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Abstract: Soil biota plays a fundamental role in many ecological processes, throughout a complex network of above/below-ground interactions. Thus, there has been an increasing interest in the use of correlates for biodiversity assessment, demonstrating their reliability with respect to proxies based on environmental data alone. Despite co-variation of species richness and composition in grassland soils has been widely discussed in literature, only few studies were developed for forest artificial stands. In this context, a EU-Life project (SelPiBioLife, LIFE13 BIO/IT/000282) started in 2014 aiming at evaluating the application of an innovative forest management along with its effects on soil biodiversity in Pinus nigra plantations (Apennines, Italy). The robustness of cross-taxon congruence before any silvicultural treatment was performed across different taxa (bacteria, vascular plants, above ground mushrooms, ectomycorrhizae on root tips, mycelium in the soil, carabids, microarthropods, nematodes), also exploring how abiotic (soil and spatial-topographic variables) and forest biotic predictors (dendrometric variables) drive the community concordances among taxa, trough the use of variation partitioning analysis. Correlations between groups were performed through Mantel and partial Mantel tests. Almost all the distribution patterns showed strong inter-group congruence and also a relationship with abiotic/biotic variables. However, only bacteria/mycelium and mushrooms/mycelium correlations remained significant after removing the environmental effect. Considering variation partitioning, the variance attributed solely to pure effect of biotic or abiotic predictors was significant only in some cases (e.g. bacteria); remarkably, in all dependent taxa, total and partial shared effect of all predictors always explained the highest portion of total ¬variation. In conclusion, the crucial importance of soil microbiome in affecting the ecosystem functioning of Pinus nigra forests was evaluated. Furthermore, results suggested a mutualistic relationship between all predictors, confirming the clutched network of ecological linkages in

soil as well as the impossibility to assess the mutual surrogate efficiency of taxa avoiding habitat influence.

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Siena, 01 August 2018

Subject: Submission to *Science of the Total Environment*

Dear Editor,

Attached for your consideration is an original manuscript entitled “Teamwork makes the dream work: disentangling cross-taxon congruence across soil biota in *Pinus nigra* Arnold plantations". The manuscript is submitted as a research paper.

This work is part of a wider multidisciplinary project (SelPiBioLife, LIFE13 BIO/IT/000282), started in 2014, aiming at evaluating the application of an innovative forest management technique along with its effects on soil biodiversity in *Pinus nigra* plantations in two mountain areas of the Apennines (Italy). Using data obtained before any silvicultural treatment, the main aim of the present research was to test the robustness of cross-taxon congruence across organisms belonging to four kingdom-levels: Bacteria, Plantae (vascular plants), Fungi (studied as ectomycorrhizae (ECM) on root tips, mushrooms above ground and mycelium in the soil) and Animalia (carabids, microarthropods, nematodes), also exploring how abiotic (soil and spatial-topographic variables) and forest biotic predictors (dendrometric variables) drive the community concordances among taxa.

The “before treatment” research activity guaranteed a high-quality dataset concerning eight different groups of taxa and a complete and objective inventory of twenty-six environmental variables, comprising soil, spatial-topographic and dendrometric factors as proxies of forest structure. This research detains an interesting potential since, to the best of our knowledge, no other researches took into account as many soil taxa as those collected in the SelpiBioLife project, focusing both on biosphere as well as on lithosphere dynamics. For these reasons we are confident that our work could well fit the Aims and Scope of the journal.

Results pointed out the crucial importance of soil microbiome and microbial taxa diversity in affecting the ecosystem functioning of artificial black pine stands. Furthermore, the overall results suggested a mutualistic relationship between all the considered variables, both biotic and abiotic, confirming the complex network of clutched ecological linkages in black pine soils as well as the impossibility to assess the mutual surrogate efficiency of taxa avoiding the environmental and habitat influence.

We are confident that our manuscript will contribute to enhance knowledge about the ecological linkages between above/below-ground biota in affecting the ecosystem functioning in artificial black pine stands, also for application in biodiversity conservation purposes.

Thank you in advance for your attention,

With best regards,

Debora Barbato

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*Title Page

Teamwork makes the dream work: disentangling cross-taxon congruence across soil biota in *Pinus nigra* Arnold plantations

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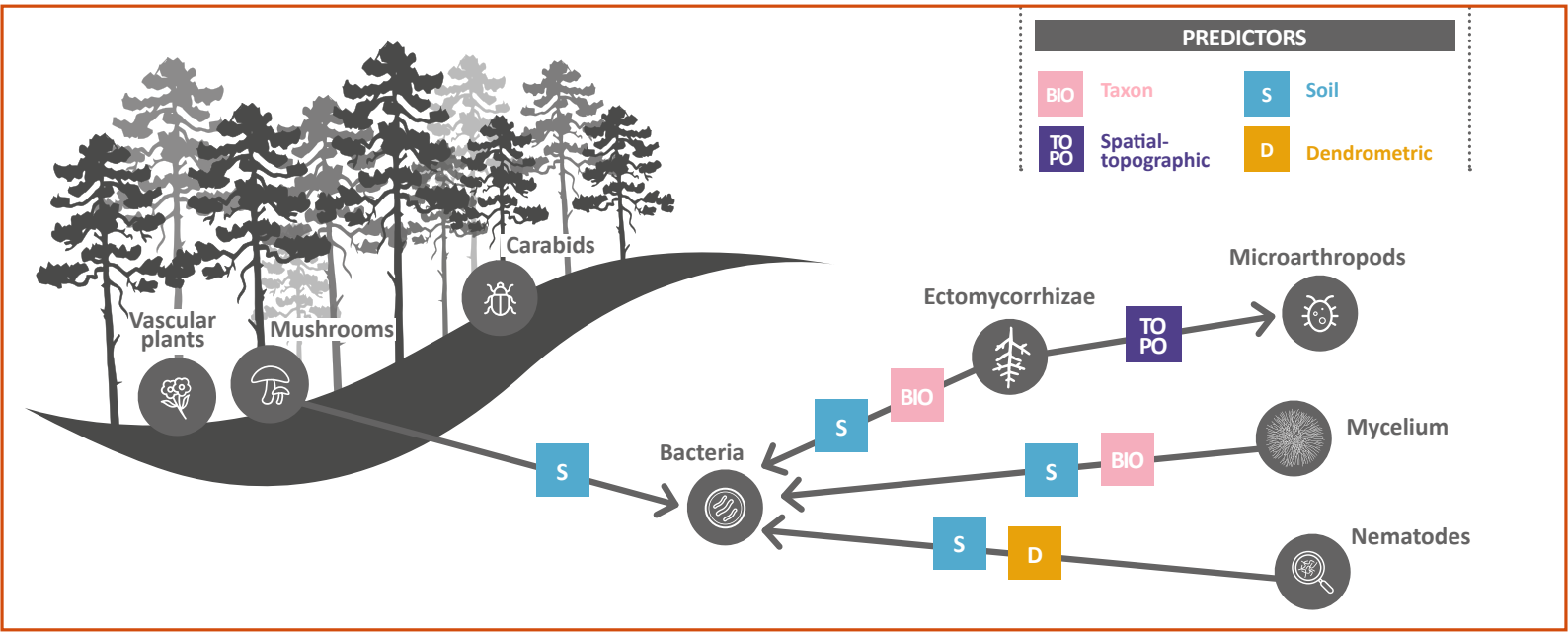
*Graphical Abstract



Highlights

- We evaluated cross-taxon congruence in black pine artificial stands
- We analysed links between soil chemical properties, forest and soil biotic communities
- Fundamental role of soil microbiome
- Complex network of clutched ecological linkages in *Pinus nigra* soil
- Impossibility to assess cross-taxon efficiency avoiding the environmental influence

Teamwork makes the dream work: disentangling cross-taxon congruence across soil biota in *Pinus nigra* Arnold plantations

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Abstract

Soil biota plays a fundamental role in many ecological processes, throughout a complex network of above/below-ground interactions. Thus, there has been an increasing interest in the use of correlates for biodiversity assessment, demonstrating their reliability with respect to proxies based on environmental data alone. Despite co-variation of species richness and composition in grassland soils has been widely discussed in literature, only few studies were developed for forest artificial stands. In this context, a EU-Life project (SelPiBioLife, LIFE13 BIO/IT/000282) started in 2014 aiming at evaluating the application of an innovative forest management along with its effects on soil biodiversity in *Pinus nigra* plantations (Apennines, Italy). The robustness of cross-taxon congruence before any silvicultural treatment was performed across different taxa (bacteria, vascular plants, above ground mushrooms, ectomycorrhizae on root tips, mycelium in the soil, carabids, microarthropods, nematodes), also exploring how abiotic (soil and spatial-topographic variables) and forest biotic predictors (dendrometric variables) drive the community concordances among taxa, trough the use of variation partitioning analysis. Correlations between groups were performed through Mantel and partial Mantel tests. Almost all the distribution patterns showed strong inter-group congruence and also a relationship with abiotic/biotic variables. However, only bacteria/mycelium and mushrooms/mycelium correlations remained significant after removing the environmental effect. Considering variation partitioning, the variance attributed solely to pure effect of biotic or abiotic predictors was significant only in some cases (e.g. bacteria); remarkably, in all dependent taxa, total and partial shared effect of all predictors always explained the highest portion of total variation. In conclusion, the crucial importance of soil microbiome in affecting the ecosystem functioning of *Pinus nigra* forests was evaluated. Furthermore, results suggested a mutualistic relationship between all predictors, confirming the clutched network of ecological linkages in soil as well as the impossibility to assess the mutual surrogate efficiency of taxa avoiding habitat influence.

Keywords: Black pine; cross-taxon congruence; soil biodiversity; forest management; above/below-ground interactions

1. Introduction

Promoting environmental conservation efforts and mitigating the effects of human-induced changes, such as habitat destruction and degradation and/or climate change, requires a solid understanding of the distribution and main drivers of patterns of biodiversity in space and time (Gaston, 1996, 2000; Howard et al., 1998; Gioria et al., 2011). However, the collection of extensive information on biodiversity is hampered by the complexity of spatio-temporal dimensions of this variable. To address these issues, there has been an increasing interest in the use of correlates for biodiversity (Noss, 1990; Prendergast et al., 1993; Margules and Pressey, 2000), which proved that the use of surrogate taxa in conservation planning is substantially more effective than that of surrogates based solely on environmental data (Rodrigues and Brooks, 2007).

Cross-taxon congruence analysis can be expressed as the spatio-temporal correlation in patterns of species richness and/or diversity (Pearson and Carroll, 1999). In other words, it occurs when diversity and/or compositional patterns of different biological groups spatially covary following a common biogeographical history, a similar response to environmental gradients or biotic interactions among taxa (Rooney and Azeria, 2015).

Despite some criticisms (Lewandowski et al., 2010; Westgate et al., 2014), the use of surrogates to predict community patterns remains an effective tool, in particular when economical resources are scarce or where taxonomy cannot provide a complete species inventory. Actually, the distribution of well-known taxa may provide insights into the processes structuring the spatial distribution of other groups; furthermore, their identification could greatly aid biodiversity monitoring and conservation initiatives (Duan et al., 2016).

Albeit most studies have traditionally examined cross-taxon congruency in above-ground terrestrial systems, some attempts are needed to identify potential surrogacy even in soil bioindicators (Keith et al., 2012). In fact, soil hosts approximately a quarter of Earth's biodiversity (FAO, 2015). This immense variety includes micro- (e.g. bacteria, fungi, protozoa and nematodes), meso- (e.g. mites and springtails) and macro- (e.g. earthworms and termites) organisms and it plays a fundamental role in several essential ecological processes, which are considered as life support functions (LSF, Schloter et al., 2018). In addition, soil interacts with above-ground biodiversity in a complex and intricate network of biological activity (Wardle et al., 2004,), so called "ecosystem multifunctionality" (Maestre et al. 2012).

A large body of recent literature deals with co-variation of species diversity in grasslands soils, especially species richness, whereas few of them are in forests and even less rely to plantation forests (Irwin et al., 2014). As the area of plantation forest expands worldwide and natural, unmanaged forests decline, the role of this artificial forest for biodiversity conservation, especially those of conifer species, resulted to be not properly understood (Marchi et al.,

2018), representing a clear gap in the process of developing reliable bioindicators for soil health across a wide range of different land use management and soil types (Keith et al., 2012).

Conifer forest plantations detain a long history, especially in Italy, where forest management has traditionally focused not only on the mere implementation of timber production but also on the biodiversity conservation and soil protection (Cantiani and Chiavetta, 2015).

The natural cycle of nutrients in a forest is highly influenced by the "soil system", mainly through the degradation of dead organic matter. Therefore, the fertility and sustainability of a natural soil depends significantly on the transformation rate of organic materials mediated by the intricate soil biota network. Thus, modern forestry management techniques should be able to meet the compromise between the economic needs of public and private entities and the conservation of biodiversity, including all its soil components (Irwin et al., 2014) as well as the many interactions between above-below ground subsystems and abiotic and biotic drivers (Wall et al., 2010; Wagg et al., 2014, Duan et al., 2016, Fujii et al., 2017).

In this context, a multidisciplinary EU-Life project (SelPiBioLife, LIFE13 BIO/IT/000282) was established in 2014 aiming at demonstrating the application of an innovative forest management technique along with its effects on a wide range of organisms belonging to four kingdom-levels: Bacteria, Plantae (vascular plants), Fungi (including above ground mushrooms, ectomycorrhizae (ECM) on root tips and mycelium in the soil) and Animalia (carabids, microarthropods, nematodes). The main goals of SelPiBioLife project were first to provide an accurate description of the native biodiversity before any type of forest management ("before treatment" phase) and then to test the effects of a selective silvicultural treatment on the overall level of soil biodiversity ("after treatment" phase) in *Pinus nigra* plantations, using a multi-taxon analysis. This new approach is in line with the EU Biodiversity Strategy to 2020 and the Global and European Atlas of Soil Biodiversity.

The "before treatment" research activity guaranteed a high-quality dataset, and a complete and objective inventory of various environmental variables, comprising soil, spatial-topographic and dendrometric factors as proxies of forest structure. This research detains an interesting potential since, to the best of our knowledge, no other researches took into account as many soil taxa as those collected in the SelpiBioLife project to carry out a cross-taxon analysis.

Based on data collected in the "before treatment" phase of SelpiBioLife, the main aims of our study were:

- to test the significance of cross-taxon congruence in community composition of different biological groups in black pine plantations;

- to assess the amount of variance explained by biotic (dendrometric variables) and abiotic predictors (soil physico-chemical and spatial-topograhic variables) along with their shared and unexplained effects driving the community concordances among taxa;
- to explore ecological linkages between above/below-ground biota in affecting the ecosystem functioning in artificial black pine stands.

2. Materials and methods

2.1 Study area

The study was carried out in two *Pinus nigra* Arn. plantations in Central Italy. The first study site (zone 1), called Monte Amiata, it is located in Southern Tuscany (Castiglion d'Orcia, Siena; 42°56'8''N, 11°38'13''E, mean elevation 780 m a.s.l.). Average slope is 15% having mainly a N-E orientation. Geological substrate is characterized by clay, calcareous and marly lithofacies, while soils are deep and very rich in organic matter. Erosion processes are apparently lacking. Average annual temperature is 12.5°C (max: 21.7 °C in July; min: 4.5 °C in January). Mean annual rainfall add up to about 687 mm, with November as the rainiest month. Pine forest is mostly dominated by *Pinus nigra* Arn. (more than 90% of plants which are, on average, 44 years old), *Quercus pubescens* Wild. and *Quercus cerris* L. (Cantiani, 2016).

Pratomagno (zone 2) is in the Northeastern part of Tuscany (Pratomagno, Arezzo; lat 45°27'8''N, long 9°11'13''E, mean elevation 960 m a.s.l.). It is lithologically characterized by quartz-feldspar sandstones alternated by siltstones and argillites. Soils are generally moderately deep, though locally deeper, due to strong erosion. Average annual temperature is 10.5°C (max: 19°C in July; min: 1.5°C in January). Rainfall follows the Apennines sub-mountain regime (mean annual rainfall: 997 mm), with a maximum peak in autumn and a second one in spring. Pine forest has absolute predominance of *Pinus nigra* Arn. with an average age of 57 years, which is locally associated with *Abies alba* Mill. (especially at higher elevation) and occasionally with broadleaved species such as *Fagus sylvatica* L., *Fraxinus ornus* L., and *Quercus cerris* L. (Cantiani, 2016).

2.2 Sampling design

Fifty-four sampling units (plots) were allocated according to a two-stage sampling design (Elzinga et al., 2001): in each of the two zones a central homogeneous area of 20 ha was chosen. Then, nine squares sectors of 1 ha were marked on the ground; afterwards, 3 concentric plots with a variable size spanning from 10 m radius for the biodiversity analysis to 15 m radius for the dendrometric and structural assessment were materialized in the field for forest surveys.

143 *2.3 Taxa datasets*

144 Eight different taxonomic groups (bacteria, vascular plants, above ground mushrooms, ectomycorrhizae (ECM) on root
145 tips, mycelium in the soil, carabids, microarthropods, nematodes) were sampled using separate protocols in 2014-2015
146 at plot or sector level, before adopting any silvicultural treatment. Organisms were identified to species or
147 morphospecies, except for bacteria, mycelium, microarthropods and nematodes that were identified to order
148 (micorarthropods), family (nematodes) or genus level (bacteria and mycelium). Prior to analysis, in order to obtain
149 comparable values, data at plot level (vascular plants, above ground mushrooms, ECM, microarthropods) were
150 aggregated at the sector spatial scale using different approaches: median method for vascular plants to reduce sensitivity
151 to outliers and sum method for the other groups. Abundances were then standardized to relative abundances (range
152 between 0-1). In total, eighteen sectors were used for the analyses: 9 relative to Monte Amiata and 9 for Pratomagno.
153 The sampling methodology for each taxonomic group is:
154
155 - for microbial analyses (bacteria and mycelium) an amount of 500 g of soil was randomly sampled in each sector from
156 the upper layer (0-20 cm) and homogenized for laboratory analysis. After sieving at 2mm, total DNA was extracted
157 from 0,5 g of soil by means of the commercial kit FastDNA^{TM} SPIN Kit for Soil (MP Biomedicals). The
158 characterization of microbial community structure was carried out through a high-throughput sequencing approach by
159 means of Miseq Illumina technology (IGA Technology Services s.r.l., Italy), targeting the 16S DNA ribosomal genes
160 using primers 515F and 806R (Caporaso et al., 2012) and ITS using primers FF390 and FR1 (Vainio and Hantula,
161 2000).
162
163 - For vascular plants, the cover abundance was estimated in each plot for all species according to the Braun Blanquet
164 phytosociological method (Braun-Blanquet 1932). For an appropriate numerical treatment, cover- abundance values
165 were transformed according to van der Maarel method (van der Maarel, 2007).
166
167 - For above ground mushrooms, mycocoenological observations were made collecting and counting all epigeous fruit
168 bodies visible to the naked eye, larger than 1 mm according among others to Arnolds (1981), at plot level in each sector.
169 Sampling activity was performed every two weeks during the period of highest fungal production (autumn) while once
170 in spring. Species identification was performed with the usual morphological techniques and employing general analytic
171 keys and monographs.
172
173 - For ECM, mycorrhized root tips present in 1 soil core of 30 cm in length and 6 cm in diameter per plot were described

as morphotypes according to Agerer (1991, 1987-2002) and counted. Morphotypes were molecularly identified using a direct PCR approach as described by Iotti and Zambonelli (2006).

- Carabids were sampled in each sector using three randomly located pitfall traps (Greenslade 1964; Adis 1979; Van den Berghe 1992), characterized by plastic glasses (height: 12 cm; diameter to the mouth: 8.5 cm) buried up to the edge and containing a saturated solution of sodium chloride, wine vinegar and little pure alcohol at 95% for the maintenance of the sample. The collection of material was carried out at intervals of 10-15 days during the season of activity of Coleoptera Carabidae.

- Concerning microarthropods, three soil samples were randomly collected at plot level in each sector, with a special 10 cm cubic corer for mesofauna sampling. Thereafter, extraction from soil samples was made using modified Berlese-Tullgren funnels following the standard methodology (Parisi et al., 2005).

- For nematodes**,** three soil samples were randomly collected in each sector with a hand auger at the depth of 15 cm in the top layer of bulk soil, after removing surface residues. Samples were then mixed to form a composite sample. Nematodes were then extracted from 100 ml of soil using the cotton-wood filter method for 48 hours at room temperature (approximately 20°C), counted and determined.

Further information on the adopted sampling design is available at www.selpibiolife.eu/en/

2.4 Explanatory variables

Soil physic-chemical properties, geographical coordinates, topographic factors and dendrometric parameters as proxies of forest structure, were collected in each plot (Table 1).

A soil sample was randomly taken from the upper layer (0-20 cm) and then analyzed to determine the percentage of clay (<0.002), coarse sand (2.0-0.2mm), fine sand (0.2-0.05mm), silt (0.050-0.002mm), total limestone, total nitrogen and total organic matter. Soil pH and electric conductivity (ms/cm) were quantified too.

Measured dendrometric variables were: number of trees per hectare, basal area per hectare, average diameter at breast height, average height of the stand (i.e total height of the plant of average diameter), dominant height (i.e arithmetic mean of the total height of 100 trees per hectare with the largest diameter at breast height), diametric differentiation (Pommerening, 2002) Clark and Evans Index (Clark and Evans, 1954), Vertical Evenness (Neuman and Starlinger, 2001), and Photosyntetic Active Radiation on the ground (PAR). Dendrometric variables are part of a wider and open-

205 access dataset, developed to assess the main structural and mensurational parameters of the studied black pine stands as
206 requested by SelPiBioLife project actions (Cantiani and Marchi, 2017).
207 To account for spatial-topographic factors, nine variables were included: aspect (sessagesimal degrees), elevation
208 (metres), flow direction of water (i.e. the direction of the greatest drop in elevation or the smallest rise if all neighbours
209 are higher), roughness (difference between the maximum and the minimum value of a cell and its 8 surrounding cells),
210 slope (percentage), Topographic Position Index (TPI; difference between the value of a cell and the mean value of its 8
211 surrounding cells), Terrain Ruggedness Index (TRI; the mean of the absolute differences between the value of a cell and
212 the value of its 8 surrounding cells), x and y geographical coordinates expressed as metric units in ETRS89/UTM 32N
213 reference system (EPSG 25832).
214 All environmental parameters obtained at plot level were aggregated at sector level using average method.
215
216 *2.5 Statistical analysis*
217 *2.5.1 Taxon Richness and Complementarity analyses*
218 To compare alpha and beta diversity among each taxon in relation to the sampling effort, rarefaction curves were
219 calculated using exact method. Generally, rarefaction curves enable to compare two or more datasets considering the
220 same sampling effort – in this case the same number of sampled sectors, nine in Amiata and nine in Pratomagno
221 (Gotelli and Colwell 2001; Bacaro et al. 2016).
222 For each taxon, classic Diversity indices (Simpson Index and the Pielou Equitability index) were calculated using the
223 available taxonomic resolution. Box and Whisker plots were used to represent the distribution of resulting values.
224 Moreover, aiming at testing differences in beta diversity among taxa, the R function 'betadispersion 2'proposed by
225 Bacaro et al. (2012, 2013) was applied using Bray-Curtis dissimilarity matrices as response variables. This procedure
226 consists of shuffling within taxon dissimilarities among taxa and disregarding between-taxa dissimilarities. In other
227 term, this analysis corresponds to a multivariate analogue of Levene's test for homogeneity of variances. By repeating
228 this operation using permutations (999), a distribution of the test statistics under the null hypothesis of no differences in
229 mean plot-to-plot dissimilarities within taxa was obtained. Where the calculated statistic resulted significant, pairwise
230 comparisons of group mean dispersions were evaluated using the Tukey's Honest Significant Differences between taxa
231 as proposed in Anderson (2006).
232
233 *2.5.2 Cross-taxon congruence between soil taxa and variation partitioning*
234 Mantel tests were used to perform pairwise cross-taxon correlation analyses among taxa, using Bray-Curtis dissimilarity
235 matrices. Similarly, Mantel correlation was calculated between each taxon and the Euclidean environmental distance

matrix obtained by all predictors (soil, spatial-topographic, dendrometric variables). Prior to the calculation, environmental factors were standardized using *decostand* function with *normalize* method in R *vegan* package (Oksanen et al., 2017).

Partial Mantel tests (Smouse et al., 1986) were then used to evaluate if a significant taxa concordance remained after the conditional effect of the environment variables was removed. The significance of correlation of each Mantel and partial Mantel statistic was obtained using 9999 permutations.

Using variation partitioning approach (Borcard et al., 1992; Legendre, 2008), we partitioned the variation in each biological group that could be explained by another taxon as well as by the environment divided into three distinct predictor sets: two abiotic (soil, spatial-topographic) and one biotic (dendrometric as a proxy of forest structure). The outputs obtained allowed us to distinguish the proportion of total variation in each taxon set as dependent variable, explained by the (a) pure effect of another taxon, (b) pure effect of soil, (c) pure effect of spatial-topographic predictors, (d) pure effects of dendrometric variables, (e+f+g+h+i+j+k+l+m+n) partial shared effects of two/three set of factors, (o) total shared effect of all the variables considered along with the variation unexplained.

The partitioning was based on the adjusted R^2 statistic as recommended by Peres-Neto et al., (2006); 999 permutations were used to assess the significance of constraints.

Before variance partitioning analysis, we minimized multicollinearity by performing a Principal Component Analysis (PCA) separately in each predictor set (taxon, soil, spatial-topographic, dendrometric), extracting the first axis of each PCA (PC1 site scores) to use as explanatory variables in next analysis, for a total of four PC1 (PC1 taxon, PC1 soil, PC1 topo and PC1 dendro).

All the statistical analyses were performed using R version 3.4.4 (R Development Core Team 2018).

3. Results

3.1 Taxon Richness and Complementarity analyses

Almost all the rarefaction curves, except mushrooms, reached the asymptote, meaning that the sampling efforts have been reliable to capture the whole diversity in the study sites (Figure 1). Concerning patterns of diversity indices (both Simpson and Pielou Equitability indices, Figure 2), alpha diversity was greater for bacteria, mycelium and plants whereas nematodes and microarthropods were the less diverse groups in terms of taxonomic composition. Bacteria, ECM and plants displayed the greater equitability (greater values of Pielou's evenness) whilst microarthropods and nematodes showed the lower evenness meaning that is the presence of few entities that dominate the assemblage.

Beta diversity average dissimilarities from individual observation units to their group centroid in multivariate space resulted to be significantly different among taxa ($F(1, 61320) = 5031.5$, $p < 0.001$). Boxplot displaying distance to centroid for each taxon are reported in Figure 3; post-hoc tests are reported in Table 2.

3.2 Cross-taxon congruence between soil taxa

Considering Mantel test results (Table 3), the highest congruence was found between bacteria and mycelium ($r = 0.88$; $p<0.001$) and the lowest between nematodes and plants ($r = -0.02$; $p > 0.05$). In general, the distribution pattern of almost all the groups analyzed showed highly supported inter-group congruence, while nematodes were not significantly correlated with other taxa. All biological groups detained close relationships with the overall dataset of environmental predictors: the highest one was found in bacteria ($r = 0.97$; $p<0.001$) followed by mycelium ($r = 0.87$; $p<0.001$) and plants ($r = 0.84$; $p<0.001$).

A partial Mantel test (Table 4), comparing the taxonomic matrices once the environmental matrix contribution was removed, showed that only bacteria and mushrooms maintained a moderate and significant ($r = 0.24$; $p<0.01$; $r = 0.19$ $p<0.05$, respectively) correlation with mycelium, independent of environmental factors. No other cross-taxon correlation remained significant.

3.3 Variation partitioning results

Considering the "pure_taxon" fraction, only ECM and mycelium were able to explain a significant degree of variance in bacteria (respectively 2.9%, p=0.02; 1.6%, p=0.05; Figure 4C and 4F). The pure taxon effect reflects the cross-taxon congruence between pairs of taxa not associated with environmental-spatial predictors and hence related purely to proxies of potential biotic interactions. The other pure taxon fractions detained an irrelevant effect on all the other groups.

In bacteria, the variation attributed solely to pure soil effect was 1.75% (p=0.05), 2.19% (p=0.05), 2.41% (p=0.04), 2.14% (p=0.06), when ECM (Figure 4C), mushrooms (Figure 4E), mycelium (Figure 4F) and nematodes (Figure 4G) were set as independent variable, respectively.

Pure effect of spatial-topographic predictors is invoked to explain a large and significant portion of variation in microarthropods, when ECM were one of the predictor taxon (11.40%, p=0.05, Figure 4C). The unique significant pure effect of dendrometric parameters as proxies of vegetation structure was found in bacteria when nematodes were set as explanatory taxon (2.07%, p=0.05, Figure 4G).

297 Remarkably, in all the dependent taxa, both totally shared and partially shared effects of all sets of predictors always
298 explained the highest portion of the total variation.
299
300
301 **4. Discussion**
302
303 Apart from some studies concerning the influence of forest management on microbiological soil properties (Lucas-
304 Borja er al., 2016), as well as the evaluation of diversity parameters in few well-known taxa (Spake et al., 2016;
305 Martìnez-Jauregui et al., 2016; Mueller et al., 2016; Hanzelka and Reif, 2016), at present no studies have
306 simultaneously assessed diversity of various types of cryptic and less studied soil organisms in *Pinus nigra* plantation
307 forests.
308 The important role of soil microbiome and microbial taxa diversity was retrieved as fundamental in affecting the
309 ecosystem functioning of artificial black pine stands. In fact, bacteria and mycelium provided the highest alpha diversity
310 values, as they represent the smallest and the most abundant organisms within soil matrix, explaining a huge amount of
311 genetic and functional diversity in any environmental sample (e.g. Thompson et al., 2017). Moreover, the high values of
312 Pielou's evenness of bacteria (Figure 2, right) indicated a low environmental selective pressure on bacterial community,
313 thus with no significant dominant species; these results are in line with previous studies which reported that these
314 microorganisms do not respond to large-scale environmental gradients in the same way as other soil meso- or macro-
315 organisms do (Decaëns, 2010).
316 The distribution pattern of almost all the taxa showed highly supported inter-group congruence, displaying close
317 relationships with the overall dataset of environmental-spatial variables (Table 3).
318 However, only bacteria/mycelium and mushrooms/mycelium correlations remained significant after removing the
319 environmental effect (Table 4), demonstrating a close biotic bacterial-fungal interaction (BFI) (Deveau et al., 2018).
320 According to recent research, BFIs are more widespread than expected and their dynamics may be crucial for many
321 ecosystems functions (Bonfante and Anca, 2009; Mocali et al., 2015; Deveau et al., 2018). On the other hand, citing the
322 well-known wood wide web network existing underground between symbionts and the root system, it is not clear why
323 ECM/plants do not have a similar important correlation (Helgason et al., 1998)
324 Overall results suggested Bacteria as the taxon most explained by the set of variables used in this study. Furthermore,
325 they resulted to be involved in the only cases where the variance attributed solely to pure effect of biotic or abiotic
326 predictors was significant (Figure 4C, 4E, 4F, 4G). In particular, among all the biotic predictors, only ECM (Figure 4C)
327 and mycelium (Figure 4F) were able to explain a significant degree of variation ascribed to pure taxon effects in

328 bacterial communities. These results are consistent with the ecological linkages and biotic interactions in forest soil
329 microbiome. For instance, ECM and bacteria are well-known to be strictly associated in rhizospheres of forest trees
330 (Baldrian, 2017b): this is demonstrated also for *Pinus sylvestris* rhizosphere where ectomycorrhizal fungi select for
331 distinct and specific associated bacterial populations (Nurmiaho-Lassila et al., 1997; Marupakula et al., 2016).
332 Mycorrhizae associated with forest trees can also model the composition of local microbial communities, selecting for a
333 broad spectrum of species with distinct enzyme functions and thus providing potential proxies for key biogeochemical
334 processes (Cheeke et al., 2017). Moreover, a large number of fungal and bacterial families engage complex interactions,
335 ranging from mutualism and antagonism (Deveau et al., 2018): while some bacteria are well known to have a positive
336 effect on symbiosis, the so-called "mycorrhiza helper bacteria" (MHB) (Garbaye, 1994; Frey-Klett et al., 2007), others
337 may have negative effect on fungi, causing diseases or using mycophagy as strategy to derive nutrition from living
338 fungi (Leveau and Preston, 2008). The co-occurrence of fungi and bacteria may result in unique contributions to
339 biogeochemical cycles (Tarkka and Deveau, 2016): for example, organic matter transformations as well as nutrient
340 bioavailability in soil strictly depend on the interaction between fungi and bacteria (Baldrian, 2017a).
341 The importance of soil as life support system was confirmed by its significant pure contribution towards bacteria
342 variability when fungi (mushrooms, ECM, mycelium) were set as explanatory variables (Figure 4E, 4C, 4F,
343 respectively). In general, spatial heterogeneity of forest topsoils determines the composition of microbial communities
344 mainly through soil/litter chemistry and vegetation composition. The latter was reported being the second major driver
345 shaping microbial communities after soil features and it detains a greater effect on fungal communities than on bacteria
346 (Baldrian, 2017a). Thus, whereas soil pH is recognized as one of the best predictors for bacterial community
347 composition, fungal community structure is more closely associated to other soil features, nutrient status or tree
348 diversity (Lauber et al., 2008). In this study, it is likely that some environmental parameter such as soil properties (i.e.
349 organic matter, soil texture, C/N ratio, etc.) or the presence of specific predators (i.e. mites and collembola), rather than
350 vegetation diversity, provided direct or indirect selection of fungal community, according with previous analyses (i.e.
351 Dirilgen et al., 2016). Despite most studies reported that soil fungal communities of forest soils are strongly dependent
352 on vegetation type (Shi et al., 2014; Urbanová et al., 2015; Baldrian, 2017b), fungal diversity appeared to be unlikely
353 related to plant diversity, with the obvious exception of ECM, suggesting that plant-soil feedbacks seem not to influence
354 the diversity of soil fungi at the global scale (Tedersoo et al., 2014). However, as distinct microbial communities
355 develop on decomposing leaf litters of different tree species, the comparisons amongst microbial communities in
356 different litters and forest floors at the same stage of decay are needed, in order to definitively deduce the influence of
357 tree species. Thus, disentangling the controversial linkages between tree species and soil microbial communities

358 requires the consideration of several factors, including soil pedoclimatic features, root exudates and the effects of soil
359 fauna (Prescott and Graystone, 2013).
360 Pure soil effect appeared to be significant when nematodes were set as predictor taxon to explain bacterial variance
361 (Figure 4G). In fact, bacterial diversity is strictly related to free nematodes community composition in soil as it includes
362 several bacteria-feeding groups, which can significantly alter the proportion of bacteria by grazing (Sundin et al., 1990;
363 Yeates et al., 1993; Yeates, 2003). Additionally, the relationship between nematodes and bacteria might be highly
364 specific, resulting in mutualistic or even symbiotic interactions (Akhurst, 1980; Forst and Clarke, 2002). Ingham et al.
365 (1985) found up to 70% of the bacterial- and fungal-feeding nematodes in the 4–5% of the total of a thin soil-layer
366 around the rhizosphere. The significance of the relationship between dendrometric parameters and nematode-bacteria
367 interaction (Figure 4G) could likely have its explanation in the variation of radical biomass, which in turn depends on
368 the epigeal biomass of the forest (Price et al., 2010; Pretzsch et al., 2012, Schepaschenko et al., 2017). In fact, the
369 radical horizon represents the natural environment of this trophic liaison (Wang et al., 2000; Eisenhauer et al. 2017).
370 However, little is still known about the relationship between plant structural components and biodiversity in managed
371 forests (Jokela et al., 2018) and further in-depth analysis are needed.
372 Because elevation gradients show a large number of correlated environmental factors, some studies have used
373 topographic factors as a surrogate for habitat heterogeneity (Moura et al., 2016). Habitat heterogeneity on its side means
374 extensive trophic niche differentiation and diverse resources availability. The significant pure effect of spatial-
375 topographic predictors in microarthropods, when ECM were one of the predictor taxon (Figure 4C), could make sense
376 observing the distribution of food resources, since it has been demonstrated the strong feeding preference of Oribatida
377 and Protura on certain ECM (Schneider and Maraun, 2005; Malmström and Persson, 2011).
378 Remarkably, in all the dependent taxa, total shared and partial shared effect of all sets of predictors always explained
379 the highest portion of total variation, testifying the highly intricate and dynamic interplay of environmental factors and
380 the potential biotic interactions in explaining cross-taxon congruence in turnover patterns in *Pinus nigra* plantations
381 (Duan et al., 2016).
382 Although above–below ground biota have been traditionally considered as isolated and independent subsystems
383 (Wardle et al., 2004), our study confirmed the complex network of clutched ecological linkages in controlling
384 ecosystem properties and processes in *Pinus nigra* soil. Considering the composite interaction between organisms
385 belonging to different taxonomic level, it resulted very difficult to assign some biota exclusively to the above or below-
386 ground environment, demonstrating the indissoluble nature of all biological relationships within soil. Furthermore, taxa
387 traditionally used in cross-taxon congruence analysis such as vascular plants and carabids, did not give further
388 information as above ground indicators, shifting the focus on the importance of below-ground system in regulating the

whole network of ecological processes. For this reason, a better understanding of the factors that influence soil biodiversity as well as the interaction mechanisms and consequences is pivotal.

5. Conclusions

Our research disentangled cross-taxon congruence across soil biota of four Kingdoms in *Pinus nigra* plantations, for the first time using a high quality multi-taxonomic dataset and an objective inventory of various environmental variables, both biotic and abiotic. This study highlighted the crucial importance of soil microbiome and especially bacteria as general biodiversity indicator potential in *Pinus nigra* plantations. However, although the understanding of bacterial ecology in forest soils has advanced dramatically in recent years, it is still incomplete. The exact extent of the contribution of bacteria to forest ecosystem processes will be recognized only in the future, when the activities of all soil community members will be studied simultaneously (Lladò et al., 2017). Apart from the fundamental role of microbial taxa, this research demonstrated that it is not a unique factor but rather the mutualistic relationship of all variables, both biotic and abiotic, to regulate the above-below ground subsystems in *Pinus nigra* plantations. Purging cross-taxon congruence from the effect of environment, only bacteria/mycelium and mushrooms/mycelium relationships maintained a strong covariation, showing the impossibility to assess the mutual surrogate efficiency of taxa avoiding the environmental and habitat influence. For this reason, in the development of improved indicators of soil quality in artificial black pine stands, it is decisive to analyze not only multiple taxa but also their relationships with biotic/abiotic features, in order to disentangle all the ecological linkages between above-below ground biota.

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Tables captions

Table 1 List of soil, dendrometric and spatial-topographic variables used as environmental predictor factors

Table 2 Output of Tukey' HSD on beta diversity analysis among taxa. Asterisks express statistical significance: *** = < 0.05; *ns* = not significant

Table 3 Mantel Test - Pearson's product moment. Asterisks express statistical significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; *ns* = not significant

Table 4 Partial Mantel Test – Environmental effect - Pearson's product moment. Asterisks express statistical significance:

Figures captions

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444 explanatory variables explain less variation than random normal variable) were interpreted as zeros. For this reason,
445 overall explained variance could exceed 100% in some cases.
446

447
448 **Table 1** List of soil, dendrometric and spatial-topographic variables used as environmental predictor factors

449

Predictor set	Variable name	Variable description
Soil	**clay**	% clay (<0.002)
	coarse sand	% coarse sand (2.0-0.2mm)
	fine sand	% fine sand (0.2-0.05mm)
	silt	% silt (0.050-0.002mm)
	tot limestone	% total limestone
	nitro	% total nitrogen
	organic matter	% total organic matter
	e-cond	electric conductivity (ms/cm)
	pH	soil pH
Dendrometric	**nr ha**	number of trees per hectare
	g ha	basal area per hectare
	d aver	average diameter at breast height
	h aver	average height of the stand
	h dom	dominant height
	size siff	diametric differentiation
	CE	Clark and Evans Index
	VE	Vertical Evenness
	PAR	Photosyntetic Active Radiation on the ground
Spatial-topographic	**aspect**	aspect (sessagesimal degrees)
	elevation	elevation (m),
	flowdir	flow direction of water
	rough	roughness
	tpi	Topographic Position Index
	tri	Terrain Ruggedness Index
	x	x geographical coordinates (metric units in ETRS89/UTM 32N)
	y	y geographical coordinates (metric units in ETRS89/UTM 32N)

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453 **Table 2** Output of Tukey' HSD on beta diversity analysis among taxa. Asterisks express statistical significance: *** =

454 < 0.05; *ns* = not significant

455

Taxa	Bacteria	Carabids	ECM	Microarthropods	Musbrooms	Mycelium	Nematodes	Vascular plants
Bacteria	-							
Carabids	***	-						
ECM	***	***ns***	-					
Microarthropods	***	*	***	-				
Mushrooms	***	***ns***	***	***	-			
Mycelium	***	***	***	***ns***	***	-		
Nematodes	***	***ns***	***	***ns***	**	**	-	
Vascular plants	***	***ns***	***	***ns***	***	***	***ns***	-

Table 3 Mantel Test - Pearson's product moment. Asterisks express statistical significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; *ns* = not significant

Taxa	Bacteria	Carabids	ECM	Microarthropods	Mushrooms	Mycelium	Nematodes	Vascular plants	Environment
Bacteria	-								
Carabids	**0.416****	-							
ECM	**0.592*****	**0.252***	-						
Microarthropods	**0.391****	0.065	**0.269****	**-**					
Mushrooms	**0.683*****	**0.343****	**0.284****	**0.326****	-				
Mycelium	**0.876*****	**0.380****	**0.552*****	**0.316****	**0.672*****	-			
Nematodes	0.091	0.118	0.129	0.142	0.136	0.050	-		
Vsscular plants	**0.787*****	**0.325***	**0.5401*****	**0.344****	**0.513*****	**0.740*****	-0.020	-	
Environment	**0.966*****	**0.451****	**0.615*****	**0.394****	**0.692*****	**0.875*****	**0.110***	**0.838*****	-

Table 4 Partial Mantel Test – Environmental effect - Pearson's product moment. Asteriks express statistical

Taxa	Bacteria	Carabids	ECM	Microarthropods	Mushrooms	Mycelium	Nematodes	Vascular plants
Bacteria	-							
Carabids	-0.086	-						
ECM	-0.009	-0.036	-					
Microarthropods	0.047	-0.137	0.038	-				
Mushrooms	0.080	0.048	-0.247	0.081	-			
Mycelium	**0.245****	-0.034	0.036	-0.063	**0.192***	-		
Nematodes	-0.057	0.077	0.080	0.108	0.085	-0.094	-	
Vasculat plants	-0.158	-0.107	0.057	0.027	-0.170	0.027	-0.207	-

significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; *ns* = not significant

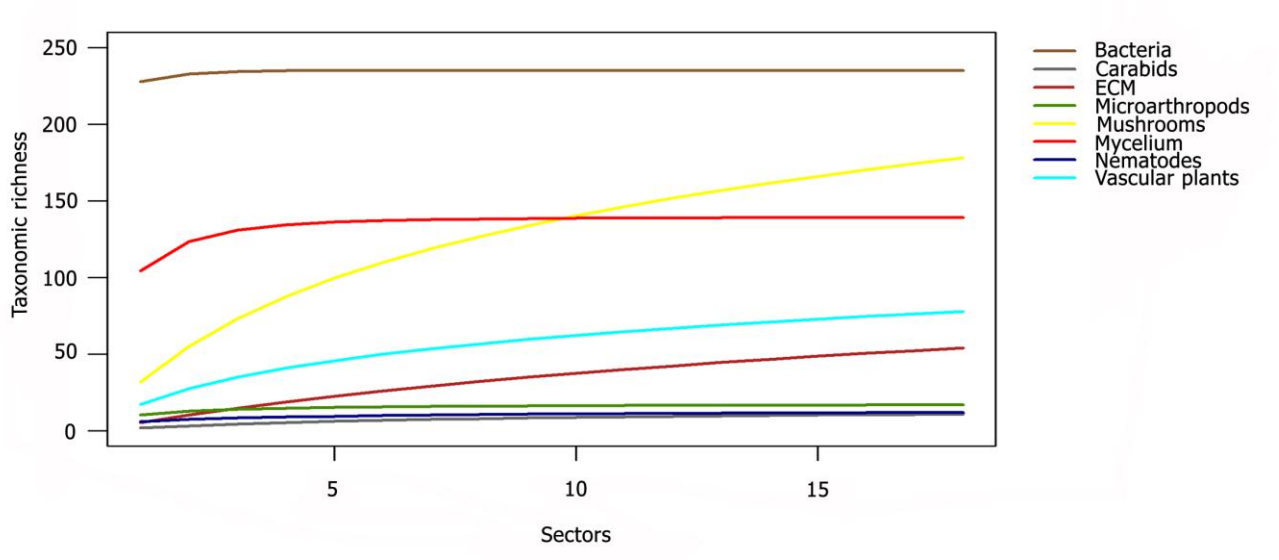


Figure 1 Rarefaction curves calculated for each taxon

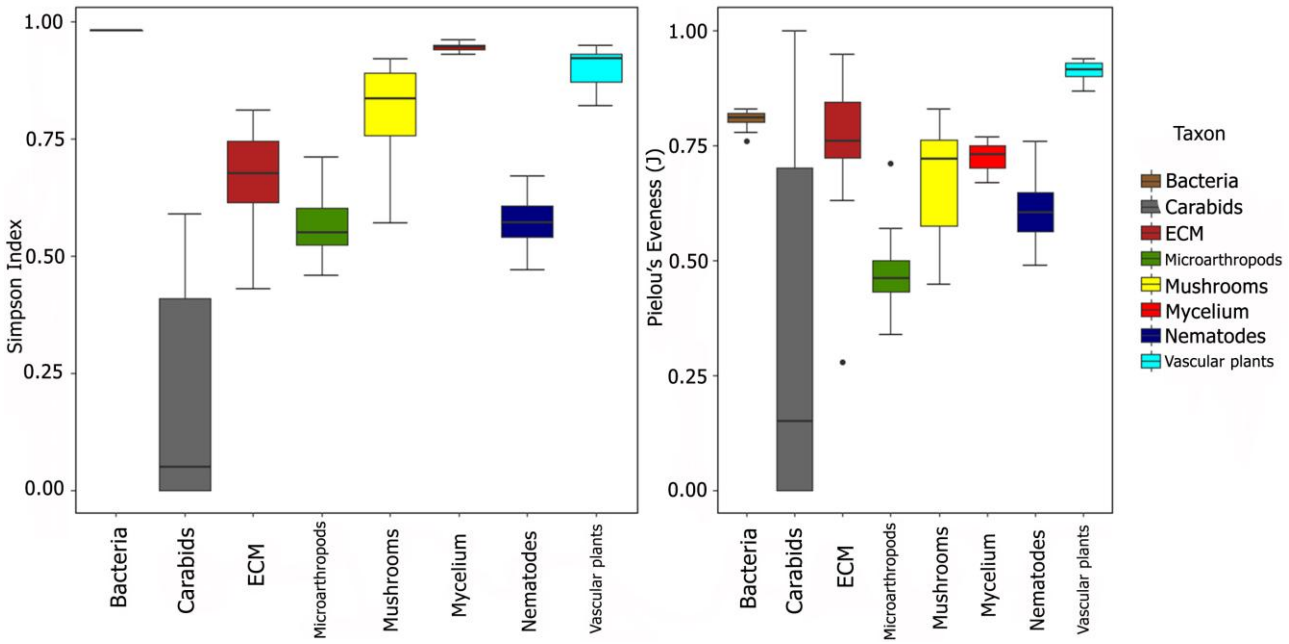


Figure 2 Summary of Simpson (left) and Pielou Equitability indeces (right) for each taxon

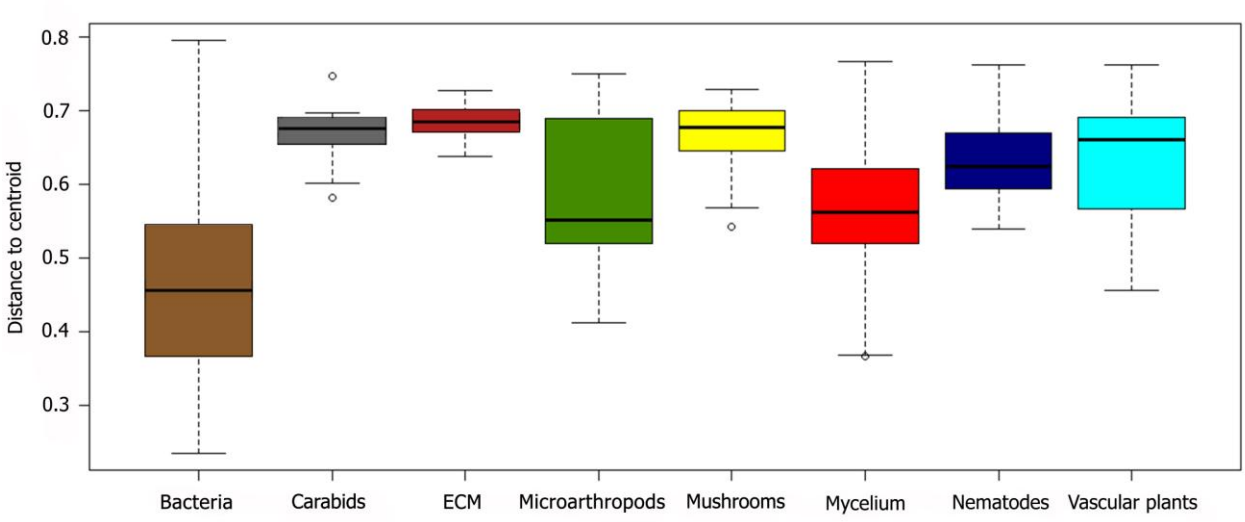
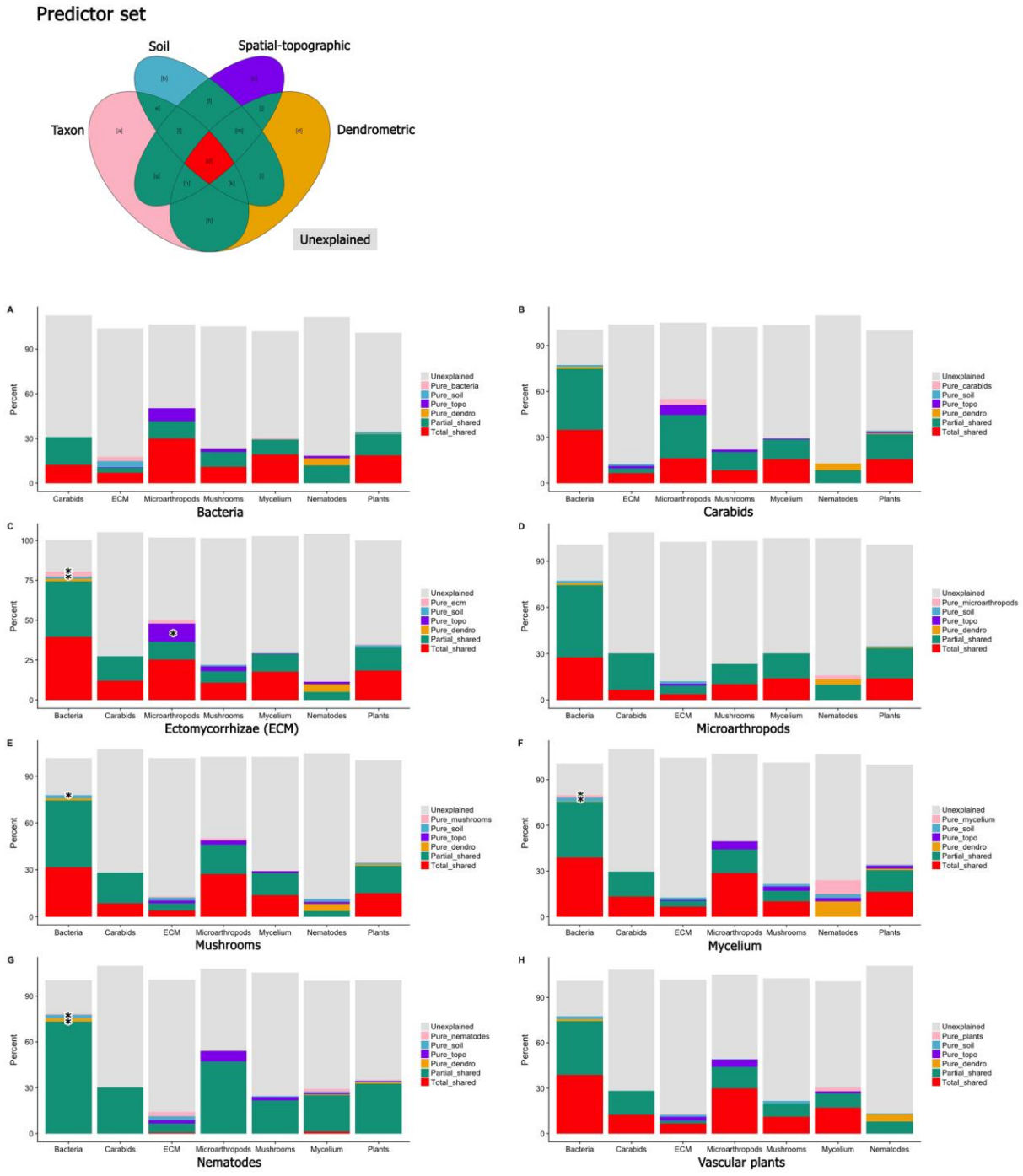


Figure 3 Boxplot displaying taxonomic β-diversity. Distance to centroid were measured by calculating the Bray Curtis distance of group members to the group centroid for each taxon



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494

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496 **References**

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Table 1 List of soil, dendrometric and spatial-topographic variables used as environmental predictor factors.

Predictor set	Variable name	Variable description
Soil	**clay**	% clay (<0.002)
	coarse sand	% coarse sand (2.0-0.2mm)
	fine sand	% fine sand (0.2-0.05mm)
	silt	% silt (0.050-0.002mm)
	tot limestone	% total limestone
	nitro	% total nitrogen
	organic matter	% total organic matter
	e-cond	electric conductivity (ms/cm)
	pH	soil pH
Dendrometric	**nr ha**	number of trees per hectare
	g ha	basal area per hectare
	d aver	average diameter at breast height
	h aver	average height of the stand
	h dom	dominant height
	size siff	diametric differentiation
	CE	Clark and Evans Index
	VE	Vertical Evenness
	PAR	Photosyntetic Active Radiation on the ground
Spatial-topographic	**aspect**	aspect (sessagesimal degrees)
	elevation	elevation (m),
	flowdir	flow direction of water
	rough	roughness
	tpi	Topographic Position Index
	tri	Terrain Ruggedness Index
	x	x geographical coordinates (metric units in ETRS89/UTM 32N)
	y	y geographical coordinates (metric units in ETRS89/UTM 32N)

Table 2 Output of Tukey' HSD on beta diversity analysis among taxa. Asterisks express statistical significance: *** = < 0.05; *ns* = not significant

Taxa	Bacteria	Carabids	ECM	Microarthropods	Musbrooms	Mycelium	Nematodes	Vascular plants
Bacteria	-							
Carabids	***	-						
ECM	***	ns	-					
Microarthropods	***	*	***	-				
Mushrooms	***	ns	***	***	-			
Mycelium	***	***	***	ns	***	-		
Nematodes	***	ns	***	ns	**	**	-	
Vascular plants	***	ns	***	ns	***	***	ns	-

Table 3
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Table 3 Mantel Test - Pearson's product moment. Asterisks express statistical significance: *** = < 0.05; *ns* = not significant

Taxa	Bacteria	Carabids	ECM	Microarthropods	Mushrooms	Mycelium	Nematodes	Vascular plants	Environment
Bacteria	-								
Carabids	**0.416****	-							
ECM	**0.592*****	**0.252***	-						
Microarthropods	**0.391****	0.065	**0.269****	**-**					
Mushrooms	**0.683*****	**0.343****	**0.284****	**0.326****	-				
Mycelium	**0.876*****	**0.380****	**0.552*****	**0.316****	**0.672*****	-			
Nematodes	0.091	0.118	0.129	0.142	0.136	0.050	-		
Vsscular plants	**0.787*****	**0.325***	**0.5401*****	**0.344****	**0.513*****	**0.740*****	-0.020	-	
Environment	**0.966*****	**0.451****	**0.615*****	**0.394****	**0.692*****	**0.875*****	**0.110***	**0.838*****	-

Table 4 Partial Mantel Test – Environmental effect - Pearson's product moment. Asterisks express statistical significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; *ns* = not significant

Taxa	Bacteria	Carabids	ECM	Microarthropods	Mushrooms	Mycelium	Nematodes	Vascular plants
Bacteria	-							
Carabids	-0.086	-						
ECM	-0.009	-0.036	-					
Microarthropods	0.047	-0.137	0.038	-				
Mushrooms	0.080	0.048	-0.247	0.081	-			
Mycelium	**0.245****	-0.034	0.036	-0.063	**0.192***	-		
Nematodes	-0.057	0.077	0.080	0.108	0.085	-0.094	-	
Vasculat plants	-0.158	-0.107	0.057	0.027	-0.170	0.027	-0.207	-

Figure 1

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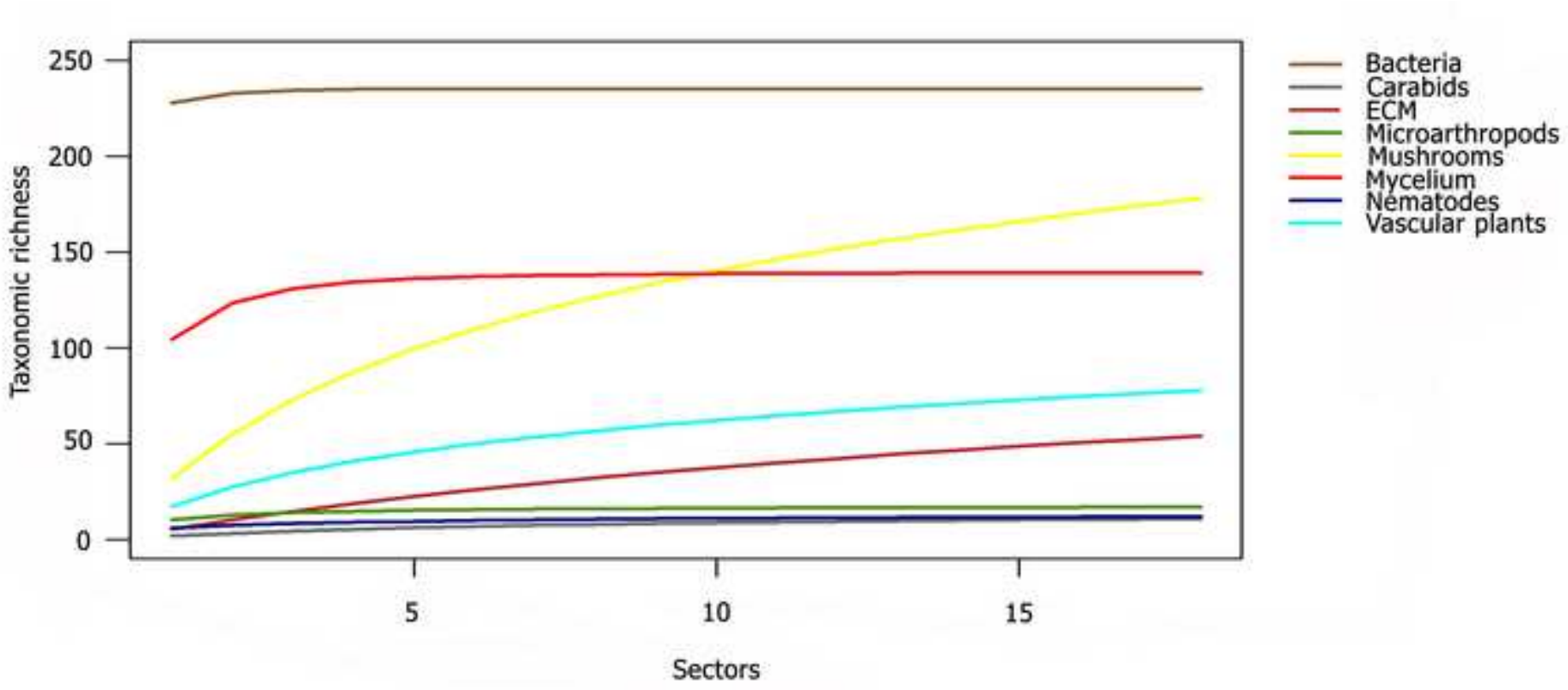

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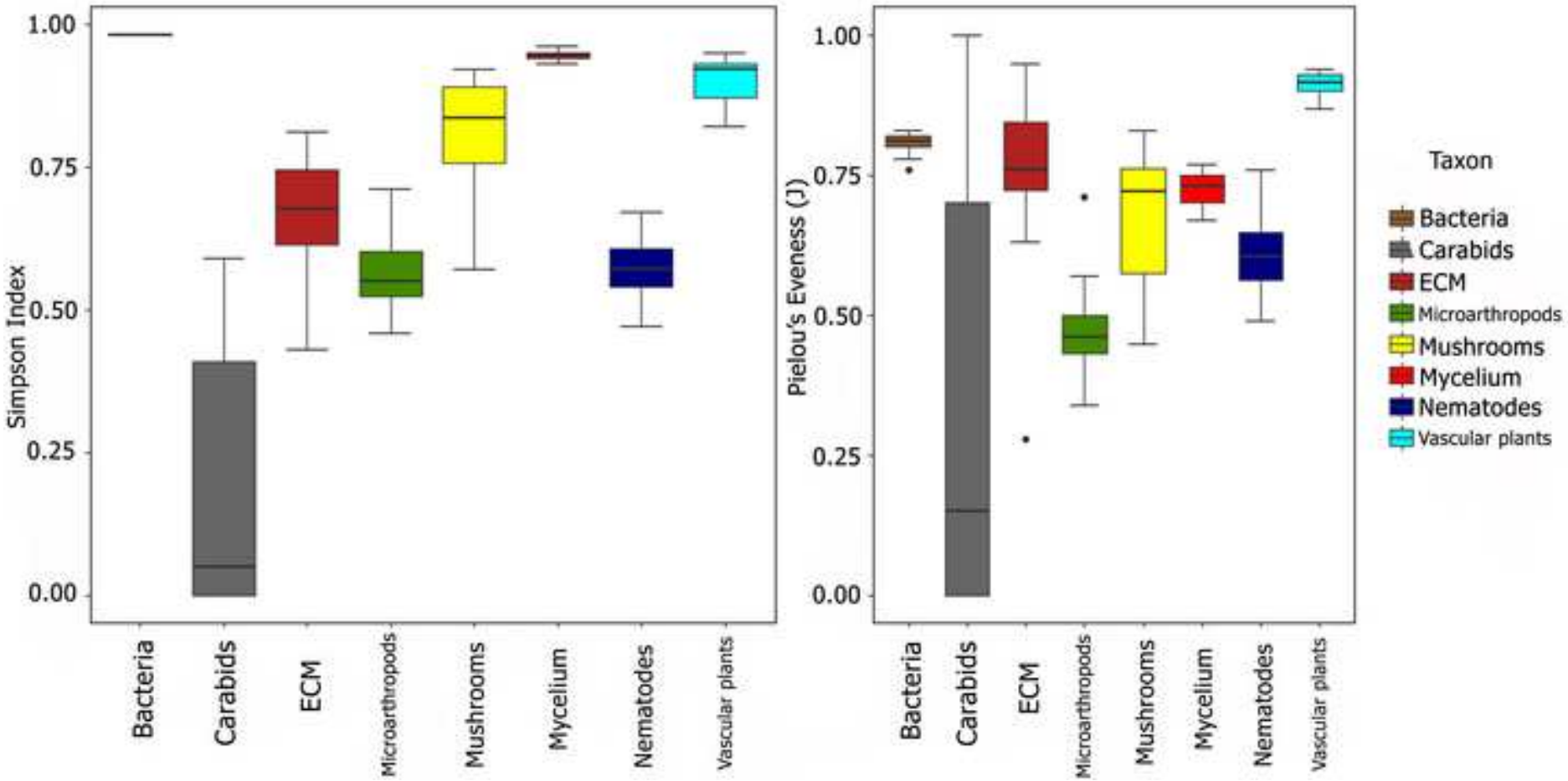

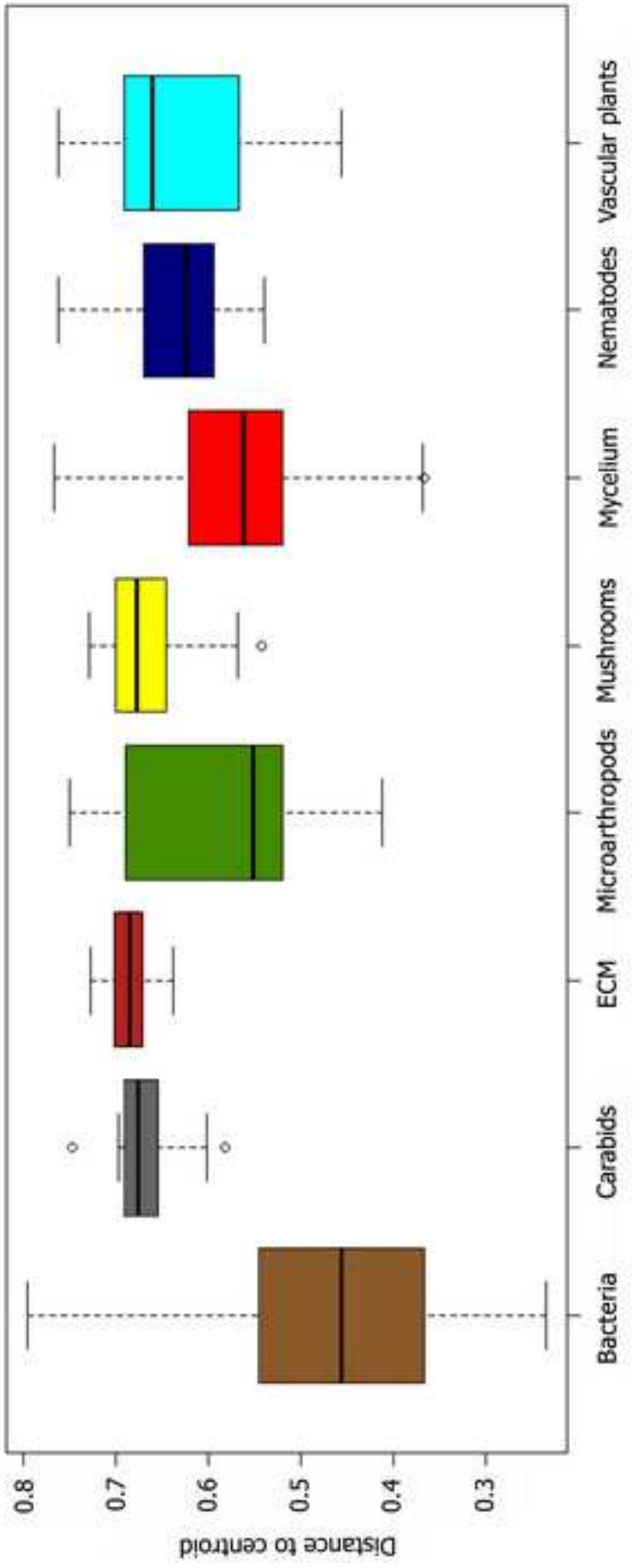

Figure 3
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Figure 4

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