A diversity of diversities: evaluating the relationships between below and aboveground biodiversity

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Abstract

Understanding the diversity and composition of ecological communities is a key component in predicting future biodiversity responses to environmental change and implications for ecosystem health. Linking across the domains of life and trophic levels is also essential for understanding whole-ecosystem dynamics but is often challenging to perform and limited in scope. In particular, it is unclear to what extent cross-domain correlations in biodiversity are determined by common abiotic drivers or species interactions. Here we analyse data from a unique biodiversity dataset gathered across a variety of oceanic temperate terrestrial habitats comprising 300 sites with co-located soil microbial, plant, bird and pollinator surveys along with climate and soil physicochemical information. Soil microbial groups are analysed using metabarcoding of the 16S, ITS and 18S DNA regions, allowing in depth characterisation of microbial community composition and diversity. Using Bayesian hierarchical regression models, we show that a positive correlation between plant diversity and soil bacterial and fungal diversity is actually driven by non-linear responses to changing soil pH, with the exception of AM fungi which show positive associations with plant diversity at low soil pH. However, positive associations between plant diversity and bird, and pollinator diversity persisted after accounting for changes in climate. The composition of soil bacteria, fungi, bees, butterflies and birds are all impacted by the plant community in conjunction with edaphic factors. The heterotrophic protistan community strongly tracks the bacterial community in both diversity and composition. The residual associations between taxa after accounting for environmental variation in a joint species distribution model revealed cross-domain correlations. Overall, our results comprehensively show the differential responses, linkages and divergences of cross-Kingdom diversity and composition in aboveground-belowground ecological communities to environmental and biotic properties.

The biodiversity of our planet is valuable in both its own right and in the provision of ecosystem resilience, functions and services (Guerra et al., 2021; IPBES, 2019). Biodiversity is under threat and monitoring change is of increasing importance. However, it is often difficult, especially for cryptic taxonomic groups and remote habitats. To address these difficulties many authors have attempted to evaluate whether certain taxa can act as indicators of other more difficult to survey taxa (e.g. Ceballos & Ehrlich, 2006; Landeiro et al., 2012; Prendergast et al., 1993; Prober et al., 2015; Wolters et al., 2006). It is theorised that diversity of certain groups can beget diversity; for example, a more diverse plant community can support a more diverse pollinator community through a proliferation of different ecological niches. The generation of biodiversity by biodiversity is somewhat supported by the presence of hotspots across the globe with consistently, geographically coincident high diversity across a multitude of taxonomic groups (Myers et al., 2000); although more detailed investigation indicates that there is limited congruence within taxonomic groups in species distributions (Ceballos & Ehrlich, 2006; Orme et al., 2005). There is still uncertainty over the strength of this diversity effect, as relationships between the diversity of different taxa aboveground have been shown to be variable and weak (Wolters et al., 2006). Results investigating the relationship between above- and belowground biodiversity have also been variable, with either positive or no correlations commonly observed between plant diversity and soil microbial diversity (e.g. Hiiesalu et al., 2014; Leff et al., 2018; Prober et al., 2015).

The relationships between the diversity of different taxonomic groups can vary by the delineation/definition of those groups, the underlying environmental conditions and the type of diversity considered. Certain taxonomic groups appear to show more positive relationships with plant diversity. For example, fungal diversity, particularly mycorrhizal diversity, is often found to be positively related to plant diversity (Hiiesalu et al., 2014; Milcu et al., 2013; Nguyen, Williams, et al., 2016; Peay et al., 2013; Ren et al., 2017; T. Yang et al., 2017). The type of plants that are considered in plant diversity can also be important, for example the number of flowering plant species and their abundance has been shown to influence bee and butterfly abundance and richness (Kearns & Oliveras, 2009; Potts et al., 2009). Some of the positive correlations that have been found between plant diversity and soil bacterial, fungal and protistan diversity are explained by shared response to

environmental variables. Soil pH and fertility have been found to drive a positive correlation between plant diversity and bacterial diversity in a variety of ecosystems (Goberna et al., 2016; Yashiro et al., 2018; Yuan et al., 2017).

While relationships between the biodiversity of different taxonomic groups may be variable, there have been many results demonstrating that the species composition of plant assemblages may be related to the composition of other taxonomic groups even when biodiversity, i.e. species richness and diversity, is not. Relationships between the composition of plants and the composition of soil bacteria, fungi and protist assemblages have been found in both experimental and observational studies (Barberán et al., 2015; Cline et al., 2017; Delgado-Baquerizo et al., 2018; Leff et al., 2018; Prober et al., 2015). These correlations in composition in observational results can persist even after controlling for environmental drivers such as climate or soil physicochemical properties (Delgado-Baquerizo et al., 2018; Prober et al., 2015). At larger scales, information on the heterogeneity of vegetation and landscape composition from satellite imagery has also been used to predict bird richness and composition (St-Louis et al., 2014), and to a lesser extent bee species (Hofmann et al., 2017).

Correlation between the biodiversity of different taxa could be due to the direct influence of one taxonomic group on another or down to shared response to environmental conditions. Taxonomic or environmental mechanisms may lead to similar associated patterns of biodiversity but have differing implications for land use management. Therefore, disentangling the relative influence of abiotic and biotic impacts upon biodiversity is key. There have been some experimental manipulations established to evaluate the impact of plant diversity upon ecosystem functioning, including changes in the biodiversity of the other groups. These have found positive relations between plant diversity and the diversity of some other organisms, particularly for aboveground herbivores and less so for soil microbial groups (Cline et al., 2017; Dassen et al., 2017; Lind et al., 2015; Weisser et al., 2017). However, by necessity these experiments are limited in scope, covering a limited set of environmental conditions and plant species combinations. The use of field-scale survey information to establish real-world correlations across taxa is essential if we are to cover a wide range of environmental and biotic conditions. Controlling for confounding variables

within statistical analysis can further help us consider what might be the direct impact of one taxonomic group upon another.

Here we present the results from a multi-trophic field survey across the entire range of terrestrial habitats in Wales, UK, where plant, bird, pollinator and soil microbial diversity were each measured at the same sites. Using an intensive biodiversity assessment spanning heterogeneous habitats at national scale enables synthesis of biodiversity data, unconstrained by major geographical or climate influences. Previous analysis of this dataset has found that plant, bird and butterfly species richness was positively associated with land use intensity and habitat heterogeneity (Alison et al., 2022; Maskell et al., 2019), while the soil microbial community was strongly driven by land use type and pH (George et al., 2019). In the present work we extend these analyses to consider the whole ecosystem, both above- and belowground and consider the roles of the plant community and abiotic environment in influencing both the diversity and composition of other taxonomic groups across diverse habitat types. Our objectives are i) to investigate if plant, bird, pollinator and soil microbial diversity are correlated with each other in a temperate ecosystem, not confounded by geographical variation, ii) to investigate if the composition of one taxonomic group is a reliable predictor of another, iii) to evaluate whether any correlations in diversity or composition are due to shared response to environmental drivers, and iv) to identify the presence of any co-occurrence relationships between specific taxa of different domains once shared response to environmental drivers is accounted for.

Methods

Field measurement programme

The data was collected as part of the Glastir Monitoring and Evaluation Programme (GMEP) field measurement program in Wales (Emmett et al., 2017; Wood et al., 2021). In total, 300 individual 1 km squares were randomly selected from within land classification strata in proportion to their extent in order to be representative of the range of habitat types across Wales or targeted to areas with high potential for agri-environment scheme uptake (Wood et al., 2021). Sampling occurred over a five month period across each of the summers of 2013 to 2016; each square was only surveyed once over the four years with different squares being surveyed each year. Every square was subjected to a habitat survey, bird

survey, two pollinator survey transects and multiple plant survey plots. For each square there were up to five 200 m^2 square plant survey plots that also had soil samples taken. Soil samples were analysed for a variety of soil physicochemical properties, including pH in 1:2.5 $CaCl_2$ suspension, total carbon, nitrogen and phosphorus, bulk density, water content, water repellency and electrical conductivity in 1:2.5 distilled water suspension. The data and full methods are available on the Environmental Information Data Centre (EIDC) (Robinson et al., 2019). Within the first two years of the survey soil samples were taken for microbial and eukaryotic community composition analysis from three of the 200 m^2 plots, randomly selected per each 1 km square.

The surveyors mapped the habitats of each square and assigned each plot to a habitat according to the UK Joint Nature Conservation Committee criteria (Jackson, 2000). The main habitats included in this study were different grassland habitats, with some woodland and heathland. The plot level measurements of microbial diversity were derived from 31% improved grassland; 23% neutral grassland; 12% acid grassland; 7% broadleaved woodland; 7% coniferous woodland; 7% bog; 4% arable; 3% dwarf shrub heath; 3% fen, marsh and swamp; and 2% bracken. Precipitation was the annual average rainfall and temperature was the annual average daily temperature for 1981-2010 calculated on a 1 km grid. All climate data came from the Met Office © Crown copyright 2019.

Biological data

Plant survey

Vegetation surveys were conducted for multiple plots per square, with the data being publicly available on the EIDC (Smart et al., 2020). Overall, there were ten types of sampling plots in total. Some plots were targeted to specific landscape features (e.g. hedges), meaning the total number and proportion of plot types varies across squares. For each plot, plant functional properties were created based on reference to literature values for growth form (e.g. forb and woody plant richness) and other indices such as Ellenberg values (Hill et al., 2004). The total number of vascular plant species recorded across the entire 1 km square was used as plant species richness for the square level analyses. Due to the differences in sampling effort across the squares, rarefaction curves were constructed to confirm that the

number of plant species found had reached saturation. Plant species that were important to the diet of lowland birds, butterfly larvae and nectar provision were identified and the species richness of those three groups calculated (Baude et al., 2016; Smart et al., 2000).

Bird and pollinator surveys

Birds were surveyed based on four morning visits to each square, equally spaced through mid-March to mid-July. Surveyors walked a route that passed within 50 m of all parts of each survey square, varying the start point for each survey in order to visit all parts of the square at least once before 08:00 h. The total number of bird species recorded across all visits per square was used to calculate total bird species richness. Pollinator surveys were split into two independent parts: two 1 km transect routes separated by at least 500 m and where possible 250 m from the edge of the 1 km square; and a 20 minute timed search in a 150 m^2 flower rich area within the 1 km square. The total number of butterfly species and bee groups recorded per square were used to calculate richness. Pollinator surveys were managed by Butterfly Conservation and bird surveys managed by the British Trust for Ornithology, and both datasets are publicly available on the EIDC (Botham et al., 2020; Siriwardena et al., 2020).

Soil microbial diversity and community composition

Soil samples for microbial biodiversity analyses were taken using a gouge auger at 5 points around the physicochemical soil core location down to 15 cm, and then bulking together the samples. DNA was extracted from the combined, homogenised samples using mechanical lysis following homogenisation in triplicate from 0.25 g of soil per sample. The 16S (V4), ITS1 and 18S regions of the rRNA marker gene were targeted for amplicon sequencing to analyse the bacterial, fungal and general eukaryotic diversity respectively. For a full description of the methods used see George et al. (2019). Sequences with associated sample metadata have been uploaded to The European Nucleotide Archive with the following primary accession codes: PRJEB27883 (16S), PRJEB28028 (ITS1) and PRJEB28067 (18S).

Amplicon Sequence Variants (ASVs) were identified from the Illumina output using the DADA2 algorithm in R (Callahan et al., 2016). First, Illumina adapters were trimmed from sequences using Cutadapt (Martin, 2011). Then, the DADA2 package was used to filter all 16S, 18S and ITS reads to be truncated after the first instance of a quality score of 2, to remove all Ns and to have no more than 2 errors. Based on the examination of the change in

quality scores with read length for a random subset of samples 16S reads were truncated to 200 bases, 18S reads truncated to 250 bases and ITS reads fewer than 100 bases in length removed. The DADA2 algorithm was then used to denoise and merge the paired reads at standard settings. Sequence tables were constructed from the resultant ASVs and chimeric sequences were removed using default settings. Taxonomy was assigned using the DECIPHER R package (Wright, 2016), with both 16S and 18S reads being matched to SILVA r138 (Glöckner et al., 2017) and ITS being matched to UNITE v2019 (Nilsson et al., 2019). Non-bacterial ASVs were removed from the 16S data, and non-fungal ASVs from the ITS data. All ASVs appearing in the negative controls were removed from the analysis. Fungal ASVs were matched to trophic mode at the genus level with FunGUILD (Nguyen, Song, et al., 2016).

Statistics

All statistical analyses were performed within R version 4.0.2 (R Core Team, 2020). To account for the differences in read depth between samples, rarefaction was used as it has been shown to preserve biological relationships (Weiss et al., 2017). The fungal data was rarefied to 10000 reads, bacteria to 20000 reads, and 18S eukaryotes to 20000 reads. Samples below this threshold were discarded, resulting in 437 fungal (ITS) measurements, 437 bacterial measurements and 438 eukaryote (18S) measurements. Eukaryote data was separated in to three sections based on higher order identification in the 18S dataset: Arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota), heterotrophic protists (Cercozoa, Ciliophora and Amoebozoa) and soil animals (kingdom Animalia). Biodiversity indices, i.e. richness, Shannon and Simpson diversity, were calculated after rarefaction, which was repeated 100 times and the rounded average result used in further analysis. For the analysis of community composition the rounded average of 20 rarefaction repeats was used.

The effect of pH upon the bacterial, fungal and heterotrophic protistan richness was modelled as a sigmoidal non-linear Bayesian model within the brms package in R (Bürkner, 2017). The square identity was included as a group-level effect on the intercept in order to account for the spatial element of the data. The impact of plant richness upon bacteria or fungi was modelled using three models: a no interaction model; a model that allowed the upper threshold of bacterial or fungi to vary with plant richness; or a model that allowed all

parameters other than the pH at maximum rate of increase to vary with plant richness. Heterotrophic protists were modelled using both a no interaction model and allowing an interaction between bacterial and plant richness. The effect of plant richness, precipitation and elevation on butterfly richness, bee richness and bird richness were modelled as a multivariate Bayesian regression model with a negative binomial response. Biological recording region (vice county) and year were used as group-level effects to account for the spatial and temporal nature of the data. Plant species richness always had precipitation and elevation as the sole fixed effect predictors. Models were compared using leave-one-out cross-validation (Vehtari et al., 2017).

Composition of the different biological communities was compared using ecological distance matrices. Distance calculation was performed using the vegan package (Oksanen et al., 2020). Binary Jaccard distance was used for plant, bird and butterfly species composition and Bray-Curtis distance used for bee and hoverfly groups due to their lower richness. All soil microbial groups were compared based upon Bray-Curtis distance. Distance matrices were compared directly using Procrustes analysis. To unpick the relative contribution of shared environmental drivers, interaction with the plant community and spatial autocorrelation that could be driving changes in the communities the variance was partitioned using the varpart function within the vegan package. The response variables were the NMDS scores of each group based on Jaccard distance for aboveground groups and Bray-Curtis distance for belowground groups and the predictors were climate (represented by temperature and precipitation), spatial distance (represented by principal coordinates of neighbour matrices), plant community composition (represented by NMDS scores in 4 dimensions). For the plot level data only the first four dimensions of a PCA upon soil physicochemical properties (pH, carbon, nitrogen, total phosphorus, bulk density, electrical conductivity, water content, water repellency) were used.

Joint species distribution models were used to identify the presence of any co-occurrence relationships between specific taxa of different domains once shared response to environmental drivers and spatial autocorrelation was accounted for. Joint species distribution models were fitted using the sjSDM package in R (Pichler & Hartig, 2021). Only common taxa were included within the analysis to reduce the number of false positive associations (Weiss et al., 2016), which we identified as being present in 25% of sites for

bacteria, heterotrophic protists, fungi and soil animals and 10% for plants, birds and pollinators. Both models had the spatial relationships between sites included as spatial eigenvectors, all taxa converted to presence/absence and fit with a binomial model with probit link, responses to environmental and spatial components modelled as linear, and lambda set to 0.01 for all model components. Within the plot-level model (i.e. including microbial groups and plant measurements from individual plots) the environmental predictors were soil pH, organic matter, carbon, nitrogen, available phosphorus (Olsen-P), conductivity, water repellency, moisture content and bulk density. Within the aboveground model (i.e. including plants at the square level, birds and pollinating insects) the environmental predictors were average annual precipitation (1981-2010) and daily temperature (1981-2010). The resulting model fit objects had the residual association between each species pair extracted and converted into a network. The resulting network was analysed for the presence of clusters using the spinglass algorithm to take account of both the positive and negative links in the igraph package (Csardi & Nepusz, 2006; Traag & Bruggeman, 2009). The resulting clusters were laid out without their interlinks using the Fruchterman-Reingold layout algorithm based on positive links only for graphical simplicity, then the layout used to graph the networks with all edges included.

Results

Alpha diversity

We found that bacterial, fungal, heterotrophic protistan, bird, bee and butterfly richness positively correlated with plant diversity. Within the soil groups, AM fungi showed the strongest correlation with plants, with bacteria, general fungi and heterotrophic protists all having lower correlations, and no correlation with animal richness (Table 1, upper triangle). The soil groups were all positively correlated with each other, however animal richness was only weakly associated with the other groups. Soil microbial richness was more strongly positively correlated to the richness of forb plant species as opposed to overall plant richness. Microbial richness was also negatively correlated to woody plant richness, particularly in AM fungi ($\rho = -0.65$) and heterotrophic protists ($\rho = -0.51$).

Table 1: The correlations between the different microbial groups and the plant community, the upper triangle shows the Spearman rank correlation coefficient for alpha diversity (richness) and the lower triangle shows the Procrustes correlation coefficient for beta diversity (Bray-Curtis distance).

Plant	0.22	0.21	0.19	-0.02	0.4	0.81
0.54	**Fungi**	0.51	0.78	0.2	0.53	0.42
0.5	0.71	**Bacteria**	0.56	0.07	0.32	0.39
0.56	0.72	0.78	**Heterotroph**	0.13	0.54	0.45
0.41	0.45	0.5	0.52	**Animals**	-0.05	-0.16
0.43	0.54	0.52	0.58	0.35	**AM Fungi**	0.57
0.55	0.47	0.46	0.51	0.32	0.4	**Forbs**

Plant diversity in the 1 km squares positively correlated most strongly with bird species richness ($\rho = 0.50$), followed by butterfly species richness ($\rho = 0.43$), then bee group and hoverfly group ($\rho \sim 0.35$) richness. Limiting the plant community to those species known to be important to the different animal groups through food provision resulted in an increase in correlation coefficients of 0.08 for birds but not for the other groups. The different pollinator groups were positively associated with each other, with butterflies and bees associated more strongly with each other than hoverflies with the other two groups ($\rho = 0.56$ compared to ρ 0.42-0.44). Bird species richness was positively correlated with butterfly and bee richness ($\rho \sim 0.5$). Average soil microbial diversity per 1 km square was also positively correlated with bird, butterfly and hoverfly richness, with correlations ranging from ~0.35 to ~0.55.

The impact of plant richness upon bacterial and fungal richness was negligible once the non-linear change in soil pH was accounted for (Figure 1). The inclusion of plant richness as well as pH to predict bacterial richness resulted in a slight improvement in predictive performance but the standard errors of the improvement were of the same magnitude as the difference (elpd difference: 1.9 ± 1.5). This was also the case for overall fungal diversity (elpd difference: 2.6 ± 1.6) but not for AM fungi which showed a persistent relationship with plant richness even after accounting for soil pH (elpd difference: 38.1 ± 11.5). Bacterial richness appear to increase with increasing plant richness, while fungal (ITS) richness showed the opposite trend, and AM fungal richness increased with increasing plant richness at pH below 5 only. Using forb richness instead of overall plant richness resulted in equivalent model predictive performance. Heterotrophic protistan richness showed no

evidence of a response to plant richness, although it did show a linear response to bacterial richness that gave equivalent predictive performance to the sigmoidal trend with soil pH (Figure 2a). Unlike all the other soil groups animal richness showed a linear decrease with increasing soil pH, and evidence of a positive interaction with soil carbon content (Figure 2b).

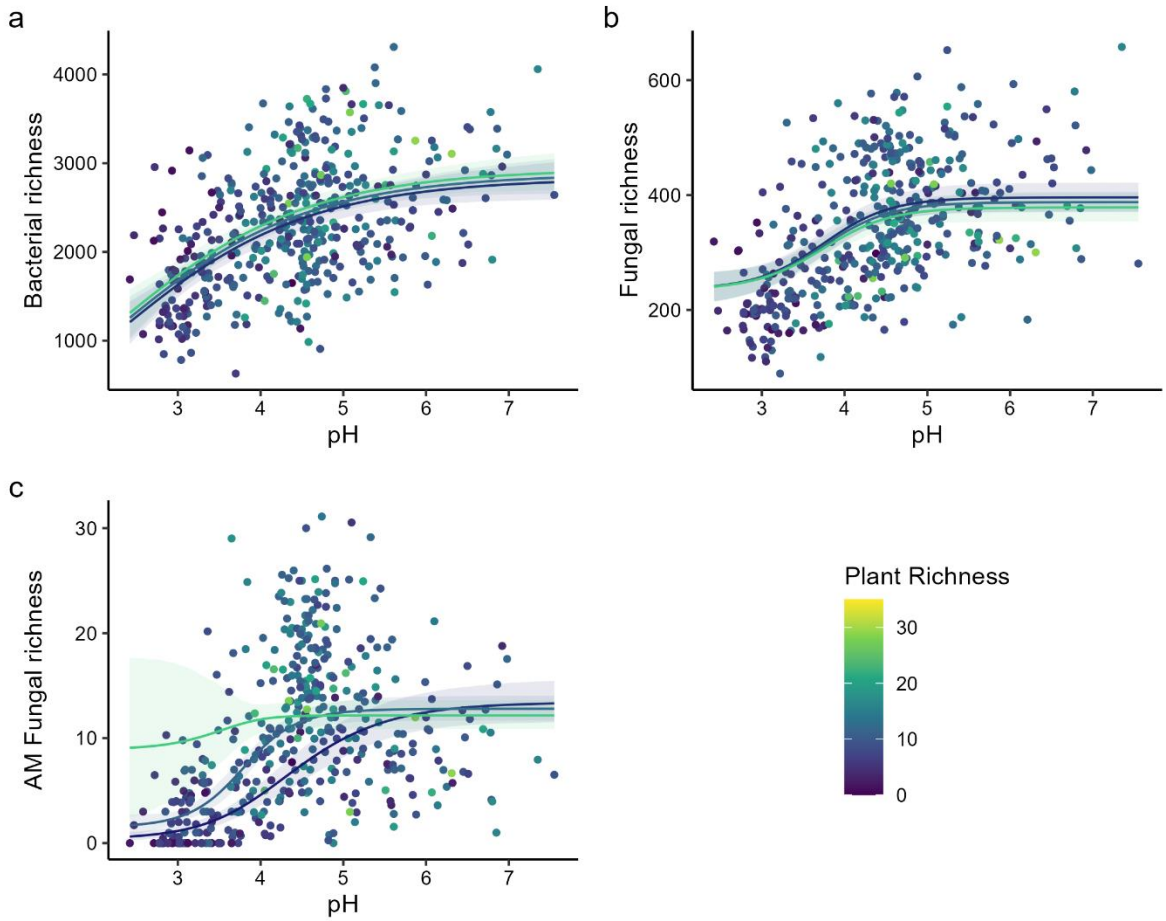

Figure 1: The impact of plant diversity upon bacterial (a), fungal (b) and AM fungal (c) richness once the gradient in pH is accounted for. Points are coloured by the plant richness and fit lines predicted microbial richness for 1 plant species (purple), 10 plant species (blue) and 20 plant species (green) are included. Note that only the AM model showed substantial improvement in predictive performance compared to pH only.

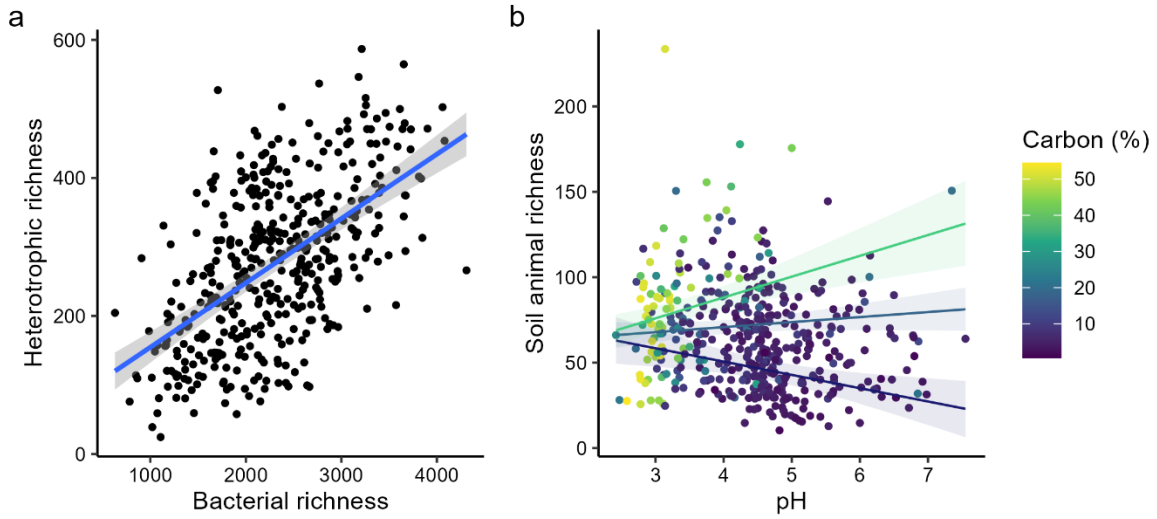

Figure 2: The impact of bacterial richness upon heterotrophic richness (a) and the impact of pH and carbon upon animal richness (b).

Plant diversity positively impacted the diversity of birds, bees and butterflies even after accounting for changes in precipitation and temperature (Figure 3, Supplementary Figure 1). The best model by leave-one-out cross validation had temperature and precipitation as predictors of plant, butterfly, bee and bird diversity and plant diversity as a predictor of butterfly, bee and bird diversity. Removing plant diversity reduced the predictive capability of the model (elpd difference = 19.2±6.7), but not as much as removing precipitation and elevation (elpd difference = 100.5±14.3). The predicted impact of going from the 53 to 132 plant species (the 10th to 90th quantile) if precipitation and temperature were kept constant (at 1500 mm and 9°C respectively) would be to increase butterfly richness by 1.2 species, bee richness by 0.5 groups and bird diversity by 13.2 species. This is in contrast to an expected increase in butterfly richness by 4 species, bee richness by 1 group and bird diversity by 25.8 species with the same increase in plant richness from the model without keeping constant temperature and precipitation.

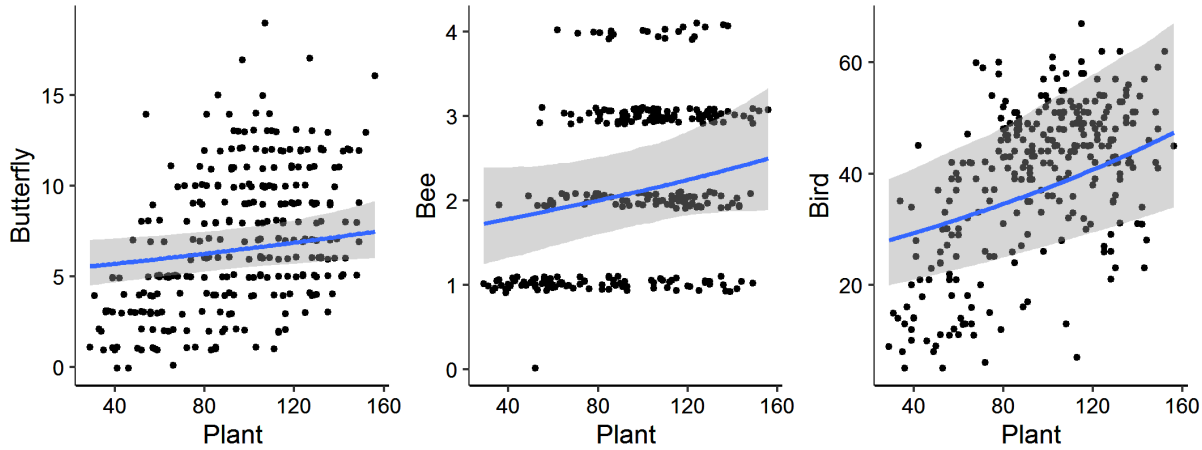

Figure 3: The predicted impact of plant diversity on butterfly, bee and bird richness once changes in precipitation and elevation were included in the model. The points are randomly jittered on the vertical axis by 0.1 to reduce data overlap.

The positive influence of plant species richness upon bee and butterfly richness may be driven by the increased variety of food sources when more plants are present. The diversity of nectar producing plants and plants identified as important in the diets of lowland birds were highly positively correlated with overall plant species richness (ρ of 0.96 and 0.87 respectively). Using the species richness of nectar producing plants resulted in marginally better predictive performance for bees and butterflies but improvement was close to the margin of error (elpd difference for butterflies: 1.6 ± 1.5; bees: 0.5 ± 0.3). The richness of nectar producing plants was more closely related to butterfly richness than was the richness of plants important to butterfly larvae, but both performed in a similar way (elpd difference: 1.0 ± 1.5). The species richness of plants identified to be important in the diet of lowland birds did no better than overall plant richness at predicting bird richness (elpd difference: -0.3 ± 3.5).

Composition

Plant community dissimilarities were positively associated with fungal, bacterial, heterotrophic protistan, bird and butterfly community dissimilarities. Bacteria, heterotrophic protists and all fungi showed a slightly stronger correlation with plant composition than AM fungi did (Table 1, lower triangle). All were significant at p = 0.001. Differences in heterotrophic protistan composition strongly tracked changes in bacterial composition, with a Procrustes correlation statistic of 0.78. Fungal composition also correlated with bacterial composition, with a Procrustes correlation statistic of 0.71. Bird

and butterfly community dissimilarity were more strongly related to plant community dissimilarity than the link between bee, hoverfly and plant dissimilarity. This was reflected by both the spearman rank correlations and the Procrustes correlation statistic (0.73, 0.59, 0.23 and 0.32 for bird, butterflies, bees and hoverflies respectively). However, all the Procrustes analyses were found to be significant at p = 0.001.

Partitioning the variance described by the spatial, soil and plant community reveals that the plant community explains unique variance in the bacterial, fungal and heterotrophic protist communities (Figure 4a). The plant community at the plot scale was partially explained by soil, climate and spatial factors but had considerable unexplained variance. Climate was initially included but did not explain any unique variance in the soil microbial communities and so was omitted from this analysis. The pattern of variance explained was similar for bacteria and fungi, with the soil physicochemical properties and plant community explaining more variation than the distance between samples. However, there was a large proportion of variation in fungi, bacteria and animals that was explained by soil, plant and spatial factors together. The heterotrophic protist community had a large proportion of their variance explained by variation in the bacterial community. Soil properties, spatial factors and the plant community explained limited variation in the heterotrophic protist community once changes in the bacterial community were accounted for but did explain joint variation with the bacterial community.

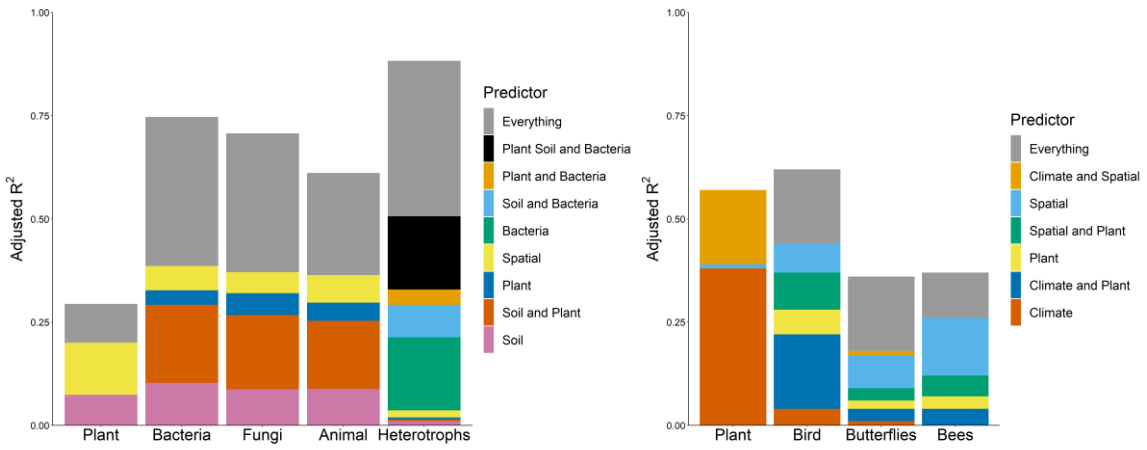

Figure 4: The properties that explain the variation in community composition at the plot level (a) and the square level (b).

The plant community explained some of the variance in bird, butterfly and bee and hoverfly community composition (Figure 4b). The plant community at the 1 km square level was largely explained by variation in precipitation and temperature, with some effect of the distance between squares interacting with climate. The bird community was explained fairly well by the plant community and the climate, whilst also incorporating a spatial interaction between the two. The pollinator communities were explained relatively poorly, the plant community, climate and spatial factors do appear to be important together but overall there is little variation explained. Precipitation and temperature are less important to bees and hoverflies than they are to the other groups, with precipitation and temperature in general being the least important factor for the animal groups but much more important for plants. Spatial factors appear to be relatively more important for the animal groups than they are for the plants.

Co-occurrence relationships

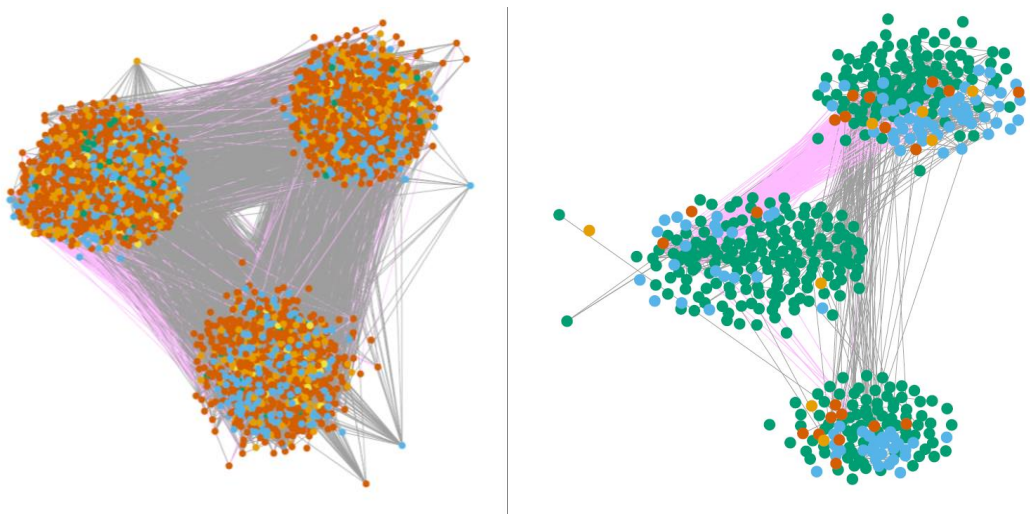

Figure 5: The co-occurrence network for the belowground community (a) and the aboveground community (b). The belowground community includes bacteria (red), fungi (blue), heterotrophic protists (orange) and plants (green). The aboveground community includes plants (green), birds (blue), butterflies (red) and bee and hoverflies (yellow). Clusters identified by the spinglass algorithm are manually separated from each other. Negative links are shown in violet (dark violet if less than -0.1), and positive links are shown in grey (medium dark grey if greater than 0.1, and dark grey if greater than 0.2). Links with absolute value less than 0.05 are not shown for graphical simplicity but are included in all calculations.

Residual co-occurrence relationships between below- and aboveground taxa were identified after joint species distribution modelling accounted for shared responses to environmental

variables. Cluster analysis of the residual microbial and plant co-occurrence network revealed the presence of three main clusters of taxa (Figure 5a), which was also the case within the aboveground model (Figure 5b). In total there were 2309 bacterial taxa, 236 heterotrophic protists, 190 fungal taxa, 22 animals and 28 plant taxa included in the belowground analysis. All taxa showed much stronger determination by soil variables than by species covariance (Supplementary Figure 2). The residual associations between taxa could be split into three clusters, including a high fertility cluster typical of semi-improved grasslands with a higher proportion of microbial pathogens, a mixed assemblage indicative of damp, somewhat semi-improved yet acidic grassland and an infertile acidic grassland cluster (Supplementary Figure 3). The aboveground taxa included 348 plant species, 101 bird species, 22 butterfly species, 4 bee groups and 4 hoverfly groups. The aboveground communities showed more variance being explained by species covariance than was the case within the belowground communities (Supplementary Figure 4). The residual associations between species could be split into three clusters (Figure 5b, Supplementary Figure 5), including a species cluster associated with infertile areas, a cluster associated with wooded landscapes, and a cluster associated with coastal areas and wetlands.

Discussion

While we found that the diversities of above- and belowground taxonomic groups positively correlated with plant diversity, the direct effect of plants was much higher aboveground than belowground. Our results indicate that the positive correlation of plant and soil microbial diversity is driven by changes in the soil environment are in agreement with previous work showing the importance of soil pH and fertility in jointly influencing plant and microbial diversity (Goberna et al., 2016; Tedersoo et al., 2016; Yashiro et al., 2018; Yuan et al., 2017). Mycorrhizal fungi have been found to be positively related to plant diversity (Milcu et al., 2013; Nguyen, Williams, et al., 2016), and we found a relationship between mycorrhizal fungal diversity and plant diversity at low pH values. We found some indication that the correlation between plant and soil microbial diversity was due to a correlation between forb diversity and soil microbial diversity. Herbs have been found to be more strongly related to prokaryotic diversity than tree diversity in forest ecosystems (J.-T. Wang et al., 2016), however, in our results it appears that the association is due to shared responses to environmental drivers rather than direct diversity relationships.

Increasing bird and pollinator diversity in conjunction with plant diversity was only partially confounded by the climate gradient, indicating that plant diversity has a direct impact upon bird and pollinator groups. This could be due to the provision of a greater variety of food sources, through increased landscape heterogeneity or potentially through the influence of an unidentified confounding variable such as anthropogenic activity (Le Provost et al., 2021; Potts et al., 2009; Stein & Kreft, 2014). Previous work upon this dataset has found that higher land-use intensity, habitat heterogeneity and the presence of wooded habitats were positively associated with the species richness of plants, birds and butterflies (Alison et al., 2022; Maskell et al., 2019). The heterogeneity of the landscape, particularly the heterogeneity of the topography, land cover and vegetation, has previously been found in many areas to be positively associated with the diversity of plants, birds and pollinators (Hofer et al., 2011; Hofmann et al., 2017; St-Louis et al., 2014). Land-use intensity can positively influence the diversity of certain animals when land-use intensity shifts from low to medium. Our data contained few high-intensity farmland sites which we would expect to have lower biodiversity due to the unimodal relationship between land use intensity and biodiversity (Maskell et al., 2013, 2019).

The very strong relationships between heterotrophic protistan diversity and composition and that of bacteria within our analysis most likely reflect the importance of the bacterial food source to heterotrophic protists. Bacteria and bacterivorous protists have been found to show similar seasonal patterns in grassland habitats, with the implication that they may be following a predator-prey cycle, but the major properties structuring heterotrophic protist communities in that grassland were spatial and soil edaphic properties (Fiore-Donno et al., 2019). The properties that influence protistan community structure do appear to be different across different ecosystems (Tedersoo et al., 2016). The lack of influence of plant species richness upon heterotrophic diversity was in agreement with previous results on experimental manipulations of plant diversity (Dassen et al., 2017). Functional changes in plant communities have been linked to changes in heterotrophic protists (Dassen et al., 2017) but in at least some cases these appear to be mediated by changes in the bacterial community (Valencia et al., 2018). Our results clearly indicate a strong linkage between bacterial and heterotrophic protistan communities that could represent the dominant role

of trophic dynamics over edaphic properties and plant inputs in structuring those communities.

We found that accounting for the influence of soil pH upon microbial diversity in a non-linear way led to the loss of a plant ~ microbe diversity relationship, with the exception of AM fungi. AM fungi are more dependent upon plant inputs and are capable of growing through large volumes of soil, meaning that they would be expected to show stronger relations with the plant community (Hiiesalu et al., 2014; Nguyen, Williams, et al., 2016). However, unexpectedly this relationship was only apparent at low pH, especially as the majority of the plants in our higher pH sites are herbs and grasses which more commonly form arbuscular mycorrhizal associations than other types of mycorrhizal associations (B. Wang & Qiu, 2006). The importance of the soil and climatic environment in influencing the links between plant and soil microbial diversity and composition have been found previously in a variety of ecosystems (Delgado-Baquerizo et al., 2018; Gao et al., 2017; Waldrop et al., 2017). This suggests that plant diversity impacts soils in different ways depending upon the soil environment and particularly that conclusions regarding the impact of plant diversity within more commonly studied neutral soils cannot be extrapolated to other environments. This offers a cautionary note to taking the results of plant biodiversity experiments conducted on neutral grassland soils, e.g. the Jena experiment pH 7.1-8.4 (Weisser et al., 2017), and applying them outside that context.

We found that the composition of above- and belowground communities was influenced by plant community composition. The proportion of variance explained by plants was much higher in the bacterial, fungal and heterotrophic protist communities than in the bird, butterfly, bee and hoverfly communities. The finding that plant community composition explains bacterial, fungal and heterotrophic protistan composition is consistent with previous findings at the field (Leff et al., 2018), regional (Barberán et al., 2015; Chen et al., 2017; T. Yang et al., 2017), and global scales (Delgado-Baquerizo et al., 2018; Prober et al., 2015). The higher proportion of explained variance in bird composition compared to butterfly, bee and hoverfly composition was unexpected as pollinators have in general been found to be closely related to plant composition (Hofmann et al., 2017; Kearns & Oliveras, 2009; Weisser et al., 2017). Overall, very little of the variation in butterfly, bee and hoverfly composition was explained by climate, plant communities or spatial factors. This may be

due to the description of the plant community through NMDS scores may not have been in sufficient detail to capture the plant-pollinator interactions. However, within the co-occurrence analysis there were several pollinator species and groups that did not show particularly strong relationships to any other taxa, potentially due to the resolution of our data. Alternatively, anthropogenic influences or other factors not incorporated into our model may be highly important in driving pollinator community assembly.

The identification of clusters of co-occurring species within the microbial and the aboveground systems that correspond to particular habitat preferences indicate the importance of cross-domain interactions in structuring ecological communities. The identified clusters largely comprised of a mix of different domains and groups. Such diversity identified within clusters raises into question the concept of a “bacterial response” versus a “fungal response” to environmental stressors, when we can show that certain taxa within a domain are more related to taxa in another domain than they are to the rest of their domain. Some of the identified linkages may represent shared response to environmental drivers while some may be true mutualistic interactions across domains (Carr et al., 2019). We attempted to control for shared response to environmental conditions within the co-occurrence analysis by modelling the response to environmental variables and examining residual species correlations. The greater influence of biotic relationships in the aboveground communities compared to belowground may be related to the lower number of environmental variables included in the model, and inclusion of information on fertility may have removed some of these relationships. As such, the presence of any correlation link still must not be taken as the presence of a true mutualistic interaction without independent verification (Blanchet et al., 2020).

Both the different taxonomic groups and the ecosystem properties and functions that occur across the landscape are relevant to different spatial and temporal scales. Previous work has shown that the scale at which biodiversity is measured, impacts the strength of the correlation found, with 10 km^2 areas showing the strongest relationship for aboveground diversity (Wolters et al., 2006). The life history traits of the community measure should be expected to impact the scale of interest, and within our dataset we have organisms that are largely limited to very short distances such as soil bacteria (P. Yang & van Elsas, 2018) ranging up to bird species that can travel vast distances. These differing communities are

both intrinsically valuable and underpin different ecosystem services that operate at different scales, ranging from nitrogen mineralisation in a grain of soil through to provision of recreational activities across the landscape. Our results indicate that the different taxonomic groups, and therefore their impact, have limited areas in which they coincide. The decoupling of aboveground and belowground diversity that we have found indicates that interventions targeted to the plant community will have predictable impact upon the bird and pollinator diversity but shift belowground composition rather than diversity. Soil microbial composition is more responsive to aboveground properties and has been found in some cases to be more relevant to soil functions (Delgado-Baquerizo et al., 2017; Zheng et al., 2019). However, it is possible that changes in land use intensity or other factors could change the very nature of the relationships between the diversity and composition of differing components of the ecosystem (Felipe-Lucia et al., 2020; Le Provost et al., 2021). Our results provide insight into the ecological communities across a wide variety of habitats and environmental conditions, and provide potential future avenues of research in evaluating whole-ecosystem state and change.

Availability of data

The data that support the findings of this study are openly available, with the soil physicochemical data at DOI: 10.5285/0fa51dc6-1537-4ad6-9d06-e476c137ed09, the vegetation data at DOI: 10.5285/71d3619c-4439-4c9e-84dc-3ca873d7f5cc, the pollinator data at DOI: 10.5285/3c8f4e46-bf6c-4ea1-9340-571fede26ee8, the bird data at DOI: 10.5285/31da0a94-62be-47b3-b76e-4bdef3037360 and the soil microbial sequences data in the European Nucleotide Archive with primary accession codes: PRJEB27883 (16S), PRJEB28028 (ITS1) and PRJEB28067 (18S).

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Author contributions

Seaton, George, Creer, Jones, and Robinson conceived the ideas and Seaton designed the methodology with input from Alison, George and Smart; Seaton analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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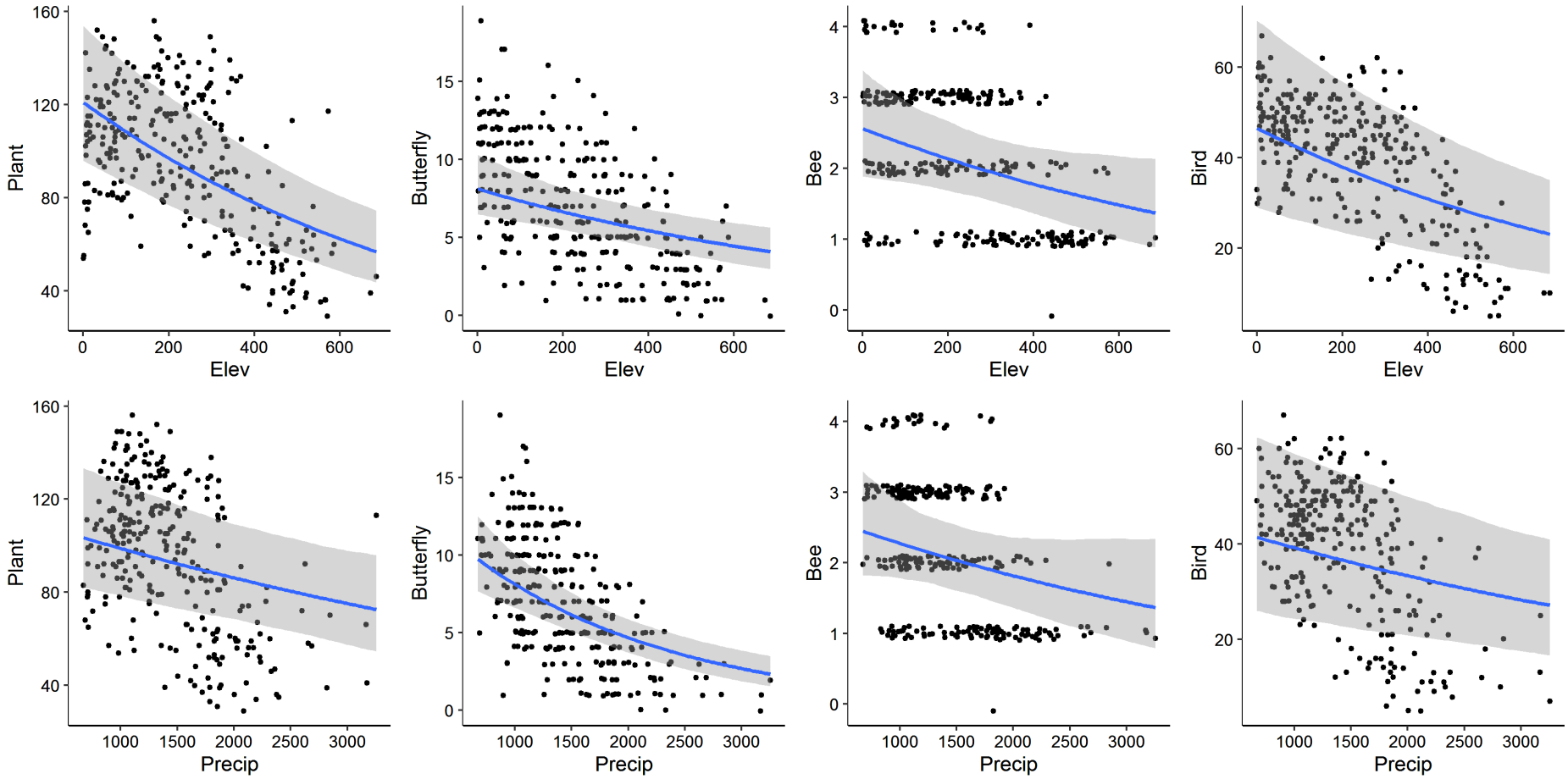
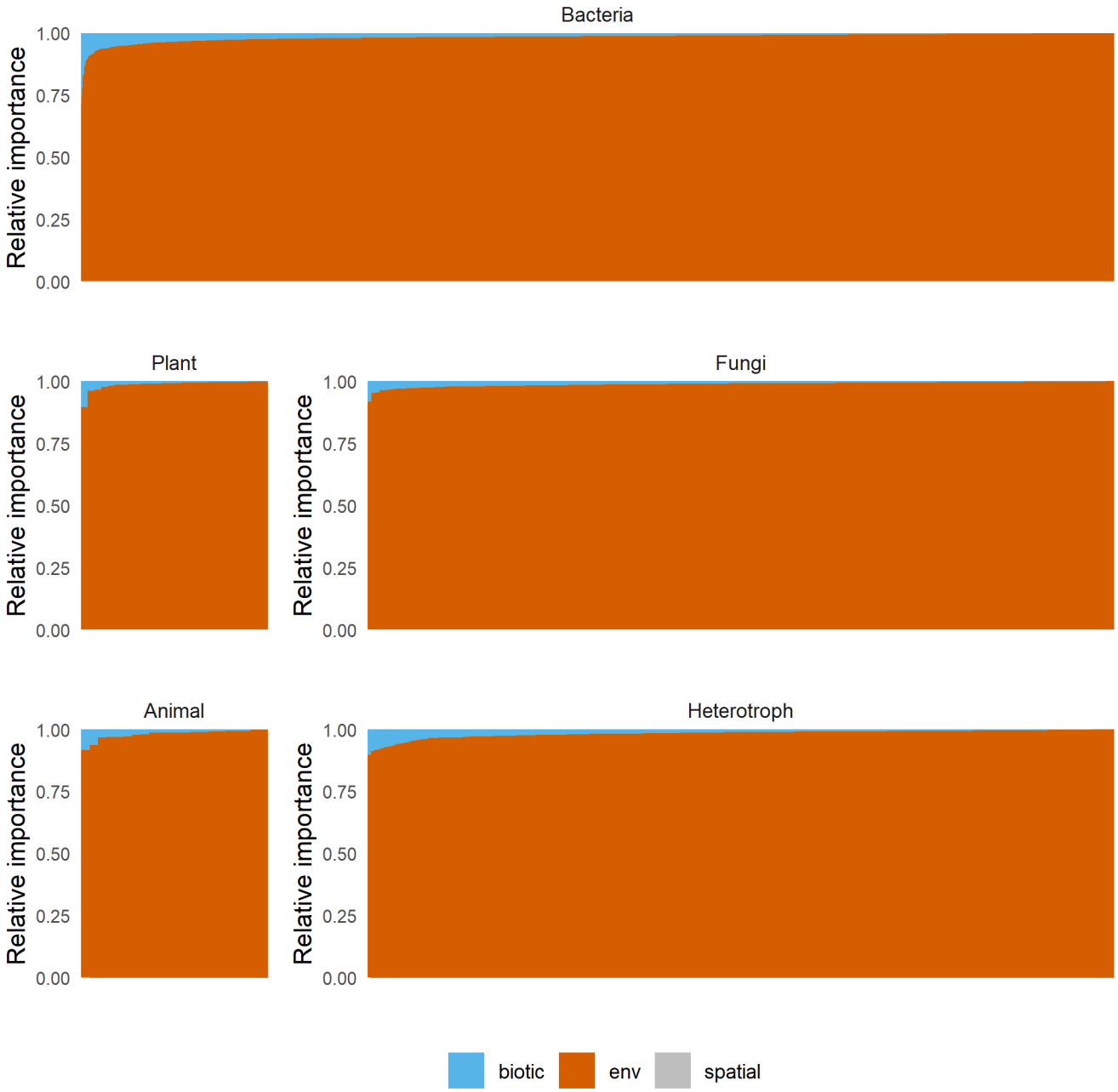
Supplementary figure 1



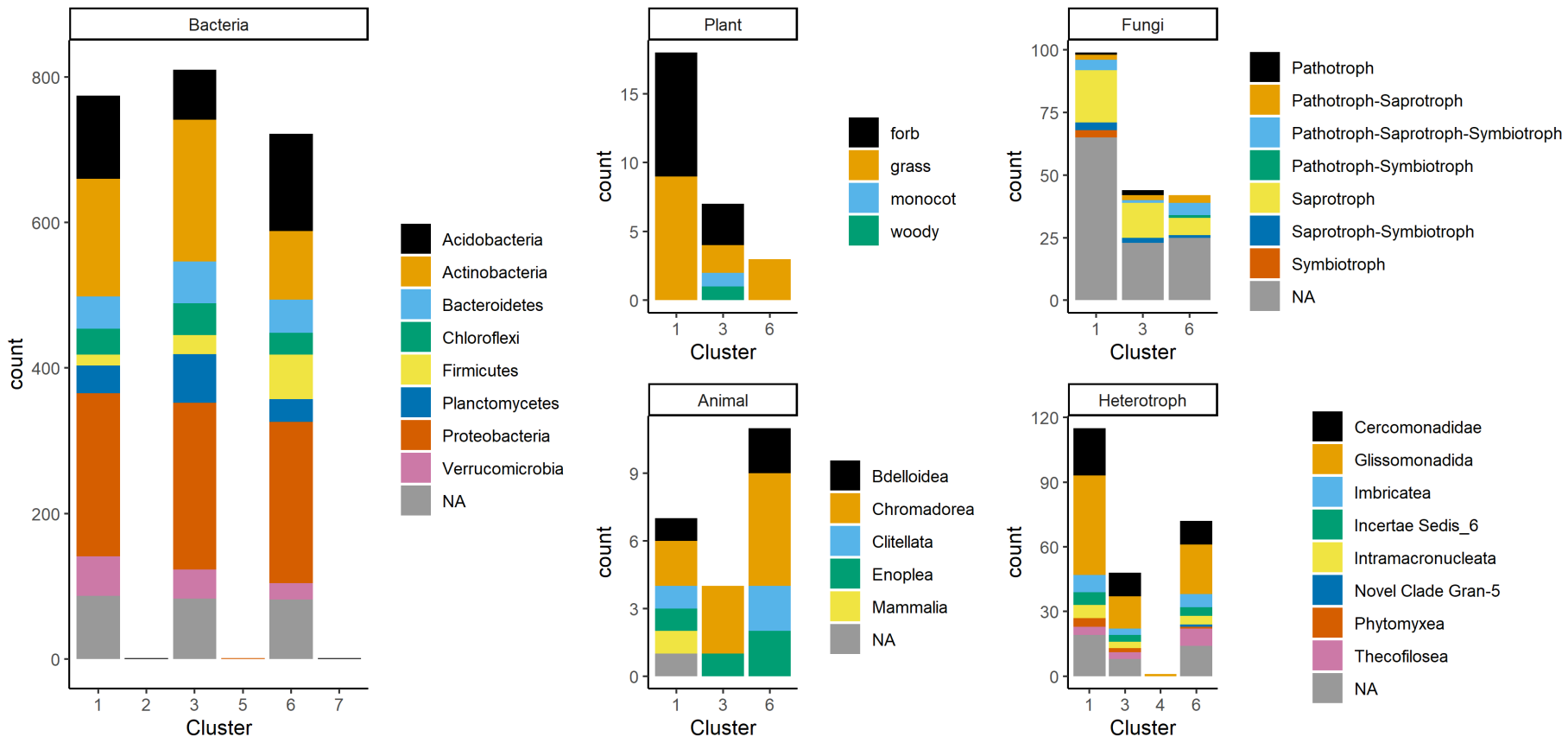
Predicted impacts of elevation (m a.s.l) and precipitation (mm y^{-1}) on aboveground diversity in model with elevation, precipitation and plant diversity as predictors and year and vice county as group-level effects. A vice-county is a geographical division of the British Isles used for the purposes of biological recording and other scientific data-gathering.

Supplementary figure 2



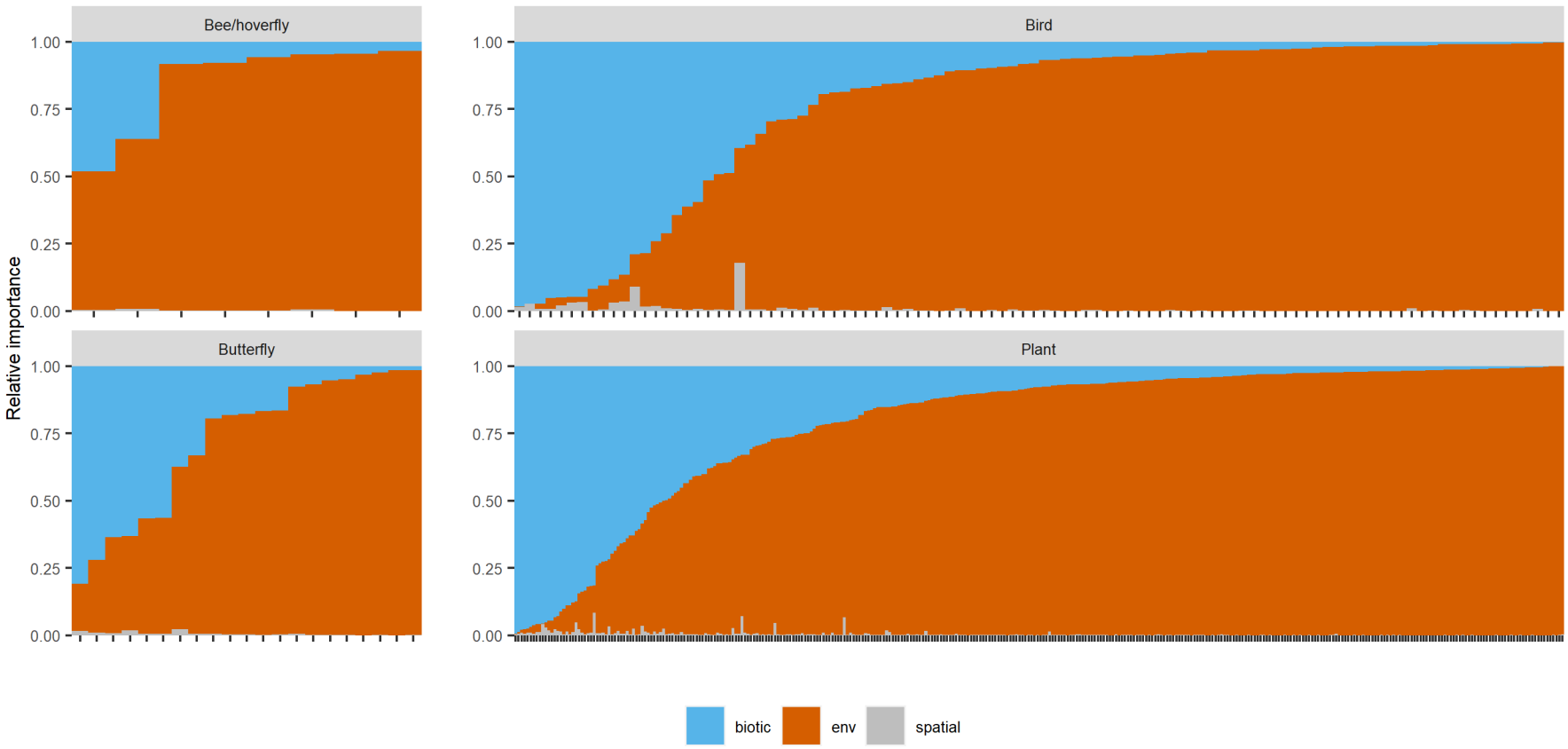
The variance partitioning for every bacterial, fungal, animal, heterotrophic protist and plant taxa. Proportion of variance explained by biotic interactions is shown in blue, proportion of variance explained by soil variables (carbon, nitrogen, pH, conductivity, organic matter, water repellency, Olsen-P phosphorus, water content, bulk density) is shown in orange and proportion of variance explained by spatial variation is shown in grey.

Supplementary figure 3



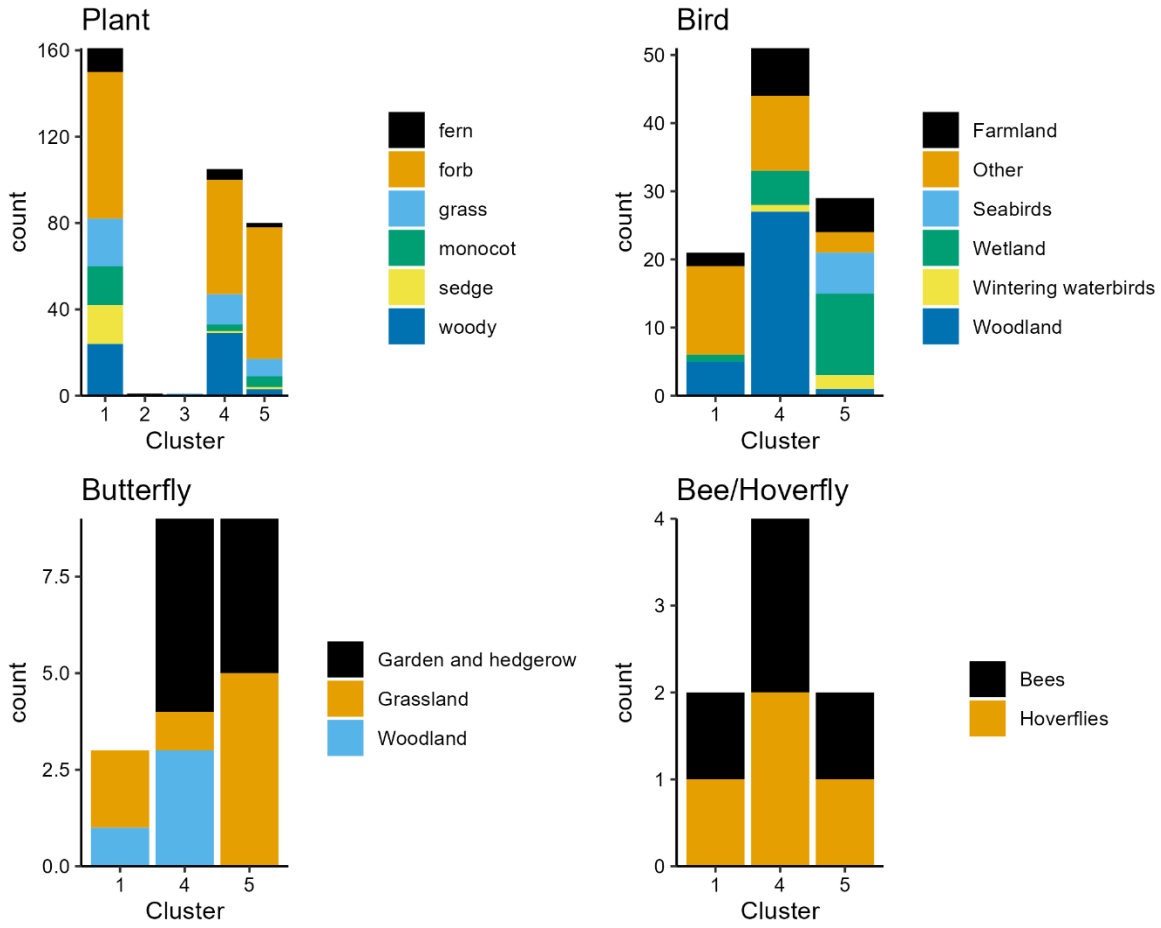
The breakdown of the network cluster membership by phylum for bacteria, by growth form for plants, by trophic mode by fungi, and by group for animals and heterotrophs.

Supplementary figure 4



The variance partitioning for every bee/hoverfly, bird, butterfly and plant species split by cluster. Proportion of variance explained by biotic interactions is shown in blue, proportion of variance explained by rainfall and temperature is shown in orange and proportion of variance explained by spatial variation is shown in grey.

Supplementary figure 5



The breakdown of the network cluster membership by growth form for plants (a), preferred habitat for birds (b) and butterflies (c), and bee/hoverfly identity (d).