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1 Mapping the imprint of biotic interactions on β -diversity

2

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48

49

50 **Abstract**

51 Investigating how trophic interactions influence the β -diversity of metacommunities is of
52 paramount importance to understanding the processes shaping biodiversity distribution. Here, we
53 propose a statistical method for inferring the strength of spatial dependencies between pairs of
54 species groups. Using simulated data generated from a model of trophic community assemblage, we
55 showed that this method can recover the global structure of the trophic network from the β -diversity
56 patterns of multiple trophic groups. When applied to multi-trophic communities in the soil along an
57 elevational gradient in the French Alps, we found that fungi make a major contribution to the
58 structuring of β -diversity across trophic groups, that there were strong spatial dependencies between
59 groups known to interact specifically (e.g. plant- symbiotic fungi, bacteria-nematodes), and that the
60 influence of environmental gradient was less significant than expected. Our method should help
61 interpret a wide range of multi-trophic biodiversity patterns and yield new testable hypotheses.

62

63

64 **Introduction**

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

72 Previous studies have sought to analyze β -diversity by teasing apart the effects of
73 environmental filtering from biotic interactions along environmental gradients on a single group of
74 species (e.g. Peay *et al.* 2016 for fungi; Hanson *et al.* 2012 for bacteria; Mazel *et al.* 2017 for
75 mammals; Chalmandrier *et al.* 2015 for plants). However, biotic interactions *across* groups are also
76 expected to drive the structure and distribution of biodiversity. For example, plant-pollinator,
77 trophic (e.g. prey-predator or plant-decomposers) and host-symbiont (including pathogens,
78 mutualistic and commensal organisms) interactions strongly impact diversity distribution and
79 ecosystem functioning (Brose & Hillebrand 2016). These interactions among groups of species,
80 although they are not necessarily species-specific (Walker *et al.* 2011; Peay *et al.* 2015), harbor
81 some degree of specificity due to trait constraints and shared habitat preferences (e.g. Allesina *et al.*
82 2008; Gonzales-Varo 2016). This interdependence among groups implies that the β -diversity of a
83 single group is likely to be contingent to that of the other groups. Hence, studying how the β -
84 diversity of multiple groups covaries along environmental gradients should help better understand
85 their spatial distribution and uncover their interactions.

86 Soil ecosystems are ideal for documenting these multi-group β -diversity patterns. Indeed,
87 they provide several examples of coupled biological systems (Wardle *et al.* 2006; Bardgett &
88 Wardle 2010), for example plant-mycorrhiza associations (Smith & Read 2008), direct plant control
89 on fungal communities (Broeckling *et al.* 2008), predator-prey relationships (Hedlund & Öhrn

90 2000) or plant-decomposer relationships (Hattenschwiler *et al.* 2005). Empirical evidence suggests
91 that these biological couplings do indeed produce spatial dependencies between the β -diversity of
92 the different groups (e.g. plants and fungi or bacterial turnover, Zinger *et al.* 2011; Prober *et al.*
93 2015; Geremia *et al.*, 2016). However, data on soil meta-communities remain scarce and there are
94 no appropriate statistical tools for exploring the β -diversity patterns in multiple soil groups (i.e.
95 more than two or three) while taking into account environmental variation.

96 Here we develop a generic method for analysing how the β -diversity of one group depends on
97 the β -diversity of the other groups and on the spatial variation in environmental conditions. This is
98 challenging due to potential confounding effects between different groups, which can generate
99 spurious correlations. Variance partitioning methods aim to disentangle the influence of several
100 explanatory variables on a response variable and they are, in principle, able to deal with
101 confounding effects by providing partial correlations among partitions (Borcard *et al.* 1992; Dray *et*
102 *al.* 2012). However, the number of partitions grows exponentially with the number of explanatory
103 variables, making the method impractical for studies encompassing a large number of species
104 groups. This is problematic since the amplicon-based DNA analysis of environmental samples (i.e.
105 environmental DNA) holds the promise of more streamlined and consistent all-biodiversity
106 environmental surveys (Taberlet *et al.* 2012; Kress *et al.* 2015) and, consequently, new statistical
107 tools are needed. One possible solution to this problem is to use statistical tools called graphical
108 models (Koller & Friedman 2009), in which each node is a random variable and edges represent
109 conditional dependencies between these random variables. Partial correlation networks represent a
110 particular type of graphical model where the edges of the network are weighted by the partial
111 correlation coefficients (i.e. the correlation between two variables while controlling the others).
112 Here, we propose studying multi-group β -diversity patterns in soil communities using partial
113 correlation networks.

114 Specifically, we hypothesise that interrelated β -diversity patterns among groups are partly
115 explained by biotic interactions along abiotic gradients, and that these spatial dependencies can be

116 detected using a method called graphical lasso to infer a partial correlation network (Friedman *et al.*
117 2007). Using simulated multi-trophic communities in a given, known trophic network, we first test
118 and validate our hypothesis and statistical method. We show that biotic interactions may indeed
119 produce interrelated β -diversity patterns (i.e. non-zero partial correlation coefficients) that can be
120 uncovered using a partial correlation network. We then apply our method to an empirical dataset
121 including bacteria, microeukaryotes, meso/macrofauna, plants and abiotic factors along an elevation
122 gradient in the French Alps. We jointly explore the co-variation between the β -diversity of multiple
123 functional and trophic groups to unravel known and unknown potential biotic interactions, while
124 controlling for the relative role of the abiotic environment and the β -diversity of the other groups.

125 **Material and Methods**

126 127 **The method: applying the Graphical lasso to multi-group β -diversity patterns**

128 From species to relevant groups – Species grouping can be defined by known trophic position (e.g.
129 symbiotic fungi), or by taxonomy (e.g. bacteria) or function. This step is essential and has to be
130 implemented in light of the prior knowledge of the study system (see our case study for an
131 example).

132 Measuring β -diversity and environmental distances – One possible measure of β -diversity between
133 two local communities, A and B, is the Jaccard dissimilarity index, defined as one minus the ratio of
134 the number of species present in both A and B over the number of species present in either A or B.
135 The Jaccard dissimilarity index equals 0 when A and B share the same species, and 1 when they do
136 not share any. We used the R package ‘vegan’ (Ricklefs 2008) to compute the Jaccard dissimilarity
137 index for multiple species groups independently (see below). Moreover, we partitioned the Jaccard
138 index into the true turnover component and the nested component (Baselga 2010), using the R
139 package 'betapart' (Baselga & Orme 2012). Environmental distances between pairs of local
140 communities were computed using Euclidean distances.

141 The graphical lasso method – The overarching goal of our approach is to use a network to
142 parsimoniously represent the correlations between the β -diversity of each group as a function of the

143 others and the environmental distances. This is challenging due to potential confounding effects (i.e.
144 collinearity among multiple variables), which can generate spurious correlations. Working with
145 partial correlations (correlation between two variables when knowing the value of the others)
146 instead of marginal correlations (Pearson correlation) avoid these confounding effects.
147 Consequently, a suitable description of the system consists of using a class of models that (1)
148 represent the conditional dependencies between random variables (here the β -diversity of multiple
149 species groups) using partial correlations while (2) allowing for a parsimonious representation of
150 the dependencies using a network. The Lasso approach (Tibshirani 1994) has been developed to
151 produce precisely this type of parsimonious set of variables. More recently, its multivariate form,
152 the Graphical lasso (Glasso), has made it possible to represent the partial correlations between
153 multiple variables in a network (here the β -diversity of multiple groups and the environmental
154 distances, Friedman *et al.* 2007; Mazumder & Hastie 2011). As a consequence, Glasso should be an
155 appropriate tool for representing the structure of the partial correlations between multi-trophic β -
156 diversity patterns.

157 In short, the Glasso uses the empirical variance-covariance matrix S (computed from the β -
158 diversity values of multiple species groups and the environmental distances) to estimate a partial
159 correlation matrix that quantifies the degree of association between pairs of variables conditional to
160 the other variables. In order to estimate the partial correlation matrix in Glasso, the S matrix is
161 inverted to produce the precision matrix P with the particular constraint that P must be sparse (i.e.
162 have many zeros). This is equivalent to the variable selection step in conventional statistical
163 approaches (see Friedman *et al.* 2007 for mathematical details). The partial correlation matrix is
164 then computed from P as follows (Eq. 1):

$$165 \quad cor(y_i, y_j | y_{I \setminus \{i, j\}}) = -\frac{p_{i, j}}{p_{i, i} p_{j, j}} \quad (\text{Eq.1})$$

166
167 where $cor(y_i, y_j | y_{I \setminus \{i, j\}})$ represents the partial correlation between the components i and j of a
168 random variable Y given all the other components, and $p_{i, j}$, $p_{i, i}$, $p_{j, j}$ are the elements of P .

169 As the precision matrices have been inverted with the constraint in order to ensure sparsity, it
170 follows that the partial correlation matrix is also sparse. This sparse representation of the
171 relationships between the β -diversity of multi-trophic groups and the environmental distances
172 means it can be represented simply and intuitively using a network. In the Glasso, this parsimonious
173 representation (i.e. the number of 0 coefficients in the partial correlation matrix) is not optimally
174 determined but is arbitrary and depends on a coefficient λ . Here, we used the Extended Bayesian
175 Information Criterion (Foygel & Drton 2010) to select optimal λ . We used the R package ‘qgraph’
176 to estimate the partial correlation matrix with graphical lasso (Epskamp & Fried 2016).

177

178 Representing conditional dependencies between β -diversity using a network representation – We
179 plotted the inferred network using Gephi (Bastian *et al.* 2009) and analysed its properties. In
180 particular, we quantified the connectivity of each group by analysing the degree and the weighted
181 degree for each group in the partial correlation network. The degree represents the number of times
182 the β -diversity of a given group is conditionally dependent on the β -diversity of other groups. If the
183 β -diversity of two groups is conditionally independent (i.e. has a zero partial correlation
184 coefficient), they cannot causally influence each other (Murphy 2012). Consequently, the more
185 connected a group is, the more central it is to structuring the β -diversity of all groups. The weighted
186 degree represents the total sum of partial correlations in β -diversity between a given group and all
187 other connected groups. The higher the sum, the more important the group.

188

189 **Validating the method using simulations**

190 In order to test whether the Glasso approach was able to recover known interactions among species
191 groups from local community β -diversity patterns, we first built a set of simulated data. We did so
192 by constructing a regional trophic web (step 1) from which local multitrophic communities were
193 sampled using a stochastic model (step 2). Then, we measured the partial correlation between the β -

194 diversity of each trophic level (step 3) and tested whether these patterns matched the simulated
195 regional trophic web.

196 Step 1 – The regional web was assumed to have six trophic levels (one basal level and five
197 consumer levels), containing twenty species each. We assumed some degree of specialization in the
198 relationships between trophic levels: each consumer species had a number of prey equals to one
199 plus a random number drawn in a Poisson law of parameter 1 (Fig. 1a). Thus, each consumer
200 species had one prey species at least, and on average two prey species. Once the number of prey
201 species had been drawn for a given consumer species, prey were drawn randomly from the lower
202 trophic level.

203 Step 2 – Based on this regional network, we generated 1,000 local multi-trophic
204 communities. Communities were simulated using a stochastic model of multi-trophic community
205 assembly inspired by the Trophic Theory of Island Biogeography (TTIB, Gravel *et al.* 2011; Massol
206 *et al.* 2017). The TTIB assumes bottom-up sequential dependencies (Holt 1997, 2009; Dunne *et al.*
207 2002) with two phases. In phase 1, each species can colonise a local community if at least one of its
208 prey species is present. In phase 2, a species which has lost its last prey species goes extinct. For the
209 sake of clarity, we assumed a homogeneous environment. The probability of each basal species
210 being present in the local community was assumed to be constant and set to $p_0 = 0.5$. The
211 probability of each consumer species C being present in the local community is related to the
212 fraction of its prey available through the relation $p_C = (k/g)^r$ where g is the diet breadth of C (i.e. the
213 number of potential prey species), k is the number of its prey species present in the community, and
214 r is a constant that controls the shape of the relation. In the TTIB, having more prey species present
215 in the community does not increase the probability of consumer presence, and the probability of
216 survival is either 0 (when $k=0$) or 1 (when $k>0$). This corresponds to the limit case $r=0$. For the
217 simulation, we used $r=1$, assuming that p_C grows linearly with the number of prey species present in
218 the community. We also studied the case $r=1/3$ presented in the appendices.

219 Step 3 – We then computed β -diversity patterns for each trophic level and inferred the partial
220 correlations between these β -diversities using the Glasso method explained above. We thus obtained
221 a distribution of partial correlations between the β -diversity at the different trophic levels. We
222 expect these partial correlations to be high between trophic levels which interact directly and low
223 between trophic levels which do not interact. Since here only two successive trophic levels interact
224 (see Fig. 1a), we expect the partial correlation between successive trophic levels to be high
225 compared to the partial correlation between non-successive trophic levels. We expect these partial
226 correlations to be more informative than marginal correlations (Pearson correlations), because they
227 avoid spurious correlations due to confounding effects.

228
229 ***Analysing multi-trophic patterns in multi-trophic soil ecosystems in the French Alps.***

230 *Study site and soil sampling* – The study was conducted in the northern French Alps (Arves Massif,
231 45.12°N, 6.40°E) along a 977 m elevation gradient (1748m to 2725m a.s.l.) located in a single cow-
232 grazed pasture, above the tree-line. The vegetation at the bottom of the gradient corresponds mainly
233 to subalpine grasslands, while alpine meadows with sparse vegetation dominate at high elevation
234 (Chalmandrier *et al.* 2017). Ten plots were established at 100m altitude intervals along the gradient,
235 each of them composed of two 10 x 10 m sub-plots. All plots were placed on the same south-facing
236 slope with a similar bedrock type and land-use to ensure a relatively homogeneous gradient. Mean
237 annual temperature along the gradient ranges between 8°C at the bottom and 3°C at the top, while
238 mean annual rainfall is 473mm over the period 2000-2012. The soil sampling field campaign was
239 conducted in September 2012.

240 We collected twenty-one soil samples per sub-plot following the two diagonals with the distance
241 increasing exponentially from the corners to the centre on one diagonal and from the centre to the
242 corners on the other. Central points were sampled only once. This sampling scheme was
243 implemented to cover as much local biodiversity as possible at the sub-plot scale (Taberlet *et al.*
244 2012; Chalmandrier *et al.* 2017) and provided an almost regular distribution of pairwise spatial
245 distances between points. Each sample contained 50g of soil from the uppermost 10 cm of soil and

246 was placed in individual plastic bags to be processed individually. Corers were cleaned and
247 sterilised using a blowtorch between each sample to prevent cross-contamination (Taberlet *et al.*
248 2012). Extracellular DNA was extracted from 15g of soil as previously described (Taberlet *et al.*
249 2012; Zinger *et al.* 2016) within four hours after sample collection to prevent microbial growth.
250 DNA was extracted twice for each sample. Blank extraction controls were included in the extraction
251 process (using solely phosphate buffer as the template).

252

253 Molecular analyses – Soil biodiversity was estimated using four DNA markers. Universal markers
254 such as 18S (amplifying all Eukaryotes, 18S nuclear rDNA) and 16S (amplifying all Bacteria, 16S
255 rRNA) were used to obtain a general overview of the multi-trophic composition of the sites.
256 Another two markers focus on Eukaryota diversity by targeting fungi (ITS1) and vascular plants
257 (Chloroplast trnL-P6 loop), respectively. For each DNA extract, PCRs were run in duplicate leading
258 to four PCR replicates per core sample. For each marker, PCR products were purified (MinElute™
259 PCR purification kit, Qiagen) with extraction and PCR blank controls included in the mix. High-
260 throughput sequencing of eukaryotes and plant amplicons was performed on an Illumina HiSeq
261 2500 platform (2x150 bp paired-end reads for Eukaryotes and 2*200bp for plants) while fungal,
262 archae and bacterial amplicons (200-350 bp) were sequenced on an Illumina MiSeq (2 x 250 bp
263 paired-end reads) platform. Data curation is presented in Appendix 1. We pooled the samples
264 together per subplot in order to obtain a single community per sub-plot and converted the data into
265 presence-absences. The raw and curated sequencing data as well as associated metadata are
266 available on the Dryad Digital Repository under accession XXX (to be provided on manuscript
267 acceptance) and the summary statistics are presented in table S1. As explained above, we computed
268 β -diversity using the Jaccard dissimilarity index. Since this index is sensitive to sequencing depth
269 difference between samples, we also used the true turnover component of the Jaccard index
270 (Baselga 2010), to remove this potential bias. The results obtained using the true turnover
271 component of the Jaccard index are similar to those using the Jaccard index so we only refer to the

272 Jaccard index in the main text, and present the results of the true turnover component of the Jaccard
273 index in Appendix 3.

274

275 Defining trophic groups of species

276 We selected *a priori* groups of soil taxa based on their distinctive role in the functioning of the soil
277 ecosystem, and in biogeochemical cycles (especially the carbon and nitrogen cycles). Our focal taxa
278 were: plants, fungi, bacteria, oribatid mites, nematodes, and springtails (Bardgett 2005). We included
279 plants since they are the primary producers and their diversity and identity drive the functioning and
280 the stability of most terrestrial ecosystems (Hooper, 1997; van der Heijen 1998). We also included
281 litter feeders that contribute to dead material fragmentation, in a particular oribatid mites and
282 springtails. Oribatid mites form one of the most abundant groups of arthropods in soil, (Behan-
283 Pelletier 1999) with up to several hundreds of thousands of individuals per square meter (Norton
284 1990). Springtails are the most numerous group of hexapods in most terrestrial ecosystems
285 (Deharveng 2004). We also included a group of taxa that mineralise the fragmented litter, such as
286 saprophytic fungi and bacteria (Bardgett 2005). Fungi are found in different compartments of the
287 soil trophic web so we classified fungal OTUs into three main functional groups, namely, symbiotic
288 fungi, saprophytic fungi and pathogenic fungi using the FUNguild database (Nguyen *et al.* 2016).
289 Symbiotic fungi represent a pivotal group in the soil ecosystem because over 90% of terrestrial
290 plant families benefit from symbiotic associations between their roots and fungi (Wang & Qiu
291 2006). Moreover, in arctic and alpine systems, 60% to 80% of the nitrogen available for plants is
292 supplied by mycorrhizal fungi (Bjorbækmoet *et al.* 2010). Bacteria also contribute to this supply by
293 fixing atmospheric nitrogen (Bonfante & Anca 2009; Haq *et al.* 2014). Finally, we included a group
294 of predators, here nematodes, the most abundant belowground multicellular animals (Bardgett
295 2005). Nematode OTUs were divided into bacterivore nematodes and herbivore/fungivore
296 nematodes using the NEMAguild database (Nguyen *et al.* 2016). In summary, the nine groups
297 included in this study were: plants, symbiotic fungi, pathogenic fungi, saprophytic fungi,

298 bacterivore nematodes, herbi/fungivore nematodes, bacteria, springtails, and oribatid mites. Most of
299 these groups interact via trophic interactions, so that this study case matches the simulations
300 described above, but not all of them. For the sake of clarity, we will hereafter refer to them as
301 trophic groups.

302 Environmental characteristics – Mean annual soil temperature was estimated from field
303 meteorological stations placed at the centre of each plot. We also estimated growing season length
304 (GSL) and number of frost days based on daily maps of snow cover at 15 m resolution for 5 years
305 falling between 2000 and 2014 and air temperature values extracted from the SAFRAN
306 meteorological model developed by Meteo France for the French Alps (Durand *et al.* 2009). More
307 methodological details and validation results for the snow cover model are available in Carlson *et*
308 *al.* (2015). For each sub-plot, topsoil (0-10 cm) characteristics were determined from the average
309 values obtained from three soil samples collected in July/August 2012, air-dried and then sieved at
310 2mm. Fine-scale topography and associated parameters (topographic wetness index and slope) were
311 inferred from airborne LIDAR data acquired the year of sampling. Mean soil pH over the gradient
312 was 5.40 (sd 0.300) whereas mean soil temperature over the year was 6.06°C (sd 2.84). The
313 environmental distances between sub plots were estimated with Euclidean distances from the first
314 two axes of a principal component analysis run for all produced (and normalised) environmental
315 variables (the variance captured by the first two axes was 34% and 25% respectively, the first axis
316 roughly represented the climatic conditions whereas the second axis roughly represented the soil
317 conditions, see Appendix 2 for more details).

318

319 **Results**

320 *Validation of the statistical method* – Our simulations showed that trophic interactions produce
321 significant relationships between β -diversity on consecutive trophic levels. Moreover, the Glasso
322 method detected the conditional relationships between the β -diversity of the different trophic groups
323 corresponding to their trophic position in the network (Fig. 1b) contrary to the marginal correlations

324 (Fig. 1c). The median of both marginal and partial correlation coefficients between pairs of trophic
325 levels decreases with the shortest path length between these trophic levels. Nevertheless, while the
326 median of the marginal correlation coefficients (Fig. 1e) decreased slowly (the distribution of
327 marginal correlation coefficients overlapped), the median of the partial correlation coefficients (Fig.
328 1d) was close to 0 once the trophic level distance was higher than 1. In other words, marginal
329 correlation analyses detected spurious correlation between non-adjacent trophic levels, but this bias
330 was strongly alleviated when considering partial correlations. Although these simulation results
331 remain qualitative, they demonstrate that specialised biotic interactions between trophic group leave
332 detectable imprints on compositional patterns and that these patterns can be detected using our
333 method. Changing the shape of the relationship linking the probability of presence of a consumer
334 species with its number of available prey species did not alter this conclusion (Fig. S4).

335

336 *β -diversity modelling of empirical soil communities* – In the French Alps, the partial correlations
337 estimated between the β -diversity of each predefined trophic group and environmental distances
338 were all positive (Fig. 2, Fig. S5, Fig. S6, table S2). The estimated partial correlation network had a
339 connectance of 0.618 and was composed of 34 undirected edges (i.e. partial correlation coefficients
340 > 0) out of 55 possible edges and 11 nodes (9 trophic groups and 2 environmental variables).

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

346 The probability of observing a non-null partial correlation between the β -diversity of a trophic
347 group and the environmental distance was 0.44 (8 edges linking environmental nodes to the trophic
348 group nodes and 18 potential edges) whereas the probability of observing a link between the β -
349 diversity of any two trophic groups was 0.69 (25 edges and 36 potential edges). Since the variables

350 associated with disconnected nodes are conditionally independent and that conditionally
351 independent variables cannot causally influence each other, this highlights the reduced influence of
352 environmental variables on the β -diversity of the trophic groups.

353

354 **Discussion**

355 In this study, we proposed a method for dissecting the joint spatial structure of multiple trophic
356 groups. This method builds on observed patterns of β -diversity in multiple trophic groups to infer
357 the conditional dependencies between pairs of groups and with the environment, in order to
358 pinpoint potential biotic interactions. Simulations confirmed that our method is able to recover the
359 overall structure of a trophic network using partial correlations. This method does not directly infer
360 the interaction network at species level, and the inferred conditional dependencies at the group level
361 do not imply causality. A similar method for producing directed networks is path analysis (Wright
362 1921; Shipley 2000 application on soil diversity Schuldt *et al.* 2017). However, the ability of path
363 analysis to draw causal inference is controversial (Shipley 2000 but see Dawid 2010; Bollen &
364 Pearl 2013). The correlative method presented here should help interpret a wide range of multi-
365 trophic biodiversity patterns. Although our approach is likely to be sensitive to the effect of a
366 missing predictor (since the structure of the partial correlation network would be affected by the
367 addition of a variable), environmental DNA sampling should facilitate comprehensive assessments.
368 One key issue remains the mapping of OTUs into functional groups, which is only possible using
369 integrative biology knowledge combined with large and comprehensive databases. An interesting
370 perspective for this method is that it could also be used to study temporal changes in biodiversity
371 (i.e., temporal β -diversity) using environmental DNA approaches (Bohan *et al.* 2017).

372 When applied to soil multi-trophic diversity along an elevation gradient of the French Alps, we
373 were able to quantify the relative importance of biotic interactions and the environment in shaping
374 the spatial structure of the meta-communities. Pairwise environmental distances displayed a low
375 correlation with the β -diversity of each group (as measured with the few non-zero partial

376 correlations). In other words, the ecological community was found to be shaped more by biotic
377 interactions than by abiotic environmental constraints. This result is rather surprising given the
378 sharpness of the elevational gradient, and the expected importance of environmental filtering in
379 shaping above and below-ground communities along elevation gradients (Meynard *et al.* 2013).
380 However, many previous studies have focused on intra-guild biotic interactions, or on
381 environmental effect only, and they have ignored the importance of inter-guild interactions (e.g.
382 Chalmandrier *et al.*, 2015). As our climatic and soil properties were sampled at plot level, they
383 might not have been measured at the appropriate scale to reflect the fine conditions experienced by
384 below-ground organisms (Falconer *et al.* 2015; Baveye *et al.* 2016; Zinger *et al.* 2017). A single
385 plot-scale measure of abiotic conditions may not be sufficient to explain the β -diversity of
386 organisms with heterogeneous sizes and capture the fine-scale heterogeneity of soil conditions.
387 Additionally, we cannot rule out the fact that some relatively important missing environmental
388 factors might explain the low predictive power of environmental distances (e.g. phosphorous for
389 symbiotic mushrooms, Liu *et al.* 2012; Camenzind *et al.* 2014). Nevertheless, while the greater β -
390 diversity was due to true-turnover (a turnover measure independent of variation of species richness;
391 on average, 80% of the β -diversity across trophic groups), climatic and soil properties had a
392 stronger influence on the true-turnover component of the β -diversity of the different trophic groups.
393 The approach described here should help interpret a wide range of multi-trophic biodiversity
394 patterns and yield new testable hypotheses. For example, in multiple pairs of trophic groups we
395 found strong spatial associations which can be interpreted in light of functional associations. In the
396 soil, plants are directly affected by symbiotic/pathogenic fungi and root herbivores, whereas the
397 complex network of detritivorous organisms affects them indirectly (Bardgett 2005; Wardle *et al.*
398 2011). Our method showed that plant β -diversity was strongly linked to the β -diversities of
399 symbiotic fungi, pathogenic fungi, oribatid mites and bacterivore nematodes. While the links with
400 the two groups of fungi most likely reflect the strong direct associations between these groups and
401 the vegetation structure, the link with oribatid mites may be explained by the fact that this group

402 feeds on plant litter fungi, especially saprophytic fungi (Schneider *et al.* 2004, Crowther *et al.* 2012;
403 2011). The graphical lasso method detected this link showing that changes in the composition of
404 saprophytic fungi lead to a change in the oribatid mite assemblages. As expected, the β -diversity of
405 bacteria correlated to that of bacterivore nematodes, which reflects this known trophic interaction
406 (Ettema 1998; Wardle 2006). Moreover, the β -diversity of herbi/fungivore nematodes correlated to
407 that of symbiotic fungi. The link between the β -diversity of oribatid mites and springtails might be
408 explained by mite predation of springtails (Ferguson & Joly 2002). Interestingly, we revealed a link
409 between the β -diversity of oribatid mites and symbiotic fungi. This result suggests that mite
410 assemblages could be influenced by fungi spatial distribution through trophic interactions, which
411 have been so far very poorly documented (Gange & Brown 2003). Interestingly, our analysis also
412 showed a strong partial correlation (the strongest partial correlation: 0.365) between the β -
413 diversities of saprophytic fungi and bacteria. Many clades of these two groups exploit the same
414 resource (in particular cellulose, which represents 30-50 % of plant dry weight, Whipps 2001; De
415 Boer *et al.* 2005) which thus creates an indirect relationship between bacteria and saprophytic fungi,
416 through an unmeasured confounding effect. The relationship uncovered between bacteria and
417 symbiotic fungi could be attributed to the fact that bacteria can assist mycorrhiza by colonising the
418 extraradical hyphae or by living in the cytoplasm of mycorrhizal fungi (Bonfante *et al.* 2009; Haq
419 *et al.* 2014).

420

421 **Conclusions**

422 The rise of environmental DNA metabarcoding and the ever-increasing availability of databases on
423 species co-occurrence have opened up a new era in quantitative and predictive ecology.
424 Comprehensive species lists of taxa are necessary, but not sufficient to provide information on how
425 co-occurring species interact and whether multi-trophic interactions shape community assembly. We
426 have developed a method that could reveal how trophic groups influence each other and respond to
427 environmental variation. As such our method helps uncover potential causes of the compositional

428 turnover of species groups from a multi-trophic interaction perspective. Gathering informative
429 expert knowledge from literature review or using automatic methods should then pave the way to
430 understanding the fine-scale structure of multi-trophic assemblages and obtaining a more holistic
431 picture of biodiversity.

432

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442

443 **Competing interests**

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

448

450 **Figure caption**

451 **Figure 1: Design and results of the simulation assessing the impact of biotic interactions on the**
452 **marginal and partial correlation of the β -diversity values of different trophic levels.** (a) the
453 trophic network used for the simulation, composed of six trophic levels. The indegree of each node
454 is one plus an integer randomly drawn from a Poisson law of parameter 1.0 (except for the basal
455 species). (b) Partial correlation network built using the median values of the partial correlations
456 (inferred using the graphical lasso) between the β -diversity values of different trophic levels. (c)
457 Marginal correlation networks built using the median values of the Pearson correlations between the
458 β -diversity values of different trophic levels. (d) Partial correlation coefficient (inferred using the
459 graphical lasso) between the β -diversity values of two trophic levels as a function of the shortest
460 path length between these trophic levels. (e) Marginal Pearson correlation coefficient between the
461 β -diversity values of two trophic levels as a function of the shortest path length between these
462 trophic levels.

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

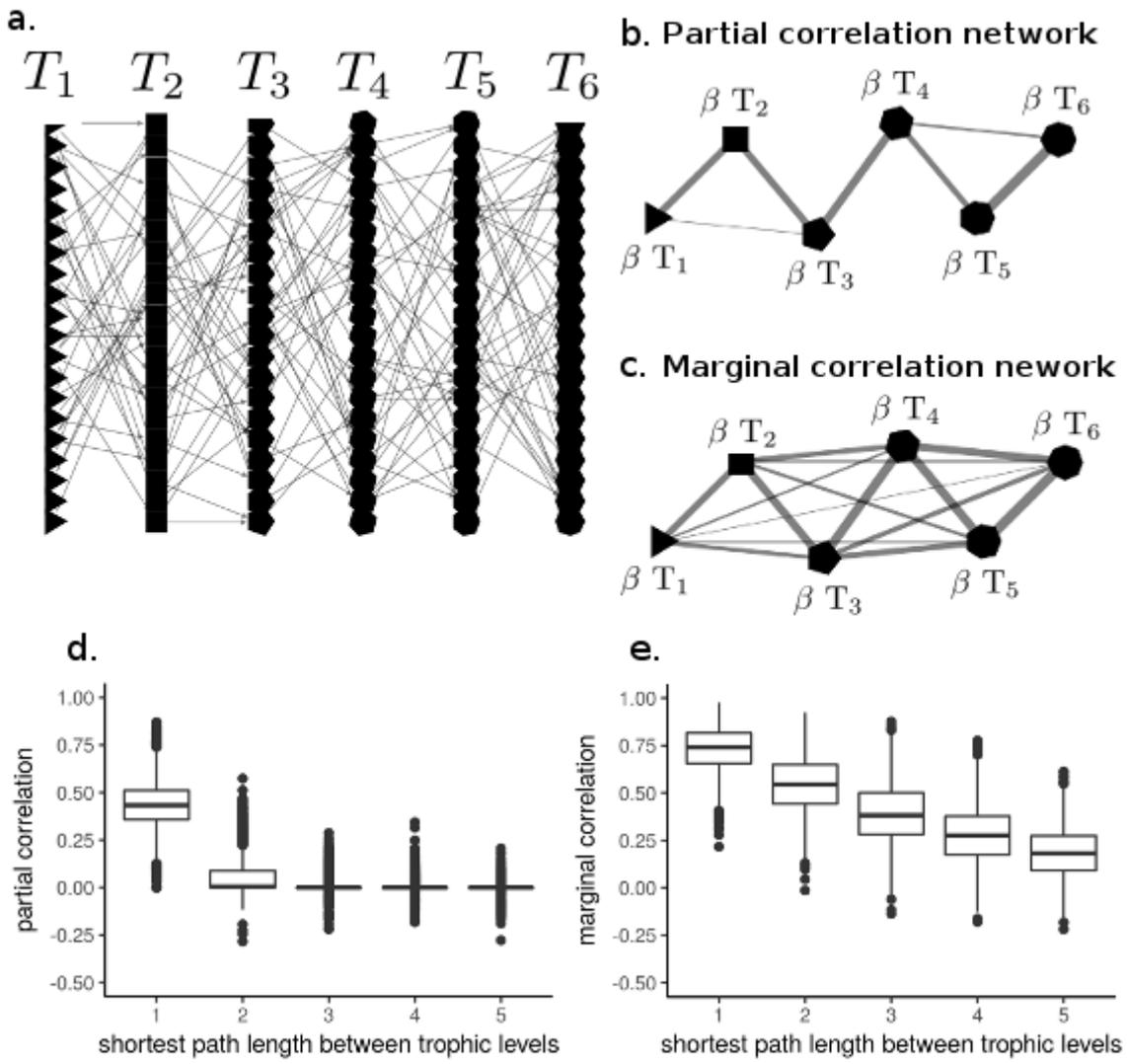
470

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

476

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478



481 **Figure 1**

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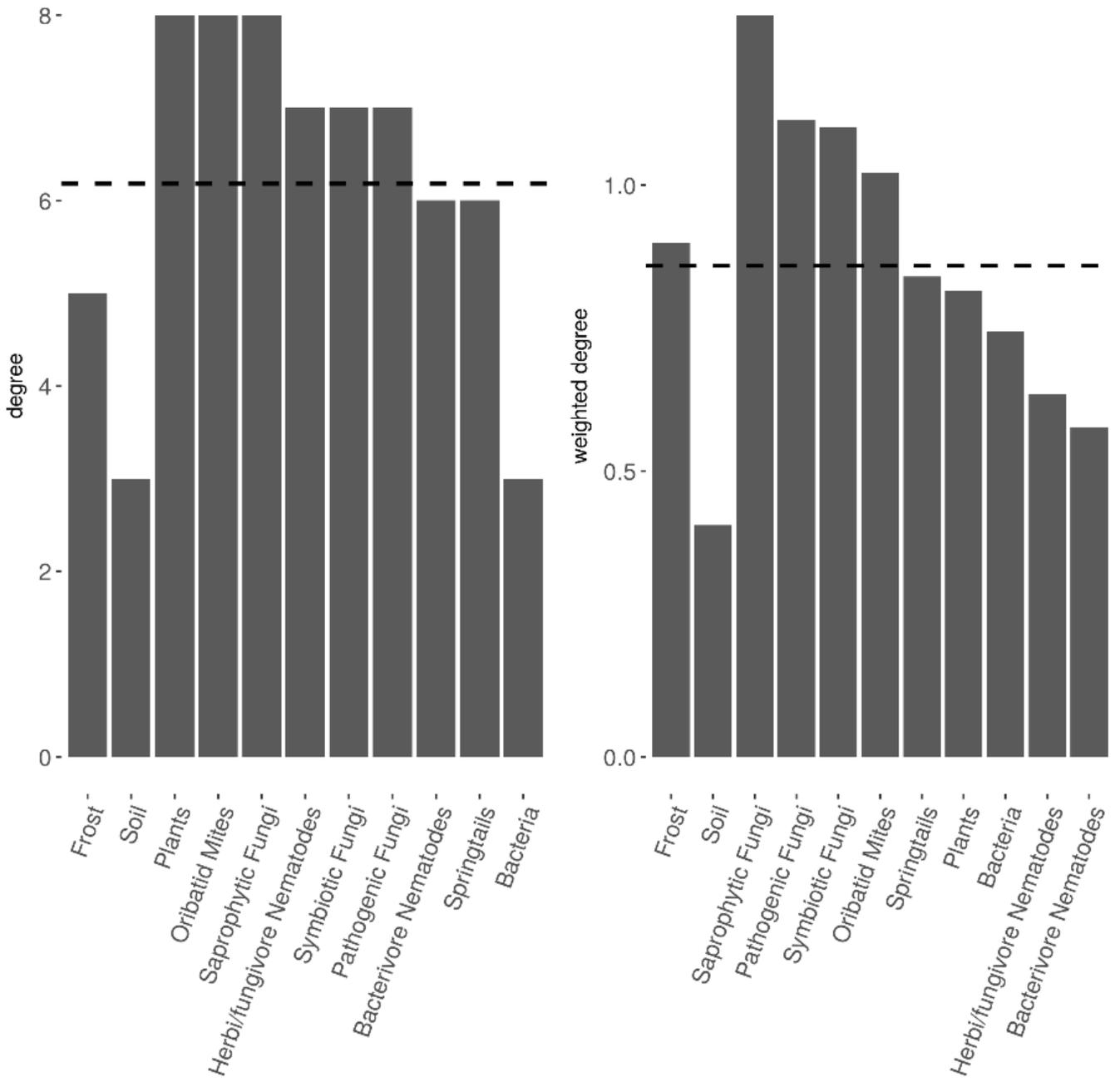
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506 **Figure 3**

507

508 **References**

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1 Appendices

2 Appendix 1 : Molecular and bioinformatics analyses

3 Data were then curated using the OBITools software package (Boyer *et al.* 2016) together with customs R scripts (R
4 Core Team 2015) following the procedure described in Zinger *et al.* (2017). Paired-end reads were assembled, assigned
5 to their respective samples/marker and dereplicated. Low-quality sequences were excluded. For the remaining ones we
6 computed pairwise dissimilarities between sequences (i.e. the number of mismatches, allowed to be 0-3) using the
7 Sumatra algorithm (Mercier *et al.* 2013), and formed Operational Taxonomic Units OTUs using the Infomap
8 community detection algorithm (Rosvall & Bergstrom 2008). Abundance of OTUs was defined as the sum of read
9 abundances of sequences belonging to them. In subsequent analyses, each OTU was represented by its most abundant
10 sequence. Each OTU was assigned a taxonomic clade using the *ecotag* program (Boyer *et al.* 2016) using a set of
11 reference databases to refine taxonomic annotations. (e.g. GENBANK, UNITE database, Abarenkov *et al.* 2010) We
12 paid particular attention to minimize PCR/sequencing errors, contaminant and false positive sequences as well as
13 potential non-functional PCRs by using the procedure described in Zinger *et al.* (2017). PCR replicates were finally
14 summed for each samples.

	Bacteria	Eukaryota	Fungi	Viridiplantae
Primers set				
Targeted region	V5-V6 regions, 16S rRNA gene	V7 region, 18S rRNA gene	ITS1	P6 loop of the chloroplast trnL intron
Forward primer (5'–3')	GGATTAGATACCC TGGTAGT [‡]	TTTGTCTGSTTAATTSCG [§]	CAAGAGATCCGTTGTT GAAAGTK [†]	GGGCAATCCTGAG CCAA [¶]
Reverse primer (5'–3')	CACGACACGAGCT GACG [‡]	TCACAGACCTGTTATTGC [§]	GGAAGTAAAAGTCGTA ACAAGG ^{§§}	CCATTGAGTCTCT GCACCTATC [¶]
PCR conditions				
Number of cycles	35	45	40	40
PCR cycles characteristics [†] (Denaturation, Annealing, Elongation – Final elongation)	95°C(30s), 57°C(30s), 72°C(90s) – 72°C(7min)	95°C(30s), 45°C(30s) 72°C(60s) – 72°C(7min)	95°C (30 sec), 55°C (30 sec), 72°C (60s) – 72°C (7 min)	95°C(30s), 50°C(30s), 72°C(60s) – 72°C(7min)
Illumina platform	MiSeq 2x250	HiSeq 2x150	MiSeq 2x250	HiSeq 2x100
Reads and Otus statistics				
Initial number of OTUs	25383	7242	4193	2153

Final number of OTUs	24058	5833	2987	555
Initial number of reads	5042640	68893592	4159074	37509301
Final number of reads	4357053	61818803	3626819	35950935

15 † this study

16 §§ White, T. J., T. Bruns, S. Lee, and J. W. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315-322 In: PCR Protocols: A Guide to Methods and Applications, eds. Innis, M. A., D. H. Gelfand, J. J. Sninsky, and T. J. White. Academic Press, Inc., New York.

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17 ‡ Fliegerova, K., Tapio, I., Bonin, A., Mrazek, J., Callegari, M. L., Bani, P., *et al.* (2014). Effect of DNA extraction and
18 sample preservation method on rumen bacterial population. *Anaerobe*, **29**, 80-84.

19 § Guardiola, M., Uriz, M. J., Taberlet, P., Coissac, E., Wangenstein, O. S., & Turon, X. (2015). Deep-Sea, Deep-
20 Sequencing: Metabarcoding Extracellular DNA from Sediments of Marine Canyons. *PLoS One*, **10**, e0139633.

21 ¶ Taberlet, P., Gielly, L., Pautou, G., & Bouvet, J. (1991). Universal primers for amplification of three non-coding
22 regions of chloroplast DNA. *Plant Molecular Biology*, **17**, 1105-1109.

23 †† All PCRs were preceded by an initial denaturation at 95°C (10 min)

24 **Table S1** Markers characteristics, PCR conditions and sequencing technology

25 *Appendix 2 : Climatic and soil variables*

26 Climatic variables: We described the bioclimatic conditions of the gradient using four variables describing both thermal
27 and nival regimes: soil temperature, solar radiations, Growing Season Length (hereafter “GSL”) and number of frost
28 days. Mean annual soil temperature was recorded using HOBO stations located at the center of each sampling site.
29 Solar radiation was averaged from simulations of solar radiation using a 2-m digital elevation model (DEM) (Carlson et
30 al. 2015) derived from a LIDAR acquisition. The number of frost days, i.e. the number of snow-free days with air
31 temperature below 0°C, was computed as described in Carlson et al. (2015). GSL, the number of snow-free days with a
32 daily mean air temperature over 0°C between snow melt-out and August 15, was computed as described in
33 Chalmandrier et al. 2016.

34 Topographical variables: Slope, Topographic Wetness Index (TWI) and Topographic Position Index (TPI) were inferred
35 with the DEM derived from the airborne LiDAR data acquired the year of sampling.

36 Soil analyses were conducted in summer 2012 from soil cores taken at the center of each subplot (1m25x1m25). Each
37 of them were weighed and 5mm-sieved (Legay et al. 2014) and processed for quantifying soil moisture, soil organic
38 matter content, pH, soil texture (gravel mass and apparent density after 2mm sieving) and soil nutrients (ammonium
39 (soil NH₄⁺), nitrates (soil NO₃⁻), total dissolved nitrogen (TDN), and dissolved organic nitrogen (DON)) from 0.5m
40 K₂SO₄ soil extracts (Jones et al. 2004; Legay et al. 2014). Soil subsamples were added 100 mL distilled water to
41 saturate each soil core and calculate the waterfilled pore space (WFPS) and then air dried and ground to measure total

42 soil C and N (Legay et al. 2014). Microbial biomass nitrogen (N) was measured using the chloroform-fumigation
 43 extraction technique of Vance et al. 1987). Potential N mineralization rates were estimated using anaerobic incubations
 44 of fresh soil subsamples (Legay et al. 2014). Potential ammonium and nitrates leaching was measured from the
 45 percolate of a site central supplementary core leached in a given volume of distilled water (Legay et al. 2016).

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	PCA axis 1	PCA axis 2
pH	-0.417	-0.368
Gravel mass	0.791	-0.277
Apparent density	0.235	-0.781
Total porosity rate	0.264	0.789
Water Filled pore space	-0.76	-0.23
Leaching NO3	-0.398	-0.029
Leaching NH4	0.0901	0.791
N rate	0.0542	-0.933
C rate	-0.587	0.713
C/N ratio	-0.332	0.896
Rate organic matter	0.332	0.863
N NO3	-0.341	-0.368
N NH4	-0.512	0.264
N TDN	0.257	-0.106
N NH4 product	-0.158	-0.0632
Year soil temperature	-0.823	0.00538
FrostDays	-0.858	-0.196
Growing Season Length	-0.983	-0.0919
Topographic wetness index	-0.652	-0.0833
slope	0.28	-0.343
Topographic position indexPI10m_mean_topo	0.35	0.101
Altitude Digital Elevation Model	0.98	0.0867
Mean solar radiation	-0.964	-0.058
Variance Growing Season Length	0.834	0.347

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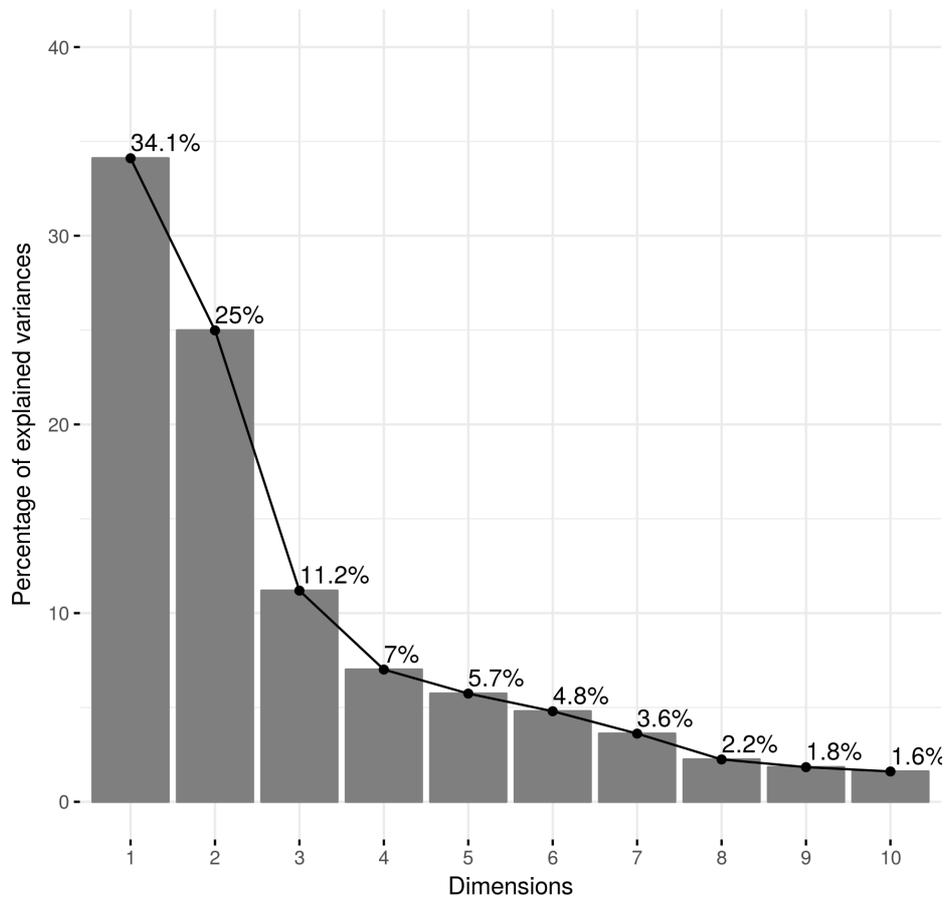
48 **Table S2** Correlations between the environmental variables and the first two axes of the Principal Component Analysis

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55 **Figure S1** Scree plot of eigenvalues on the principal component on environmental variables

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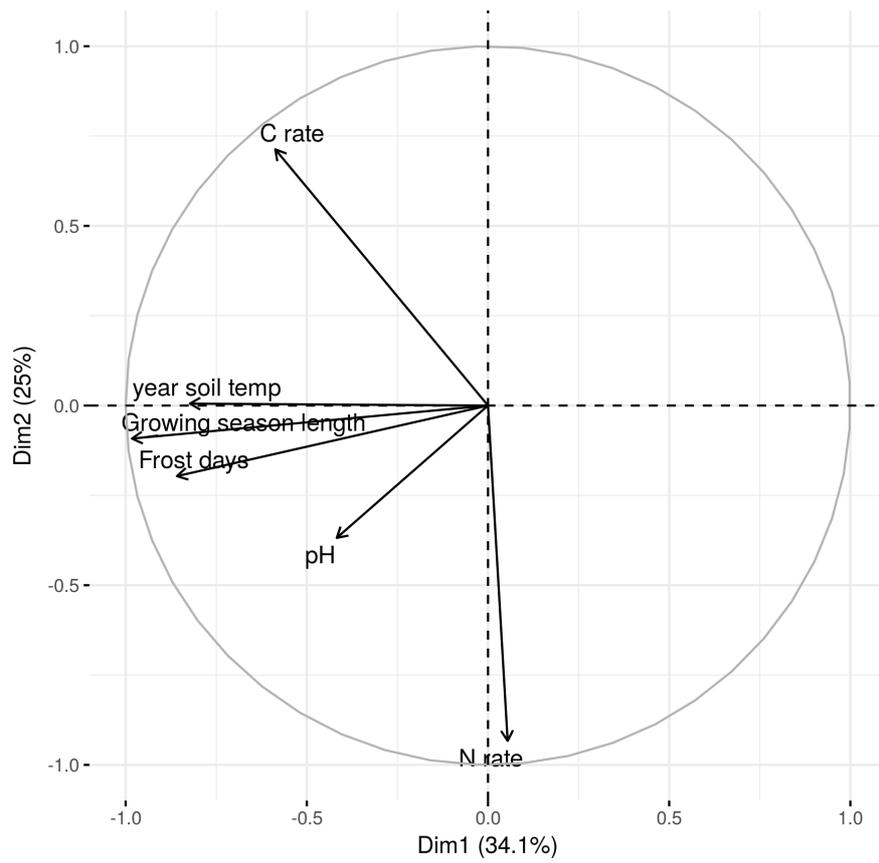
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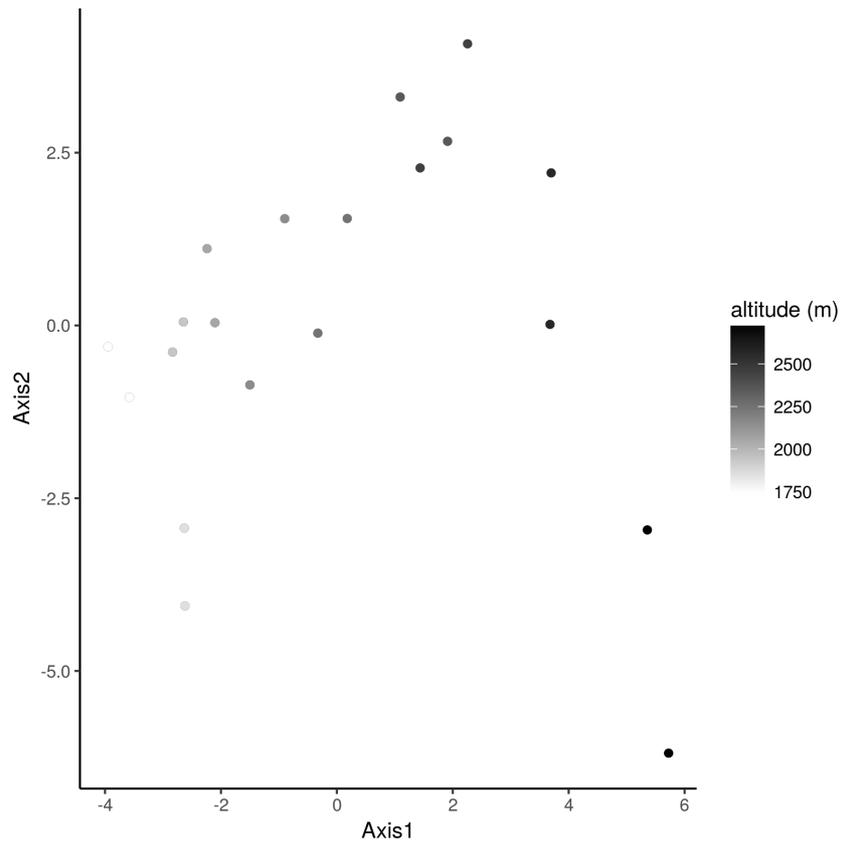
69 **Figure S2** Correlation circles of the principal component analysis. Only 6 variable over the 24 variables are represented

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75 **Figure S3** Plots represented on the first factorial plan on the principal component analysis. The color of the points
76 correspond to their altitude.

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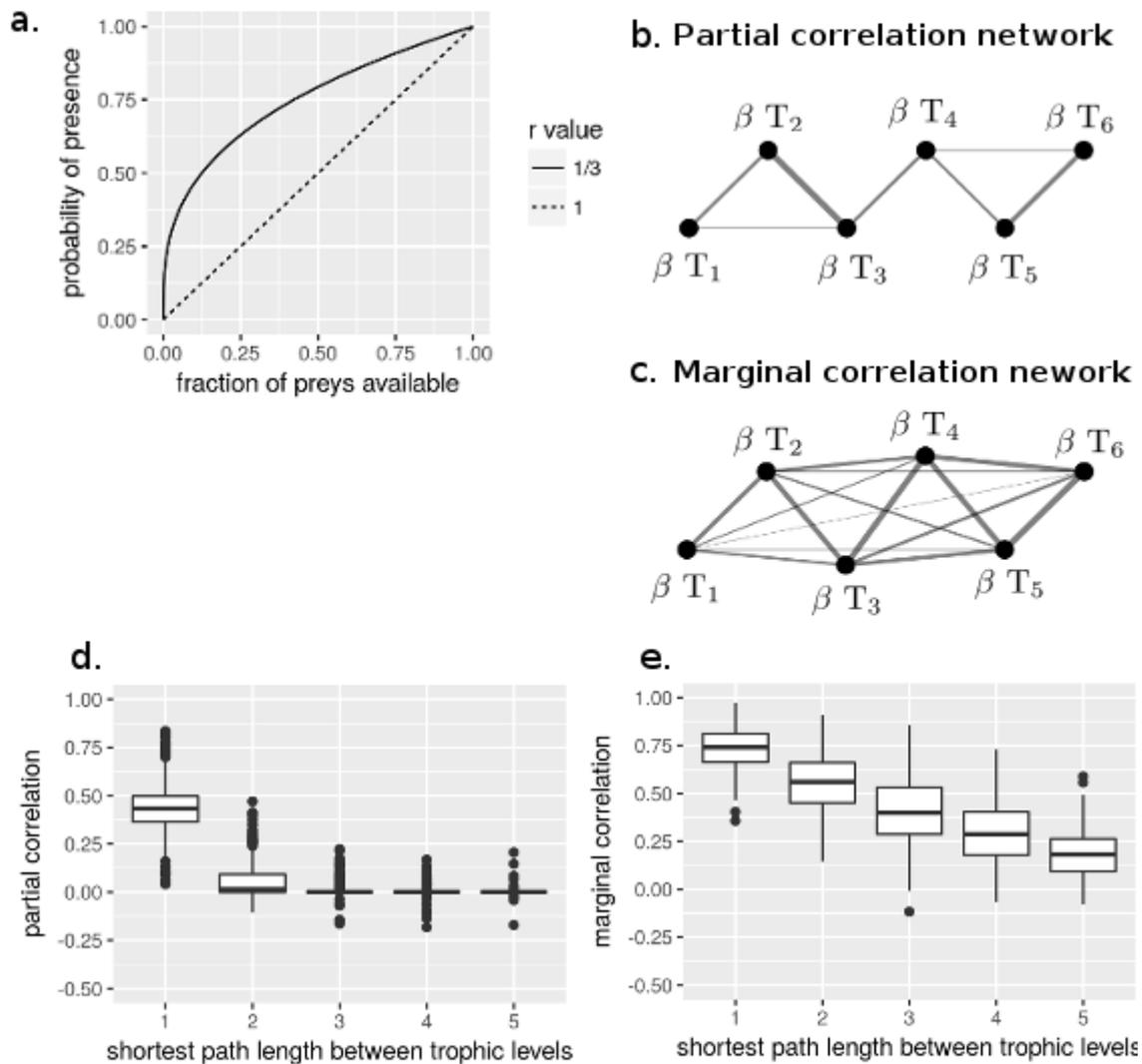
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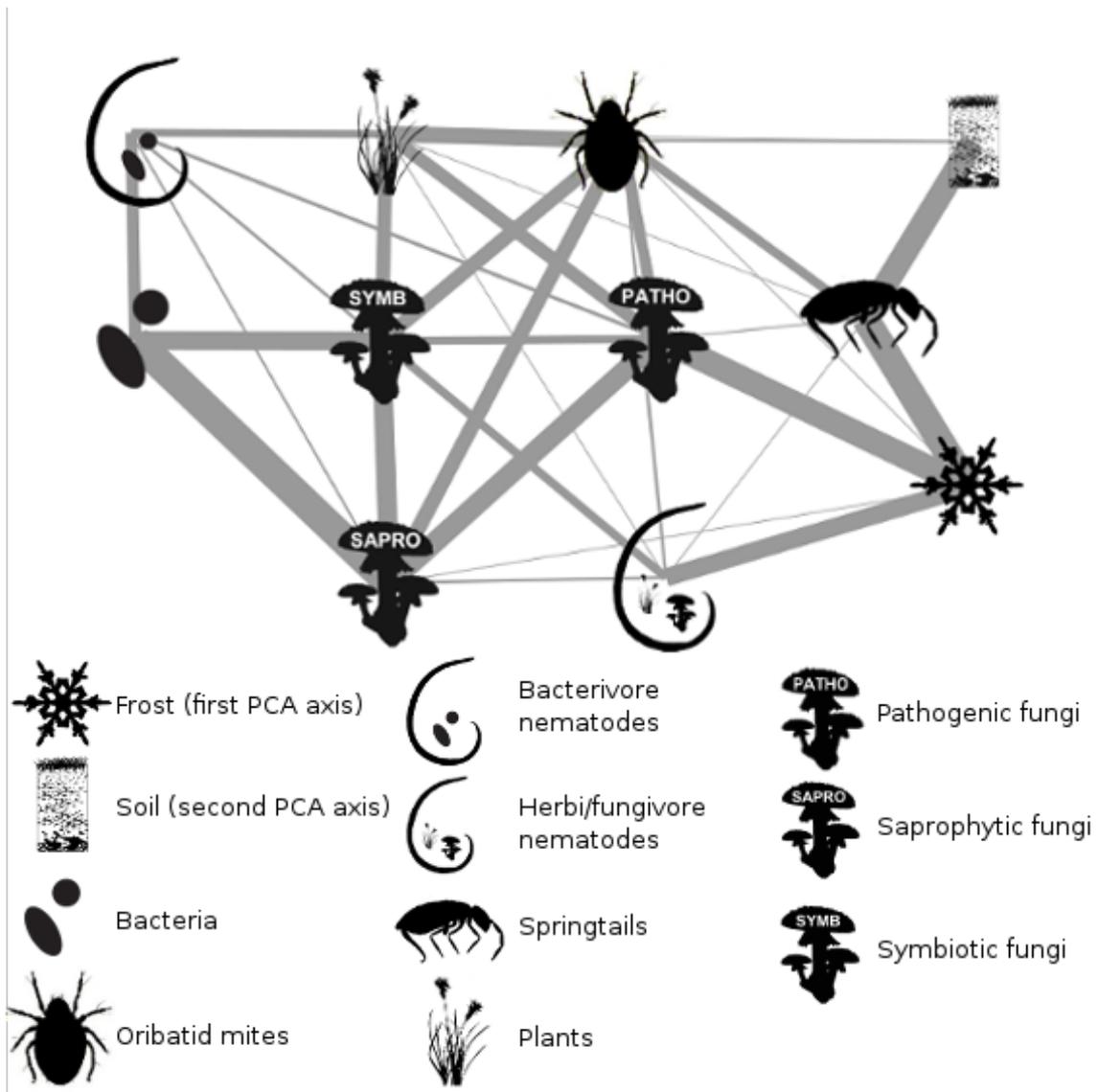
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94 **Figure S4** Design and results of the simulation assessing the impact of biotic interactions on the marginal and partial
 95 correlation of the β -diversity values of different trophic levels for another shape of the relationship linking the
 96 probability of presence of a consumer species with its number of available preys. (a) Two different shapes of the
 97 relationship, the value used in the following plots is $r=1/3$, while the main text $r=1$ (b) Partial correlation network built
 98 using the median values of partial correlations (inferred using Glasso) between the β -diversity values of different
 99 trophic levels. (c) Marginal correlation networks built using the median values of the Pearson correlations between the
 100 β -diversity values of different trophic levels. (d) Partial correlation coefficient (inferred using the graphical lasso)
 101 between the β -diversity values of two trophic levels in function of the shortest path length between these trophic levels.
 102 (e) Marginal Pearson correlation coefficient between the β -diversity values of two trophic levels in function of the
 103 shortest path length between these trophic levels.

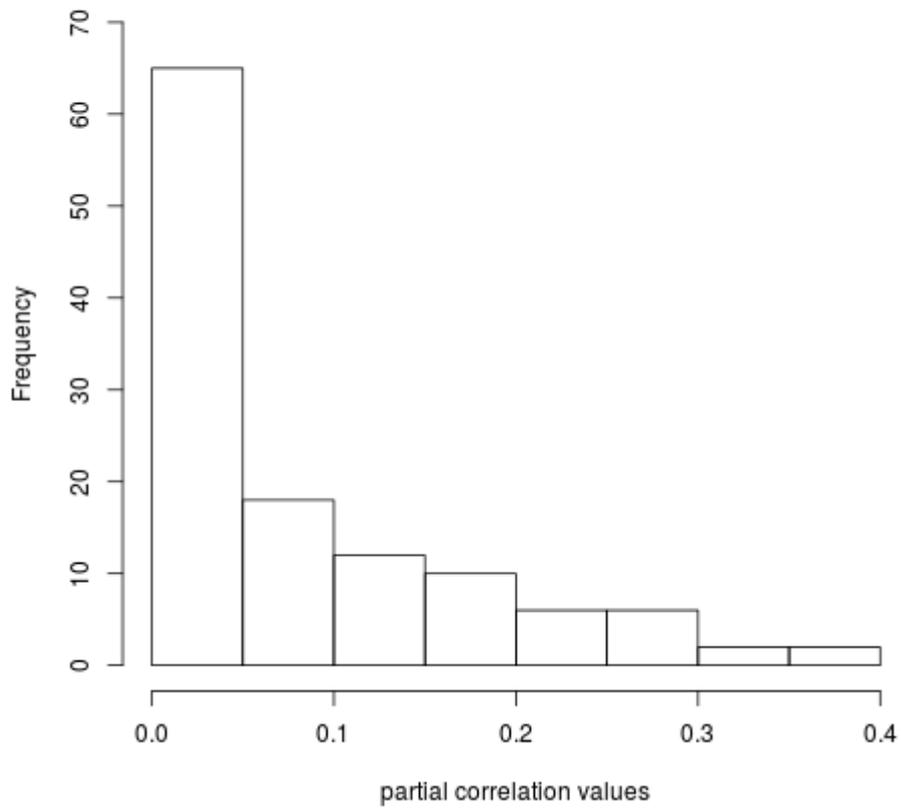
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107 **Figure S5** Undirected partial correlation network between β -diversity of the major trophic groups constituting of soil
 108 biodiversity and environmental distances. Each node represent the β -diversity of a trophic group or an abiotic
 109 environmental distance. Each edge represent a non-nul partial correlation between the variables associated to each node
 110 and was estimated using a graphical lasso. Consequently, if two nodes are disconnected, then the associated variables
 111 (β -diversity or environmental distances) are conditionally independent. The connectance of the network is 0.618.

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122 **Figure S6** Histogram of the partial correlation coefficients estimated between β -diversity of major trophic groups
123 constituting of soil biodiversity and environmental distances. Partial correlation coefficients are all positive.

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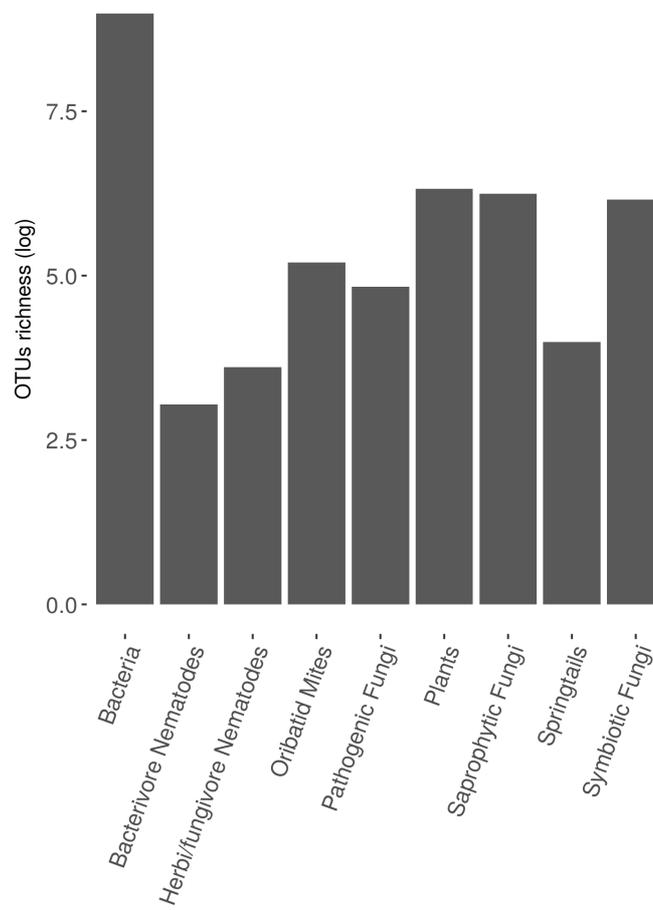
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141 **Figure S7** Histogram of the natural logarithm of the numbers of Operational Taxonomic Units (OTUs) assigned to each
 142 trophic group.

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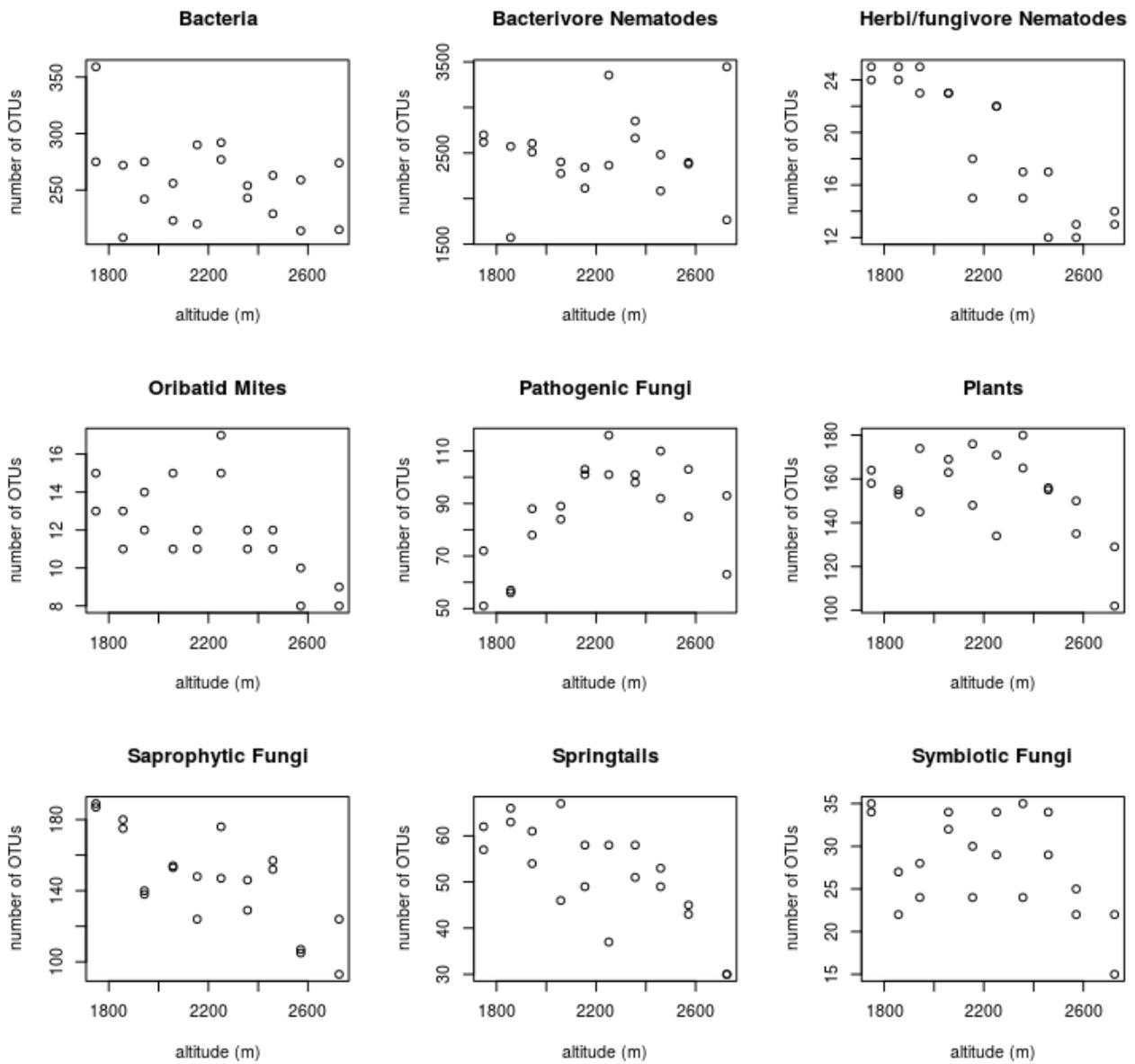
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156 **Figure S8** Number of OTUs per trophic group in function of the altitude of the plots

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	Frost	Soil	Plants	Bacteria	Herbi/Fun givre nematodes	Bacterivor e nematodes	Oribatida	Saprophyt ic fungi	Symbiotic fungi	Pathogeni c fungi	Springtails
Frost	0	0	0	0	0.222	0	0.0358	0.0149	0	0.3	0.327
Soil	0	0	0.0347	0	0	0	0.0807	0	0	0	0.29
Plants	0	0.0347	0	0	0.0274	0.101	0.197	0.0914	0.169	0.166	0.0284
Bacteria	0	0	0	0	0	0.149	0	0.365	0.23	0	0
Herbi/Fun givre nematodes	0.222	0	0.0274	0	0	0.0833	0.084	0.084	0.11	0	0.0238
Bacterivor e nematodes	0	0	0.101	0.149	0.0833	0	0	0.0708	0.0739	0.0994	0
Oribatida	0.0358	0.0807	0.197	0	0.084	0	0	0.185	0.182	0.14	0.116
Saprophyt ic fungi	0.0149	0	0.0914	0.365	0.084	0.0708	0.185	0	0.234	0.252	0
Symbiotic fungi	0	0	0.169	0.23	0.11	0.0739	0.182	0.234	0	0.102	0
Pathogeni c fungi	0.3	0	0.166	0	0	0.0994	0.14	0.252	0.102	0	0.0541
Springtail s	0.327	0.29	0.0284	0	0.0238	0	0.116	0	0	0.0541	0

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168 **Table S3** Partial correlation between β -diversity values of trophic groups constituting of soil diversity and abiotic
169 environmental distances inferred using Glasso.

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	Frost	Soil	Plants	Bacteria	Herbi/Fun givre Nematode s	Bacterivor e nematodes	Oribatida	Saprophyt ic fungi	Symbiotic fungi	Pathogeni c fungi	Springtails
Frost	1	0.305	0.581	0.405	0.648	0.497	0.672	0.678	0.575	0.772	0.703
Soil	0.305	1	0.392	0.235	0.325	0.0994	0.443	0.33	0.27	0.347	0.545
Plants	0.581	0.392	1	0.644	0.585	0.611	0.775	0.778	0.78	0.774	0.546
Bacteria	0.405	0.235	0.644	1	0.47	0.642	0.688	0.857	0.808	0.687	0.34
Herbi/Fun givre nematodes	0.648	0.325	0.585	0.47	1	0.531	0.64	0.664	0.657	0.626	0.513
Bacterivor e nematodes	0.497	0.0994	0.611	0.642	0.531	1	0.573	0.675	0.656	0.645	0.346
Oribatida	0.672	0.443	0.775	0.688	0.64	0.573	1	0.836	0.818	0.808	0.622
Saprophyt ic fungi	0.678	0.33	0.778	0.857	0.664	0.675	0.836	1	0.888	0.864	0.553
Symbiotic fungi	0.575	0.27	0.78	0.808	0.657	0.656	0.818	0.888	1	0.81	0.476
Pathogeni c fungi	0.772	0.347	0.774	0.687	0.626	0.645	0.808	0.864	0.81	1	0.628
Springtail s	0.703	0.545	0.546	0.34	0.513	0.346	0.622	0.553	0.476	0.628	1

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172 **Table S4** Marginal (Pearson correlation) between β -diversity values of trophic groups constituting of soil diversity and
173 abiotic environmental distances.

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176 *Appendix 3 : Statistical analysis using the true-turnover component of the β -diversity*

177 We ran the statistical analysis on the true turnover component of the β -diversity (Baselga 2010) of each predefined
178 trophic group. while the larger amount of β -diversity was due to true-turnover (Fig. 9) and on average, 80% of the β -
179 diversity across trophic groups. The partial correlations estimated between the true turnover component of the β -
180 diversity of each predefined trophic group and environmental distances were all positive except one coefficient (Fig.
181 S10, Fig. S11, Fig. S12, table S4). The estimated partial correlation network had a connectance of 0.60 and was
182 composed of 33 undirected edges (i.e. partial correlation coefficients > 0) out of 55 possible edges and 11 nodes (9
183 trophic groups and 2 environmental variables). The mean value of non null partial correlation coefficients was 0.133,
184 the median was 0.102 and the maximum 0.459.

185 Saprophytic fungi seemed to be the most influential group in conditioning the β -diversity of the others group (highest
186 degree value, 9, and highest weighted degree value, 1.37, Fig. S12). Environmental variables had a moderate impact on
187 the β -diversity of the trophic groups (degree of 6 for the first PCA axis, 4 for the second PCA axis and whereas the
188 mean degree of the partial correlation network was 6; weighted degree of 1.13 for the first PCA-axis, 0.381 for the
189 second pca axis node whereas the mean value is 0.759).

190 The probability of observing a non-null partial correlation between the β -diversity of a trophic group and the
191 environmental distance was 0.44 (8 edges linking environmental nodes to the trophic groups nodes and 18 potential
192 edges) whereas the probability of observing a link between the β -diversity of any two trophic groups was 0.67 (24 edges
193 and 36 potential edges), highlighting the weaker influence of environmental variables on the true turnover component of
194 the β -diversity of the trophic groups.

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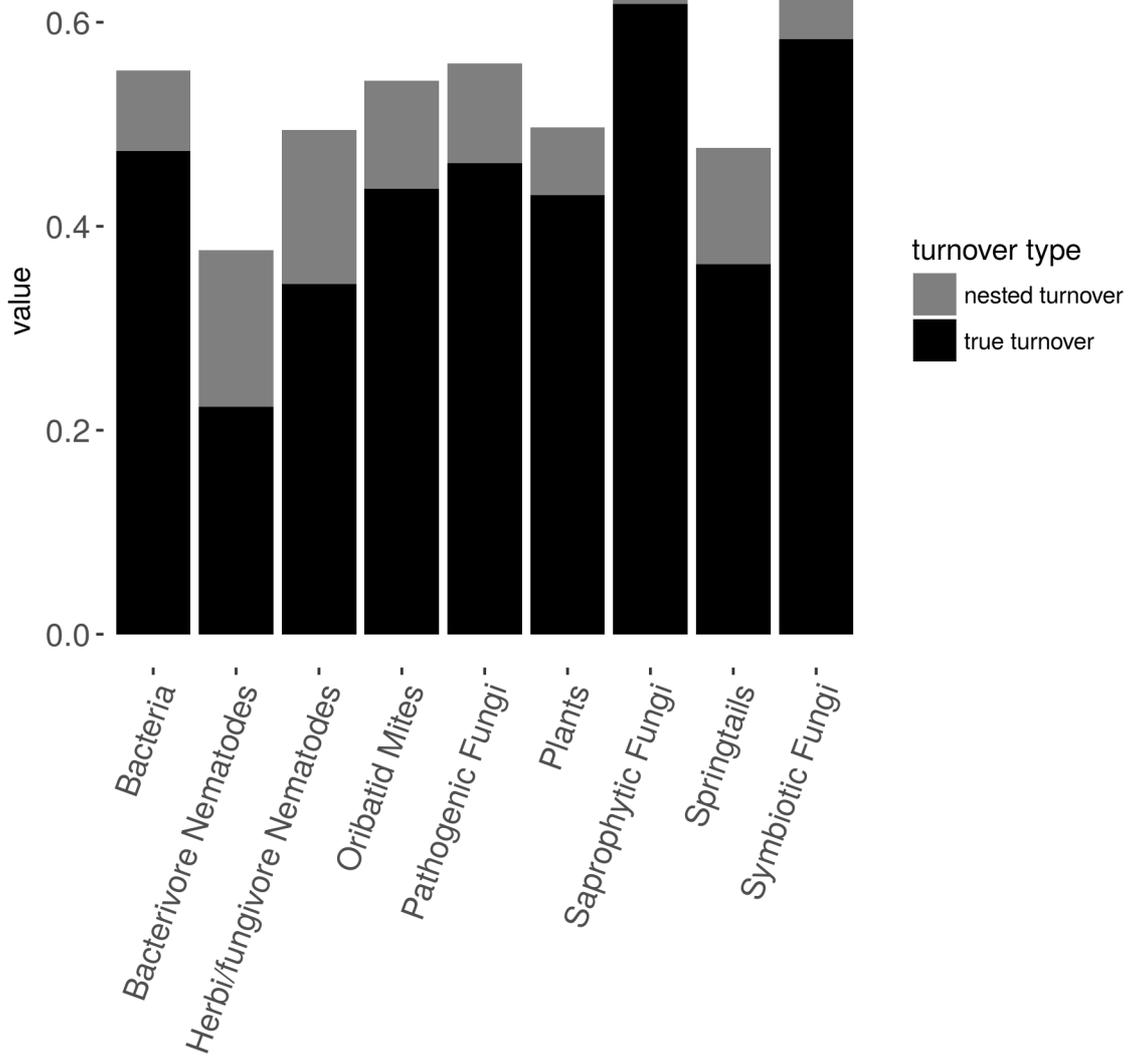
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208 **Figure S9** Mean true turnover and nested turnover components of the Jaccard index for each trophic group.

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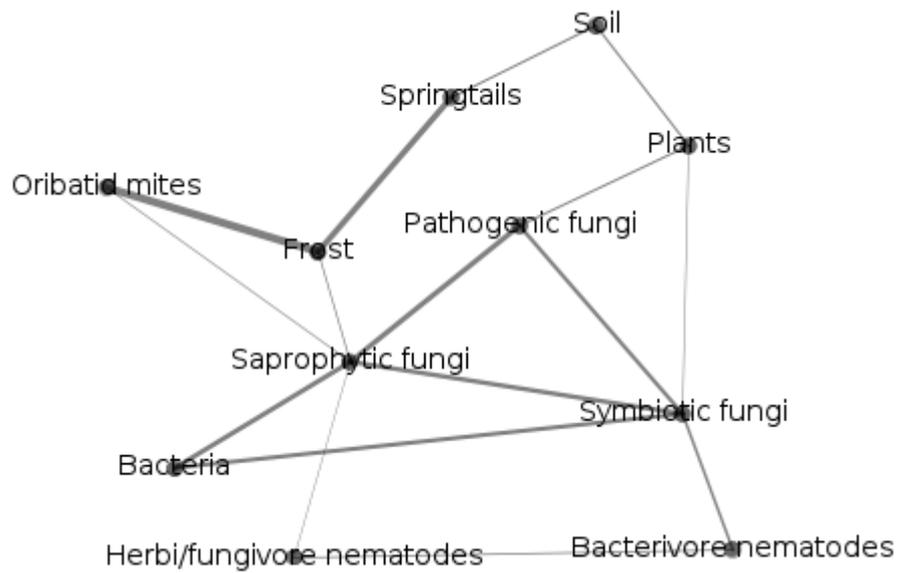
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219 **Figure S10** Undirected partial correlation network inferred by the graphical lasso method between the true turnover
 220 component of the β -diversity of the major trophic groups constituting of soil biodiversity and the environmental
 221 distances. Each node represent the β -diversity of a trophic group or an environmental distance. Here, are only shown the
 222 partial correlations above the median value of the non-null partial correlation coefficients (0.102). The non-filtered
 223 network is presented in Figure S11. Edge thickness is proportional to the value of the partial correlation coefficient and
 224 the partial correlation coefficients are all positive.

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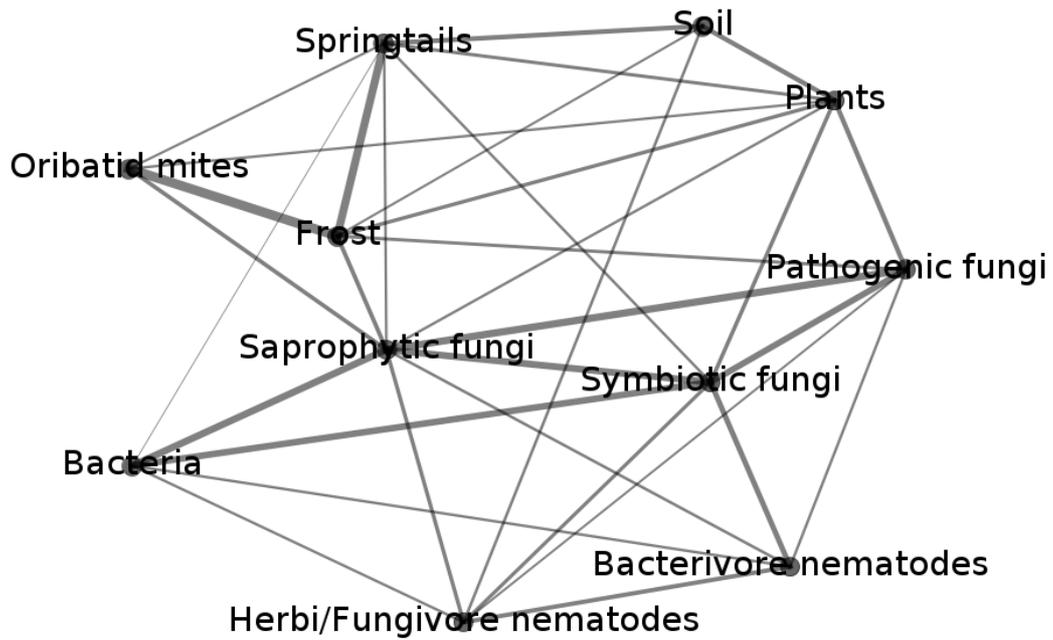
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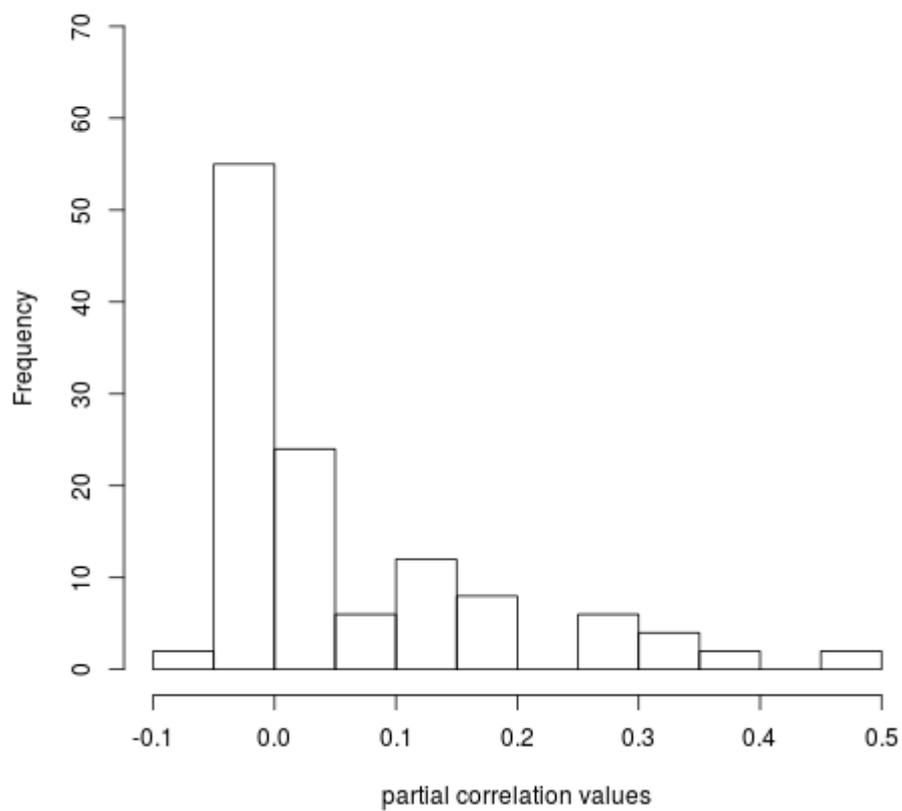
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240 **Figure S11** Undirected partial correlation network inferred by the graphical lasso method between the true turnover
 241 component of the β -diversity of the major trophic groups constituting of soil biodiversity and the environmental
 242 distances. Each node represent the β -diversity of a trophic group or an environmental distance. The connectance of the
 243 graph is 0.600 . Edge thickness is proportional to the value of the partial correlation coefficient and the partial
 244 correlation coefficients are all positive.



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247 **Figure S12** Histogram of the partial correlation coefficients estimated between the true turnover component of the β -
248 diversity of major trophic groups constituting of soil biodiversity and environmental distances. Partial correlation
249 coefficients are all positive.

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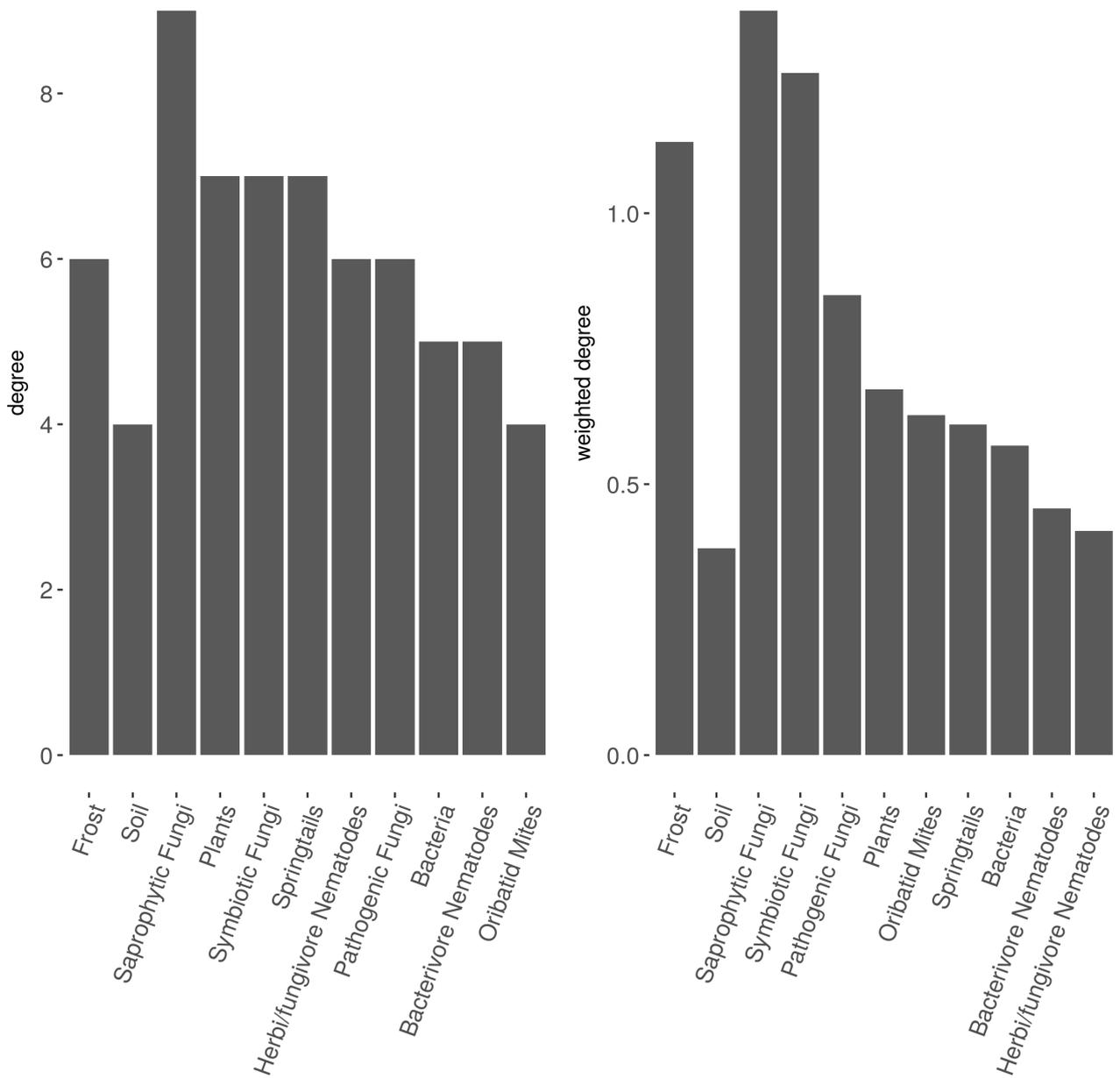
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261 **Figure S13 Properties of the inferred network.** The mean degree (left panel) is the number of neighbors of nodes in a
 262 graph (here, the undirected partial correlation network). It measures the number of variables that are conditionally
 263 dependent to the variable associated to this node. The weighted degree (right panel) is the sum of the partial correlation
 264 coefficients attached to the edges adjacent this node.

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	Frost	Soil	Plants	Bacteria	Herbi/Fun givre nematodes	Bacterivor e nematodes	Oribatida	Saprophyt ic fungi	Symbiotic fungi	Pathogeni c fungi	Springtails
Frost	0	0.0122	0.1	0	0	0	0.459	0.129	0	0.0725	0.359
Soil	0.0122	0	0.0161	0	0.0442	0	0	0	0	0	0.164
Plants	0.1	0.161	0	0	0	0	0.0289	0.0314	0.112	0.162	0.0796
Bacteria	0	0	0	0	0.0327	0.0354	0	0.0302	0.275	0	-0.0744
Herbi/Fun givre nematodes	0	0.0422	0	0.0327	0	0.139	0	0.104	0.0896	0.00466	0
Bacterivor e nematodes	0	0	0	0.0354	0.139	0	0	0.0457	0.2	0.0353	0
Oribatida	0.459	0	0.0289	0	0	0	0	0.122	0	0	0.0181
Saprophyt ic fungi	0.129	0	0.0314	0.302	0.104	0.0457	0.122	0	0.292	0.321	0.0268
Symbiotic fungi	0	0	0.112	0.275	0.0896	0.2	0	0.292	0	0.254	0.0366
Pathogeni c fungi	0.0725	0	0.162	0	0.00466	0.0353	0	0.321	0.254	0	0
Springtail s	0.359	0.164	0.0796	-0.0744	0	0	0.0181	0.0268	0.0366	0	0

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273 **Table S5** Partial correlation between the true turnover component of β -diversity values of trophic groups constituting
274 of soil diversity and abiotic environmental distances inferred using Glasso.

	Frost	Soil	Plants	Bacteria	Herbi/Fun givre Nematode s	Bacterivor e nematodes	Oribatida	Saprophyt ic fungi	Symbiotic fungi	Pathogeni c fungi	Springtails
Frost	1	0.305	0.503	0.313	0.102	0.117	0.734	0.619	0.471	0.551	0.637
Soil	0.305	1	0.363	0.0432	0.216	-0.0226	0.249	0.255	0.207	0.158	0.367
Plants	0.503	0.363	1	0.276	0.231	0.235	0.416	0.535	0.54	0.557	0.417
Bacteria	0.313	0.0432	0.276	1	0.395	0.439	0.346	0.743	0.732	0.593	0.0491
Herbi/Fun givre nematodes	0.102	0.216	0.231	0.395	1	0.398	0.0963	0.468	0.467	0.396	0.158
Bacterivor e nematodes	0.117	-0.0226	0.235	0.439	0.398	1	0.196	0.499	0.557	0.456	0.0921
Oribatida	0.734	0.249	0.416	0.346	0.0963	0.196	1	0.556	0.448	0.463	0.461
Saprophyt ic fungi	0.619	0.255	0.535	0.743	0.468	0.499	0.556	1	0.835	0.799	0.422
Symbiotic fungi	0.471	0.207	0.54	0.732	0.467	0.557	0.448	0.835	1	0.768	0.382
Pathogeni c fungi	0.551	0.158	0.557	0.593	0.396	0.456	0.463	0.799	0.768	1	0.331
Springtail s	0.637	0.367	0.417	0.0491	0.158	0.0921	0.461	0.422	0.382	0.331	1

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276 **Table S6** Marginal (Pearson correlation) between the true turnover component of β -diversity values of trophic groups
277 constituting of soil diversity and abiotic environmental distances.

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