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LETTER

Mapping the imprint of biotic interactions on β-diversity

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Abstract

Investigating how trophic interactions influence the β-diversity of meta-communities is of paramount importance to understanding the processes shaping biodiversity distribution. Here, we apply a statistical method for inferring the strength of spatial dependencies between pairs of species groups. Using simulated community data generated from a multi-trophic model, we showed that this method can approximate biotic interactions in multi-trophic communities based on β-diversity patterns across groups. When applied to soil multi-trophic communities along an elevational gradient in the French Alps, we found that fungi make a major contribution to the structuring of β-diversity across trophic groups. We also demonstrated that there were strong spatial dependencies between groups known to interact specifically (e.g. plant-symbiotic fungi, bacteria-nematodes) and that the influence of environment was less important than previously reported in the literature. Our method paves the way for a better understanding and mapping of multi-trophic communities through space and time.

Keywords

β-diversity, graphical lasso, graphical model, interaction network, meta-communities, partial correlation networks.

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INTRODUCTION

Understanding the processes that determine the spatial structure of biodiversity is one of the overarching goals of ecology (Ricklefs 1987). In particular, the study of β-diversity, the change in species identities (or species groups) across sampled locations, sheds light on different ecological, evolutionary and biogeographic processes (e.g. Graham & Fine 2008; Anderson *et al*. 2011). For a given regional species pool, the processes responsible for β-diversity are usually assumed to be environmental filtering, dispersal limitations and biotic interactions (HilleRisLambers *et al*. 2012; Meynard *et al*. 2013).

Previous studies have sought to analyse β-diversity by teasing apart the effects of environmental filtering from biotic interactions along environmental gradients on a single group of species (e.g. Peay *et al*. 2016 for fungi; reviewed in Hanson *et al*. 2012 for bacteria; Mazel *et al*. 2017 for mammals; Chalmandrier *et al*. 2015 for plants). However, biotic interactions *across* groups are also expected to drive the structure and distribution of biodiversity. For example, plant-pollinator, trophic (e.g. prey–predator or plant-decomposers) and host-symbiont (including pathogens, mutualistic and commensal organisms) interactions strongly impact diversity distribution and ecosystem functioning (Brose & Hillebrand 2016). These interactions among groups of species, although not necessarily species-specific (Walker *et al*. 2011; Peay *et al*. 2015), harbour some degree of specificity due to trait constraints and shared habitat preferences (e.g. Allesina *et al*. 2008; Gonzalez-Varo & Traveset 2016). This spatial interdependence among groups implies that the β-diversity of a single group is likely to be contingent to that of the other groups. Hence, studying how the β-diversity of multiple groups covaries along environmental gradients should help better understand their spatial distribution and uncover their interactions. In particular, soil systems provide several examples of coupled biological systems (Wardle 2006; Bardgett & Wardle 2010); for example plant-mycorrhiza associations (Smith *et al*. 2008), direct plant control on fungal communities (Broeckling *et al*. 2008), predator-prey relationships (Hedlund & Öhrn 2000) or plant-decomposer relationships (Hättenschwiler *et al*. 2005). Empirical evidence suggests that these biological couplings could indeed produce spatial dependencies between the β-diversity of the different groups (e.g. plants and fungi or bacterial turnover, Zinger *et al*. 2011; Prober *et al*. 2015; Geremia *et al*. 2016; aquatic macro/micro consumers and producers Matias *et al*. 2016). However, such studies remain seldom due to difficulties in compiling comprehensive multi-trophic inventories (but see De Bie *et al*. 2012; Matias *et al*. 2016; Kéfi *et al*. 2016). While, amplicon-based DNA analysis of environmental samples (i.e. environmental DNA, Taberlet *et al*. 2012; Kress *et al*. 2015) holds the promise to unlock this limit by enabling consistent all-biodiversity environmental surveys in soils (Tedersoo *et al*. 2016; Zinger *et al*. 2017) or aquatic environments (Lima-Mendez *et al*. 2015), we still critically miss appropriate

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statistical tools to explore these multi-trophic β-diversity patterns while taking into account environmental variation.

Indeed, analysing how the β-diversity of a given trophic group depends not only on the β-diversity of the other groups but also on the spatial variation in environmental conditions is challenging as soon as the number of groups becomes large. Indeed, many groups will inevitably show multiple correlations leading to multi-collinearity in the analysis. Path analyses (Wright 1921; Shipley 2000; Schuldt *et al.* 2017) are one of the available tools to deal with this issue. However, they require assumptions on the overall structure of the network and they depict hierarchical dependences. Alternatively, probabilistic graphical models have been designed to account for conditional dependencies among multiple variables (Koller & Friedman 2009). For instance, partial correlation networks, a type of Markov networks, do not require any predefined structure, has also been used to model species interactions (Harris 2016) and can be inferred using graphical lasso (Friedman *et al.* 2007; Mazumder & Hastie 2011). Partial correlation networks could then be applied to multi-trophic systems in order to provide a map of dependencies between β-diversities of trophic groups without any *a priori* structure.

Here, we propose to document multi-group β-diversity patterns in soil communities using partial correlation networks. Specifically, we hypothesise that interrelated β-diversity patterns among groups are partly explained by biotic interactions along abiotic gradients, and that these spatial dependencies can be detected with the graphical lasso method to infer a partial correlation network. First, using a simulation model of multi-trophic communities with several trophic networks, we show that biotic interactions may indeed produce interrelated β-diversity patterns (i.e. non-zero partial correlation coefficients) that can be uncovered using a partial correlation network. Second, we apply the method to an empirical dataset including bacteria, micro-eukaryotes, meso/macrofauna, plants and abiotic factors along an elevation gradient in the French Alps. We jointly explore the co-variation between the β-diversity of multiple trophic groups to unravel known and unknown potential biotic interactions, while controlling for the relative role of the abiotic environment and the β-diversity of the other groups.

MATERIAL AND METHODS

The method: applying the Graphical lasso to multi-trophic β-diversity patterns

From species identity to (trophic) groups, and measuring β-diversity and environmental distances

Species grouping can be defined by known trophic position (e.g. symbiotic fungi), or by taxonomy (e.g. bacteria) or function. This step is essential and has to be implemented in the light of the prior knowledge of the study system (see our case study for an example). Then, one possible measure of β-diversity between two local communities, A and B, is the Jaccard dissimilarity index, defined as one minus the ratio of the number of species present in both A and B over the number of species present in either A or B. It equals 0 when A and B share the same species, and 1 when they do not share any. We used the R package 'vegan' (Oksanen *et al.* 2015) to compute the Jaccard dissimilarity matrix for multiple species groups (see below). Since the Jaccard index is sensitive to sample size, and since metabarcoding data often produce samples of heterogeneous sizes (Figs S1, S2), we partitioned the Jaccard index into the true turnover component and the nested component (Baselga 2010; the true turnover component reflects the turnover independently of richness variation while the nested component is deduced by subtracting true turnover component to total turnover), using the R package 'betapart' (Baselga & Orme 2012). Environmental distances between pairs of local communities were computed using Euclidean distances. For the sake of comparison, we also ran the analysis using the Sorensen dissimilarity index and its true turnover component.

The graphical lasso method

The goal of our approach is to use a network to parsimoniously represent the partial correlations between the β-diversity matrix of each group as a function of the others and the environmental distances. Consequently, a suitable description of the system consists of using a class of models that (1) represent the conditional dependencies between random variables (here the β-diversity matrices of multiple species groups) using partial correlations, while (2) allowing for a parsimonious representation of the dependencies using a network. While the Lasso approach was created to produce this type of parsimonious set of variables (Tibshirani 1994), its multivariate form, the Graphical lasso (Glasso), allows representing the partial correlations among multiple variables in a network (here the β-diversity matrix of multiple groups and the environmental distances, Friedman *et al.* 2007; Mazumder & Hastie 2011).

In short, the Glasso uses the empirical variance-covariance matrix S to estimate a partial correlation matrix that quantifies the degree of association between pairs of variables conditional to the other variables. Here a variable is a $n \times n$ β-diversity matrix for a given group (n being the number of plots), or a $n \times n$ environmental distance matrix. To estimate the partial correlation matrix in Glasso, the S matrix is inverted, and its inverse is called the precision matrix P. Moreover, a penalty term in the likelihood (modulated by a coefficient λ) ensures the sparsity of the matrix P (i.e. P have many zeros, see Friedman *et al.* 2007 for mathematical details). The partial correlation matrix is then computed from P as follows (eqn 1):

$$cor(y_i, y_j | y_{I\setminus i,j}) = -\frac{p_{i,j}}{p_{i,i}p_{j,j}} \quad (1)$$

where $cor(y_i, y_j | y_{I\setminus i,j})$ represents the partial correlation between the components i and j of a random variable Y given all the other components, and $p_{i,j}$, $p_{i,i}$, $p_{j,j}$ are the elements of P. The elements of P consist in partial correlations between the β-diversity matrices of the different trophic groups and the environmental distances. As the precision matrices have been inverted with the constraint to ensure sparsity, it follows that the partial correlation matrix is also sparse. This sparse representation of the relationships between the β-diversity of multi-trophic groups and the environmental distances means it can

be represented using a network. In the Glasso, the number of coefficients equal to 0 in the partial correlation matrix depends on the coefficient λ. Here, we used the Extended Bayesian Information Criterion (Foygel & Drton 2010) to select an optimal λ. We used the R package 'qgraph' to estimate the partial correlation matrix with graphical lasso (Epskamp & Fried 2016). We expected partial correlations to be more informative than marginal correlations (Pearson correlations), because they avoid spurious correlations due to confounding effects.

Representing conditional dependencies between β-diversity using a network

We assessed how the β-diversity of each group is influenced by environmental change and the β-diversity of the other groups by analysing the degree and the weighted degree of the correspondent node in the network (using Gephi, Bastian *et al*. 2009). The degree of a node in the network is its number of direct neighbours. If the β-diversity of two groups is conditionally independent (i.e. has a zero partial correlation coefficient), they cannot causally influence each other (Murphy 2012). Consequently, the more connected a group is, the more central it is to structuring the β-diversity of all groups. The weighted degree represents the total sum of partial correlations in β-diversity between a given group and the groups that are directly connected to this group. The higher the sum, the greater the interdependencies with other groups.

Approximating the structure of a simulated trophic network

We then tested whether the Glasso approach was able to recover known interactions among species groups from local community β-diversity patterns. We first built a set of simulated data by constructing a regional trophic web (step 1) from which local multi-trophic communities were sampled using a stochastic model (step 2). Then, we measured the partial correlation between the β-diversity of each trophic level (step 3) and tested whether these patterns matched the simulated regional trophic web.

Step 1 – The regional web was assumed to have six trophic groups and three trophic levels (three basal groups, two intermediate groups and one top group), containing 20 species each. We assumed some degree of specialisation in the relationships between trophic levels: each species from the intermediate and top trophic levels had a number of prey equals to one plus a random number drawn in a Poisson law of parameter three (Fig. 1a). Thus, each consumer species had one prey species at least, and on average four prey species. Once the number of prey species had been drawn for a given consumer species, prey were drawn randomly from the species belonging to the lower trophic levels (T4 had preys in T1 and T2, T5 in T3 and T4 and T6 in T4 and T5)

Step 2 – Based on this regional network, we generated 1000 local multi-trophic communities. Communities were simulated using a stochastic model of multi-trophic community assembly inspired by the Trophic Theory of Island Biogeography (TTIB, Gravel *et al*. 2011; Massol *et al*. 2017). The TTIB assumes bottom-up sequential dependencies (Holt 1997, 2009; Dunne *et al*. 2002) with two phases. In phase 1, each species can colonise a local community if at least one of its prey species is present. In phase 2, a species which has lost its last prey species goes extinct. For the sake of clarity, we assumed a homogeneous environment. The probability of each basal species being present in the local community was assumed to be constant and set to $p_0 = 0.5$. The probability of each consumer species C being present in the local community is related to the fraction of its prey available through the relation $p_C = (k/g)^r$ where g is the diet breadth of C (i.e. the number of potential prey species), k is the number of its prey species present in the community and r is a constant that controls the shape of the relation. In the TTIB, having more prey species present in the community does not increase the probability of consumer presence, and the probability of survival is either 0 (when $k = 0$) or 1 (when $k > 0$). This corresponds to the case $r = 0$. For the simulation, we used $r = 1$, assuming that p_C grows linearly with the number of prey species present in the community. We also studied the case $r = 1/3$ presented in the appendices.

Step 3 – We then computed β-diversity matrices for each trophic group. We inferred then the partial correlations and computed the marginal correlations between these β-diversities using the Glasso method. We thus obtained a distribution of partial and marginal correlations between pairs of the β-diversity at the different trophic levels. We expected these partial correlations to be high between trophic groups which interact directly and low between trophic groups which do not interact.

Analysing multi-trophic patterns in soil ecosystems in the French Alps

Study site and soil sampling

The study was conducted in the northern French Alps (Arves Massif, 45.12° N, 6.40° E) along a 977 m elevational gradient (1748 m to 2725 m a.s.l.) located in a single cow-grazed pasture, above the tree-line. The vegetation at the bottom of the gradient corresponds mainly to subalpine grasslands, while alpine meadows with sparse vegetation dominate at high elevation (Chalmandrier *et al*. 2017). Ten plots were established at 100 m altitude intervals along the gradient, each of them composed of two 10×10 m^2 subplots. All plots were placed on the same south-facing slope with a similar bedrock type and land-use to ensure a relatively homogeneous gradient. Mean annual temperature ranges between 8 °C at the bottom and 3 °C at the top, while mean annual rainfall is 473 mm over the period 2000–2012. The soil sampling field campaign was conducted in September 2012. We collected 21 soil samples per subplot. More details are presented in Appendix S1.

Molecular analyses

Soil biodiversity was estimated using four DNA markers. Universal markers such as 18S (amplifying all Eukaryotes, 18S nuclear rDNA) and 16S (amplifying all Bacteria, 16S rRNA) were used to obtain a general overview of the multi-trophic composition of the sites. Another two markers focus on Eukaryota diversity by targeting fungi (ITS1) and vascular plants (Chloroplast trnL-P6 loop) respectively. Molecular analysis and data curation are presented in Appendix S1. We pooled the samples together per subplot in order to obtain a single community per subplot and converted the data into

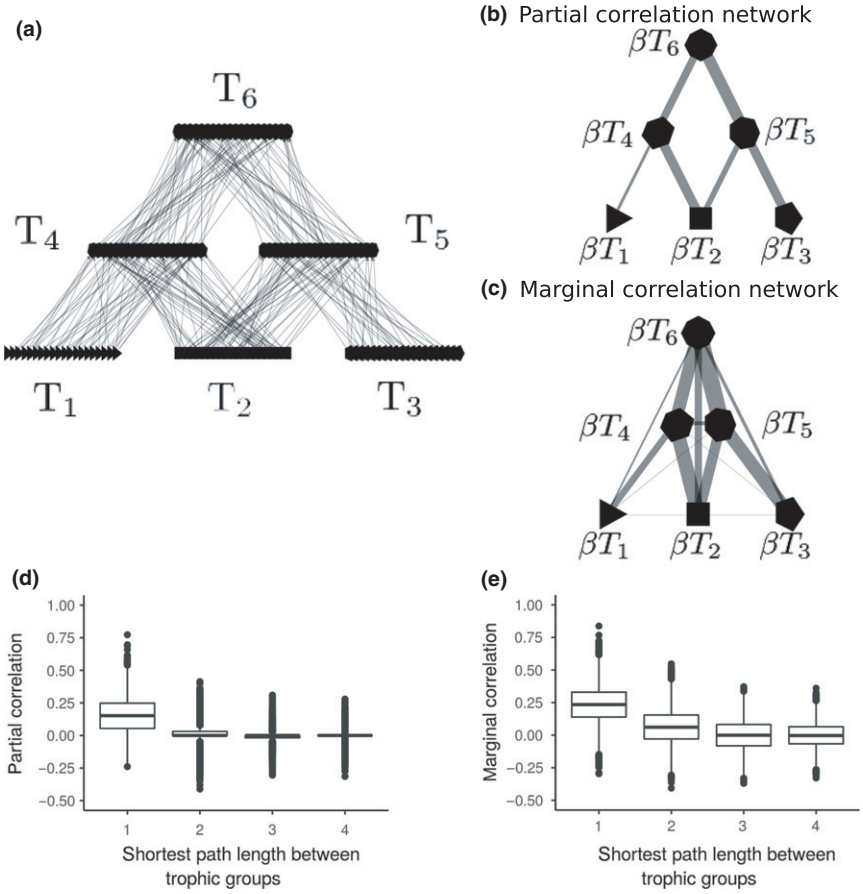

Figure 1 Design and results of the simulation assessing the impact of biotic interactions on the marginal and partial correlation of the β-diversity values of different trophic groups. (a) the trophic network used for the simulation, composed of six trophic groups and three trophic levels. The indegree of each node is one plus an integer randomly drawn from a Poisson law of parameter three (except for the basal species). (b) Partial correlation network built using the median values of the partial correlations (inferred using the graphical lasso) between the β-diversity values of different trophic groups. (c) Marginal correlation networks built using the median values of the Pearson correlations between the β-diversity values of different trophic groups. (d) Partial correlation coefficient (inferred using the graphical lasso) between the β-diversity values of two trophic groups as a function of the shortest path length between these trophic groups. (e) Marginal Pearson correlation coefficient between the β-diversity values of two trophic groups as a function of the shortest path length between these trophic groups.

presence-absences. The raw and curated sequencing data as well as associated data and codes are available on the Dryad Digital Repository under accession https://doi.org/10.5061/dryad.5b58400 and the summary statistics are presented in Table S1. As explained above, we computed β-diversity using the Jaccard dissimilarity index. Since this index is sensitive to sequencing depth difference between samples, we also used the true turnover component of the Jaccard index (Baselga 2010). The results obtained using the true turnover component of the Jaccard index are similar to those using the Jaccard index; so, we only refer to the Jaccard index in the main text, and present the results of the true turnover component of the Jaccard index in Appendix S2 (Figs S3–S7, Tables S2–S3). Moreover, we present the analysis using the Sorensen dissimilarity index and its true turnover component in Appendix S3 (Figs S8–S11).

Defining trophic groups of species

We selected *a priori* groups of soil taxa based on their distinctive role in the functioning of the soil ecosystem, namely: plants, fungi, bacteria, oribatid mites, nematodes and springtails (Bardgett 2005). We included plants since they are the primary producers and their diversity and identity drive the functioning and the stability of most terrestrial ecosystems (Hooper 1997; van der Heijden *et al.* 1998). We also included litter feeders that contribute to dead material fragmentation, in particular oribatid mites and springtails. Oribatid mites form one of the most abundant groups of arthropods in soil, (Behan-Pelletier 1999) with up to several hundreds of thousands of individuals per square metre (Norton 1990). Springtails are the most numerous group of hexapods in most terrestrial ecosystems (Deharveng 2004). We also included a group of taxa that mineralise the fragmented litter, such as saprophytic fungi and bacteria (Bardgett 2005). Fungi are found in different compartments of the soil trophic web so we classified fungal OTUs into three main functional groups, namely, symbiotic fungi, saprophytic fungi and pathogenic fungi using the FUNguild database (Nguyen *et al.* 2016). Root associated symbiotic fungi rare found on over 90% of terrestrial plant families (Wang & Qiu 2006). Moreover, in arctic and alpine systems, 60–80% of the nitrogen available

for plants is supplied by mycorrhizal fungi (Bjorbækmo *et al*. 2010). Bacteria also contribute to this supply by fixing atmospheric nitrogen (Bonfante & Anca 2009; Haq *et al*. 2014). Finally, we included a group of predators, here nematodes, the most abundant belowground multicellular animals (Bardgett 2005). Nematode OTUs were divided into bacterivore nematodes and herbivore/fungivore nematodes using the NEMAguild database (Nguyen *et al*. 2016). In summary, the nine groups included in this study were: plants, symbiotic fungi, pathogenic fungi, saprophytic fungi, bacterivore nematodes, herbi/fungivore nematodes, bacteria, springtails and oribatid mites. Most of these groups interact via trophic interactions, so that this study case matches the simulations described above, but not all of them. For the sake of clarity, we will hereafter refer to them as trophic groups.

Environmental characteristics

Mean annual soil temperature was estimated from field meteorological stations placed at the centre of each plot. We also estimated growing season length and number of frost days based on daily maps of snow cover at 15 m resolution for 5 years falling between 2000 and 2014 and air temperature values extracted from the SAFRAN meteorological model developed by Météo France for the French Alps (Durand *et al*. 2009). More methodological details and validation results for the snow cover model are available in Carlson *et al*. (2015). Fine-scale topography and associated parameters (topographic wetness index and slope) were inferred from airborne LIDAR data acquired the year of sampling. Mean soil pH over the gradient was 5.40 (SD 0.300), whereas mean soil temperature over the year was 6.06 °C (SD 2.84). The environmental distances between subplots were estimated with Euclidean distances from the first two axes of a principal component analysis run for all produced (and normalised) environmental variables (the variance captured by the first two axes was 34 and 25% respectively, the first axis roughly represented the climatic conditions, whereas the second axis was related to the soil conditions, see Appendix S4 (Figs S12–S14, Table S4) for more details).

RESULTS

Approximating the structure of a simulated trophic network

Our simulations showed that trophic interactions do produce non-zero marginal and partial correlations between β-diversity on consecutive trophic levels. Moreover, the Glasso method detected the conditional dependencies (i.e. an edge in the partial correlation network) between the β-diversity of the different trophic groups corresponding to their trophic position in the network contrary to the marginal correlations (Fig. 1b,c). The median of both marginal and partial correlation coefficients between pairs of trophic levels decreased with the shortest path length between these trophic levels. Nevertheless, while the median of the marginal correlation coefficients decreased slowly, the median of the partial correlation coefficients dropped to values close to 0 once the trophic level distance was higher than 1 (Fig. 1d,e). Changing the shape of the relationship linking the probability of presence of a consumer species with its number of available prey species did not alter this conclusion (Fig. S15).

β-diversity modelling of empirical soil communities

In the French Alps, the partial correlations estimated between the β-diversity of each predefined trophic group and environmental distances were all positive (Figs 2, S16, S17, Table S5). The estimated partial correlation network had 11 nodes (9 trophic groups and 2 environmental variables), was composed of 34 undirected edges out of 55 possible edges and had a connectance of 0.618.

Saprophytic fungi were the most influential group in conditioning the β-diversity of the other groups (highest degree value, 8, and highest weighted degree value, 1.30, Fig. 3). Plants and oribatid mites also had a strong influence on the β-diversity of other groups, as did pathogenic and symbiotic fungi. In contrast, environmental variables had a relatively small direct impact on the β-diversity of the trophic groups.

The probability of observing a non-null partial correlation between the β-diversity of a trophic group and the environmental distance was 0.44 (8 edges linking environmental nodes to the trophic group nodes and 18 potential edges), whereas the probability of observing a link between the β-diversity of any two trophic groups was 0.69 (25 edges and 36 potential edges). Since the variables associated with disconnected nodes were conditionally independent and that conditionally independent variables could not causally influence each other, this result demonstrates that, in general, environmental variables had a lower influence on the β-diversity of the trophic groups than the other trophic groups.

DISCUSSION

In this study, we applied a method for dissecting the joint spatial structure of multiple trophic groups. This method builds on observed patterns of β-diversity in multiple trophic groups to infer the conditional dependencies between pairs of groups and with the environment, in order to pinpoint potential biotic interactions and influential effects of environmental variables on some specific groups. Simulations confirmed that our method is able to recover the overall structure of a trophic network using partial correlations of β-diversity between pairs of groups.

When applied to soil multi-trophic diversity along an elevation gradient of the French Alps, we were able to quantify the relative importance of biotic interactions and the environment in shaping the spatial structure of the meta-communities. Pairwise environmental distances displayed a low correlation with the β-diversity of each group (as measured with the few non-zero partial correlations). This result implies that the overall ecological community is primarily driven by biotic interactions and, to a lower extent, by environmental constraints (but still important on some groups like springtails or pathogenic fungi). This result is surprising, given the sharpness of the elevational gradient, and the expected importance of environmental filtering in shaping above and below-ground communities along elevation gradients (Meynard *et al*. 2013). However, many previous studies have focused on intraguild biotic interactions, or on environmental effect only (see Kraft *et al*.

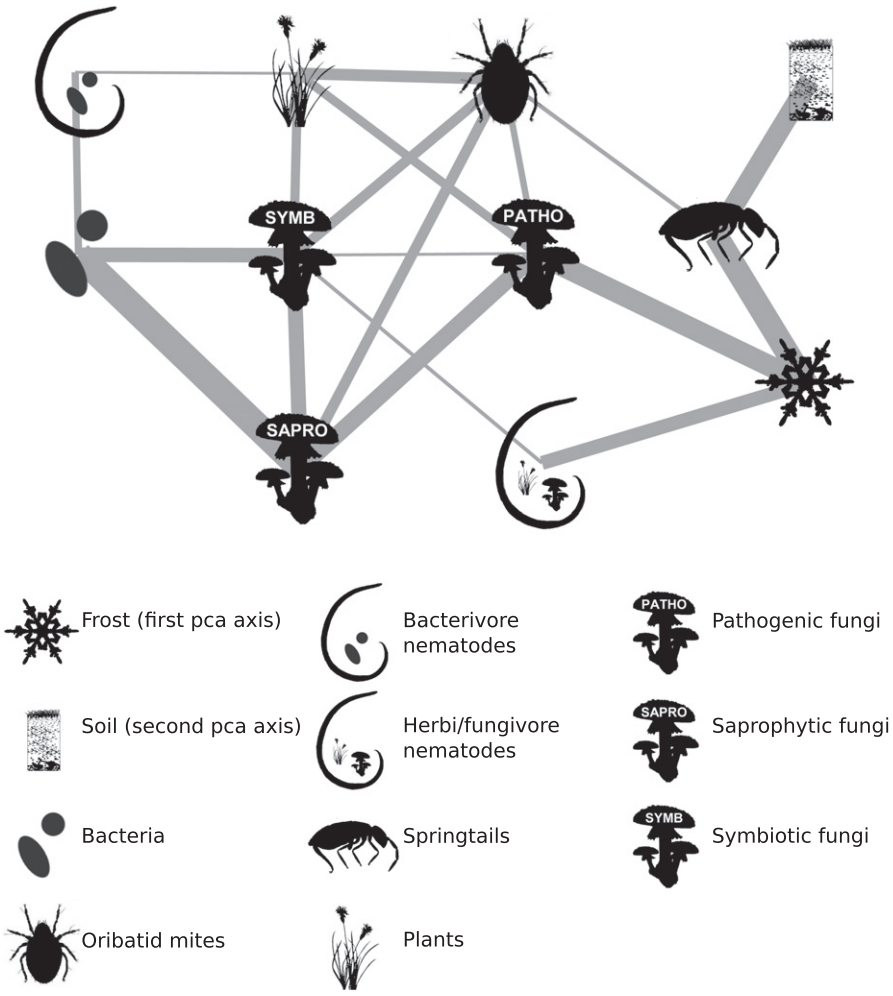

Figure 2 Undirected partial correlation network inferred using the graphical lasso method between the β-diversity of the major trophic groups constituting soil biodiversity and the environmental distances. Each node represents the β-diversity of a trophic group or an environmental distance. Here, only the partial correlations above the median value of the non-null partial correlation coefficients (0.106) are shown. The non-filtered network is presented in Fig. S1. Edge thickness is proportional to the value of the partial correlation coefficient and the partial correlation coefficients are all positive.

2015 for a critical synthesis), and they have ignored the importance of interguild interactions (e.g. Chalmandrier *et al.* 2015).

As our climatic and soil properties were sampled at plot level, they might not have been measured at the appropriate scale to reflect the fine conditions experienced by belowground organisms (Falconer *et al.* 2015; Baveye *et al.* 2016; Matias *et al.* 2016; Zinger *et al.* 2017). Further studies should empirically investigate the β-diversity area relationships of the different groups (see Barton *et al.* 2013) and exhibit at which scale the spatial turnover of the different groups match together and with the environment (Barberán *et al.* 2015; Zinger *et al.* 2017). Ultimately, this will give an idea of the appropriate scale of sampling and collecting environmental information for such multi-trophic analyses.

Finally, we cannot rule out that some important missing environmental factors might explain the lower than expected predictive power of environmental distances (e.g. phosphorous for symbiotic mushrooms, Liu *et al.* 2012; Camenzind *et al.* 2014). Interestingly, focusing on the true turnover, instead of total turnover, reveals a stronger influence of environmental variation in structuring the β-diversity of the different trophic groups. This means that the effects of the other groups are pivotal to explain the overall turnover and change in species richness (nestedness component) across space, while environmental variation is important in driving the pure turnover between groups.

The strong advantage of Graphical lasso over other related approaches (e.g. Bayesian network, path analyses) is that the partial correlation network can be inferred without assuming any *a priori* structure. This is important when the goal is of exploring and mapping co-variations between different groups and when little knowledge of the system is available. As explained in the introduction, the graphical lasso is expected to be sensitive to the effect of a missing predictor since the structure of the partial correlation network may be affected by the addition of a variable. In our case, we tested to what extent the addition of an environmental variable impacted the structure of the partial correlation network. We showed a moderate impact on the network topology, guaranteeing so the robustness of the analysis (Appendix S5, Figs S18–S20). This method does not directly infer the interaction network at

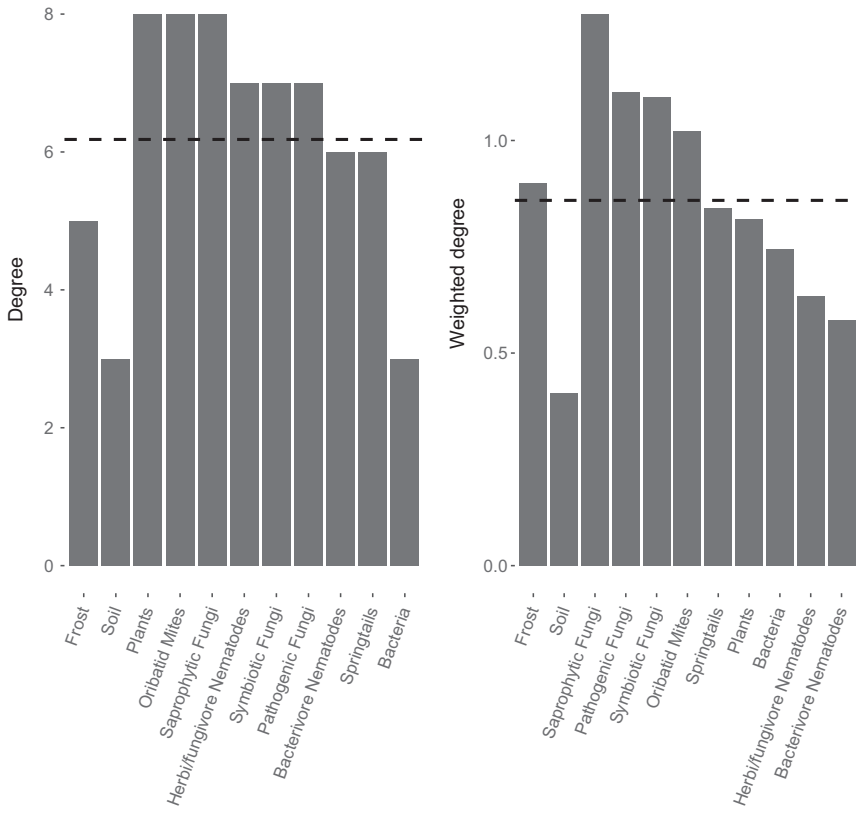

Figure 3 Properties of the inferred network. The degree (left panel) is the number of neighbours of nodes in a graph (here, the undirected partial correlation network). It measures the number of variables that are conditionally dependent on the variable associated with this node. The weighted degree (right panel) is the sum of the partial correlation coefficients attached to the edges adjacent to this node. Dashed lines represent the mean values of degree and weighted degree.

the species level, and the inferred conditional dependencies at the group level do not imply causality. However, they shed light on potential interactions and pave the way for more analyses along identified co-variations.

The approach we proposed here should help interpret a wide range of multi-trophic biodiversity patterns and yield new testable hypotheses. For example, in multiple pairs of trophic groups, we found strong spatial associations which can be interpreted in light of functional associations. In the soil, plants are directly affected by symbiotic/pathogenic fungi and root herbivores, whereas the complex network of detritivorous organisms affects them indirectly (Bardgett 2005; Wardle *et al*. 2011). Our method showed that plant β-diversity was strongly linked to the β-diversities of symbiotic fungi, pathogenic fungi, oribatid mites and bacterivore nematodes. While the links with the two groups of fungi most likely reflect the strong direct associations between these groups and the vegetation structure, the link with oribatid mites may be explained by the fact that this group feeds on plant litter fungi, especially saprophytic fungi (Schneider *et al*. 2004; Crowther *et al*. 2011; Crowther & A'Bear 2012). The graphical lasso method detected this link showing that changes in the composition of saprophytic fungi lead to a change in the oribatid mite assemblages. As expected, the β-diversity of bacteria correlated with that of bacterivore nematodes, which reflects this known trophic interaction (Ettema 1998; Wardle 2006). Moreover, the β-diversity of herbi/fungivore nematodes correlated with that of symbiotic fungi. The link between the β-diversity of oribatid mites and springtails might be explained by mite predation of springtails (Ferguson & Joly 2002). We also highlighted a link between the β-diversity of oribatid mites and symbiotic fungi. This result suggests that mite assemblages could be influenced by fungi spatial distribution through trophic interactions, which have been so far very poorly documented (Gange & Brown 2003). Interestingly, our analysis also showed a strong partial correlation (the strongest partial correlation: 0.365) between the β-diversities of saprophytic fungi and bacteria. Indeed, bacteria can rely on decomposition products from organic matter, which are provided by saprophytic fungi fully equipped from an enzymatic point of view (De Boer *et al*. 2005; Romaní *et al*. 2006). The relationship uncovered between bacteria and symbiotic fungi could be attributed to the fact that bacteria can assist mycorrhiza by colonising the extraradical hyphae or by living in the cytoplasm of mycorrhizal fungi (Bonfante & Anca 2009; Haq *et al*. 2014). We did not observe direct relationship between bacteria and plants, probably because we lumped together bacterial taxa typical from the bulk soil (e.g. acidobacteria) with those interacting with plants (e.g. N-fixing bacteria or pathogens). A better functional assignment of bacterial OTUs would probably help to clarify this identified relationship likely due to mutualistic bacterial OTUs.

CONCLUSIONS

The rise of environmental DNA metabarcoding and the ever-increasing availability of databases on species co-occurrence have opened up a new era in quantitative and predictive ecology. While comprehensive species lists of taxa are necessary, they do tell much on how species interact across space and time and how multi-trophic interactions shape community assembly. The method we proposed here addresses this challenge by revealing how trophic groups influence each other and respond to environmental variation. As such, our method is able to uncover the potential determinants of the compositional turnover of species groups from a multi-trophic interaction perspective. This paves the way for larger applications of this method to ecological data where comprehensive biodiversity assessments are becoming more and more available and where knowledge of the structure of the system is still limited.

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AUTHORSHIP

WT, FM and MO conceived the ideas with the help of LC. LC, EC, LG, JP, FM, PT, LZ and WT collected the soil and environmental data in the field. LG, JP and PT ran the PCR and DNA extractions. LZ and VS ran the bioinformatic analyses. MO ran all statistical analyses and developed the method together with FM and WT. MO, FM and WT wrote the first version of the paper, and all authors contributed substantially to the revisions.

COMPETING INTERESTS

LG and PT are co-inventors of patents related to the gh primers and the use of the P6 loop of the chloroplast trnL (UAA) intron for plant identification using degraded template DNA. These patents only restrict commercial applications and have no impact on the use of this locus by academic researchers.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5b58400

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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