

Research

Simple attributes predict the value of plants as hosts to fungal and arthropod communities

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Fungal and arthropod consumers constitute the vast majority of global terrestrial biodiversity. Yet, the link from richness and composition of producer (plant) communities to the richness of consumer communities is poorly understood. Fungal and arthropod species richness could be a simple function of producer species richness at a site. Alternatively, it could be a complex function of chemical and structural properties of the producer species making up communities. We used databases on plant–fungus and plant–arthropod trophic links to derive the richness of consumer biota per associated plant species (coined link score). We assessed how well link scores could be predicted by simple attributes of plant species. Next, we used a multi-taxon inventory of 130 sites, representing all major habitat types in a country (Denmark), to investigate whether link scores summed over plant species in communities (coined link sum) could outperform simple plant species richness as predictor of fungal and arthropod richness at the sites. We found plant species' link scores for both fungi and arthropods to be positively related to plant size, regional occupancy, nativeness and ectomycorrhizal status. Link-based indices generally improved the prediction of richness of fungal and arthropod communities. For fungal communities, both observed link sum (from databases) and predicted link sum (from plant attributes) had high predictive power, while plant richness alone had none. For arthropod communities, predictive performance varied between functional groups. For both fungi and arthropods, richness predictions were further improved by considering abiotic habitat conditions. Our results underline the importance of plants as niche space for the megadiverse groups of arthropods and fungi. The plant–attribute approach holds promise for predicting local and regional consumer richness in areas of the world lacking detailed plant–consumer databases.

Keywords: consumer diversity, ecospace, multi-taxon biodiversity, mycorrhizal fungi, phytophagous arthropods, plant traits, trophic interactions



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Introduction

Consumers, including the megadiverse groups of arthropods and fungi, constitute a major part of terrestrial biodiversity. Producers, i.e. plants, provide structural habitats and resources to consumers and species-rich plant communities have been shown to accommodate species-rich communities of consumers (Brunbjerg et al. 2018). However, the link from producer to consumer richness is modulated by the host specificity of trophic interactions, as some producers are hosts to a much greater diversity of associated consumers than others (Southwood 1961). Therefore, plant identity may be more important than plant species richness to local consumer diversity. There are, however, only few areas of the world where host–consumer interactions have been mapped sufficiently to test this hypothesis.

Most insects, mites and fungi associated with living plants are strongly specialised, i.e. each species depends on a single or a few plant species as both resource and habitat (Strong et al. 1984, Hawksworth 2001). Even decomposers may show a high degree of specificity, due to after-life effects of plant structure and chemical composition (Heilmann-Clausen et al. 2016). Not only primary consumers show host-plant specificity, also consumers on the third and fourth trophic levels may be associated with specific plant hosts (Godfray 1995).

The direct effect of plants on higher trophic levels is encapsulated in the ecospace dimension coined expansion, signifying the build-up and diversification of organic carbon in ecosystems (Brunbjerg et al. 2017). However, the predictive power of plant richness on consumer richness may be indirect, if consumers and producers respond in similar ways to extrinsic factors (Kemp and Ellis 2017), in particular abiotic conditions such as microclimate, soil moisture, soil pH, soil nutrients and inorganic substrates, i.e. the position component of ecospace (Brunbjerg et al. 2017). Thus, rigorously testing the effect of plant diversity on consumer diversity should account for effects of the abiotic environment.

While understanding the causes of variation in richness of arthropods and fungi is a goal in itself, there are important applications as well. Prediction of local or regional multi-taxon biodiversity provides essential knowledge to prioritization of conservation efforts. While biodiversity surrogacy has been questioned in general (Larsen et al. 2009, Lindenmayer et al. 2015), plant species richness has been demonstrated to promote multi-taxon diversity, provided that – on top of plant species richness – plant species identities are used for bioindication of key habitat conditions (Brunbjerg et al. 2018). However, it remains to be tested if a higher predictive power may be attained by including plant species' attractiveness as food and habitat to consumer species.

A number of key plant functional attributes are known to correlate with the richness of associated arthropod and fungal biotas. In particular, properties associated with plant apparency and predictability as a resource to consumers have been found important (Feeny 1976), i.e. species range size and local abundance, size and life span, time since immigration

and nativeness (Southwood 1961, Lawton and Schröder 1977, Kennedy and Southwood 1984, Brändle and Brandl 2001, Miller 2012). In addition, chemical defences and phylogenetic isolation are among the proposed plant determinants of associated arthropod richness (Tahvanainen and Niemelä 1987, Brändle and Brandl 2006) and, for symbiotic fungi, the ability of plants to form mycorrhiza of different types (Tedersoo et al. 2015). The body of literature relating arthropod richness to plants as hosts is huge. In contrast, the similar literature for plant–fungal interactions is much smaller. Very few analyses have combined the two consumer groups (Strong and Levin 1979, Brändle and Brandl 2003), and even fewer – if any – have taken investigations from the level of whole biotas to local communities.

Here, we use a survey of species richness of vascular plants, arthropods and macrofungi at 130 sites representing most terrestrial ecosystems in a country (Denmark). First, for all plant species in the survey, we collated independent data on plant–consumer interactions in order to determine the size of the associated arthropod and fungal biotas per plant species (observed link score). The observed link score was used to build predictive models of plant species attractiveness from key plant attributes, such as range size and growth form (predicted link score). Next, link scores were summed over the plant species occurring in each local site to obtain an observed and a predicted link sum per community. We modelled total fungal and total arthropod richness across study sites and, in addition, the richness of individual functional response groups, which could potentially be controlled by different abiotic and biotic drivers.

Specifically, we asked: 1) which plant attributes can predict the number of trophic interaction links between plants and associated arthropods and fungi? 2) Is community link sum a better predictor of observed species richness of fungi and arthropods (and functional subgroups thereof) than plant species richness alone? 3) Can the observed link score be substituted by a plant–attribute predicted link sum in the prediction of arthropod and fungal richness?

Methods

Study area and collection of biodiversity data

The study area was Denmark (Fig. 1). In the field, we collected data from 130 sites, each with an area of 40 × 40 m, deemed homogenous with respect to topography and vegetation structure, but accepting the inherent heterogeneity of some habitat types. The study design aimed for coverage of the major environmental gradients, including naturalness of habitat (i.e. the intensity of silviculture and agriculture). Thirty sites were allocated to cultivated habitats and 100 sites to more natural habitats. The cultivated subset was stratified according to major land-use classes and the natural subset was stratified across gradients in soil fertility, soil moisture and vegetation openness. The design has been described in detail by Brunbjerg et al. (2019).

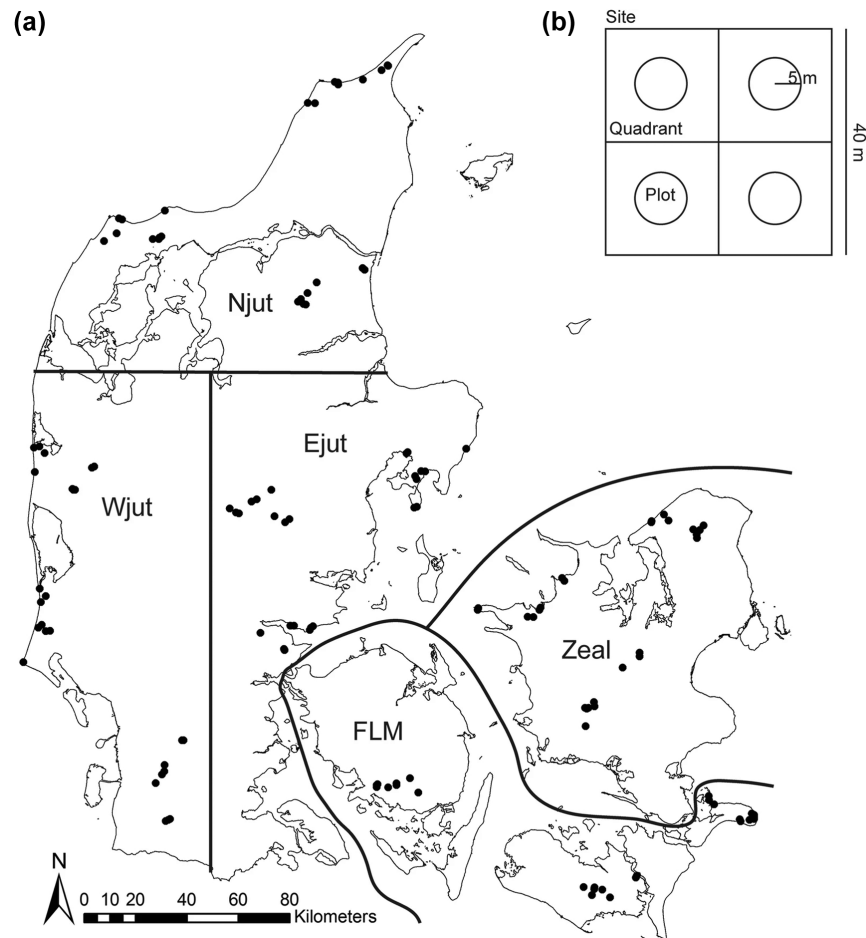


Figure 1. (A) Map of Denmark showing the location of the 130 sites grouped into 15 clusters within five regions (Njut: Northern Jutland, Wjut: Western Jutland, Ejut: Eastern Jutland, FLM: Funen, Lolland, Møn, Zeal: Zealand). (B) Site layout with four 20×20 m quadrants, each containing a central 5 m radius circular plot. Reprinted and modified from Ejrnæs et al. (2018), Copyright (2018), with permission from Elsevier.

We collected data on the occurrence of vascular plants, macrofungi and arthropods, aiming for an unbiased and representative assessment of the multi-taxon species diversity in each of the 130 sites. For vascular plants, the sampling included abundance assessment on a coarse scale. Each site was divided into four quadrants and, at the centre of each quadrant, a circular plot (5 m radius) with an embedded 50×50 cm inner quadrat was situated. Presence of plant species was recorded in inner quadrats and 5 m plots separately, in addition to records for the whole site. Plant species judged by visual inspection to be dominant at site-level were noted. For the present analysis, we assigned an ordinal abundance of 3 to plants species either judged as dominants or recorded in all four inner quadrats. Plant species recorded in at least one inner quadrat and at least one additional 5 m plot were assigned an ordinal abundance of 2. The remaining species were assigned an abundance of 1. Proxy variables for site environmental conditions were derived from site plant lists by bioindication using Ellenberg indicator values for light, soil nutrients, soil moisture and soil pH (Ellenberg et al. 1991, Brunbjerg et al. 2018).

The data for vascular plants may be considered as exhaustive, while for the remaining species groups, which are more demanding to find or catch and to identify, the data represent a standardized in-depth sampling effort across the 130 sites. For arthropods, we operated with a standard set of pitfall traps, yellow-pan traps and Malaise traps during two set periods in 2014. Furthermore, two active-search approaches were used to retrieve externally and internally feeding phytophagous arthropods, respectively: 1) sweep netting and beating with a focus on true bugs (Heteroptera) and leaf beetles (Chrysomelidae), 2) strategic search for plant galling and mining arthropods, including non-galling Cecidomyiinae (Diptera: Cecidomyiidae). For macrofungi, we visited each site three times during the main season (August to early November), obtaining an exhaustive list of fruiting species on each occasion focussing on all groups of Basidiomycota and Ascomycota, but excluding non-stromatic Pyrenomycetes and Discomycetes with fruitbodies smaller than 1 mm and lichenized fungi. For full details on methods applied and the taxonomic coverage of

the obtained results, see Brunbjerg et al. (2019, Supporting information).

Interaction data and observed link score calculation

We extracted data for interaction links from existing databases for each plant species found at the 130 field sites. For both fungi and arthropods, the estimation had to take into account that many interaction links have been recorded at the level of plant genus only, either because consumers do not discriminate between different species of the same plant genus (Savile 1979) or because of incomplete identification of the host by the human observer.

We mined two databases for reported links to the list of vascular plants found in the studied 130 sites: 1) a Danish fungal database (Danish Mycological Society 2016, accessed 03-01-2018) for fungi and 2) the Biological Records Centre's host plant database for arthropods (DBIF, <www.brc.ac.uk/dbif/hosts.aspx>, accessed 15 January 2018). We included interaction links reported on the levels of plant subspecies, species and genus. Due to difference in structure, the two databases were handled in somewhat different ways, in order to obtain comparable data for analysis.

The Danish fungal database consists of observations of fungi made by citizens and professionals, with records accompanied by observational data on substrate, i.e. live plants or dead plant parts, or – for ectomycorrhizal (ECM) fungi – close association with plants, identified at least to plant genus. The British BRC host plant database is a meta-database, compiling arthropod–plant associations reported in the scientific literature. The geographic focus is Great Britain and adjacent continental Europe. The database has been updated regularly, but curation of insect and mite taxonomy and nomenclature is no better than the most recent source for each taxonomic group, which for many little studied groups may be several decades old. Because of the heterogeneity and vast size of the body of literature sources, cleaning the arthropod names for synonyms was considered intractable. The reliability of published host records collated in the database has been found to be well supported (Brändle and Brandl 2001). We retrieved arthropod links for all vascular plant species found across the 130 field sites, under the assumption that the BRC database would give an unbiased picture of the size of the total biota of associated arthropods on Danish vascular plants.

A particular challenging task was to distribute fungal and arthropod links reported at the plant genus level onto the plant species belonging to that genus. The procedure is detailed in the following (Supporting information).

Link score calculation: plant-associated fungi

We retrieved all observations of fungi with an associated plant host record from the Danish fungal database ($n = 255\,700$). From that, we extracted all recorded interactions between fungi and vascular plants at the species or genus level and filtered to plant species found at the 130 study sites, which resulted in 20 309 unique interaction links between 4549 fungal and 538 vascular plant taxa (at species or genus level),

of which 50% were reported at the plant genus level. For each fungal species, each of its plant links was given a weight corresponding to 1 divided by the number of linked plant taxa. Thus, all fungal species would contribute identical total weights to the final link score, but a specialist fungus would contribute more to the link score of its single host plant than would a generalist fungus to the link scores of each of its many hosts. These link weights were summed for each vascular plant taxon (at both species and genus level) over all fungal taxa, accepting that some fungal species had links reported at both levels. When calculating the final link score for a plant species, we allocated the plant genus score to the species belonging to a given genus in the following way (a worked example is given in the Supporting information):

- 1) Plant species having link records at both the species and genus levels were allocated a percentage of the genus link score proportional to their species-level link score relative to the link score of the species within the genus with the highest species-level link score. This rule applied to interactions involving 265 plant species.
- 2) Plant species belonging to a genus with fungal link records at the genus level only (no species-level records for any constituent species) were allocated an arbitrary 90% of the genus link score, equal for all species in the genus. This was done to down-weight species-level links inferred with less certainty from genus-level records. This rule applied to interactions involving 104 plant species.
- 3) Plant species having fungal link records at the genus level only, but belonging to a genus containing other species with species-level records, were scored as 'NA', based on the assumption that neither zero nor an inferred link score would be correct. This rule applied to interactions involving 245 plant species.
- 4) Plant species without reported fungal links at neither genus nor species level were given a zero link score. This rule applied to interactions involving 293 plant species.

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

Link score calculation: phytophagous arthropods

For each of the plant species encountered at the 130 sites, we retrieved all reported interactions involving insects and mites from the BRC host plant database, considering also commonly used plant synonyms. Interactions reported on plant subspecies level were aggregated to the species level. We found 31 890 interaction links, involving 6870 arthropod species and 1215 vascular plant taxa (at the species or genus level), of which 32% were reported at the plant genus level. Similar to the procedure for fungal links, each plant link of an arthropod species was given a weight corresponding to 1 divided by the number of linked plant genera. However, we first partitioned the unity link score to plant genera only, ignoring links at the plant species level. This procedure was chosen for two reasons: 1) specialist phytophagous insects and mites are very often tightly specialized to plant genera, 2) the database was compiled from heterogeneous primary

sources, some of which would report species-specific links on the plant genus level. In a second round, the link score at the plant genus level was partitioned onto all constituent species equally, except for plant species with reported arthropod links, which had their share of the genus score tripled. This additional weighing was done because some genera contain exotic or biologically deviating members, which host only a fraction of the genus' arthropod biota. The final link score for each plant species was calculated as the sum of genus-level link weights (Supporting information).

Plant attributes and predicted link score

In order to predictively model the interaction link score of plants species from their attributes, we compiled plant attributes for the plant species found across the 130 field sites. Information on ectomycorrhizal (ECM) associations was extracted from the MycoFlor database (Hempel et al. 2013). Information on nativeness of plant species at 1) the scale of Denmark, 2) the European scale and 3) nativeness to Denmark of the genus were taken from Buchwald et al. (2013). Plant species were assigned to one of the following phylogenetic groupings: Angiosperm, Gymnosperm and Pteridophyte (ferns, horsetails, clubmosses), based on standard plant classification. Lifespan was scored as 1) annuals+short-lived perennials, 2) medium-lived perennials, 3) long-lived perennials. Lifeform was scored as 1) tree = macrophanerophyte, 2) shrub + liana = nanophanerophyte, 3) dwarf-shrub = hemiphanerophyte, 4) herb = hemicryptophyte + geophyte + chamaephyte + therophyte + hydrophyte + pseudophanerophyte (Klotz et al. 2002). Plant size was based on maximum canopy height and classified as 1) huge, 2) large, 3) medium-sized, 4) small and 5) tiny, following the LEDA trait database (Kleyer et al. 2008). These attributes were extracted using the R package TR8 (Bocci 2015). We used family, genus and species descriptions in Hansen (2004) for filling gaps in information on plant size (canopy height). Plant species regional occupancy was extracted from a national plant survey (Atlas Flora Danica), carried out in 5 × 5 km grid cells, of which 1300 were thoroughly surveyed, resulting in reliable presence-absence data (Hartvig and Vestergaard 2015). Species incidence frequency across reference grid cells was re-coded as high (> 0.75), moderate (0.26 – 0.75) and low (< 0.25) occupancy. Because of a bimodal frequency distribution, there were approximately equal numbers of species in the three occupancy classes.

To obtain predicted link scores, we used an ANOVA model with plant species' observed link score, for fungal and arthropod links separately, as response to plant attributes, i.e. ECM status, national nativeness, European nativeness, nativeness on the genus level, regional occupancy phylogenetic group, life form, lifespan and plant size as explanatory variables. All explanatory variables were coded as categorical variables. Fungal link score was log transformed and arthropod link score was squareroot transformed prior to analysis in order to minimize skewness of error structure. Model performance was assessed with type 3 sum of squares based on reducing a

full model with the least significant variable until all variables were significant. The parameters of the resulting models were used to predict the expected number of fungal and arthropod links per plant species based on species attributes, and coined predicted link score as opposed to the observed link score derived from databases. The correlation between fungal and arthropod observed links scores across plant species was assessed with Spearman rank correlation.

Community link sum per site

For each of the 130 sites, we calculated a simple sum of link scores as well as a weighted link sum, the latter using plant species abundance as weight. The use of plant abundance as weight was based on the reasoning that the local abundance of a plant species would increase the chance that the plant was used as host by fungal or arthropod species. Simple and weighted link sum values were calculated for both observed and predicted link score values. The community link sum for a given site increases with local plant species richness and with the average host attractiveness (link score) of the plant community members, and thus can also be seen as a link-weighted plant species richness of 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 as follows according to their relation to plants as resources and ecospace at large: Observed fungi were divided into symbionts (mainly ECM fungi, but also including biotrophic parasites) and decomposers (saprotrophic fungi). Observed arthropods were divided into 1) predators, 2) flying insects, 3) externally feeding herbivores and 4) internally feeding arthropods, i.e. galls and miners. The group 'flying insects' was defined by mode of movement and dispersal more or less tightly coupled with specialization to ephemeral resources and a habitat decoupling of juvenile and adult life stages. For detailed information on assignment of fungal and arthropod taxa to functional groups – see the Supporting information.

We modelled species richness with GLM, using negative binomial error structure to account for frequent overdispersion of Poisson models (Hilbe 2011). For each taxonomic group, we fitted binomial GLMs with link sum as response. In order to avoid confounding effects from variation in the abiotic environment potentially co-varying with community link sum, 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 a set of co-variables. We applied multiple regression model 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 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 Akaike information criterion in most cases – particularly for response groups with strong dependence on host richness. We also modelled abundance-weighted plant richness, but results were almost identical to the simple richness models, so only the latter are reported.

Results

Field-collected data from the 130 sites comprised 650 vascular plant species, 1774 species of macrofungi (90% of which were Basidiomycetes), which were divided into symbionts (n=788) and decomposers (n=915) (71 species of primary mycoparasitic species were omitted; Supporting information). In total, 2345 species of arthropods were recorded and divided into external herbivores (n=836), internal herbivores (n=241), predators (n=544) and flying insects (n=649) (75 most detritivorous species were omitted; Supporting information). For full details of the taxonomic coverage, see Brunbjerg et al. (2019, Supporting information) and Frøslev et al. (2019).

The plant taxa with most fungal interaction links in our database were *Fagus sylvatica*, *Quercus robur*, *Picea abies*, *Pinus sylvestris* and *Salix cinerea*, i.e. all woody plants and all shown previously to be important fungal hosts (Heilmann-Clausen et al. 2016). The herbaceous plants with most fungal links were large graminoids, i.e. *Phragmites australis* and *Carex paniculata*. For arthropods, the plant taxa with most recorded interaction links were *Salix* spp. (e.g. *S. cinerea* and *S. repens*), *Quercus* (*Q. robur*), *Pinus sylvestris*, *Betula* and *Populus* (*P. tremula*), similarly in agreement with previously published evidence (Kelly and Southwood 1999, Brändle

and Brandl 2003). The herbaceous plants with most arthropod links were *Achillea millefolium* (Asteraceae) and *Medicago sativa* (Fabaceae).

The attribute-based model of observed fungal link scores across plant species revealed that plants' capacity to form ectomycorrhiza (ECM), high regional occupancy, nativeness to Europe and intermediate to long lifespan all had strong positive effects on plant 'attractiveness' to fungi and arthropods, while small size and herbaceous life form had negative effects (Table 1). The adjusted model R² was 0.64. The parallel model for observed arthropod link score showed that ECM capacity, high regional occupancy (on the level of plant genus), dwarf shrub lifeform (as opposed to tree, herb and shrub + liana) had significantly positive effects on the arthropod link score, while short life span and fern phylogenetic group had significant negative effects (Table 2). The adjusted model R² was 0.52, i.e. somewhat lower than for the fungal model. Observed link scores for fungi and arthropods were positively correlated, albeit moderately so (Rho = 0.30, p < 0.001).

The bivariate models showed that observed and predicted link sum were in general equally good predictors, with the observed link sum performing slightly better in most cases. Only for internally feeding phytophagous arthropods, the predicted link sum performed much better than the observed link sum (Fig. 2).

Comparing the predictive power of community link sum to simple plant richness gave contrasting results for fungi and arthropods. Simple plant species richness was a very poor predictor of fungal richness. In contrast, both observed and predicted link sum were quite strong and significant predictors of fungal richness, and with observed link sum providing consistently better modelling results than predicted link sum, accounting for more than 50% of the variation in fungal richness (Fig. 2). Moreover, this result was almost equally attributable to decomposer and symbiotic fungi. The modelling outcome of the bivariate models was very different for total arthropod richness and most arthropod subgroups, for

Table 1. Fungal observed link score per plant taxon as predicted from plant attributes using ANOVA. Overall model adjusted R² 0.64; F_{11,295} = 50.2, p-value < 0.001. p-values are marked with asterisks thus: * < 0.05, ** < 0.01, *** < 0.001".

	Coefficient	SE	t-value	p-value
Intercept	2.051	0.533	3.81	< 0.001***
Ectomycorrhizal (ECM)	1.669	0.227	7.34	< 0.001***
European native	0.683	0.220	3.11	0.002**
Occupancy: High	–	–	–	–
Moderate	–0.358	0.102	–3.52	< 0.001***
Low	–0.728	0.135	–5.38	< 0.001***
Lifespan: Long	–	–	–	–
Short	–0.356	0.140	–2.55	0.011*
Life form: Dwarf shrub	–	–	–	–
Herb	–0.683	0.264	–2.59	0.010*
Shrub + Liana	–0.104	0.323	–0.32	0.748
Tree	0.581	0.459	1.27	0.206
Size: Huge	–	–	–	–
Large	–0.249	0.271	–0.92	0.360
Medium	–0.142	0.432	–0.33	0.742
Small	–0.883	0.440	–2.01	0.046*

Table 2. Arthropod observed link score per plant taxon as predicted from plant attributes using ANOVA. Overall model adjusted R^2 0.53; $F_{12,649} = 59.9$, p -value < 0.001 . p -values are marked with asterisks thus: * < 0.05 , ** < 0.01 , *** < 0.001 ".

	Coefficient	SE	t-value	p-value
Intercept	5.000	0.534	9.37	< 0.001 ***
Ectomycorrhizal (ECM)	1.231	0.251	5.00	< 0.001 ***
Phylum: Angiosperm	–	–	–	–
Gymnosperm	0.045	0.382	0.12	0.905
Fern ally	–0.664	0.215	–3.08	0.002**
Occupancy: High	–	–	–	–
Moderate	–1.195	0.091	–13.09	< 0.001 ***
Low	–1.828	0.092	–19.81	< 0.001 ***
Lifespan: Long	–	–	–	–
Short	–0.435	0.093	–4.69	< 0.001 ***
Life form: Dwarfshrub	–	–	–	–
Herb	–1.235	0.234	–5.27	< 0.001 ***
Shrub + Liana	–0.794	0.288	–2.75	0.006**
Tree	–1.094	0.474	–2.31	0.021*
Size: Huge	–	–	–	–
Large	–0.245	0.295	–0.83	0.407
Medium	–0.404	0.470	–0.86	0.390
Small	–0.798	0.474	–1.68	0.093

which plant richness was a superior predictor. For the subgroup of internally feeding phytophagous arthropods (gallers and miners), however, link sum performed markedly better than simple plant richness. The best models reached 39% explained variation for total arthropod richness (simple plant

richness) and 38% explained variation for internal feeders (predicted link score).

After fitting environmental proxies (community-mean Ellenberg indicator values) as covariates in a multiple regression model, plant species richness became a significant

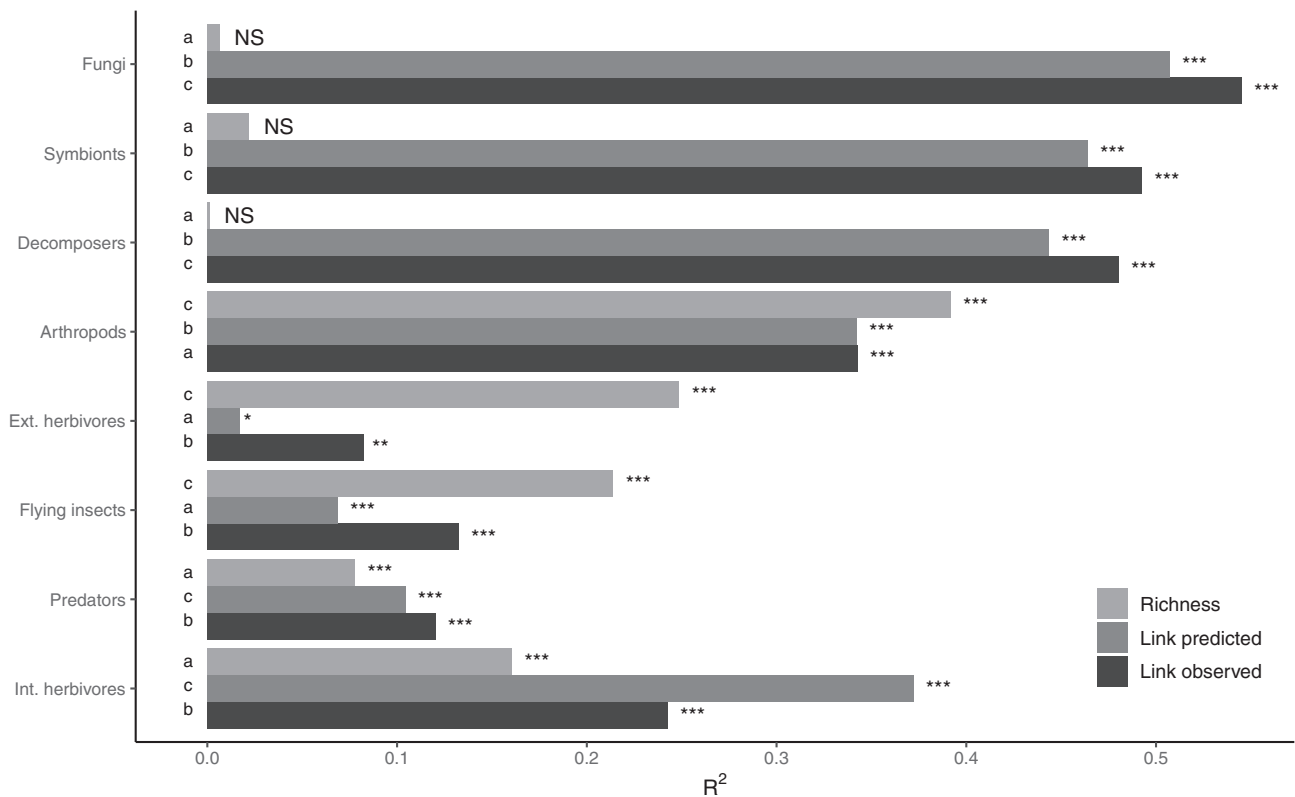


Figure 2. Bivariate models. Bars represent pseudo- R^2 for regression models of consumer species richness in response to simple vascular plant species richness and plant richness weighted link scores for consumer associations. Small letters to the left of columns show significant differences in predictive power of the three candidate models. Significance of plant richness or link effects is indicated by asterisks (NS $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

predictor of all three measures of fungal richness (Fig. 3). However, both observed and predicted link sum per site remained stronger predictors of fungal richness, and for the richness of most arthropod response groups, than simple plant species richness. Observed link sum was generally stronger than predicted link sum, although the difference was modest. The multiple regression model for total fungal richness using observed link sum reached 54% explained variation. Multiple regression including environmental proxies only contributed with a minor improvement of predictions compared to the best bivariate model (53% explained variation). Environmental proxies alone explained less than half of the variation of fungal richness, a little more than half of the variation for decomposers and one third of the variation in fungal symbiont richness (Fig. 3).

Arthropod models improved markedly after fitting environmental proxy variables, with 48% explained variation for total arthropod richness (predicted link sum), 43% for internal feeders (predicted link sum) and 42% for external feeders (simple plant richness). The difference between the predictive power of plant richness and link scores was reduced compared to the bivariate models. The amount of variation explained by environmental proxies alone was low for internal feeders and total arthropod richness (23 and 36%, respectively), moderate for predators and flying insects (43 and 47%, respectively) and high for external feeders (89%).

Discussion

An overarching question of this study was whether plant species composition of ecosystems may work as an efficient predictor of co-occurring consumer species richness. We have demonstrated that simple plant attributes are good predictors of the richness of plant-associated consumer biotas and that the host value of plants thus assessed improves prediction of local consumer community richness from plant community composition. Plant community richness had consistent positive effects on co-occurring consumer richness, which is mediated through expanded structural and functional diversity of the plant communities (Brunbjerg et al. 2017, Schuldt et al. 2019).

In a previous study in the same system of 130 sites, we showed that plants may predict general species richness across taxonomic and functional groups, given that predictions are based on both plant species richness and plant-based bioindication of habitat conditions (Brunbjerg et al. 2018). In the present study, we have demonstrated that plant surrogacy of arthropod and fungal biodiversity can be taken one step further by including plant growth form and other plant attributes, such as range size.

The size of biotas of plant-associated arthropods and fungi varies considerably and predictably across plant taxa, a notion that was first established more than half a century ago (Southwood 1961). Large-bodied, long-lived, structurally

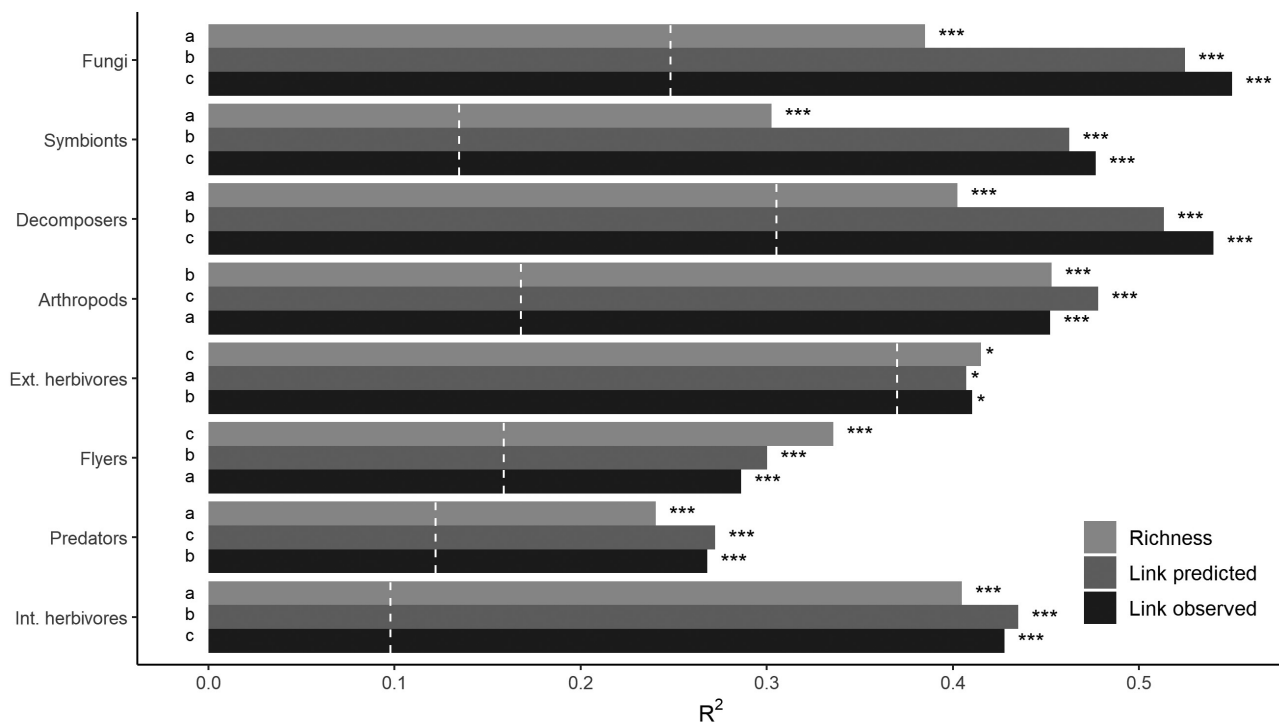


Figure 3. Multiple regression. Bars represent pseudo- R^2 for regression models of consumer species richness in response to simple vascular plant species richness, in response to plant richness weighted link scores for consumer associations, and with environmental calibration by mean Ellenberg indicator values as co-variables. The R^2 for the model on environmental calibration alone is indicated by white lines. Small letters to the left of columns show significant differences in predictive power of the three candidate models. Significance of plant richness or link effects is indicated by asterisks (NS $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

complex, widely distributed and locally abundant plant species have repeatedly been shown to harbour comparatively large faunas of phytophagous arthropods (Tahvanainen and Niemelä 1987, Brändle and Brandl 2001) and fungus (Strong and Levin 1975, Miller 2012). This has been encapsulated in the concept of apparency, which comprises both species' attributes (e.g. size and longevity) and their history of immigration and fate in community dynamics (regional occupancy and local abundance). We found plant taxon nativeness, which is positively related to time since immigration, to be a correlate of consumer richness, but only in the model for fungal richness and, interestingly, only nativeness on the scale of Europe, not Denmark. Thus, the results suggest that associated consumers effectively track their host plants on the regional scale, but not on continental or over-seas scales.

We found an expected effect of the capacity of plant taxa to form ectomycorrhiza (ECM) as a predictor for associated fungal richness (Hiiesalu et al. 2017, Awad et al. 2019). For arthropod richness, in contrast, to find that ECM capacity was a similarly strong predictor was highly unexpected. This surprising pattern was not simply due to the fact that almost all ECM host plants are trees, as plant size and growth form were also included as model predictors. Thus, within plant life-form groups, ECM plant taxa were on average hosts to a larger arthropod fauna than non-ECM taxa. For trees and shrubs, ECM-forming genera such as *Fagus*, *Quercus*, *Betula* and *Salix* hosted more arthropod species than did the non-ECM genera *Ulmus*, *Acer*, *Fraxinus* and *Crataegus*, and similarly the ECM dwarf-shrub *Salix repens* had a richer associated fauna than did non-ECM dwarf-shrubs. The mechanism behind this non-random co-occurrence escapes immediate explanation and calls for more detailed investigations (Koricheva et al. 2009).

When predicting observed species richness of arthropods and fungi in actual communities at 130 sites, models based on predicted link sum, i.e. based on simple plant attributes, performed almost as well as models based on observed link sum and even better for total arthropod richness. This result is encouraging for the use of plant community data to predict multi-taxon biodiversity, also outside a well-studied region as the one used here. Basic knowledge on fungus and arthropod faunas is far from complete in large parts of the world, in particular much less so than vascular floras (Mora et al. 2011, Hawksworth and Lücking 2017), and knowledge on host–parasite relations is even more incomplete. In contrast, simple plant traits, such as size and life form, are available for plant species globally, at least on a coarse scale. Thus, our finding is promising, and calls for further validation across biomes.

The predictive power of our modelled community-level host suitability (plant community link sum) on observed site consumer richness varied considerably across functional groups of fungi and arthropods (Fig. 2). The effect of including plant attributes was strongest on the richness of decomposer fungi, symbiotic fungi and internally feeding arthropods. To a large extent, the physical and chemical properties of host plants define the habitat of species in these groups, which

live in close intimacy with their host (Mazziotta et al. 2017). These intimate consumers cannot escape factors such as chemical plant defence, not even as after-life effects in dead wood and other plant litter (Purahong et al. 2018). The comparatively smaller predictive power for externally feeding arthropods was surprising at first glance, because a fraction of these herbivorous species are oligophagous or monophagous. On the other hand, a similarly large fraction of externally feeding phytophagous insects are associated with habitat type such as lake margins or heathlands, and use a variety of host plants within that habitat, e.g. taxa such as leaf beetles (*Chrysomelidae*) and plant bugs (*Miridae*). The richness of external feeders, thus, was largely predictable from general habitat conditions derived from plant community composition via bioindication (Fig. 3). For predatory arthropods, in contrast, there was a surprising effect of plant species richness. This relationship between the first and the third trophic levels could relate to the host specificity of insect parasitoids in particular, and to their use of plant species chemistry as cue to locate their herbivorous hosts (Godfray 1995).

There was an appreciable indirect effect of extrinsic habitat conditions – position in ecospace (Brunbjerg et al. 2017) – on the observed consumer richness (Fig. 3), yet we could clearly demonstrate an added effect of community link sum across all functional groups. This effect was particularly evident for fungi, both symbionts and decomposers. For fungi, it is noteworthy that a significant effect of plant richness per se was only apparent after taking ecospace position into account. This suggests the effect to be nested within habitat types, e.g. differing in relative magnitude from closed forest to open grasslands. For arthropods, the additive predictive power of link sum over simple plant richness was generally small. However, a strong effect of plant richness remained on top of environmental calibration and after including environmental co-variables, predicted link score turned out to be the most significant predictor.

A core component in the ecospace framework for understanding consumer biodiversity is the diversification of carbon pools. While there is no easy way to directly characterize and quantify different pools of dead organic matter in ecosystems, the use of plant traits and other attributes offers an opportunity for investigating the importance of carbon diversification for heterotrophic diversity on the parasitic–mutualistic–saprotrophic continuum (Pöhlme et al. 2018). However, important carbon pools such as dung, carcass and dead wood, which were not part of our assessment, deserve further investigations.

Prediction of multi-taxon consumer diversity from plant attributes may be applied in conservation science in order to improve planning and management decisions. This is particularly relevant in regions with limited knowledge of consumer biotas and their host relationships. Further, our results may be applied to novel ecosystems, e.g. in planning and management of urban greenspace to support a richer biodiversity of insects and fungi.

Our results strongly support the idea that site-level biodiversity is an emergent property of site conditions

(Brunbjerg et al. 2020), within the bounds of the regional species pool. This calls for reconsidering the widespread focus on biodiversity determining ecosystem function. Likewise, the results demonstrate that biodiversity begets biodiversity, as proposed by Whittaker (1975), with plant species richness in the role as a central bottom-up driver with strong effects across taxonomic groups and trophic levels.

Speculations

Few regions of the world are as well-studied in terms of interactions between plants and plant-associated fungi and arthropods as central and northern Europe, which is also the geographic scope of Ellenberg indicator values (EIVs). From that perspective, it may seem almost impossible to apply the predictive framework laid out here to most other regions. In most parts of the world, however, the flora is reasonably well known and simple attributes of plants species, such as body size and range size, are likewise. Thus, prediction of consumer richness from simple plant attributes is only rarely limited by data. Further, EIVs may easily be replaced by species scores from an ordination of vegetation plot data, as long as most important gradients in habitat conditions filtering plant species into communities are covered. We therefore call for validation of our findings in different biogeographic regions.

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Data availability statement

All data and code are openly accessible from the Dryad Digital repository: <<https://doi.org/10.5061/dryad.hx3ffbgg8>>. (Bruun et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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