Simple attributes predict the importance of plants as hosts to the richness of fungi and arthropods

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Abstract

Consumers constitute the vast majority of global terrestrial biodiversity. Yet, local consumer

richness is poorly understood. Plant species richness offers a simple hypothesis to how the

diversification of carbon substrates may promote the diversity of arthropods and fungi. We took

this one step further and used databases on plant-consumer interaction links to derive the

richness of associated biota per plant species (link score). Using a species inventory of 130 sites

we investigated 1) how well the link score could be predicted by plant attributes and 2) if the

sum of plant species' observed or predicted link scores could predict site richness of arthropods

and macrofungi better than plant species richness alone. We found plant link scores to be

positively related to plant size, abundance, nativeness and ectomycorrhizal status. Link based

indices generally improved prediction of richness, stressing the importance of plants as niche

space for the megadiverse groups of insects and fungi.

Keywords: trophic interactions, plant traits, mycorrhizal fungi, phytophagous arthropods,

consumer diversity, ecospace, multi-taxon species richness

Introduction

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

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

Prediction of local site biodiversity provides essential knowledge to prioritization of 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 funga and

87   arthopod 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?

Methods

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 nuclear16S 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).
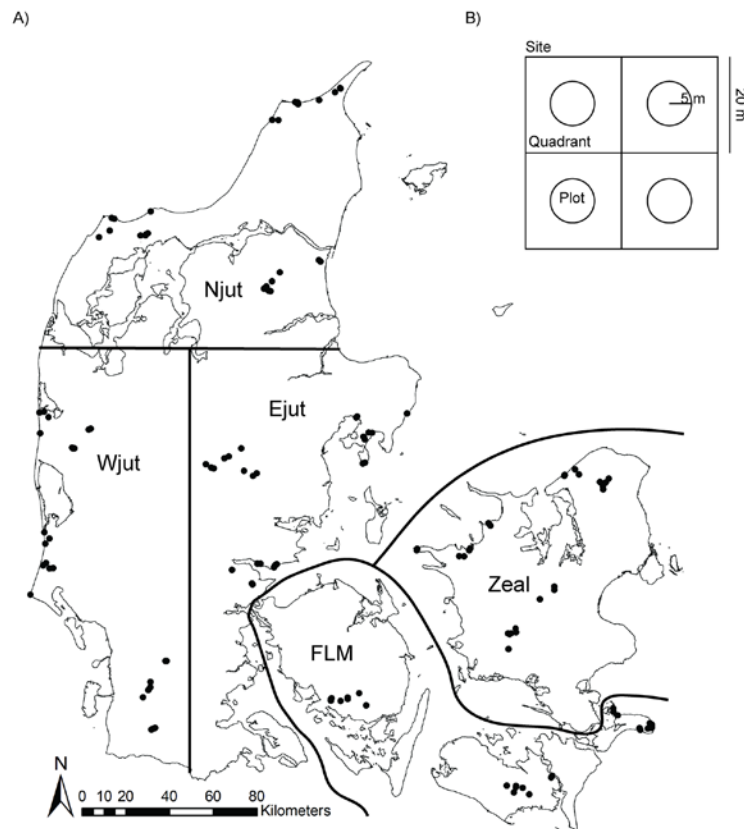
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132   *Fig. 1. Map of Denmark showing the location of the 130 sites grouped into 15 clusters within five regions (Njut: Northern*
133   *Jutland, Wjut: Western Jutland, Ejut: Eastern Jutland, FLM: Funen, Lolland, Møn, Zeal: Zealand). B) Site layout with four 20 × 20*
134   *m quadrants each containing a central 5 m radius circular plot.*

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-

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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.

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 5×5 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.

Testing the prediction of biodiversity by interaction scores

We tested the predictive power of interaction link scores on observed multi-taxon species

richness data from the 130 field sites. We used total observed species richness of fungi and

arthropods as response variable, but also investigated models for functional subgroups of fungi

and arthropods, divided according to their relation to plants as resources and ecospace at large.

Fungi were divided into symbionts (mainly ectomycorrhizal fungi, but also including biotrophic

parasites) and decomposers (saprotrophs). Arthropods were divided into 1) predators, 2) flyers,

3) externally feeding herbivores and 4) internally feeding arthropods, i.e. gallers and miners. The

group 'flyers' differ from the trophically defined subgroups and was defined by mode of

movement and dispersal, reflecting an assumed decoupling of adult and juvenile life stages.

We modelled species richness with GLM, using negative binomial error structure to account for

frequent overdispersion of Poisson models. For each taxonomic response group we made a

bivariate GLM in response to the link sum. In order to avoid confounding effects from variation

in the abiotic environment potentially co-varying with plant link scores, we subsequently ran

parallel GLM modelling, in which community mean Ellenberg Indicator Values for light, soil

nutrients, soil moisture and soil pH were added to the models as co-variables. We applied

multiple regression to test if link sum remained important after fitting a general environmental

calibration of the habitat. Both types of model were made for three different sets of plant host

richness variables: 1) simple plant richness (corresponding to a null hypothesis of all plant

species having equal abundance and equal value as consumer species' resource), 2) the observed

link sum and 3) the predicted link sum. We log-transformed these plant ecospace variables, as

this led to decreasing model AIC in most cases – particularly for response groups with strong

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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.

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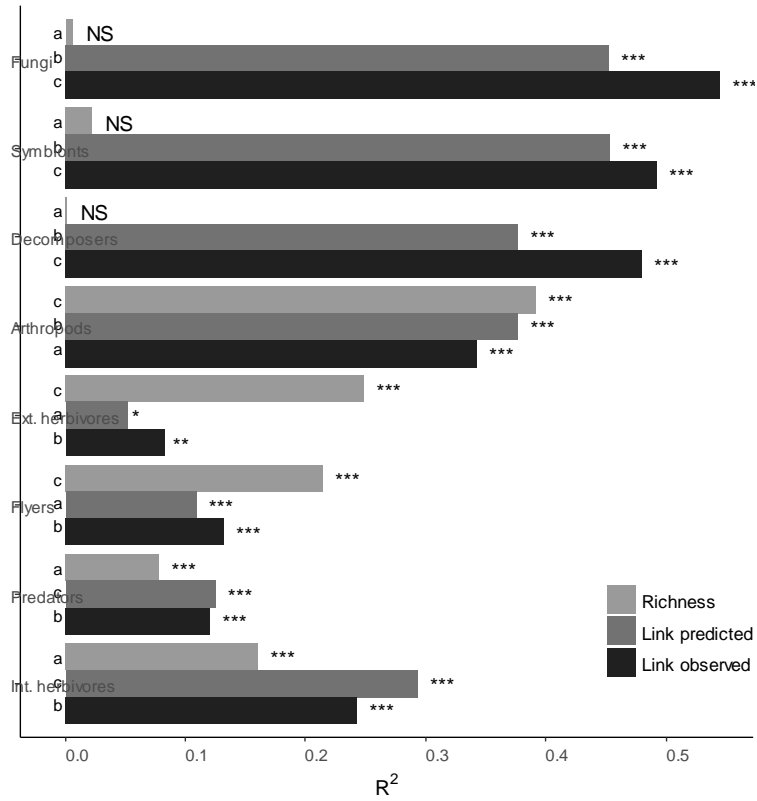
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313   *Fig. 2. Bivariate models. Bars represent pseudo-R^2 for regression models of consumer species richness in response to simple*
314   *vascular plant species richness and plant richness weighted link scores for consumer associations. Significance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

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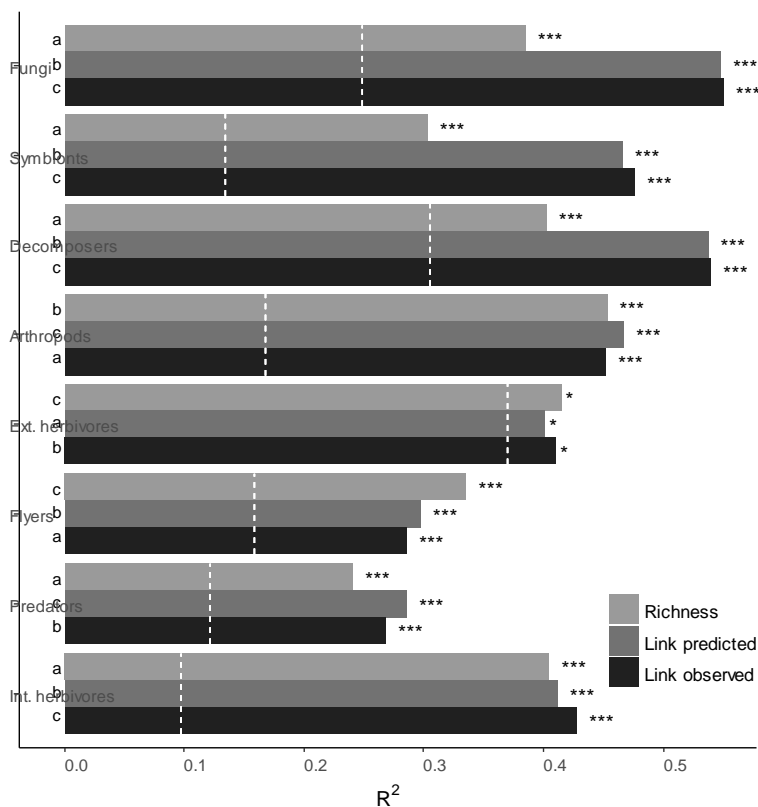
Fig. 3. Multiple regression. Bars represent pseudo-R^2 for regression models of consumer species richness in response to simple vascular plant species richness and plant richness weighted link scores for consumer associations, and with environmental calibration by mean Ellenberg Indicator Values as co-variables.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

After fitting environmental proxies (community mean Ellenberg Indicator Values) as

covariates in a multiple regression model, plant species richness became a significant predictor

of all three measures of fungal richness. However, link sum, observed and predicted alike,

remained stronger predictors of fungi richness and richness of most arthropod response groups

than simple species richness. Observed link score was generally stronger than predicted link

score, although the difference was modest. The multiple regression model for total fungi richness

using observed link score reached 55% explained variation. Multiple regression including

environmental proxies only contributed with a minor improvement of predictions compared to

the best bivariate model (54.5% explained variation). Environmental proxies alone explained less

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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%).

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 fungas 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 continuum~~a~~ (Põlme

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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Tables

Table 1. Regression model of fungal link score per plant taxon as predicted from plant attributes. Overall 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 *

Table 2. Regression model of arthropod link score per plant taxon as predicted from plant attributes. 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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