungi varies considerably and predictably  
348 across plant taxa, a notion that was firmly established more than half a century ago (Southwood  
349 1961). The results obtained in the present analysis are, for the most part, well aligned with the  
350 rich body of literature on the topic. Large-bodied, long-lived, structurally complex, widely  
351 distributed and locally abundant plant species have repeatedly been shown to harbour a larger  
352 fauna of phytophagous arthropods (e.g. Tahvanainen & Niemelä 1987; Brändle & Brandl 2001)

353 and fungi (Strong & Levin 1975; Miller 2012). This has been encapsulated in the concept of  
354 apparency, which comprises both species' attributes (e.g. body size and longevity) and of their  
355 history of immigration and fate in community dynamics (regional occupancy and local  
356 abundance). We found plant taxon nativeness, which is positively related to time since  
357 immigration, to be a correlate of consumer richness, but only in the model for fungi richness and,  
358 interestingly, only nativeness on the scale of Europe, not Denmark. Thus, it seems that associated  
359 consumers effectively track their host plants on the larger regional scale.

360 The capacity of plant taxa to form ectomycorrhiza (ECM) was little surprising as a predictor  
361 for associated fungal richness. It was, however, not anticipated that ectomycorrhizal capacity  
362 was a strong predictor of associated arthropod richness. This surprising pattern was not simply  
363 due to the fact that almost all ectomycorrhizal host plants are trees, as plant body size and growth  
364 form were also included as model predictors. Thus, within life-form groups, ectomycorrhizal  
365 plant taxa are on average hosts to a larger arthropod fauna than are non-ECM taxa. For trees and  
366 shrubs, genera such as *Fagus*, *Quercus*, *Betula* and *Salix* host more arthropod species than do  
367 *Ulmus*, *Acer*, *Fraxinus* and *Crataegus*, and similarly the dwarf-shrub *Salix repens* has a richer  
368 associated fauna than other similar-sized plant species. The mechanism behind this non-random  
369 co-occurrence escapes explanation, but calls for more detailed investigations.

370 When predicting observed species richness of arthropods and fungi in actual communities,  
371 models based on simple plant traits (predicted link sum) generally performed almost as good as  
372 models based on databased interaction links (observed link sum) or even better for all pooled  
373 arthropods. This result is encouraging for the use of plants in biodiversity surrogacy outside the  
374 study region used here. Basic knowledge on fungus and arthropod faunas is very far from  
375 complete in large parts of the world, and much more so than vascular floras (Mora *et al.* 2011;

376 Hawksworth & Lücking 2017), and knowledge on species' host relations is even more  
377 incomplete. In contrast, simple plant traits, such as life form and body size, are available for  
378 almost all plant species on the Globe, at least on a coarse scale. Thus, our finding is promising,  
379 and calls for further validation across global biomes.

380 The predictive power of interaction link sum on observed consumer richness varied  
381 considerably across functional groups of fungi and arthropods (Fig. 2). The effect of plant  
382 properties was strongest on the richness of biotrophs, decomposers and internally feeding  
383 arthropods. To a large extent, the physical and chemical properties of host plants define the  
384 habitat of species in these groups, which live in close intimacy with their host (Mazziotta *et al.*  
385 2017) and cannot escape factors such as chemical plant defence, not even as after-life effects  
386 (Purahong *et al.* 2018). The small effect for externally feeding arthropods was surprising at first  
387 glance, because these species are herbivores and quite many of them oligophagous. On the other  
388 hand, many externally feeding phytophagous insects are associated with habitat type, such as  
389 lake margins or heathlands, and use a variety of host plants within that habitat, e.g. taxa such as  
390 the leaf beetles (Chrysomelidae) and the plant bugs (Miridae). The richness of external feeders,  
391 thus, was largely predictable from general habitat conditions derived from plant community  
392 composition through bioindication (Fig. 3). For predators, in contrast, one could think that “meat  
393 is meat” and plant species identity would have no effect. Nonetheless, we found secondary  
394 consumer richness to have a direct relationship with plant species richness. This communication  
395 between the first and the third trophic levels may be because many predators, in particular insect  
396 parasitoids, are quite host specific and use plant species chemistry as cue to locate their host  
397 (Godfray 1995).

398        There was an appreciable indirect effect of extrinsic habitat conditions – *position* in ecospace  
399 (Brunbjerg *et al.* 2017b) – on the observed consumer richness (Fig. 3), yet we could clearly  
400 demonstrate an added effect of interaction link sum across all functional groups. This effect was  
401 particularly evident for fungi, both biotrophs and decomposers. For arthropods, the additive  
402 predictive power of link sums over simple plant richness was generally dwarfed. However, a  
403 strong effect of plant richness remained on top of environmental calibration and after including  
404 environmental co-variates, predicted link score turned out to be the most significant predictor.

405        A core component in the *ecospace* approach to understanding consumer biodiversity is the  
406 diversification of carbon pools. While there is no easy way to directly characterize and classify  
407 different pools of dead organic matter in ecosystems, the classification of plants offer an  
408 opportunity for investigating the importance of carbon diversification for heterotrophic diversity.  
409 However, important carbon pools such as dung, carcass and dead wood, which were not part of  
410 our assessment, deserve further investigations.

411        Our results lend support to the notion that site-level biodiversity is an emergent property of  
412 site conditions (Brunbjerg *et al.* 2020 OIKOS), within the bounds of the regional species pool.  
413 Likewise, the results demonstrate that biodiversity begets biodiversity, with community-level  
414 plant species richness in the role as a central bottom-up driver with strong effects across  
415 taxonomic groups, trophic levels and the parasitic-mutualistic-saprotrophic continuuma (Pöhlme  
416 *et al.* 2018). Our results may be applied in conservation science in order to improve the  
417 evaluation of planning and management choices, also in areas without much knowledge of the  
418 consumer biotas and their host relationships. Further, our results may be applied to novel  
419 ecosystem in the management of urban biodiversity.

420 **Author contributions statement:** HHB, RE, AKB and JHC conceived the ideas and  
421 designed the methodology; AKB, IG, TL, SH, HHB, RE, TGF, JHC and CF collected the data;  
422 RE, AKB, HHB and LD analysed the data; HHB, RE and AKB led the writing of the manuscript.  
423 All authors contributed critically to the drafts and gave final approval for publication.

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428 **Tables**

429

430 *Table 1. Regression model of fungal link score per plant taxon as predicted from plant attributes. Overall*  
 431 *model adjusted R-squared 0.6459; F-statistic: 52.57 on 11 and 300 DF, p-value << 0.0001*

	Coefficient	Std. Error	t value	P value
Intercept	2.0858	0.5330	3.914	0.000113 ***
Ectomycorrhizal	1.6682	0.2256	7.394	1.43e-12 ***
Native: Europe	0.6850	0.2179	3.144	0.001834 **
Occupancy: Low	-0.7532	0.1314	-5.732	2.42e-08 ***
Occupancy: Moderate	-0.3661	0.1001	-3.658	0.000300 ***
Lifespan: Short	-0.3598	0.1368	-2.631	0.008957 **
Life form: Herbaceous	-0.6941	0.2617	-2.652	0.008426 **
Life form: Shrub+Liana	-0.1338	0.3206	-0.417	0.676661
Life form: Tree	0.5542	0.4551	1.218	0.224311
Body size: Large	-0.2523	0.2688	-0.939	0.348619
Body size: Medium	-0.1369	0.4280	-0.320	0.749322
Body size: Small	-0.9172	0.4362	-2.103	0.036323 *

432

433

434 *Table 2. Regression model of arthropod link score per plant taxon as predicted from plant attributes.*  
 435 *Overall model adjusted R-squared 0.4521; F-statistic 46.52 on 12 and 650 DF, p-value << 0.0001*

	Coefficient	Std. Error	t value	P value
Intercept	13.5028	1.7653	7.649	7.33e-14 ***
Ectomycorrhizal	7.0742	0.8313	8.509	<2e-16 ***
Occupancy:Low	-3.9968	0.3053	-13.093	<2e-16 ***
Occupancy:Moderate	-2.3160	0.3018	-7.674	6.11e-14 ***
Phylum: Fern ally	-2.0130	0.7118	-2.828	0.00483 **
Phylum: Gymnosperm	-1.7946	1.2649	-1.419	0.15646
Body size: Large	-0.4597	0.9749	-0.471	0.63744
Body size: Medium	-2.7934	1.5533	-1.798	0.07259
Body size: Small	-4.0444	1.5687	-2.578	0.01015 *
Lifespan: Short	-1.7315	0.3061	-5.657	2.32e-08 ***
Life form: Herbaceous	-3.5787	0.7750	-4.618	4.67e-06 ***
Life form: Shrub+Liana	-2.7042	0.9535	-2.836	0.00471 **
Life form: Tree	-4.6355	1.5671	-2.958	0.00321 **

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## 438 References

- 439 Bocci, G. (2015) TR8: an R package for easily retrieving plant species traits. *Methods in Ecology*  
440 *and Evolution*, **6**, 347-350.
- 441 Brunbjerg, A.K., Bruun, H.H., Broendum, L., Classen, A.T., Fog, K., Froeslev, T.G., Goldberg,  
442 I., Hansen, M.D.D., Hoeye, T.T., Laessoe, T., Newman, G., Skipper, L., Soechting, U.  
443 & Ejrnaes, R. (2017a) A systematic survey of regional multitaxon biodiversity:  
444 evaluating strategies and coverage. *bioRxiv*.
- 445 Brunbjerg, A.K., Bruun, H.H., Dalby, L., Fløjgaard, C., Frøslev, T.G., Høye, T.T., Goldberg, I.,  
446 Læssøe, T., Hansen, M.D.D., Brøndum, L., Skipper, L., Fog, K. & Ejrnæs, R. (2018)  
447 Vascular plant species richness and bioindication predict multi-taxon species richness.  
448 *Methods in Ecology and Evolution*, **9**, 2372-2382.
- 449 Brunbjerg, A.K., Bruun, H.H., Moeslund, J.E., Sadler, J.P., Svenning, J.-C. & Ejrnæs, R. (2017b)  
450 Ecospace: A unified framework for understanding variation in terrestrial biodiversity.  
451 *Basic and Applied Ecology*, **18**, 86-94.
- 452 Brändle, M. & Brandl, R. (2001) Species richness of insects and mites on trees: expanding  
453 Southwood. *Journal of Animal Ecology*, **70**, 491-504.
- 454 Brändle, M. & Brandl, R. (2003) Species richness on trees: a comparison of parasitic fungi and  
455 insects. *Evolutionary Ecology Research*, **5**, 941-952.
- 456 Brändle, M. & Brandl, R. (2006) Is the composition of phytophagous insects and parasitic fungi  
457 among trees predictable? *Oikos*, **113**, 296-304.
- 458 Buchwald, E., Wind, P., Bruun, H.H., Møller, P.F., Ejrnæs, R. & Svart, H.E. (2013) Hvilke  
459 planter er hjemmehørende i Danmark? *Flora og Fauna*, **118**, 73-96.
- 460 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1991) *Zeigerwerte*  
461 *von Pflanzen in Mitteleuropa*. Verlag E. Goltze KG, Göttingen.
- 462 Feeny, P. (1976) Plant apparency and chemical defense. *Biological Interactions Between Plants*  
463 *and Insects* (eds J.W. Wallace & R.L. Nansel), pp. 1-40. Plenum Press, New York, USA.
- 464 Godfray, H.C.J. (1995) Communication between the first and third trophic levels: An analysis  
465 using biological signalling theory. *Oikos*, **72**, 367-374.
- 466 Hansen, K. (2004) *Dansk Feltflora*, 1. udg. 9. opl. edn. Gyldendal, Copenhagen.
- 467 Hartvig, P. & Vestergaard, P. (2015) Atlas Flora Danica. pp. 1230. Gyldendal, København.
- 468 Hawksworth, D.L. (2001) The magnitude of fungal diversity: the 1.5 million species estimate  
469 revisited. *Mycological Research*, **105**, 1422-1432.

- 470 Hawksworth, D.L. & Lücking, R. (2017) Fungal diversity revisited: 2.2 to 3.8 million species.  
471 *Microbiology Spectrum*, **5**.
- 472 Heilmann-Clausen, J., Maruyama, P.K., Bruun, H.H., Dimitrov, D., Læssøe, T., Frøslev, T.G. &  
473 Dalsgaard, B. (2016) Citizen science data reveal ecological, historical and evolutionary  
474 factors shaping interactions between woody hosts and wood-inhabiting fungi. *New*  
475 *Phytologist*, **212**, 1072–1082.
- 476 Hempel, S., Götzenberger, L., Kühn, I., Michalski, S.G., Rillig, M.C., Zobel, M. & Moora, M.  
477 (2013) Mycorrhizas in the Central European flora: relationships with plant life history  
478 traits and ecology. *Ecology*, **94**, 1389-1399.
- 479 Kelly, C.K. & Southwood, T.R.E. (1999) Species richness and resource availability: a  
480 phylogenetic analysis of insects associated with trees. *Proceedings of the National*  
481 *Academy of Sciences of the United States of America*, **96**, 8013-8016.
- 482 Kemp, J.E. & Ellis, A.G. (2017) Significant local-scale plant-insect species richness relationship  
483 independent of abiotic effects in the temperate Cape floristic region biodiversity hotspot.  
484 *PLoS ONE*, **12**, e0168033.
- 485 Kennedy, C.E.J. & Southwood, T.R.E. (1984) The number of species of insects associated with  
486 British trees: a re-analysis. *Journal of Animal Ecology*, **53**, 455-478.
- 487 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M.,  
488 Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M.,  
489 Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P.,  
490 Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A.,  
491 Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O.,  
492 Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008) The  
493 LEDA Traitbase: a database of life-history traits of the Northwest European flora.  
494 *Journal of Ecology*, **96**, 1266-1274.
- 495 Klotz, S., Kühn, I. & Durka, W. (2002) *BIOLFLOR - Eine Datenbank mit biologisch-*  
496 *ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz /  
497 Landwirtschaftsverlag, Bonn.
- 498 Larsen, F.W., Bladt, J. & Rahbek, C. (2009) Indicator taxa revisited: useful for conservation  
499 planning? *Diversity and Distributions*, **15**, 70-79.
- 500 Lawton, J.H. & Schröder, D. (1977) Effects of plant type, size of geographical range and  
501 taxonomic isolation on number of insect species associated with British plants. *Nature*,  
502 **265**, 137-140.
- 503 Lindenmayer, D., Barton, P., Westgate, M., Lane, P. & Pierson, J. (2015) Biodiversity  
504 surrogates. *Indicators and Surrogates of Biodiversity and Environmental Change* (eds D.  
505 Lindenmayer, P. Barton & J. Pierson), pp. 15-24. CRC Press, Boca Raton, Florida, USA.

- 506 Mazziotta, A., Vizentin-Bugoni, J., Tøttrup, A.P., Bruun, H.H., Fritz, Ö. & Heilmann-Clausen, J.  
507 (2017) Interaction type and intimacy structure networks between forest-dwelling  
508 organisms and their host trees. *Basic and Applied Ecology*, **24**, 86-97.
- 509 Miller, Z.J. (2012) Fungal pathogen species richness: why do some plant species have more  
510 pathogens than others? *The American Naturalist*, **179**, 282-292.
- 511 Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011) How many species are  
512 there on Earth and in the Ocean? *PLoS Biology*, **9**, e1001127.
- 513 Nilsson, R.H., Larsson, K.-H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D.,  
514 Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U. & Abarenkov,  
515 K. (2019) The UNITE database for molecular identification of fungi: handling dark taxa  
516 and parallel taxonomic classifications. *Nucleic Acids Research*, **47**, D259–D264.
- 517 Pölme, S., Bahram, M., Jacquemyn, H., Kennedy, P., Kohout, P., Moora, M., Oja, J., Öpik, M.,  
518 Pecoraro, L. & Tedersoo, L. (2018) Host preference and network properties in biotrophic  
519 plant–fungal associations. *New Phytologist*, **217**, 1230-1239.
- 520 Purahong, W., Wubet, T., Krüger, D. & Buscot, F. (2018) Molecular evidence strongly supports  
521 deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate  
522 forests. *The ISME Journal*, **12**, 289-295.
- 523 Savile, D.B.O. (1979) Fungi as aids to plant taxonomy: methodology and principles. *Symbolae*  
524 *Botanicae Upsalienses*, **22**, 135-145.
- 525 Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D. & Müller,  
526 J. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity  
527 in dead wood. *Journal of Applied Ecology*, **53**, 934-943.
- 528 Southwood, T.R.E. (1961) The number of species of insect associated with various trees. *Journal*  
529 *of Animal Ecology*, **30**, 1-8.
- 530 Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants: Community Patterns*  
531 *and Mechanisms*. Blackwell Scientific Publications, Oxford.
- 532 Strong, D.R. & Levin, D.A. (1975) Species richness of parasitic fungi of British trees.  
533 *Proceedings of the National Academy of Sciences of the United States of America*, **72**,  
534 2116-2119.
- 535 Strong, D.R. & Levin, D.A. (1979) Species richness of plant parasites and growth form of their  
536 host. *American Naturalist*, **114**, 1-22.
- 537 Tahvanainen, J. & Niemelä, P. (1987) Biogeographical and evolutionary aspects of insect  
538 herbivory. *Annales Zoologici Fennici*, **24**, 239-247.

539 Tedersoo, L., Bahram, M., Cajthaml, T., Põlme, S., Hiiesalu, I., Anslan, S., Harend, H., Buegger,  
540 F., Pritsch, K., Koricheva, J. & Abarenkov, K. (2015) Tree diversity and species identity  
541 effects on soil fungi, protists and animals are context dependent. *ISME J*, **10**, 346–362.

542