



HAL
open science

Mountain soil multitrophic networks shaped by the interplay between habitat and pedoclimatic conditions

Irene Calderón-Sanou, Marc Ohlmann, Tamara Münkemüller, Lucie Zinger, Mickael Hedde, Clément Lionnet, Camille Martinez-Almoyna, Amélie Saillard, Julien Renaud, Nicolas Le Guillarme, et al.

► To cite this version:

Irene Calderón-Sanou, Marc Ohlmann, Tamara Münkemüller, Lucie Zinger, Mickael Hedde, et al.. Mountain soil multitrophic networks shaped by the interplay between habitat and pedoclimatic conditions. *Soil Biology and Biochemistry*, 2024, 190, pp.109282. 10.1016/j.soilbio.2023.109282 . hal-04409236

HAL Id: hal-04409236

<https://hal.science/hal-04409236>

Submitted on 24 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 **Mountain soil multitrophic networks shaped by the interplay between habitat and**
2 **pedoclimatic conditions**

3
4 Irene Calderón-Sanou^{1,2*§}, Marc Ohlmann^{1§†}, Tamara Münkemüller¹, Lucie Zinger^{3,4},
5 Mickael Hedde⁵, Clément Lionnet¹, Camille Martinez-Almoyna^{1,6}, Amélie Saillard¹, Julien
6 Renaud¹, Nicolas Le Guillaume¹, Ludovic Gielly¹, Orchamp Consortium & Wilfried Thuiller¹
7

8 § Joint first co-authors

9 † Deceased shortly before submission (17/06/2023).

10 1. Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, F-38000 Grenoble, France

11 2. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig,
12 Germany

13 3. Institut de Biologie de l'ENS (IBENS), Département de biologie, École normale supérieure,
14 CNRS, INSERM, Université PSL, 75005 Paris, France

15 4. Naturalis Biodiversity Center, 2300 RA Leiden, The Netherlands

16 5. Eco&Sols, INRAE – IRD – CIRAD – Institut Agro, Montpellier, France

17 6. Univ. Grenoble Alpes, LESSEM, INRAE, Grenoble, France

18 *Corresponding author: irecalso@gmail.com
19
20

21 **Number of words:**

22 -abstract: 148

23 -main text: 5169

24 Number of references: 92

25 Number of figures: 5

26 Number of tables: 1
27

28 **Supplementary information:**

29 Supplementary Figures and Tables

30 Appendix 1 & 2
31
32

33 **Statement of authorship:** WT, TM, MO and IC-S conceptualised the study. AS and WT led
34 the field work, with participation of MO, CM-A, JR, CL, LG, IC-S and several members of the
35 Orchamp consortium. LG executed eDNA extractions and all laboratory samples processing.
36 CL and IC-S processed and cleaned the sequenced eDNA data. JR and CM-A provided the
37 code for extracting the environmental data. IC-S, LZ, MH, CM-A, MO and NLG participated
38 in the assignment of the taxa to trophic groups and the construction of the metaweb. IC-S and
39 MO ran the analyses. All co-authors participated in the writing led by IC-S, MO, WT and TM.

40

41 **Data accessibility statement:** Should the manuscript be accepted, the data supporting the
42 results will be archived in an appropriate public repository (Dryad, Figshare or Hal) and the
43 data DOI will be included at the end of the article.

44

45 **Acknowledgments:**

46 This project was possible thanks to the many people that participated in the field work and in
47 the lab procedures, including students, interns, postdoctoral fellows, field assistants, park
48 managers and rangers. We thank Cindy Arnoldi for conducting the soil physicochemical
49 analyses.

50 This research was funded by the French Agence Nationale de la Recherche (ANR) through the
51 GlobNet & EcoNet projects (ANR-16-CE02-0009, ANR-18-CE02-0010-01), from two
52 ‘Investissement d’Avenir’ grant (Idex UGA: ANR-15-IDEX-02; Montane: OSUG@2020:
53 ANR-10-LAB-56, MIAI@Grenoble Alpes: ANR-19-P3IA-0003), the METRO Grenoble
54 Alpes, the Isere departement and the Office Français de la Biodiversité (OFB). Support was
55 also received from the Lautaret Garden-UMS 3370 (Univ. Grenoble Alpes, CNRS, SAJF,
56 38000 Grenoble, France), member of AnaEE-France (ANR-11-INBS-0001AnaEE-Services,
57 Investissements d’Avenir frame) and of the LTSER Zone Atelier Alpes, a member of the
58 eLTER-Europe network.

59

60 **Abstract**

61

62 Our knowledge of the factors influencing the distribution of soil organisms is limited to specific
63 taxonomic groups. Consequently, our understanding of the drivers shaping the entire soil
64 multitrophic network is constrained. To address this gap, we conducted an extensive soil
65 biodiversity monitoring program in the French Alps, using environmental DNA to obtain multi-
66 taxon data from 418 soil samples. The spatial structure of resulting soil multitrophic networks
67 varied significantly between and within habitats. From forests to grasslands, we observed a
68 shift in the abundance of trophic groups from fungal to bacterial feeding channels, reflecting
69 different ecosystem functioning. Furthermore, forest soil networks were more strongly
70 spatially structured which could only partly be explained by abiotic conditions. Grassland soil
71 networks were more strongly driven by plant community composition and soil characteristics.
72 Our findings provide valuable insights into how climate and land-use changes may
73 differentially affect soil multitrophic networks in mountains.

74

75 **Keywords:** network dissimilarity, soil biodiversity, trophic interactions, environmental DNA
76 metabarcoding, ecological filters, metaweb.

77

78

79

80 **1. Introduction**

81

82 Soil biodiversity encompasses a complex network of interactions among functionally and
83 trophically diverse organisms, playing a vital role in supporting ecosystem functions and
84 services such as carbon sequestration, organic matter decomposition, and enhancing plant
85 performance and resistance to pests and stress (Bardgett and van der Putten, 2014; Delgado-
86 Baquerizo et al., 2020). Over the past decades, our understanding of the spatial distribution of
87 soil taxa has improved, particularly for specific groups like bacteria (Fierer and Jackson, 2006;
88 Delgado-Baquerizo et al., 2018) and fungi (Tedersoo et al., 2014; Davison et al., 2015).
89 However, our current knowledge primarily relies on a few specific taxa, while the broader
90 ecological processes shaping the whole soil communities and their organisation into interaction
91 networks remain poorly understood. This knowledge gap stem from challenges associated with
92 capturing the intricate spatial heterogeneity inherent to the soil environment (Ettema and
93 Wardle, 2002), and the methodological complexities of sampling and analysing the vast
94 diversity of the soil biota (Geisen et al., 2019). These limitations have hindered the application
95 of existing theoretical frameworks on soil biota (Thakur et al., 2020). Advancing research in
96 this direction promises to unravel the ecological processes that structure soil biodiversity and
97 to predict the impacts of global change on terrestrial ecosystems (Soliveres et al., 2016;
98 Eisenhauer et al., 2021).

99

100 Gaining insights into the organization of soil communities necessitates studying spatial,
101 environmental, and biotic drivers, and this poses challenges (Decaëns, 2010; Münkemüller et
102 al., 2020; Eisenhauer et al., 2022). First, capturing the full complexity of soil systems requires
103 accounting for their inherent spatial heterogeneity from landscape to local scales (Ettema and
104 Wardle, 2002; Thakur et al., 2020). At the landscape scale, dominant habitat types, such as
105 grasslands or forests, are crucial for soil taxonomic and functional composition (Fiore-Donno
106 et al., 2020; Arribas et al., 2021; Sepp et al., 2021). Consequently, the heterogeneity between
107 habitats within a landscape can give rise to mosaic patterns of soil communities. Moreover, the
108 spatial connectivity of habitats and the varying dispersal capacities of soil organisms can
109 influence the local composition and structure of soil communities (Arribas et al., 2021). But
110 even at the local scale of a few meters, variable abiotic conditions, including microclimate and
111 soil physico-chemical properties, along with stochastic processes, can lead to pronounced
112 differences in soil communities (Ramirez et al., 2014; O'Brien et al., 2016; Zinger et al., 2019).
113 The structure of the vegetation within an habitat or its taxonomy or functional composition can

114 also affect the abundance and diversity of different soil taxa or trophic groups (Ganault et al.,
115 2021; Noguerales et al., 2021; Calderón-Sanou et al., 2022). Effectively disentangling the
116 effects of spatial, environmental and biotic processes necessitates a sampling design that
117 encompasses multiple spatial scales, ranging from the heterogeneity between habitats to small-
118 scale soil variations.

119

120 Second, comprehensive sampling and cross-taxa analysis are required to capture the high
121 diversity in soils. Recent advancements in monitoring techniques, such as environmental DNA
122 metabarcoding (eDNA) (Taberlet et al., 2012), offer cost-effective means to obtain extensive
123 data on soil biota at large spatial extent (Taberlet et al., 2018; Geisen et al., 2019). To more
124 concisely present the different taxa they can be classified into trophic groups that share similar
125 resources or prey (Eltonian niche; Elton 1927), e.g. fungivorous nematodes or photoautotrophic
126 bacteria (Louca et al., 2016; Potapov et al., 2022). To better comprehend the complex
127 interactions, we can construct multitrophic networks that consider multiple trophic groups
128 (nodes) and their linkages across trophic levels (links) (Thompson et al., 2012; Gravel et al.,
129 2019). However, constructing multitrophic networks from large eDNA datasets is not without
130 challenges. It entails handling and classifying thousands of sequences into trophic groups, and
131 subsequently linking these groups based on known interactions. Obstacles include the
132 resolution limitations of DNA markers for species-level assignment, the incompleteness of
133 sequence reference databases, inconsistent terminology in trophic ecology across soil taxa
134 (Hedde et al., 2022), and the sparse trophic information available for soil organisms in literature
135 and repositories (but see Potapov et al., 2022). Nevertheless, the application of artificial
136 intelligence tools now offers the potential for automating classification tasks (Compson et al.,
137 2018; Le Guillarme and Thuiller, 2023).

138

139 Third, if we are to understand soil biodiversity, not as a group of independent taxa, but rather
140 as multitrophic networks, we need the appropriate methods and frameworks to investigate how
141 ecological processes act on soil trophic groups and their interactions. The mono-trophic
142 community assembly framework (Keddy, 1992; Thuiller et al., 2013) can be extended to
143 multitrophic networks using the metaweb concept (Dunne, 2006). At the regional scale, the
144 metaweb represents the potential ecological network encompassing all species (or trophic
145 groups) from the regional pool and their potential interactions (Fig. 1c). At the local scale,
146 realised local networks emerge as subsets of the metaweb due to ecological filtering of species
147 (Bauer et al., 2022). This filtering process can be influenced by spatial filters like landscape

148 barriers, limiting dispersal (Peay et al., 2010; Gobbi et al., 2022; Blasbichler et al., 2023),
149 abiotic factors filtering out species lacking physiological adaptations (Maaß et al., 2015;
150 Glassman et al., 2017; Steinwandter and Seeber, 2023), and biotic interactions such as
151 mutualisms, herbivory and predation (Vályi et al., 2016). By using the metaweb concept, we
152 can evaluate the effects of ecological filters not only on the taxonomic composition of the local
153 community but also on its network structure (i.e. composition of interactions). Important biotic
154 interactions in the soil are via plant–soil feedbacks, where the taxonomic or functional
155 composition of plant communities influences soil multitrophic networks and vice-versa
156 (Kardol and De Long, 2018; Kardol et al., 2018). Moreover, trophic interactions within the
157 network can elucidate its local structure and composition (Thakur and Geisen, 2019). We
158 anticipate that interactions between taxa or groups within the network should result in co-
159 variation across environmental and spatial gradients. For instance, environments characterised
160 by decomposer communities dominated by bacteria (rather than fungi) should promote the
161 dominance of bacteria consumers and related higher-level consumers within the multitrophic
162 network (Moore and de Ruiter, 1991), see e.g. Martinez-Almoyna *et al.* 2022. Null models can
163 be used to test the significance of such co-variation in the assembly of ecological communities
164 (Caruso et al., 2022).

165

166 Here, we analysed the spatial variation in soil multitrophic network structure, encompassing
167 trophic group and interaction composition. We used data from all over the French Alps
168 including lowland forests and high-elevation grassland ecosystems. To represent their spatial
169 heterogeneity, we employed a stratified and nested sampling design, consisting of 24 elevation
170 gradients with multiple plots at varying elevations (Fig. 1a). We measured soil biodiversity in
171 418 soil samples, using environmental DNA (eDNA). Using an ontology-based data integration
172 pipeline, combining multiple databases with existing knowledge on the trophic habits of soil
173 organisms (Le Guillarme and Thuiller, 2023; Le Guillarme et al., 2023), we constructed a
174 metaweb comprising 55 soil trophic groups with 383 potential trophic interactions (Fig. 1b).
175 Finally, we applied the metaweb framework to characterise the importance of ecological filters
176 on soil multitrophic networks (Fig. 1c), using a combination of network diversity indices based
177 on Hill numbers (Ohlmann et al., 2019) and associated null models. We quantified local
178 variations in soil multitrophic network structure both between and within habitats, addressing
179 three specific questions: (Q1) Do different habitats differ in soil multitrophic networks? (Q2)
180 Do trophic interactions contribute to variations in group abundances between habitats?, and,

181 (Q3) How do abiotic conditions, spatial factors, and plant communities shape soil multitrophic
182 networks within habitats?

183

184 **2. Material and Methods**

185 **2.1. Study site**

186 The data come from the Orchamp long-term biodiversity observatory (www.orchamp.osug.fr,
187 Appendix 1). It encompasses 24 elevation gradients (at the time of this study) across the French
188 Alps sampled between 2016 and 2020 (Fig. 1a). These gradients represent diverse climatic,
189 vegetation and soil conditions. Each gradient consists of four to nine 30 x 30 m permanent
190 plots, spaced approximately 200 m apart in elevation. The elevation range covered by each
191 gradient varies between 585 and 1380 m (Fig. S1). We worked with 127 plots, ranging in total
192 from 280 m and 2780 m above sea level.

193 Habitat type (forest, grassland, shrubland) was determined on-site. Most gradients covered all
194 three types of habitats, with some exceptions where only one or two types were present (e.g.
195 grassland and shrubland in high-elevation mountains). Plant species abundances were
196 estimated at the peak of the vegetation along a linear transect traversing each plot, using the
197 pin-point method (Jonasson, 1988). Soil sampling was performed at the end of the summer
198 season in three subplots (2 x 2 m) located along a separate 4 m wide transect within each plot.
199 In each subplot, we collected ten soil cores, 5 cm in diameter and ~15 cm in depth (excluding
200 litter), pooled together to a biological sample. Some elevation gradients (37 plots) were
201 sampled twice (i.e. in different years).

202

203 **2.2. Soil biota sampling**

204 Soil biodiversity was measured using environmental DNA (eDNA) metabarcoding from the
205 soil samples. In the field, we extracted eDNA from a 15 g aliquot following Taberlet *et al.*
206 (2012, 2018). The remaining soil was sieved at 2 mm and used to measure soil physico-
207 chemical properties (Table 1).

208 We employed six DNA markers, including two universal markers (Euka02 for eukaryote,
209 Bact01 for bacteria) and four clade-specific markers (Fung02 for fungi, Inse01 for insect,
210 Olig01 for oligochaeta, and Coll02 for collembola) (Taberlet *et al.*, 2018). Details regarding
211 the markers and molecular analyses are detailed in Appendix 2. A standardised bioinformatic
212 pipeline was applied to curate the retrieved sequences from contaminants and errors (Calderón-
213 Sanou *et al.*, 2020), using the OBITools software (Boyer *et al.*, 2016) and the ‘metabaR’ R
214 package (R Core Team, 2020; Zinger *et al.*, 2021). Sequences were clustered into Molecular

215 Operational Taxonomic Unit (MOTU) with SUMACLUSt (Mercier et al., 2013) using a
216 clustering threshold of 97% for Euka02, Fung01 and Bacte01, 85% for Coll01, 88% for Olig01
217 and 95% for Inse01, following the recommendations in Bonin *et al.* (2023). Taxonomic
218 annotations were performed on MOTUs with the SILVAngs pipeline (Quast et al., 2013)
219 (SILVA version 138.1) for ribosomal universal markers. For clade specific markers, we used
220 the ecotag program from the OBITools, and marker-specific databases built with the ecoPCR
221 program (Ficetola et al., 2010), from the EMBL database version 136. Metazoan taxa not
222 registered in the European region were removed from the data (<1% of total reads) using the
223 GBIFfilter tool (<https://github.com/nleguillarme/gbif-filter-python>).

224

225 **2.3. Multitrophic network construction**

226 Trophic groups and classes: We assigned the retrieved taxonomically annotated MOTUs to 10
227 trophic classes including autotrophs, decomposers, detritivores, phytophages or phytoparasites,
228 plant mutualists, bacterivores, fungivores, omnivores, predators and zooparasites. We then
229 refined those trophic classes by subdividing them into 55 trophic groups in total. These were
230 defined by separating phylogenetic distant groups that could have a different set of
231 prey/predators (e.g. bacterivorous mites vs. bacterivorous nematodes) and groups differing in
232 their resources acquisition strategy (e.g. different types of mycorrhiza and saprotrophs). The
233 taxonomic rank used to delimitate phylogenetic distant groups comprised Bacteria, Fungi,
234 Protista, the different phyla within Metazoa, and the different classes or orders within
235 Arthropoda and Annelida. (Appendix 2).

236 To facilitate the assignment of the taxonomically annotated MOTUs to trophic classes, we first
237 built a knowledge graph integrating information about the trophic interactions and feeding
238 habits of soil-associated consumers from multiple data sources using the ontology-based data
239 integration pipeline described in Le Guillaume & Thuiller (2023). This trophic knowledge
240 graph uses the NCBITaxon ontology and the Soil Food Web Ontology (SFWO) (Le Guillaume
241 et al., 2023) as global schemas for reconciling taxonomic and semantic heterogeneities between
242 the data sources. It provides a unified access to multisource trophic information across
243 taxonomic groups and trophic levels. The list of data sources and details on the assignment
244 criteria can be found in Appendix 2.

245

246 Building the metaweb: A metaweb is a potential network containing all trophic groups and
247 their potential interactions (Dunne, 2006). We added three basal resources to construct our
248 metaweb: light (or chemical energy), plants, and organic matter. Trophic links were then added

249 between groups based on their main feeding preferences. Therefore, plant mutualists and
250 phytoparasites were linked with the plant resource, detritivores and decomposers were linked
251 with the organic matter resource and autotrophs were associated with the light resource.
252 Bacterivores were linked with all trophic groups containing bacteria, and fungivores with all
253 trophic groups containing fungi. The trophic interactions of omnivores, predators and
254 zooparasites, were determined through a literature review of dietary preferences of taxa
255 representing over 90% of the read abundance of the group (Appendix 2).

256

257 Local networks: From the metaweb, the composition and structure of the local soil multitrophic
258 networks were deduced based on locally present trophic groups, i.e. local networks are
259 subgraphs of the metaweb. This assumes that co-occurring groups interact locally as defined
260 in the metaweb. We approximated local relative abundance of each trophic group using a
261 double-transformation, where first, total read counts were transformed into proportions within
262 the sample, and second, the resulting proportions were standardised by the largest proportion
263 observed across samples for each trophic group ('eDNA index' in Kelly *et al.* 2019). The
264 relative abundance of each trophic group varied thus between 0 (absent) to 1 (largest observed
265 proportion), allowing to have a comparable measure across trophic groups. Abundance values
266 of the basal resources (light, plant, organic matter) were set to non-null (0.001) to not affect
267 diversity measurements. For trophic class abundance estimates, we summed group relative
268 abundances.

269

270 **2.4. Network analyses**

271 With the aim of analysing spatial variation in soil multitrophic network structure, we used beta
272 diversity metrics that account for compositional changes in the network across samples. We
273 used a set of network diversity indices based on the generalisation of Hill numbers proposed
274 by Ohlmann *et al.* (2019). These indices allow to quantify diversity in trophic groups and
275 trophic interactions, varying the weight of the relative abundance of groups and links. Here,
276 we focussed on Shannon diversity ($q=1$, see Calderón-Sanou *et al.* 2020) but also replicated
277 the analyses using species richness ($q=0$) and Simpson diversity ($q=2$) to assess the extent to
278 which the observed changes are compositional versus structural. Since interactions in the
279 metaweb are binary (either presence or absent), we approximated the abundance of interactions
280 as the product of the relative abundances of the interacting groups. These diversity indices can
281 be further decomposed into alpha, gamma, and β -diversity (β_T), and be used to calculate the
282 pairwise dissimilarities for both groups (β_P) and links (β_L). β -diversity (β_T) quantifies the

283 effective number of different communities, based on shared groups (β_{TP}) or interactions (β_{TL}),
284 ranging from 1 (indicating identical group or interaction abundance distribution) to the total
285 number of communities, when networks do not share any common group or interaction. The
286 diversity metrics were computed using the R package 'econetwork' (Miele et al., 2021).

287

288 To quantify changes in the spatial structure of soil multitrophic networks across habitats, we
289 calculated pairwise dissimilarity measures for both groups (β_{pP}) and interactions (β_{pL}) among
290 all pairs of local networks. Subsequently, we used UMAP, a non-linear dimension reduction
291 algorithm, to visualize the local networks in a two-dimensional space based on their group and
292 interaction dissimilarities (McInnes et al., 2020). Given the strong structural differences
293 observed in local soil multitrophic networks between forests and grasslands (Fig. 2, S3), and
294 the high variability in network composition in shrublands due their intermediate state along the
295 elevation gradient, our analysis focused exclusively on grasslands and forests for further
296 comparison. We compared the relative abundances of trophic groups and classes between
297 forests and grasslands with a Wilcoxon test and used the 'group-TL-tsne' network layout from
298 the R package 'metanetwork' (Ohlmann et al., 2023) together with edge bundling provided by
299 'edgebundle' R package (Schoch, 2022) to represent the difference network between average
300 networks in forests vs. grasslands.

301

302 We tested the imprint of trophic interactions on community assembly with null models. Firstly,
303 we constructed an average soil multitrophic network for each habitat by using the average
304 relative abundances of trophic groups per habitat. We then calculated the β -diversity (β_T) for
305 both group and link interactions between the two habitats. Next, we built the null model. Since
306 group and interaction diversities are strongly correlated, we aimed at keeping group diversity
307 constant in the null model while modifying interaction diversity. This was achieved by
308 permuting the node labels within the metaweb. Consequently, group β -diversity remains
309 unchanged as this diversity index is invariant to label permutation. However, interaction β -
310 diversity was affected since it relies on the product of relative abundances of interacting groups.
311 If dominant interacting groups differ between the two habitats, the observed interaction β -
312 diversity would be higher than expected under a random distribution of group abundances. To
313 evaluate the significance of our findings, we conducted 3000 permutations and compared the
314 observed diversities with the corresponding null distribution.

315

316 Finally, to quantify the relative importance of environmental and spatial distances in explaining
317 network dissimilarity within habitats (i.e. grasslands and forests), we used Generalised
318 Dissimilarity Models (GDM) (Ferrier et al., 2007). We built two GDM per habitat using trophic
319 group turnover (βpP) and interaction turnover (βpL) as response variables, with the R package
320 ‘gdm’ (Fitzpatrick et al., 2022). For the environmental predictors we selected a set of weakly
321 correlated variables (Pearson’s $r < 0.5$, Fig. S2) representing climatic, soil and vegetation
322 conditions that could influence soil organisms (Table 1). The spatial coordinates of the samples
323 and all the selected environmental variables were used as predictors. The environmental
324 distance between samples was directly calculated by the ‘gdm’ package, but for plant
325 composition, we used our own dissimilarity indices to represent changes in vegetation
326 composition from both a taxonomic and functional point of view (Table 1). Plant taxonomic
327 dissimilarity between plots was calculated using the *beta.pair* function from the R package
328 ‘betapart’ (Baselga et al., 2022). To estimate plant functional dissimilarity we retrieved trait
329 values for species of which cumulative abundances represented at least 90% of the plot
330 coverage. Missing values (<15% of the total data) were estimated using the imputation method
331 offered by the R package ‘mice’ (van Buuren and Groothuis-Oudshoorn, 2011). Plant
332 functional dissimilarity was estimated using the *beta.fd.multidim* function from the R package
333 ‘mFD’ (Magneville et al., 2021). In the analysis, soil samples from the same subplot collected
334 in different years (i.e. 95 of the 418 samples) were treated as separate samples as they differed
335 in environmental conditions, except for climate and NDVI that were averaged across a period
336 of 10 years. Their spatial dependency was considered through the spatial coordinates of the
337 plot.

338

339 **3. Results**

340

341 The metaweb constructed for the French Alps region using the taxa identified in 418 soil
342 samples consisted of 55 trophic groups, three basal resources and a total of 383 potential
343 interactions (Fig. S3). On average, local networks were composed of 41 ± 4 trophic groups
344 (and resources), with 206 ± 37 interactions. All 10 trophic classes were present in all local
345 networks, with a single exception where no group from the fungivore class was detected. The
346 mean dissimilarity between local soil multitrophic networks was primarily influenced by
347 changes in the dominance of trophic groups, rather than by changes in the presence or absence
348 of groups (as indicated by increasing dissimilarity when increasing parameter q , which
349 represents the weight of trophic group abundance and interaction, Fig. S4).

350

351 Overall, we found that multitrophic network composition varied across the environmental
352 range covered in this study. The habitat type, particularly when comparing grassland and forest
353 habitats, strongly structured the network composition, both in terms of trophic group and
354 interaction composition (Q1) (Fig. 2, Fig. S5). The influence of habitat type on interaction
355 composition was more pronounced compared to trophic group composition (Table S1). When
356 examining shrubland areas, which represent ongoing shifts from grassland to forest, we found
357 highly variable network structures (Fig. 2). These structures exhibited similarities to both forest
358 and grassland networks, potentially due to the spatial proximity of shrubland sampling sites to
359 forests or grasslands, or the specific stage of succession in the shrubland areas. By contrasting
360 the average networks of forests and grasslands, we identified compositional differences in the
361 abundance of trophic groups and classes between the two habitats (Fig. 3). Forest soil
362 multitrophic networks were enriched in ectomycorrhizal fungi, litter and wood saprotrophic
363 fungi, macro-detritivores like earthworms and diplopods at basal level, fungivores (particularly
364 eudaphic collembola and protura), soil top predators including predatory mites, centipedes,
365 predatory coleoptera and pseudoscorpions, as well as zooparasites. In contrast, grassland soil
366 multitrophic networks had a higher proportion of decomposers and detritivores, particularly
367 soil saprotrophic fungi, enchytraeids and coprophagous coleoptera (e.g. dung beetles),
368 arbuscular mycorrhizal fungi and root endophytes, and most groups of plant phytoparasites and
369 autotrophs. Grasslands also exhibited a higher proportion of bacterivores and omnivores
370 compared to forests, notably bacterivorous nematodes, rotifers and epigeic collembola, at
371 higher trophic levels. We further examined the β -diversity of interactions between habitats and
372 compared it to null expectations derived from randomising trophic group abundances while
373 preserving trophic group diversity and network structure (see methods). The observed β -
374 diversity was significantly higher than expected by chance (Fig. 4), indicating that trophic
375 groups enriched in each habitat were not randomly distributed in the network, but instead
376 formed pairs of trophically linked groups. This suggests that differences in trophic group
377 abundance between habitats (Fig. 3) are influenced by the structure of trophic links within the
378 network (Q2).

379

380 The composition of forest and grassland soil multitrophic networks was influenced by distinct
381 ecological filters (Q3). In both habitats, predictors associated with these filters accounted for
382 approximately 10% of the variance in soil multitrophic network dissimilarity (Fig. 5, Fig. S6).
383 In forests, spatial and environmental predictors played a more important role, particularly soil

384 C/N ratio (related to organic matter degradability), pH, and frozen degree days (FDD) as
385 indicators of abiotic stress (Fig. 5a). Dissimilarities in trophic groups and interactions were
386 more pronounced between sites separated by large spatial distances and remained consistent
387 along the gradients of FDD and pH (Fig. 5b). Changes in soil C/N ratio primarily influenced
388 interaction dissimilarity, particularly at higher values of the C/N ratio gradient (>20).
389 In contrast, grassland soil multitrophic networks were predominantly driven by plant
390 taxonomic and functional composition, as well as soil C/N ratio (Fig. 5a). Soil C/N ratio and
391 plant taxonomic/functional composition better explained interaction dissimilarity (Fig. 5c),
392 while plant taxonomic composition was more effective in predicting trophic group
393 dissimilarity. Dissimilarities in trophic groups and interactions remained relatively constant
394 along the plant dissimilarity gradient but were more pronounced in the lower part of the FDD
395 gradient (> 40 cumulative degrees) and the upper part of the C/N ratio gradient (>15).

396

397 **4. Discussion**

398

399 Our study employed high-resolution data spanning contrasted habitats and extensive
400 environmental gradients to quantify the variability of soil multitrophic network structure. This
401 approach revealed new insights into how the environment, space and biotic interactions shape
402 soil multitrophic network assembly in the French Alps. We observed significant differences in
403 dominant trophic groups between habitats, that was associated with the structure of the trophic
404 links in the network (i.e. the abundance of trophically linked groups co-vary across habitats).
405 Furthermore, we uncovered notable discrepancies in the relative importance of the ecological
406 filters between forests and grasslands.

407

408 **4.1. Habitat filtering in soil multitrophic networks**

409 This study encompassed diverse climatic regions in the French Alps (e.g. alpine, continental,
410 mediterranean) and an elevation range of 2500m, resulting in significant environmental
411 variability within and across habitat. As anticipated, habitat filtering strongly influenced soil
412 multitrophic network structure, especially when comparing forests and grasslands (Crotty et
413 al., 2014; Arribas et al., 2021; Sepp et al., 2021). Differences in abiotic conditions and resource
414 availability between habitats could explain the observed differences in the proportions of
415 trophic groups. Grassland soils exhibit lower acidity, higher P and N availability and a lower
416 C/N ratio (Joimel *et al.* 2016, Fig. S1), and have a higher below-ground plant biomass, which
417 is more easily decomposed, leading to significant inputs of readily decomposable organic

418 matter into the soil (Mason and Zanner, 2005; Hedě́nec et al., 2022). These factors likely
419 enhanced resource availability for detritus-based trophic groups, resulting in the higher
420 dominance of copiotroph decomposers (e.g. saprophytic fungi and bacteria), micro- or meso-
421 detritivores (i.e. Enchytraeidae) and microbivores in grasslands. In contrast, plant detritus in
422 forests, which is more challenging to decompose, serves as a direct resource for litter and wood
423 saprotrophic fungi and provide a habitat for macro-detritivores, which feed on plant litter and
424 associated fungi (David and Handa, 2010; Zuo et al., 2014). Light availability in grasslands
425 may favour the presence of photoautotrophic bacteria that use light as their primary resource,
426 and facilitate interactions, such as arbuscular mycorrhiza (Konvalinková and Jansa, 2016).
427 Moreover, grasslands had a higher proportion of phytoparasites, likely due to the higher
428 biomass of fine roots in this habitat (Jackson et al., 1997; Hedě́nec et al., 2022), which are more
429 easy to colonise by symbionts, while forests had a higher proportion of zooparasites, benefiting
430 from a greater abundance of potential hosts, predominantly arthropods, molluscs or
431 earthworms, for the taxa belonging to our zooparasite groups. These findings align with our
432 results showing that trophic interactions within the soil multitrophic network contributed to
433 explain network dissimilarities between habitats (Fig. 4) and are consistent with previous
434 studies examining changes in the trophic composition of protists (de Araujo et al., 2018; Fiore-
435 Donno et al., 2020) and nematodes (Zhao and Neher, 2014) across habitats. The distinct
436 identities of soil antagonists in the soil multitrophic networks from grassland to forests warrant
437 further investigation as they could provide insights for land management strategies in mountain
438 ecosystems (Wall et al., 2015).

439

440 **4.2. Impact of ecological filters within habitats**

441 Our study design aimed to investigate the impact of ecological processes on soil multitrophic
442 network structure across elevation gradients and diverse environmental conditions. It is
443 important to note that the studied mountain system included various forest types (e.g. low-
444 elevation deciduous, high-elevation coniferous) and grassland types (e.g. subalpine, alpine).
445 To capture this ecological heterogeneity within habitats, our research incorporated variations
446 in abiotic conditions, plant composition, and geographic distance, offering a comprehensive
447 analysis of the complex environmental variation characterising our mountainous systems.
448 Although the GDM explained a relatively low percentage of variance when quantifying
449 changes in the structure of local networks (Fig. 5a), it is important to note that typical deviance
450 explained for models of compositional dissimilarity ranges from 20% to 50%, and this
451 percentage can decrease with an increasing number of sites, which was relatively high in our

452 study (Ferrier et al., 2007; Mokany et al., 2022). Furthermore, the resolution of our soil
453 multitrophic networks using trophic groups instead of species led to low average dissimilarities
454 (0.27 and 0.48 in forests, and 0.30 and 0.53 in grasslands for groups and interactions
455 respectively), reducing model predictability (Mokany et al., 2022). Importantly, we found that
456 trophic link structure significantly influenced changes in trophic groups abundance
457 composition (Fig. 4). However, current models cannot account for this factor, and
458 incorporating network structure in diversity models may enhance predictability but requires
459 further implementation (Poggiato et al., 2022).

460

461 Spatial processes, environmental filtering, and changes in plant community composition
462 explained variation in soil multitrophic networks within habitats. In forests, spatial distance
463 played a significant role, explaining a substantial portion of trophic group (31%) and
464 interaction dissimilarity (58%), even when accounting for confounding environmental changes.
465 Limited dispersal opportunities in closed forest habitats, particularly for organisms dispersed
466 through wind (anemochory), might influence soil multitrophic network structure in mountain
467 forests. Conversely, open grassland habitats subject to strong winds (Tackenberg and Stöcklin,
468 2008) and high levels of herbivory, both domestic and wild, can facilitate the dispersal of soil
469 organisms. Furthermore, mountain massifs and large distances between forested areas (up to
470 250 km) can impact meso- and macrofauna, susceptible to ecological drift due to their limited
471 dispersal capacity or smaller population sizes (Arribas et al., 2021; Kang et al., 2022). This is
472 in line with our results showing that network dissimilarity increased with greater spatial
473 distances (Fig. 5b). Yet, the spatial distance used in the model may not fully capture the
474 complexity of the spatial structure, and further investigation using experimental setups to
475 clarify spatial connectivity and dispersal limitation effects is required.

476

477 Environmental filtering played a significant role in both habitats, primarily influenced by soil
478 edaphic properties. In the French Alps, the soil C/N ratio emerged as the most influential abiotic
479 factor in shaping soil multitrophic network composition. It reflects organic matter
480 decomposability and resource availability, as discussed above, impacting decomposer groups,
481 their consumers, and the entire feeding channel. Conversely, variables related to total energy
482 or resources, such as the NDVI, GDD and SOM, had a smaller impact on soil multitrophic
483 network dissimilarity. While this contrasts with previous studies emphasizing the role of these
484 variables in diversity patterns of soil groups in mountains (Zinger et al., 2011; Calderón-Sanou
485 et al., 2022; Steinwandter and Seeber, 2023), it highlights the emergence of different ecological

486 drivers at different levels of biodiversity organization. In our study, resource quality,
487 particularly litter quality, seemed to dominate network composition rather than quantity.
488 Additionally, environmental factors associated with harsh conditions, such as pH and frozen
489 degree days, known drivers of soil taxonomic diversity and composition (Fierer and Jackson,
490 2006; Decaëns, 2010; Gobbi et al., 2022), also played a major role in shaping soil multitrophic
491 networks.

492
493 Plant-soil interactions likely play a crucial role in shaping grasslands soil multitrophic networks
494 in the French Alps. Although we did not directly measure these interactions, the taxonomic
495 and/or functional composition of plant communities had a major impact on soil multitrophic
496 network structure. Mountain grasslands exhibit high variability in plant species richness and
497 the presence of functionally important taxa such as Fabaceae, Brassicaceae or Poaceae across
498 different elevations and massifs. Changes in plant diversity can influence the composition of
499 soil multitrophic networks (Eisenhauer et al., 2013) , and altering plant identity can affect
500 different soil taxa (Zinger et al., 2011). Interestingly, taxonomic dissimilarity had a larger effect
501 than plant functional dissimilarity, possibly because above-ground traits used in our study may
502 have a lesser role in plant-soil interactions compared to root traits (Kardol and De Long, 2018;
503 Wilschut et al., 2019). Surprisingly, in forests, plant composition had a minor impact on soil
504 multitrophic network structure. Soil variables like pH and C/N ratio may better capture
505 variations in forest type (e.g. broadleaf vs coniferous forests), directly influencing soil
506 multitrophic networks.

507

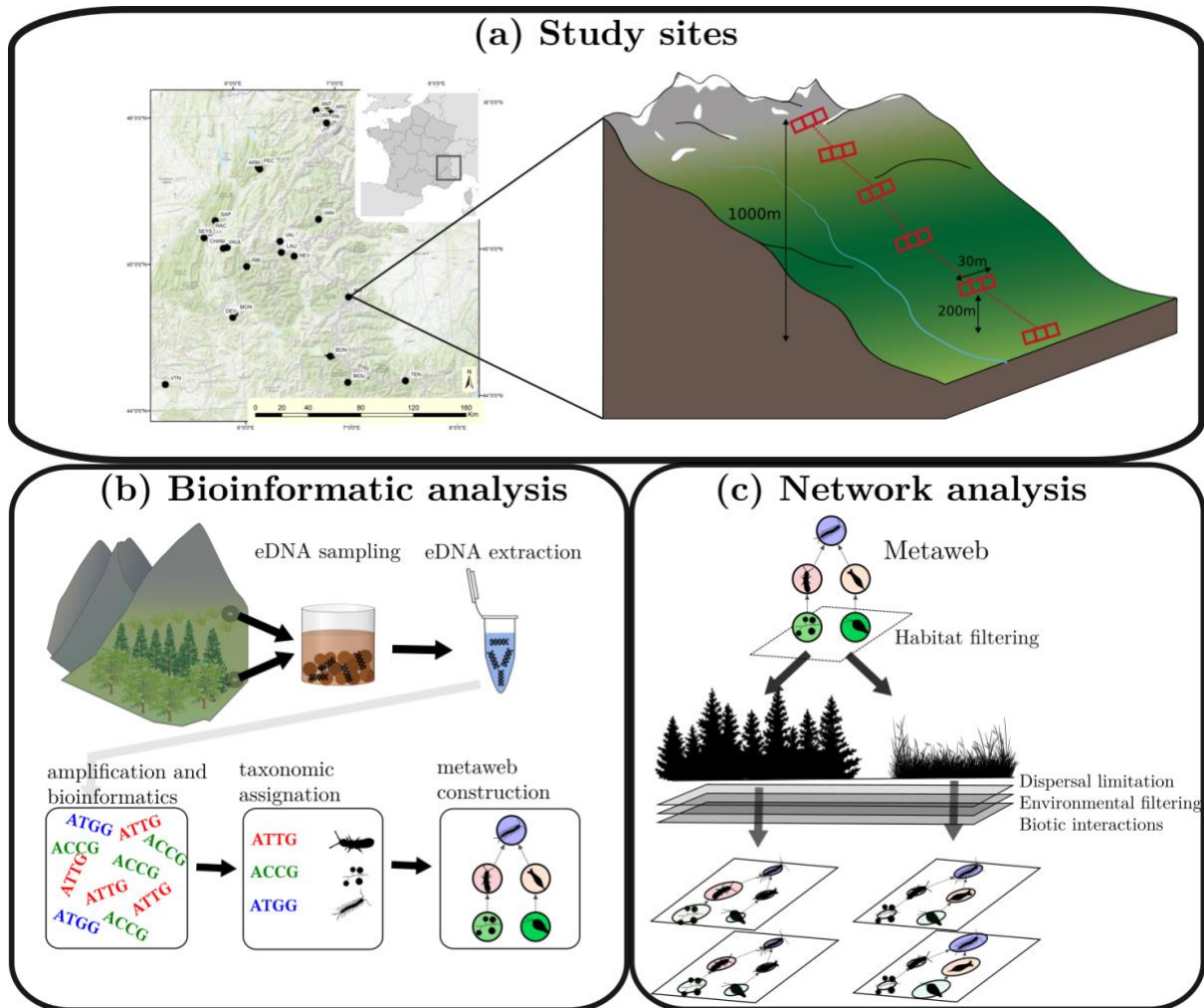
508 **5. Conclusions**

509 This study enhances our understanding of how ecological processes operate in below-ground
510 communities and networks, thereby extending our knowledge of ecological communities as a
511 whole. Furthermore, our research offers valuable insights into the impacts of global change on
512 soil biodiversity and terrestrial ecosystem functioning, particularly in vulnerable mountainous
513 systems experiencing climate change and land-use modifications. Land management decisions,
514 such as forestry, agriculture, and tourism, can alter local land-use and habitats, necessitating
515 consideration of their effects on soil multitrophic networks and ecosystem functioning.
516 However, further investigations are needed to explore the underlying mechanisms driving
517 spatial changes in network structure. Additionally, studying the recovery and resilience of soil
518 multitrophic networks to land-use changes is essential, considering the dynamic nature of
519 ecosystems in the face of a constantly changing climate. These future studies will enhance our

520 understanding of soil multitrophic networks and their responses to environmental changes,
521 aiding informed land management decisions and sustainable practices.
522
523

524 Table 1. Environmental variables used in this study.

	Environmental variable	Abbr.	Description	Temporal range	Resolution	Source
Climate	Growing degree days	GDD	Annual sum of degree-days over a 0°C soil temperature	Average across 2009-2019	Plot	SAFRAN- SURFEX/ISBA-Crocus-MEPRA reanalysis (Vernay et al., 2021)
	Annual precipitation	AP	The sum of all the monthly precipitation estimates			
	Frost degree days	FDD	Annual sum of average daily degrees below zero in soil temperature. Summarizes the duration and intensity of ground freezing events.			
Soil	Soil pH	pH	Top-soil wahter pH	Same year than the sample was collected (2016-2020)	Sample	Measured in the lab
	Soil Organic Matter	SOM	Soil organic matter content		Sample	
	Soil C/N	C/N	Soil carbon to nitrogen ration in organic matter		Sample	
Vegetation	Plant taxonomic dissimilarity		Jaccard pairwise dissimilarity index between subplots.	Same year than the sample was collected (2016-2020)	Plot	Botanical surveys
	Plant functional dissimilarity		Jaccard-like functional index. Traits: specific leaf area (SLA), leaf C/N, root depth (ordered variable), vegetative plant height, and woodyness index (categorical variable ranging from herbaceous to woody).		Plot	Botanical surveys and our own trait measurement values for species (median values across individuals). Root depth was , extracted from (Landolt et al., 2010).
	Normalised Difference Vegetation Index	NDVI	Estimated from the surface spectral reflectance at a resolution of 250 m. Raw NDVI times series were pre-processed following (Choler, 2015), and we kept the mean yearly sum of NDVI greater than 0.2	Average across 2010-2020	Plot	MODIS (Moderate Resolution Imaging Spectroradiometer), available online: https://lpdaac.usgs.gov/products/mod09q1v006/ .



527

528 **Figure 1. Study design to investigate soil multitrophic network structure in the French Alps (a)**

529 Study sites across the French Alps were selected using a stratified sampling design across elevations

530 and nested design with subplots within gradients. The collected 418 soil samples were distributed across

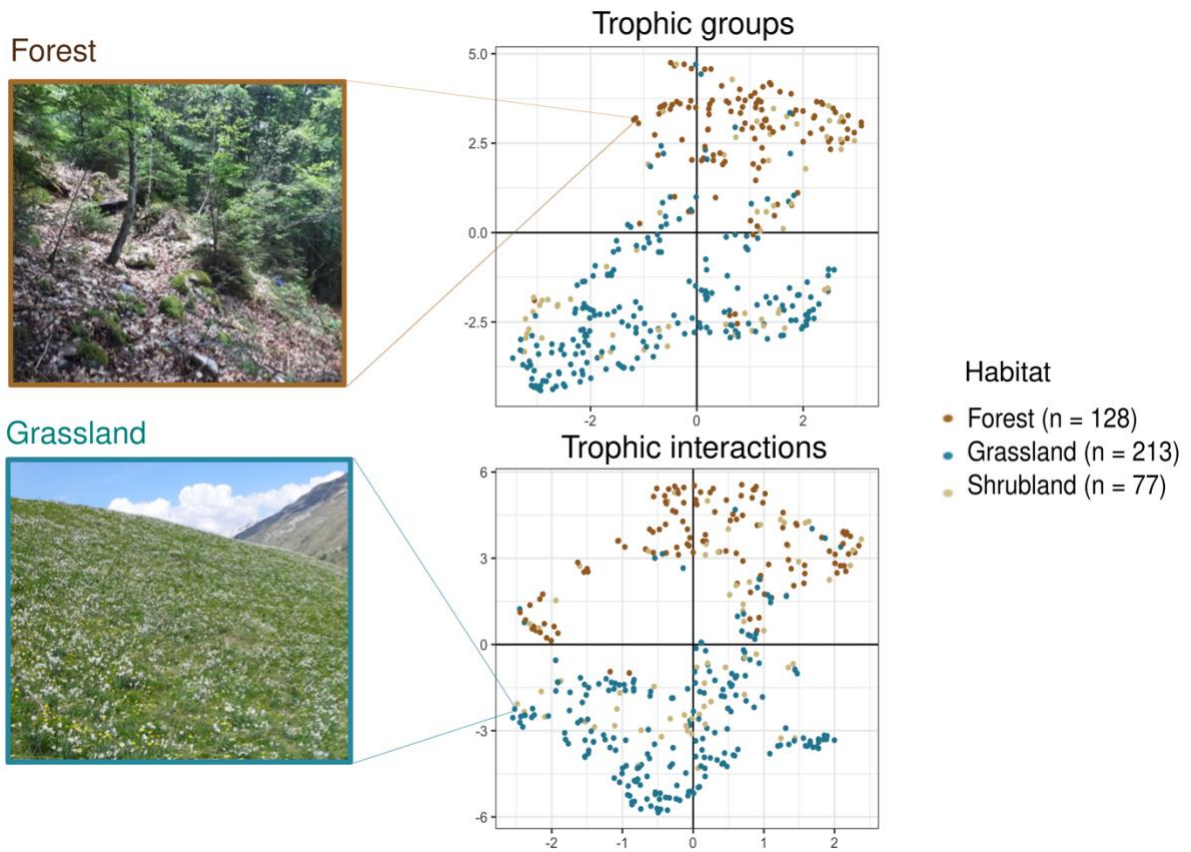
531 nested spatial distances ranging from 8 m to 250 km. (b) eDNA and bioinformatic analysis were used

532 to assign detected organisms to taxonomic and functional information. (c) The metaweb framework was

533 used to quantify spatial changes in the structure of soil multitrophic networks across the study area and

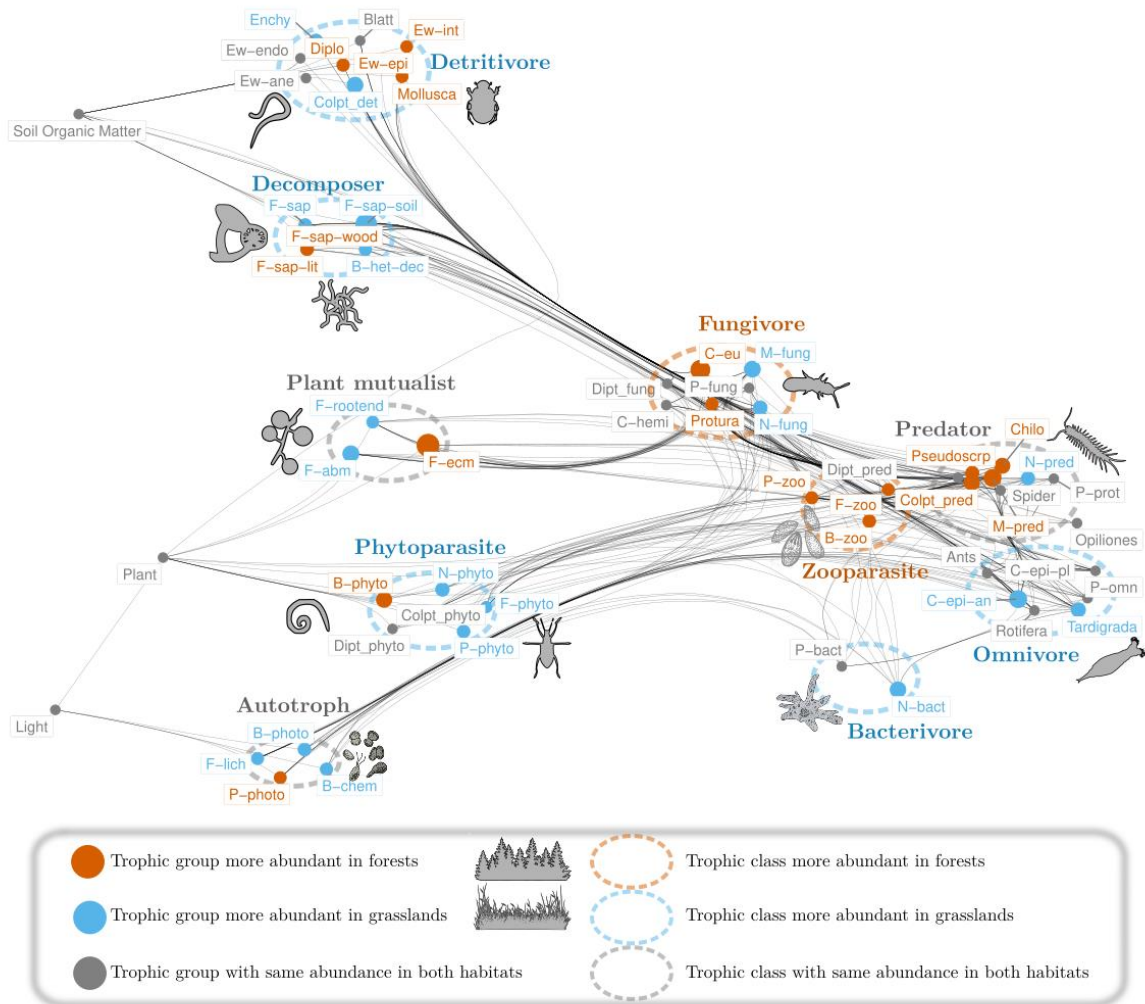
534 examine their associations with environmental and spatial factors.

535



536
 537
 538
 539
 540
 541

Figure 2. 2-D plane representing the dissimilarity between soil multitrophic networks based on the composition of trophic groups and trophic interactions with a colour scale representing the habitat type. Each dot is a local network from a single sub-plot. Dots that are close to each other in the 2D plane have similar trophic group compositions or interactions.



542

543 **Figure 3. Differences in trophic group and class abundances between soil multitrophic networks**

544 **in forests and grasslands.** Colours indicate the significance of Wilcoxon tests calculated for the

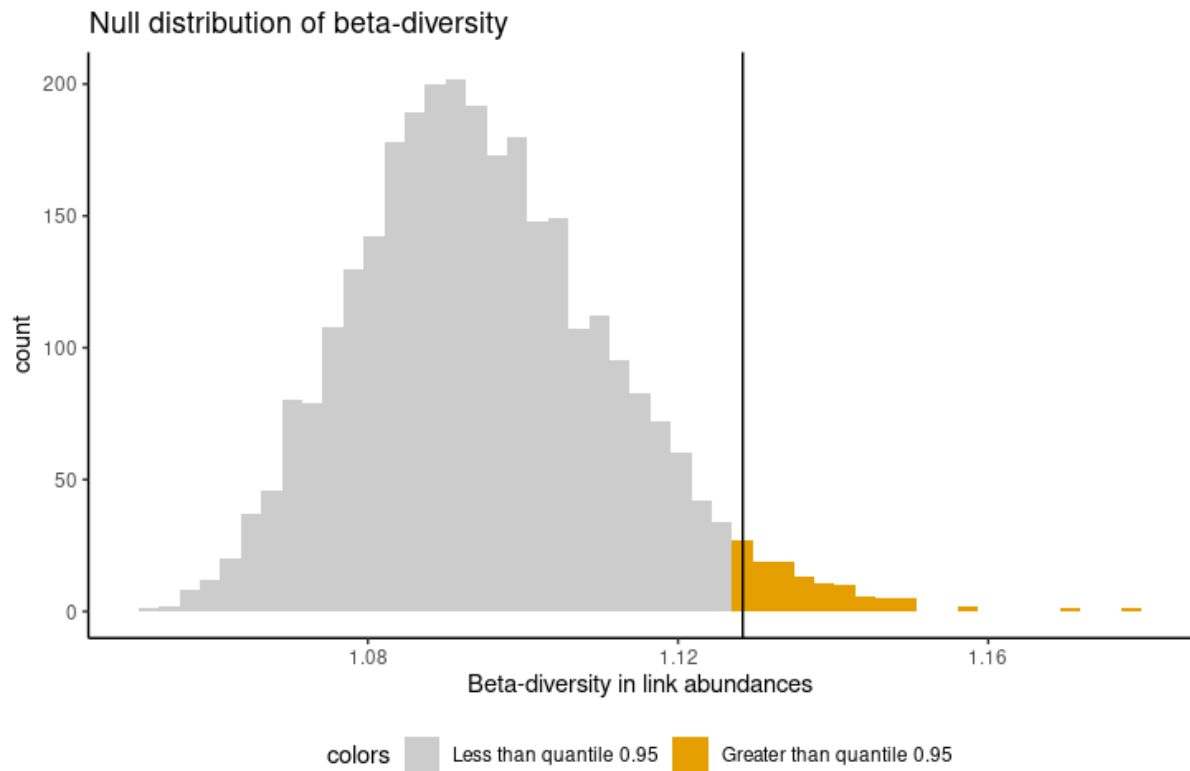
545 difference in abundances of each group between habitats ($p < 0.05$) while node sizes are proportional to

546 significant abundance differences. A Wilcoxon test was also applied to compare differences in trophic

547 class abundances (dashed circles) between habitats. Abundance of trophic classes correspond to the sum

548 of trophic groups relative abundances.

549



550

551 **Figure 4. Null distribution of the β -diversity of interactions (β TL) at fixed trophic group diversity.**

552 The values of the histogram show the β TL between the average soil multitrophic networks of forest and

553 grassland computed using 3000 permutations of trophic group abundances at fixed network structure,

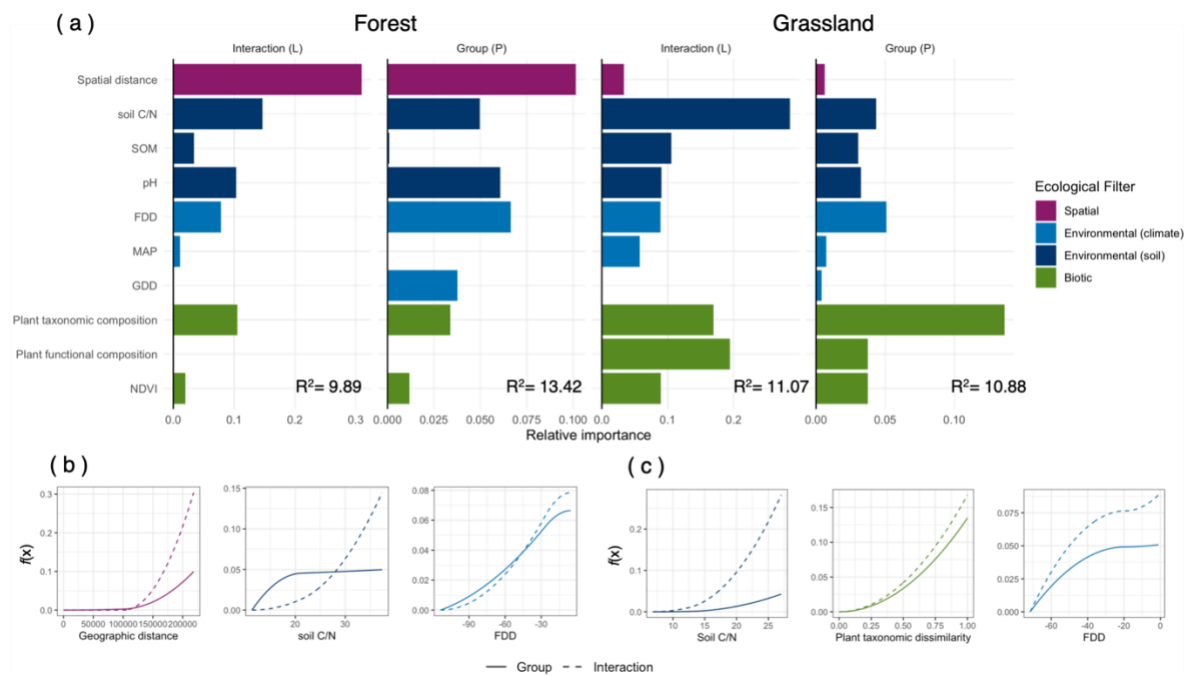
554 leading to various β TL values while keeping trophic group β -diversity constant. The vertical line shows

555 the observed β TL across habitats. The value of β TL varies from one when the average network of forest

556 and grassland have identical interaction abundances distribution, to two, when the networks do not share

557 any common group or interaction.

558



559
 560
 561
 562
 563
 564
 565
 566
 567
 568
 569
 570
 571
 572

Figure 5. Main predictors of soil multitrophic network dissimilarity within forest and grassland habitats. The relative importance of each predictor was estimated using Generalised Dissimilarity Models (a). It is measured as the sum of the coefficients of the three I-splines of the focus predictor and represents the total amount of change along the predictor gradient and represents the total amount of change along the predictor gradient. Partial curves for three of the most important predictors of network dissimilarity in forest (b) and grassland (c). Each panel shows the network dissimilarity as a function of an environmental predictor when holding all other variables to their mean. The slope at any point on the curve indicates the rate of network dissimilarity at that position along the environmental gradient (x-axis), while the total height reached by the function indicates the total amount of network dissimilarity due to that environmental predictor. SOM: Soil Organic Matter, FDD: Frost Degree Days, GDD: Growing Degree Days, AP: Annual Precipitation, NDVI: Normalised Difference Vegetation Index.

573 **References**

574

- 575 Arribas, P., Andújar, C., Salces-Castellano, A., Emerson, B.C., Vogler, A.P., 2021. The limited spatial
576 scale of dispersal in soil arthropods revealed with whole-community haplotype-level
577 metabarcoding. *Molecular Ecology* 30, 48–61. doi:10.1111/mec.15591
- 578 Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning.
579 *Nature* 515, 505–511. doi:10.1038/nature13855
- 580 Baselga, A., Orme, D., Villeger, S., Bortoli, J.D., Leprieur, F., Logez, M., Henriques-Silva, R.,
581 Martínez-Santalla, S., Martín-Devasa, R., Gómez-Rodríguez, C., Crujeiras, R., 2022. betapart:
582 Partitioning Beta Diversity into Turnover and Nestedness Components.
- 583 Bauer, B., Berti, E., Ryser, R., Gauzens, B., Hirt, M.R., Rosenbaum, B., Digel, C., Ott, D., Scheu, S.,
584 Brose, U., 2022. Biotic filtering by species' interactions constrains food-web variability
585 across spatial and abiotic gradients. *Ecology Letters* 25, 1225–1236. doi:10.1111/ele.13995
- 586 Blasbichler, H., Plunger, J., Seeber, J., Steinwandter, M., 2023. Abrupt boundaries between mountain
587 meadows and forests separate ground-dwelling invertebrate communities: a case study from
588 South Tyrol, Italy. *Soil Organisms* 95, 203–216. doi:10.25674/so95iss3id338
- 589 Bonin, A., Guerrieri, A., Ficetola, G.F., 2023. Optimal sequence similarity thresholds for clustering of
590 molecular operational taxonomic units in DNA metabarcoding studies. *Molecular Ecology* 23,
591 368–381. doi:10.22541/au.163398436.69595421/v1
- 592 Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P., Coissac, E., 2016. OBITOOLS : a UNIX -
593 inspired software package for DNA metabarcoding. *Molecular Ecology Resources* 16, 176–
594 182. doi:10.1111/1755-0998.12428
- 595 Calderón-Sanou, I., Münkemüller, T., Boyer, F., Zinger, L., Thuiller, W., 2020. From environmental
596 DNA sequences to ecological conclusions: How strong is the influence of methodological
597 choices? *Journal of Biogeography* 47, 193–206. doi:https://doi.org/10.1111/jbi.13681
- 598 Calderón-Sanou, I., Zinger, L., Hedde, M., Martinez-Almoyna, C., Saillard, A., Renaud, J., Gielly, L.,
599 Khedim, N., Lionnet, C., Ohlmann, M., Consortium, O., Münkemüller, T., Thuiller, W., 2022.
600 Energy and physiological tolerance explain multi-trophic soil diversity in temperate
601 mountains. *Diversity and Distributions* 28, 2549–2564. doi:10.1111/ddi.13529
- 602 Caruso, T., Clemente, G.V., Rillig, M.C., Garlaschelli, D., 2022. Fluctuating ecological networks: A
603 synthesis of maximum-entropy approaches for pattern detection and process inference.
604 *Methods in Ecology and Evolution* 13, 2306–2317. doi:10.1111/2041-210X.13985
- 605 Choler, P., 2015. Growth response of temperate mountain grasslands to inter-annual variations in
606 snow cover duration. *Biogeosciences* 12, 3885–3897. doi:10.5194/bg-12-3885-2015
- 607 Compson, Z.G., Monk, W.A., Curry, C.J., Gravel, D., Bush, A., Baker, C.J.O., Al Manir, M.S.,
608 Riazanov, A., Hajibabaei, M., Shokralla, S., Gibson, J.F., Stefani, S., Wright, M.T.G., Baird,
609 D.J., 2018. Chapter Two - Linking DNA Metabarcoding and Text Mining to Create Network-
610 Based Biomonitoring Tools: A Case Study on Boreal Wetland Macroinvertebrate
611 Communities, in: Bohan, D.A., Dumbrell, A.J., Woodward, G., Jackson, M. (Eds.), *Advances
612 in Ecological Research, Next Generation Biomonitoring: Part 2*. Academic Press, pp. 33–74.
613 doi:10.1016/bs.aecr.2018.09.001
- 614 Crotty, F.V., Blackshaw, R.P., Adl, S.M., Inger, R., Murray, P.J., 2014. Divergence of feeding
615 channels within the soil food web determined by ecosystem type. *Ecology and Evolution* 4,
616 1–13. doi:10.1002/ece3.905
- 617 David, J.-F., Handa, I.T., 2010. The ecology of saprophagous macroarthropods (millipedes, woodlice)
618 in the context of global change. *Biological Reviews* 85, 881–895. doi:10.1111/j.1469-
619 185X.2010.00138.x
- 620 Davison, J., Moora, M., Öpik, M., Adholeya, A., Ainsaar, L., Bâ, A., Burla, S., Diedhiou, A.G.,
621 Hiiesalu, I., Jairus, T., Johnson, N.C., Kane, A., Koorem, K., Kochar, M., Ndiaye, C., Pärtel,
622 M., Reier, Ü., Saks, Ü., Singh, R., Vasar, M., Zobel, M., 2015. Global assessment of
623 arbuscular mycorrhizal fungus diversity reveals very low endemism. *Science* 349, 970–973.
624 doi:10.1126/science.aab1161
- 625 de Araujo, A.S.F., Mendes, L.W., Lemos, L.N., Antunes, J.E.L., Beserra, J.E.A., de Lyra, M. do
626 C.C.P., Figueiredo, M. do V.B., Lopes, Â.C. de A., Gomes, R.L.F., Bezerra, W.M., Melo,

627 V.M.M., de Araujo, F.F., Geisen, S., 2018. Protist species richness and soil microbiome
628 complexity increase towards climax vegetation in the Brazilian Cerrado. *Communications*
629 *Biology* 1, 135. doi:10.1038/s42003-018-0129-0

630 Decaëns, T., 2010. Macroecological patterns in soil communities. *Global Ecology and Biogeography*
631 19, 287–302. doi:10.1111/j.1466-8238.2009.00517.x

632 Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J.,
633 Bardgett, R.D., Maestre, F.T., Singh, B.K., Fierer, N., 2018. A global atlas of the dominant
634 bacteria found in soil. *Science* 359, 320–325. doi:10.1126/science.aap9516

635 Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F.,
636 Berhe, A.A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., He, J.-
637 Z., Hseu, Z.-Y., Hu, H.-W., Kirchmair, M., Neuhauser, S., Pérez, C.A., Reed, S.C., Santos, F.,
638 Sullivan, B.W., Trivedi, P., Wang, J.-T., Weber-Grullon, L., Williams, M.A., Singh, B.K.,
639 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature*
640 *Ecology & Evolution* 4, 210–220. doi:10.1038/s41559-019-1084-y

641 Dunne, J.A., 2006. The network structure of food webs, in: Pascual, M., Dunne, J.A. (Eds.),
642 *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press,
643 pp. 27–86.

644 Eisenhauer, N., Bender, S.F., Calderón-Sanou, I., de Vries, F.T., Lembrechts, J.J., Thuiller, W., Wall,
645 D.H., Zeiss, R., Bahram, M., Beugnon, R., Burton, V.J., Crowther, T.W., Delgado-Baquerizo,
646 M., Geisen, S., Kardol, P., Krashevskaya, V., Martínez-Muñoz, C.A., Patoine, G., Seeber, J.,
647 Soudzilovskaia, N.A., Steinwandter, M., Sünemann, M., Sun, X., van der Heijden, M.G.A.,
648 Guerra, C.A., Potapov, A., 2022. Frontiers in soil ecology—Insights from the World
649 Biodiversity Forum 2022. *Journal of Sustainable Agriculture and Environment* 1, 245–261.
650 doi:10.1002/sae2.12031

651 Eisenhauer, N., Buscot, F., Heintz-Buschart, A., Jurburg, S.D., Küsel, K., Sikorski, J., Vogel, H.-J.,
652 Guerra, C.A., 2021. The multidimensionality of soil macroecology. *Global Ecology and*
653 *Biogeography : A Journal of Macroecology* 30, 4–10. doi:10.1111/geb.13211

654 Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K., Reich, P.B., 2013. Plant
655 diversity effects on soil food webs are stronger than those of elevated CO₂ and N deposition
656 in a long-term grassland experiment. *Proceedings of the National Academy of Sciences* 110,
657 6889–6894. doi:10.1073/pnas.1217382110

658 Elton, C.S., 1927. *Animal ecology*. Macmillan Co., New York., doi:10.5962/bhl.title.7435

659 Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. *Trends in Ecology & Evolution* 17, 177–183.
660 doi:10.1016/S0169-5347(02)02496-5

661 Ferrier, S., Manion, G., Elith, J., Richardson, K., 2007. Using generalized dissimilarity modelling to
662 analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity*
663 *and Distributions* 13, 252–264. doi:10.1111/j.1472-4642.2007.00341.x

664 Ficetola, G.F., Coissac, E., Zundel, S., Riaz, T., Shehzad, W., Bessière, J., Taberlet, P., Pompanon, F.,
665 2010. An In silico approach for the evaluation of DNA barcodes. *BMC Genomics* 11, 434.
666 doi:10.1186/1471-2164-11-434

667 Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities.
668 *Proceedings of the National Academy of Sciences* 103, 626–631.

669 Fiore-Donno, A.M., Richter-Heitmann, T., Bonkowski, M., 2020. Contrasting Responses of Protistan
670 Plant Parasites and Phagotrophs to Ecosystems, Land Management and Soil Properties.
671 *Frontiers in Microbiology* 11. doi:10.3389/fmicb.2020.01823

672 Fitzpatrick, M., Mokany, K., Manion, G., Nieto-Lugilde, D., Ferrier, S., Lisk, M., Ware, C., Woolley,
673 S., Harwood, T., 2022. gdm: Generalized Dissimilarity Modeling.

674 Ganault, P., Nahmani, J., Hättenschwiler, S., Gillespie, L.M., David, J.-F., Henneron, L., Iorio, E.,
675 Mazzia, C., Muys, B., Pasquet, A., Prada-Salcedo, L.D., Wambsganss, J., Decaëns, T., 2021.
676 Relative importance of tree species richness, tree functional type, and microenvironment for
677 soil macrofauna communities in European forests. *Oecologia* 196, 455–468.
678 doi:10.1007/s00442-021-04931-w

679 Geisen, S., Briones, M.J.I., Gan, H., Behan-Pelletier, V.M., Friman, V.-P., de Groot, G.A., Hannula,
680 S.E., Lindo, Z., Philippot, L., Tiunov, A.V., Wall, D.H., 2019. A methodological framework

681 to embrace soil biodiversity. *Soil Biology and Biochemistry* 136, 107536.
682 doi:10.1016/j.soilbio.2019.107536

683 Glassman, S.I., Wang, I.J., Bruns, T.D., 2017. Environmental filtering by pH and soil nutrients drives
684 community assembly in fungi at fine spatial scales. *Molecular Ecology* 26, 6960–6973.
685 doi:10.1111/mec.14414

686 Gobbi, M., Corlatti, L., Caccianiga, M., Ter Braak, C.J.F., Pedrotti, L., 2022. Hay meadows’
687 overriding effect shapes ground beetle functional diversity in mountainous landscapes.
688 *Ecosphere* 13, e4193. doi:10.1002/ecs2.4193

689 Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., Poisot, T., Stouffer,
690 D.B., Tylianakis, J.M., Wood, S.A., Rosling, T., 2019. Bringing Elton and Grinnell Together:
691 a quantitative framework to represent the biogeography of ecological interaction networks.
692 *Ecography* 42, 401–620.

693 Hedde, M., Blight, O., Briones, M.J.I., Bonfanti, J., Brauman, A., Brondani, M., Calderón Sanou, I.,
694 Clause, J., Conti, E., Cortet, J., Decaëns, T., Erktan, A., Gérard, S., Goulpeau, A., Iannelli,
695 M., Joimel-Boulanger, S., Jouquet, P., Le Guillarme, N., Marsden, C., Martinez Almoyna, C.,
696 Mulder, C., Perrin, W., Pétilion, J., Pey, B., Potapov, A.M., Si-moussi, S., Thuiller, W., Trap,
697 J., Vergnes, A., Zaitsev, A., Capowiez, Y., 2022. A common framework for developing
698 robust soil fauna classifications. *Geoderma* 426, 116073.
699 doi:10.1016/j.geoderma.2022.116073

700 Heděnc, P., Jiménez, J.J., Moradi, J., Domene, X., Hackenberger, D., Barot, S., Frossard, A., Oktaba,
701 L., Filser, J., Kindlmann, P., Frouz, J., 2022. Global distribution of soil fauna functional
702 groups and their estimated litter consumption across biomes. *Scientific Reports* 12, 17362.
703 doi:10.1038/s41598-022-21563-z

704 Jackson, R.B., Mooney, H.A., Schulze, E.-D., 1997. A global budget for fine root biomass, surface
705 area, and nutrient contents. *Proceedings of the National Academy of Sciences* 94, 7362–7366.
706 doi:10.1073/pnas.94.14.7362

707 Joimel, S., Cortet, J., Jolivet, C.C., Saby, N.P.A., Chenot, E.D., Branchu, P., Consalès, J.N., Lefort,
708 C., Morel, J.L., Schwartz, C., 2016. Physico-chemical characteristics of topsoil for contrasted
709 forest, agricultural, urban and industrial land uses in France. *Science of The Total*
710 *Environment* 545–546, 40–47. doi:10.1016/j.scitotenv.2015.12.035

711 Jonasson, S., 1988. Evaluation of the Point Intercept Method for the Estimation of Plant Biomass.
712 *Oikos* 52, 101–106. doi:10.2307/3565988

713 Kang, L., Chen, L., Zhang, D., Peng, Y., Song, Y., Kou, D., Deng, Y., Yang, Y., 2022. Stochastic
714 processes regulate belowground community assembly in alpine grasslands on the Tibetan
715 Plateau. *Environmental Microbiology* 24, 179–194. doi:10.1111/1462-2920.15827

716 Kardol, P., De Long, J.R., 2018. How anthropogenic shifts in plant community composition alter soil
717 food webs. *F1000Research* 7, 4. doi:10.12688/f1000research.13008.1

718 Kardol, P., De Long, J.R., Mariotte, P., 2018. Soil Biota as Drivers of Plant Community Assembly, in:
719 Ohgushi, T., Wurst, S., Johnson, S.N. (Eds.), *Aboveground–Belowground Community*
720 *Ecology, Ecological Studies*. Springer International Publishing, Cham, pp. 293–318.
721 doi:10.1007/978-3-319-91614-9_13

722 Keddy, P.A., 1992. Assembly and Response Rules: Two Goals for Predictive Community Ecology.
723 *Journal of Vegetation Science* 3, 157–164. doi:10.2307/3235676

724 Kelly, R.P., Shelton, A.O., Gallego, R., 2019. Understanding PCR Processes to Draw Meaningful
725 Conclusions from Environmental DNA Studies. *Scientific Reports* 9, 12133.
726 doi:10.1038/s41598-019-48546-x

727 Konvalinková, T., Jansa, J., 2016. Lights Off for Arbuscular Mycorrhiza: On Its Symbiotic
728 Functioning under Light Deprivation. *Frontiers in Plant Science* 7.

729 Landolt, E., Bäumler, B., Ehrhardt, A., Hegg, O., Klötzli, F., Lämmli, W., Nobis, M., Rudmann-
730 Maurer, K., Schweingruber, F.H., Theurillat, J.-P., Urmi, E., Vust, M., Wohlgenuth, T.,
731 2010. *Flora indicativa: Okologische Zeigerwerte und biologische Kennzeichen zur Flora der*
732 *Schweiz und der Alpen*. Haupt, Bern.

733 Le Guillarme, N., Hedde, M., Potapov, A.M., Berg, M.P., Briones, M.J.I., Calderón-Sanou, I.,
734 Degrune, F., Hohberg, K., Martinez-Almoyna, C., Martínez-Muñoz, C.A., Pey, B., Russell,
735 D.J., Thuiller, W., 2023. The Soil Food Web Ontology: aligning trophic groups, processes,

736 and resources to harmonise and automatise soil food web reconstructions.
737 doi:10.1101/2023.02.03.526812

738 Le Guillarme, N., Thuiller, W., 2023. A practical approach to constructing a knowledge graph for soil
739 ecological research. *European Journal of Soil Biology* 117, 103497.
740 doi:10.1016/j.ejsobi.2023.103497

741 Louca, S., Parfrey, L.W., Doebeli, M., 2016. Decoupling function and taxonomy in the global ocean
742 microbiome. *Science* 353, 1272–1277. doi:10.1126/science.aaf4507

743 Maaß, S., Maraun, M., Scheu, S., Rillig, M.C., Caruso, T., 2015. Environmental filtering vs. resource-
744 based niche partitioning in diverse soil animal assemblages. *Soil Biology and Biochemistry*
745 85, 145–152. doi:10.1016/j.soilbio.2015.03.005

746 Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire,
747 E., Mouillot, D., Villeger, S., 2021. mFD: Compute and Illustrate the Multiple Facets of
748 Functional Diversity.

749 Martinez-Almoyna, C., Saillard, A., Zinger, L., Lionnet, C., Arnoldi, C., Foulquier, A., Gielly, L.,
750 Piton, G., Münkemüller, T., Thuiller, W., 2022. Differential effects of soil trophic networks
751 on microbial decomposition activity in mountain ecosystems. *Soil Biology and Biochemistry*
752 172, 108771. doi:10.1016/j.soilbio.2022.108771

753 Mason, J.A., Zanner, C.W., 2005. GRASSLAND SOILS, in: Hillel, D. (Ed.), *Encyclopedia of Soils in*
754 *the Environment*. Elsevier, Oxford, pp. 138–145. doi:10.1016/B0-12-348530-4/00028-X

755 McInnes, L., Healy, J., Melville, J., 2020. UMAP: Uniform Manifold Approximation and Projection
756 for Dimension Reduction. doi:10.48550/arXiv.1802.03426

757 Mercier, C., Boyer, F., Bonin, A., Coissac, E., 2013. SUMATRA and SUMACLUST: fast and exact
758 comparison and clustering of sequences, in: *Programs and Abstracts of the SeqBio 2013*
759 *Workshop*. Abstract. Citeseer, pp. 27–29.

760 Miele, V., Matias, C., Dray, S., Botella, C., Ohlmann, M., Poggiato, G., Thuiller, W., 2021.
761 econetwork: Analyzing Ecological Networks.

762 Mokany, K., Ware, C., Woolley, S.N.C., Ferrier, S., Fitzpatrick, M.C., 2022. A working guide to
763 harnessing generalized dissimilarity modelling for biodiversity analysis and conservation
764 assessment. *Global Ecology and Biogeography* 31, 802–821. doi:10.1111/geb.13459

765 Moore, J.C., de Ruiter, P.C., 1991. Temporal and spatial heterogeneity of trophic interactions within
766 below-ground food webs. *Agriculture, Ecosystems & Environment* 34, 371–397.
767 doi:10.1016/0167-8809(91)90122-E

768 Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F.,
769 Mokany, K., Roquet, C., Smyčka, J., Talluto, M.V., Thuiller, W., 2020. Dos and don'ts when
770 inferring assembly rules from diversity patterns. *Global Ecology and Biogeography* 29, 1212–
771 1229. doi:10.1111/geb.13098

772 Noguerales, V., Meramveliotakis, E., Castro-Insua, A., Andújar, C., Arribas, P., Creedy, T.J.,
773 Overcast, I., Morlon, H., Emerson, B.C., Vogler, A.P., Papadopoulou, A., 2021. Community
774 metabarcoding reveals the relative role of environmental filtering and spatial processes in
775 metacommunity dynamics of soil microarthropods across a mosaic of montane forests.
776 *Molecular Ecology* 1–19. doi:10.1111/mec.16275

777 O'Brien, S.L., Gibbons, S.M., Owens, S.M., Hampton-Marcell, J., Johnston, E.R., Jastrow, J.D.,
778 Gilbert, J.A., Meyer, F., Antonopoulos, D.A., 2016. Spatial scale drives patterns in soil
779 bacterial diversity. *Environmental Microbiology* 18, 2039–2051. doi:10.1111/1462-
780 2920.13231

781 Ohlmann, M., Garnier, J., Vuillon, L., 2023. 'metanetwork': a R package dedicated to handling and
782 representing trophic metanetworks. *Ecology and Evolution* in press.

783 Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L., Thuiller, W., 2019. Diversity
784 indices for ecological networks: a unifying framework using Hill numbers. *Ecology Letters*
785 22, 737–747. doi:10.1111/ele.13221

786 Peay, K.G., Garbelotto, M., Bruns, T.D., 2010. Evidence of dispersal limitation in soil
787 microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology* 91,
788 3631–3640. doi:10.1890/09-2237.1

789 Poggiato, G., Andréoletti, J., Shirley, L., Thuiller, W., 2022. Integrating food webs in species
790 distribution models improves ecological niche estimation and predictions (preprint). Preprints.
791 doi:10.22541/au.166853394.45823739/v1

792 Potapov, A.M., Beaulieu, F., Birkhofer, K., Bluhm, S.L., Degtyarev, M.I., Devetter, M., Goncharov,
793 A.A., Gongalsky, K.B., Klärner, B., Korobushkin, D.I., Liebke, D.F., Maraun, M., Mc
794 Donnell, R.J., Pollierer, M.M., Schaefer, I., Shrubovych, J., Semenyuk, I.I., Sendra, A.,
795 Tuma, J., Tůmová, M., Vassilieva, A.B., Chen, T., Geisen, S., Schmidt, O., Tiunov, A.V.,
796 Scheu, S., 2022. Feeding habits and multifunctional classification of soil-associated
797 consumers from protists to vertebrates. *Biological Reviews* brv.12832. doi:10.1111/brv.12832

798 Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O.,
799 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-
800 based tools. *Nucleic Acids Research* 41, D590–D596. doi:10.1093/nar/gks1219

801 R Core Team, 2020. *A Language and Environment for Statistical Computing*.

802 Ramirez, K.S., Leff, J.W., Barberán, A., Bates, S.T., Betley, J., Crowther, T.W., Kelly, E.F., Oldfield,
803 E.E., Shaw, E.A., Steenbock, C., Bradford, M.A., Wall, D.H., Fierer, N., 2014. Biogeographic
804 patterns in below-ground diversity in New York City’s Central Park are similar to those
805 observed globally. *Proceedings of the Royal Society B: Biological Sciences* 281, 20141988.
806 doi:10.1098/rspb.2014.1988

807 Schoch, D., 2022. *edgebundle: Algorithms for Bundling Edges in Networks and Visualizing Flow and*
808 *Metro Maps*.

809 Sepp, S.-K., Davison, J., Moora, M., Neuenkamp, L., Oja, J., Roslin, T., Vasar, M., Öpik, M., Zobel,
810 M., 2021. Woody encroachment in grassland elicits complex changes in the functional
811 structure of above- and belowground biota. *Ecosphere* 12, e03512.
812 doi:https://doi.org/10.1002/ecs2.3512

813 Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H.,
814 Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S.,
815 Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V.H.,
816 Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E.K., Müller, J., Oelmann, Y.,
817 Overmann, J., Pašalić, E., Rillig, M.C., Schaefer, H.M., Schloter, M., Schmitt, B., Schöning,
818 I., Schruppf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel,
819 J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Türke, M., Venter, P.C., Weiner,
820 C.N., Weissner, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst,
821 S., Fischer, M., Allan, E., 2016. Biodiversity at multiple trophic levels is needed for
822 ecosystem multifunctionality. *Nature* 536, 456–459. doi:10.1038/nature19092

823 Steinwandter, M., Seeber, J., 2023. Ground-dwelling invertebrates of the high alpine: Changes in
824 diversity and community composition along elevation (1500–3000 m). *Applied Soil Ecology*
825 190, 104988. doi:10.1016/j.apsoil.2023.104988

826 Taberlet, P., Bonin, A., Zinger, L., Coissac, E., 2018. *Environmental DNA: for biodiversity research*
827 *and monitoring*. Oxford University Press, New York.

828 Taberlet, P., Coissac, E., Hajibabaei, M., Rieseberg, L.H., 2012. Environmental DNA. *Molecular*
829 *Ecology* 21, 1789–1793. doi:10.1111/j.1365-294X.2012.05542.x

830 Tackenberg, O., Stöcklin, J., 2008. Wind dispersal of alpine plant species: A comparison with lowland
831 species. *Journal of Vegetation Science* 19, 109–118. doi:10.3170/2007-8-18338

832 Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-
833 Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas,
834 M., Riit, T., Ratkowsky, D., Pritsch, K., Poldmaa, K., Piipenbring, M., Phosri, C., Peterson,
835 M., Parts, K., Partel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado,
836 L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout,
837 P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L. -d., Greslebin, A., Grelet, G.,
838 Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang,
839 T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K.,
840 2014. Global diversity and geography of soil fungi. *Science* 346, 1256688–1256688.
841 doi:10.1126/science.1256688

842 Thakur, M.P., Geisen, S., 2019. Trophic Regulations of the Soil Microbiome. *Trends in Microbiology*
843 27, 771–780. doi:10.1016/j.tim.2019.04.008

844 Thakur, M.P., Phillips, H.R.P., Brose, U., Vries, F.T.D., Lavelle, P., Loreau, M., Mathieu, J., Mulder,
845 C., Putten, W.H.V. der, Rillig, M.C., Wardle, D.A., Bach, E.M., Bartz, M.L.C., Bennett, J.M.,
846 Briones, M.J.I., Brown, G., Decaëns, T., Eisenhauer, N., Ferlian, O., Guerra, C.A., König-
847 Ries, B., Orgiazzi, A., Ramirez, K.S., Russell, D.J., Rutgers, M., Wall, D.H., Cameron, E.K.,
848 2020. Towards an integrative understanding of soil biodiversity. *Biological Reviews* 95, 350–
849 364. doi:10.1111/brv.12567

850 Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladysz, S., Kitching, R.L., Martinez, N.D.,
851 Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling
852 the structure and function of biodiversity. *Trends in Ecology & Evolution* 27, 689–697.
853 doi:10.1016/j.tree.2012.08.005

854 Thuiller, W., Münkemüller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffrers, K., Gravel, D.,
855 2013. A road map for integrating eco-evolutionary processes into biodiversity models.
856 *Ecology Letters* 16, 94–105. doi:10.1111/ele.12104

857 Vályi, K., Mardhiah, U., Rillig, M.C., Hempel, S., 2016. Community assembly and coexistence in
858 communities of arbuscular mycorrhizal fungi. *The ISME Journal* 10, 2341–2351.
859 doi:10.1038/ismej.2016.46

860 van Buuren, S., Groothuis-Oudshoorn, K., 2011. mice: Multivariate Imputation by Chained Equations
861 in R. *Journal of Statistical Software* 45, 1–67. doi:10.18637/jss.v045.i03

862 Vernay, M., Lafaysse, M., Monteiro, D., Hagenmuller, P., Nheili, R., Samacoïts, R., Verfaillie, D.,
863 Morin, S., 2021. The S2M meteorological and snow cover reanalysis over the French
864 mountainous areas, description and evaluation (1958–2020) (preprint). *Cryosphere – Snow*
865 *and Sea Ice*. doi:10.5194/essd-2021-249

866 Wall, D.H., Nielsen, U.N., Six, J., 2015. Soil biodiversity and human health. *Nature* 528, 69–76.
867 doi:10.1038/nature15744

868 Wilschut, R.A., van der Putten, W.H., Garbeva, P., Harkes, P., Konings, W., Kulkarni, P., Martens,
869 H., Geisen, S., 2019. Root traits and belowground herbivores relate to plant–soil feedback
870 variation among congeners. *Nature Communications* 10, 1564. doi:10.1038/s41467-019-
871 09615-x

872 Zhao, J., Neher, D.A., 2014. Soil energy pathways of different ecosystems using nematode trophic
873 group analysis: a meta analysis. *Nematology* 16, 379–385. doi:10.1163/15685411-00002771

874 Zinger, L., Lejon, D.P.H., Baptist, F., Bouasria, A., Aubert, S., Geremia, R.A., Choler, P., 2011.
875 Contrasting Diversity Patterns of Crenarchaeal, Bacterial and Fungal Soil Communities in an
876 Alpine Landscape. *PLoS ONE* 6, e19950. doi:10.1371/journal.pone.0019950

877 Zinger, L., Lionnet, C., Benoiston, A.-S., Donald, J., Mercier, C., Boyer, F., 2021. metabar: An r
878 package for the evaluation and improvement of DNA metabarcoding data quality. *Methods in*
879 *Ecology and Evolution* 12, 586–592. doi:10.1111/2041-210X.13552

880 Zinger, L., Taberlet, P., Schimann, H., Bonin, A., Boyer, F., De Barba, M., Gaucher, P., Gielly, L.,
881 Giguët-Covex, C., Iribar, A., Réjou-Méchain, M., Rayé, G., Rioux, D., Schilling, V., Tymen,
882 B., Viers, J., Zouiten, C., Thuiller, W., Coissac, E., Chave, J., 2019. Body size determines soil
883 community assembly in a tropical forest. *Molecular Ecology* 28, 528–543.
884 doi:10.1111/mec.14919

885 Zuo, J., Fonck, M., van Hal, J., Cornelissen, J.H.C., Berg, M.P., 2014. Diversity of macro-detritivores
886 in dead wood is influenced by tree species, decay stage and environment. *Soil Biology and*
887 *Biochemistry* 78, 288–297. doi:10.1016/j.soilbio.2014.08.010

888