Mountain soil food webs shaped by the interplay between habitat and pedoclimatic conditions

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Abstract

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

Introduction

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

Gaining insights into the organization of soil communities necessitates studying spatial, environmental, and

biotic drivers and this poses challenges (Decaëns 2010; Münkemüller *et al.* 2020; Eisenhauer*et al.* 2022). First, capturing the full complexity of soil systems requires accounting for their inherent spatial heterogeneity from landscape to local scales (Ettema & Wardle 2002; Thakur *et al.* 2020). At the landscape scale, dominant habitat types, such as grasslands or forests, are crucial for soil taxonomic and functional composition (Fiore-Donno *et al.* 2020; Arribas *et al.* 2021; Sepp *et al.* 2021). Consequently, the heterogeneity between habitats within a landscape can give rise to mosaic patterns of soil communities. Moreover, the spatial connectivity of habitats and the varying dispersal capacities of soil organisms can influence the local composition and structure of soil communities (Arribas *et al.*2021). But even at the local scale of a few meters, variable abiotic conditions, including microclimate and soil physico-chemical properties, along with stochastic processes, can lead to pronounced differences in soil communities (Ramirez *et al.* 2014; O'Brien *et al.*2016; Zinger *et al.* 2019). The structure of the vegetation within an habitat or its taxonomy or functional composition can also affect the abundance and diversity of different soil taxa or trophic groups (Noguerales *et al.* 2021; Calderón-Sanou *et al.* 2022; Ganault *et al.* 2022). Effectively disentangling the effects of spatial, environmental and biotic processes necessitates a sampling design that encompasses multiple spatial scales, ranging from the heterogeneity between habitats to small-scale soil variations.

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

Third, if we are to understand soil biodiversity, not as a group of independent taxa, but rather as food webs, we need the appropriate methods and frameworks to investigate how ecological processes act on soil trophic groups and their interactions. The mono-trophic community assembly framework (Keddy 1992; Thuiller *et al.* 2013) can be extended to food webs using the metaweb concept (Dunne 2006). At the regional scale, the metaweb represents the potential food web encompassing all species (or trophic groups) from the regional pool and their potential interactions (Fig.1c). At the local scale, realised local food webs emerge as subsets of the metaweb due to ecological filtering of species (Bauer *et al.* 2022). This filtering process can be influenced by spatial filters like landscape barriers, limiting dispersal (Peay *et al.* 2010), abiotic factors filtering out species lacking physiological adaptations (Maass *et al.* 2015; Glassman *et al.* 2017), and biotic interactions such as mutualisms, herbivory and predation (Valyi *et al.* 2016). By using the metaweb concept, we can evaluate the effects of ecological filters not only on the taxonomic composition of the local community but also on its network structure (i.e., composition of interactions). Important biotic interactions in the soil are via plant-soil feedbacks, where the taxonomic or functional composition of plant communities influences soil food webs and vice-versa (Kardol & De Long 2018; Kardol *et al.*2018). Moreover, trophic interactions within the food web can elucidate its local structure and composition (Thakur & Geisen 2019). We anticipate that interactions between taxa or groups within the food web should result in co-variation across environmental and spatial gradients. For instance, environments characterized by decomposer communities dominated by bacteria (rather than fungi) should promote the dominance of bacteria consumers and related higher-level consumers within the food web (Moore & de Ruiter 1991), see e.g. Martinez-Almoyna*et al.* 2022. Null models can be used to test the significance of such co-variation in the assembly of ecological communities

(Caruso*et al.* 2022).

Here, we analysed the spatial variation in soil food web structure, encompassing trophic group and interaction composition. We used data from all over the French Alps including lowland forests and high-altitude grassland ecosystems. To represent their spatial heterogeneity, we employed a stratified and nested sampling design, consisting of 24 elevational gradients with multiple plots at varying altitudes (Fig. 1a). We measured soil biodiversity in 418 soil samples, using environmental DNA (eDNA). Using an ontology-based data integration pipeline, combining multiple databases with existing knowledge on the trophic habits of soil organisms (Le Guillarme *et al.* 2023; Le Guillarme & Thuiller 2023), we constructed a metaweb comprising 55 soil trophic groups with 383 potential trophic interactions (Fig.1b). Finally, we applied the metaweb framework to characterise the importance of ecological filters on soil food webs (Fig.1c), using a combination of network diversity indices based on Hill numbers (Ohlmann *et al.*2019) and associated null models. We quantified local variations in soil food web structure both between and within habitats, addressing three specific questions: (Q1) Do different habitats differ in soil food webs?, (Q2) Do trophic interactions contribute to variations in group abundances between habitats?, and, (Q3) How do abiotic conditions, spatial factors, and plant communities shape soil food webs within habitats?

Material and Methods

Study site

The data come from the Orchamp long-term biodiversity observatory (*www.orchamp.osug.fr*, Appendix 1). It encompasses 24 elevation gradients (at the time of this study) across the French Alps sampled between 2016 and 2020 (Fig.1a). These gradients represent diverse climatic, vegetation and soil conditions. Each gradient consists of four to nine 30 x 30 m permanent plots, spaced approximately 200 m apart in altitude. We thus worked with 127 plots ranging from 280 m and 2780 m above sea level.

Habitat type (forest, grassland, shrubland) was determined on-site. Plant species abundances were estimated at the peak of the vegetation along a linear transect traversing each plot, using the pin-point method (Jonasson 1988). Soil sampling was performed at the end of the summer season in three subplots (2 x 2 m) located along a separate 4 m wide transect within each plot. In each subplot, we collected ten soil cores, 5 cm in diameter and ~15 cm in depth (excluding litter), pooled together to a biological sample. Some elevational gradients (37 plots) were sampled twice (i.e., in different years).

Soil biota sampling

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

We employed six DNA markers, including two universal markers (euka02 for eukaryote, bact01 for bacteria) and four clade-specific markers (fung02 for fungi, inse01 for insect, olig01 for oligochaeta, and coll02 for collembola) (Taberlet *et al.* 2018). Details regarding the markers and molecular analyses are detailed in Appendix 2. A standardised bioinformatic pipeline was applied to curate the retrieved sequences from contaminants and errors (Calderon-Sanou *et al.* 2020), using the OBITools software (Boyer *et al.* 2016) and the 'metabaR' R package (R Core Team 2020; Zinger *et al.* 2021). Sequences were clustered into Molecular Operational Taxonomic Unit (MOTU) with SUMACLUST (Mercier *et al.* 2013) using a clustering threshold of 97% for Euka02, Fung01 and Bacte01, 85% for Coll01, 88% for Olig01 and 95% for Inse01, following the recommendations in Bonin *et al.* (2023). Taxonomic annotations were performed on MOTUs with the SILVAngs pipeline (Quast *et al.* 2013) (SILVA version 138.1) for ribosomal universal markers. For clade specific markers, we used the ecotag program from the OBITools, and marker-specific databases built with the ecoPCR program (Ficetola *et al.* 2010), from the EMBL database version 136. Metazoan taxa not registered in the European region were removed from the data (<1% of total reads) using the GBIFfilter tool (*https://github.com/nleguillarme/gbif-filter-python*).

Food web construction

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

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

Building the metaweb: A metaweb is a potential network containing all trophic groups and their potential interactions (Dunne 2006). We added three basal resources to construct our metaweb: light (or chemical energy), plants, and organic matter. Trophic links were then added between groups based on their main feeding preferences. Therefore, plant mutualists and phytoparasites were linked with the plant resource, detritivores and decomposers were linked with the organic matter resource and autotrophs were associated with the light resource. Bacterivores were linked with all trophic groups containing bacteria, and fungivores with all trophic groups containing fungi. The trophic interactions of omnivores, predators and zooparasites, were determined through a literature review of dietary preferences of taxa representing over 90% of the read abundance of the group (Appendix 2).

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

Network analyses

With the aim of analysing spatial variation in soil food web structure, we used beta diversity metrics that account for compositional changes in the food web across samples. We used a set of network diversity indices based on the generalisation of Hill numbers proposed by (Ohlmann *et al.* 2019) These indices allow to quantify diversity in trophic groups and trophic interactions, varying the weight of the relative abundance of groups and links. Here, we focussed on Shannon diversity (q=1, see Calderon-Sanou *et al.* 2020) but also replicated the analyses using species richness (q=0) and Simpson diversity (q=2) to assess the extent to which the observed changes are compositional versus structural. Since interactions in the metaweb are binary (either presence or absent), we approximated the abundance of interactions as the product of the relative abundances of the interacting groups. These diversity indices can be further decomposed into alpha, gamma, and ss-diversity (ssT), and be used to calculate the pairwise dissimilarities for both groups (sspP) and links (sspL). ss-diversity (ssT) quantifies the effective number of different communities, based on shared groups (ssTP) or interactions (ssTL), ranging from 1 (indicating identical group or interaction abundance distribution) to the

total number of communities, when networks do not share any common group or interaction. The diversity metrics were computed using the R package 'econetwork' (Miele*et al.* 2021).

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

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

Finally, to quantify the relative importance of environmental and spatial distances in explaining food web dissimilarity within habitats (i.e., grasslands and forests), we used Generalised Dissimilarity Models (GDM) (Ferrier *et al.* 2007). We built two GDM per habitat using trophic group turnover (sspP) and interaction turnover (sspL) as response variables, with the R package *gdm* (Fitzpatrick *et al.*2022). For the environmental predictors we selected a set of weakly correlated variables (Pearson's $r < 0.5$, Fig.S6) representing climatic, soil and vegetation conditions that could influence soil organisms (Table 1). The spatial coordinates of the samples and all the selected environmental variables were used as predictors. The environmental distance between samples was directly calculated by the *gdm* package, but for plant composition, we used our own dissimilarity indices to represent changes in vegetation composition from both a taxonomic and functional point of view (Table 1). Plant taxonomic dissimilarity between plots was calculated using the*beta.pair* function from the R package 'betapart' (Baselga*et al.* 2022). To estimate plant functional dissimilarity we retrieved trait values for species of which cumulative abundances represented at least 90% of the plot coverage. Missing values (<15% of the total data) were estimated using the imputation method offered by the R package 'mice' (van Buuren & Groothuis-Oudshoorn 2011). Plant functional dissimilarity was estimated using the *beta.fd.multidim* function from the R package 'mFD' (Magneville *et al.* 2021). In the analysis, soil samples from the same subplot collected in different years (i.e., 95 of the 418 samples) were treated as separate samples as they differed in environmental conditions, except for climate and NDVI that were averaged across a period of 10 years. Their spatial dependency was considered through the spatial coordinates of the plot.

Results

The metaweb constructed for the French-Alps region using the taxa identified in 418 soil samples consisted of 55 trophic groups, three basal resources and a total of 383 potential interactions (Fig. S1). On average, local food webs were composed of 41 +- 4 trophic groups (and resources), with 206 +- 37 interactions. All 10 trophic classes were present in all local food webs, with a single exception where no group from the fungivore class was detected. The mean dissimilarity between local soil food webs was primarily influenced

by changes in the dominance of trophic groups, rather than by changes in the presence or absence of groups (as indicated by increasing dissimilarity when increasing parameter q, which represents the weight of trophic group abundance and interaction, Fig.S2).

Overall, we found that food web composition varied across the environmental range covered in this study. The habitat type, particularly when comparing grassland and forest habitats, strongly structured the food web composition, both in terms of trophic group and interaction composition (Q1) (Fig.2, Fig.S3). The influence of habitat type on interaction composition was more pronounced compared to trophic group composition (Table S1). When examining shrubland areas, which represent ongoing shifts from grassland to forest, we found highly variable food web structures (Fig. 2). These structures exhibited similarities to both forest and grassland food webs, potentially due to the spatial proximity of shrubland sampling sites to forests or grasslands, or the specific stage of succession in the shrubland areas. By contrasting the average food webs of forests and grasslands, we identified compositional differences in the abundance of trophic groups and classes between the two habitats (Fig.3). Forest soil food webs were enriched in ectomycorrhizal fungi, litter and wood saprotrophic fungi, macro-detritivores like earthworms and diplopods at basal level, fungivores (particularly eudaphic collembola and protura), soil top predators including predatory mites, centipedes, predatory coleoptera and pseudoscorpions, as well as zooparasites. In contrast, grassland soil food webs had a higher proportion of decomposers and detritivores, particularly soil saprotrophic fungi, enchytraeids and coprophagous coleoptera (e.g., dung beetles), arbuscular mycorrhizal fungi and root endophytes, and most groups of plant phytoparasites and autotrophs. Grasslands also exhibited a higher proportion of bacterivores and omnivores compared to forests, notably bacterivorous nematodes, rotifers and epigeic collembola, at higher trophic levels. We further examined the ss-diversity of interactions between habitats and compared it to null expectations derived from randomising trophic group abundances while preserving trophic group diversity and network structure (see methods). The observed ss-diversity was significantly higher than expected by chance (Fig.4), indicating that trophic groups enriched in each habitat were not randomly distributed in the food webs, but instead formed pairs of trophically linked groups. This suggests that differences in trophic group abundance between habitats (Fig.3) are influenced by the structure of trophic links within the food web (Q2).

The composition of forest and grassland food webs was influenced by distinct ecological filters (Q3). In both habitats, predictors associated with these filters accounted for approximately 10% of the variance in soil food web dissimilarity (Fig.5, Fig.S4). In forests, spatial and environmental predictors played a more important role, particularly soil C/N ratio (related to organic matter degradability), pH, and frozen degree days (FDD) as indicators of abiotic stress (Fig.5a). Dissimilarities in trophic groups and interactions were more pronounced between sites separated by large spatial distances and remained consistent along the gradients of FDD and pH (Fig.5b). Changes in soil C/N ratio primarily influenced interaction dissimilarity, particularly at higher values of the C/N ratio gradient (>20).

In contrast, grassland soil food webs were predominantly driven by plant taxonomic and functional composition, as well as soil C/N ratio (Fig.5a). Soil C/N ratio and plant taxonomic/functional composition better explained interaction dissimilarity (Fig.5c), while plant taxonomic composition was more effective in predicting trophic group dissimilarity. Dissimilarities in trophic groups and interactions remained relatively constant along the plant dissimilarity gradient but were more pronounced in the lower part of the FDD gradient (> 40 cumulative degrees) and the upper part of the C/N ratio gradient (>15).

Discussion

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

Habitat filtering in soil food webs

As anticipated, habitat filtering strongly influenced soil food web structure (Crotty *et al.* 2014; Arribas *et al.* 2021; Sepp*et al.* 2021). Differences in abiotic conditions and resource availability between habitats could explain the observed differences in the proportions of trophic groups. Grassland soils exhibit lower acidity, higher P and N availability and a lower C/N ratio (Joimel*et al.* 2016, Fig.S5), and have a higher below-ground plant biomass, which is more easily decomposed, leading to significant inputs of readily decomposable organic matter into the soil (Mason & Zanner 2005; Heděnec *et al.* 2022). These factors likely enhanced resource availability for detritus-based trophic groups, resulting in the higher dominance of copiotroph decomposers (e.g., saprophytic fungi and bacteria), micro- or meso- detritivores (i.e., Enchytraeidae) and microbivores in grasslands. In contrast, plant detritus in forests, which is more challenging to decompose, serves as a direct resource for litter and wood saprotrophic fungi and provide a habitat for macro-detritivores, which feed on plant litter and associated fungi (David & Handa 2010; Zuo *et al.* 2014). Light availability in grasslands may favour the presence of photoautotrophic bacteria that use light as their primary resource, and facilitate interactions, such as arbuscular mycorrhiza (Konvalinková & Jansa 2016). Moreover, grasslands had a higher proportion of phytoparasites, likely due to the higher biomass of fine roots in this habitat (Jackson *et al.* 1997; Heděnec *et al.* 2022), which are more easy to colonise by symbionts, while forests had a higher proportion of zooparasites, benefiting from a greater abundance of potential hosts, predominantly arthropods, molluscs or earthworms, for the taxa belonging to our zooparasite groups. These findings align with our results showing that trophic interactions within the soil food web contributed to explain food web dissimilarities between habitats (Fig. 4) and are consistent with previous studies examining changes in the trophic composition of protists (de Araujo *et al.* 2018; Fiore-Donno *et al.* 2020) and nematodes (Zhao & Neher 2014) across habitats. The distinct identities of soil antagonists in the soil food webs from grassland to forests warrant further investigation as they could provide insights for land management strategies in mountain ecosystems (Wall *et al.*2015).

Impact of ecological filters within habitats

Our study design aimed to investigate the impact of ecological processes on soil food web structure across altitudinal gradients and diverse environmental conditions. Although the GDM explained a relatively low percentage of variance when quantifying changes in the structure of local food webs (Fig. 5a), it's important to note that typical deviance explained for models of compositional dissimilarity ranges from 20% to 50%, and this percentage can decrease with an increasing number of sites, which was relatively high in our study (Ferrier *et al.*2007; Mokany *et al.* 2022). Furthermore, the resolution of our soil food webs using trophic groups instead of species led to low average dissimilarities (0.27 and 0.48 in forests, and 0.30 and 0.53 in grasslands for groups and interactions respectively), reducing model predictability (Mokany *et al.* 2022). Importantly, we found that trophic link structure significantly influenced changes in trophic groups abundance composition (Fig.4). However, current models cannot account for this factor, and incorporating network structure in diversity models may enhance predictability but requires further implementation (Poggiato *et al.* 2022).

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

Environmental filtering played a significant role in both habitats, primarily influenced by soil edaphic properties. In the French Alps, the soil C/N ratio emerged as the most influential abiotic factor in shaping soil food web composition. It reflects organic matter decomposability and resource availability, as discussed above, impacting decomposer groups, their consumers, and the entire feeding channel Conversely, variables related to total energy or resources, such as the NDVI and SOM, had a smaller impact on soil food web dissimilarity. While this contrasts with previous studies emphasizing the role of these variables in diversity patterns of soil groups in mountains (Zinger *et al.*2011; Calderón-Sanou *et al.* 2022), it highlights the emergence of different ecological drivers at different levels of biodiversity organization. In our study, resource quality, particularly litter quality, seemed to dominate food web composition rather than quantity. Additionally, environmental factors associated with harsh conditions, such as pH and frozen degree days, known drivers of soil taxonomic diversity and composition (Fierer & Jackson 2006; Decaens 2010), also played a major role in shaping soil food webs.

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

Conclusion and perspectives

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

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)

	Environmental variable	Abbr.	Description	Temporal range	Resolution	Source
	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

	Environmental variable	Abbr.	Description	Temporal range	Resolution	Source
	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).
	Normalized 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 Spectrora-diometer), available online: https://lpdaac.us cts/mod09q1v006

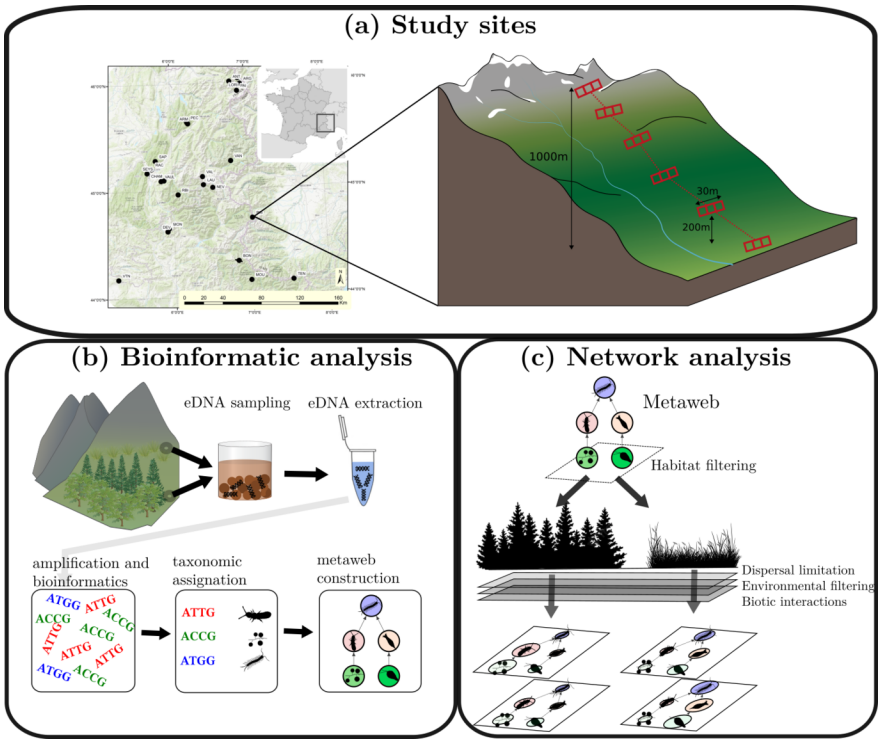

Figure 1. Study design to investigate soil food web structure in the French Alps (a) Study sites across the French Alps were selected using a stratified sampling design across elevations and nested design with subplots within gradients. The collected 418 soil samples were distributed across nested spatial distances ranging from 8 m to 250 km. (b) eDNA and bioinformatic analysis were used to assign detected organisms to taxonomic and functional information. (c) The metaweb framework was used to quantify spatial changes in the structure of soil food webs across the study area and examine their associations with environmental and spatial factors.

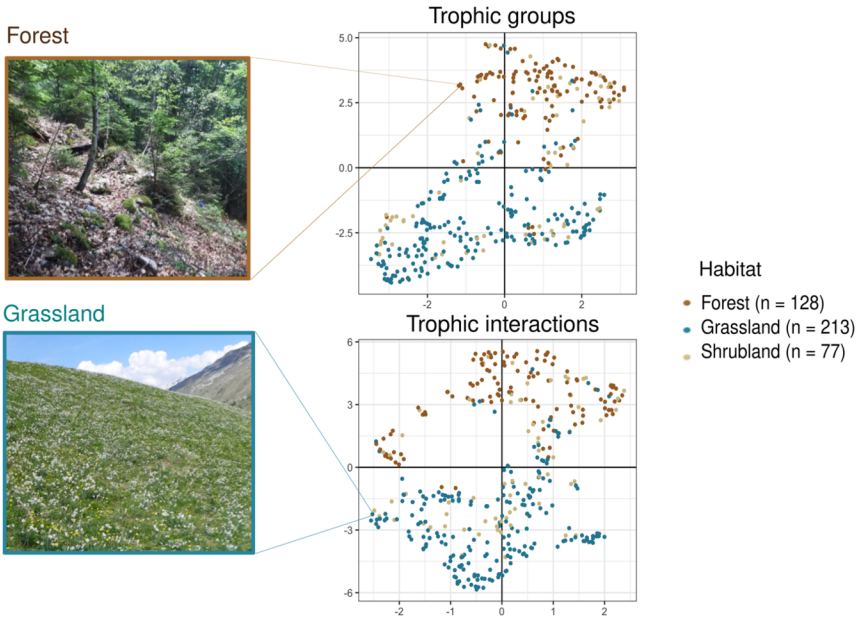

Figure 2. 2-D plane representing the dissimilarity between soil food webs based on the composition of trophic groups and trophic interactions with a colour scale representing the habitat type. Each dot is a local food web from a single sub-plot. Dots that are close to each other in the 2D plane have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

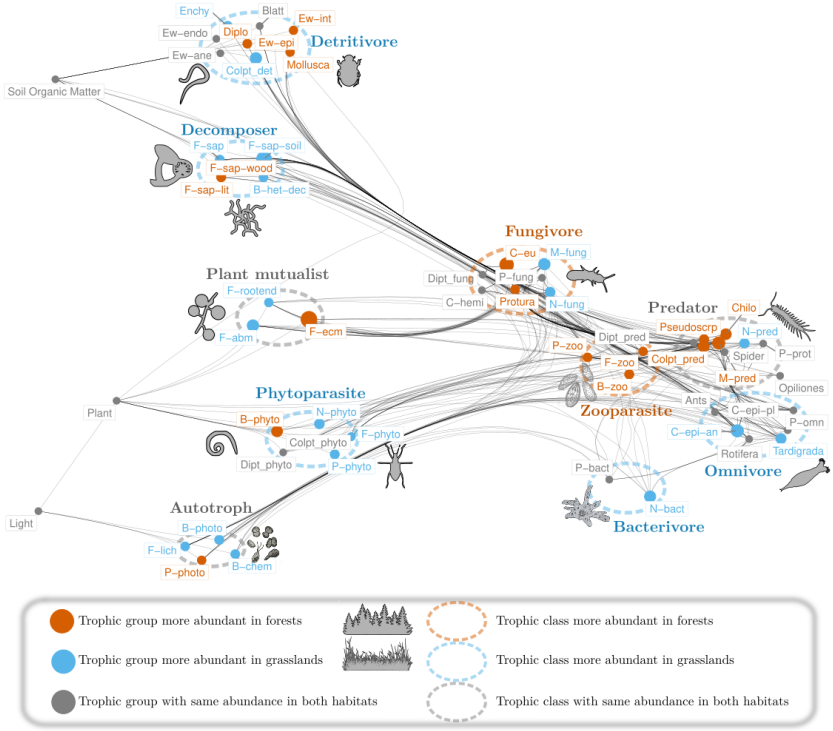

Figure 3. Differences in trophic group and class abundances between soil food webs in forests and grasslands . Colours indicate the significance of Wilcoxon tests calculated for the difference in abundances of each group between habitats ($p<0.05$) while node sizes are proportional to significant abundance differences. A Wilcoxon test was also applied to compare differences in trophic class abundances (dashed circles) between habitats. Abundance of trophic classes correspond to the sum of trophic groups relative abundances.

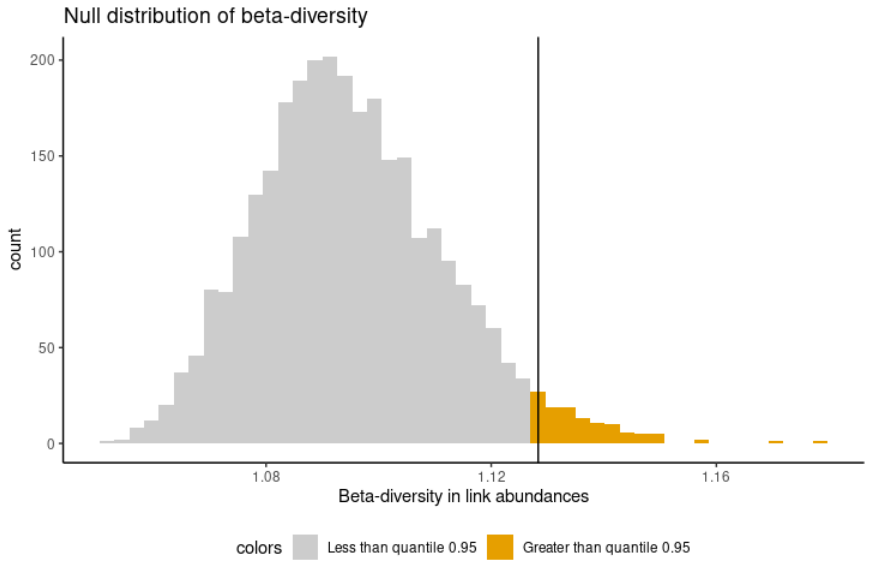

Figure 4. Null distribution of the ß-diversity of interactions (ßTL) at fixed trophic group diversity. The values of the histogram show the ßTL between the average food webs of forest and grassland computed using 3000 permutations of trophic group abundances at fixed network structure, leading to various ßTL values while keeping trophic group ß-diversity constant. The vertical line shows the observed ßTL across habitats. The value of ßTL varies from one when the average food web of forest and grassland have identical interaction abundances distribution, to two, when the food webs do not share any common group or interaction.

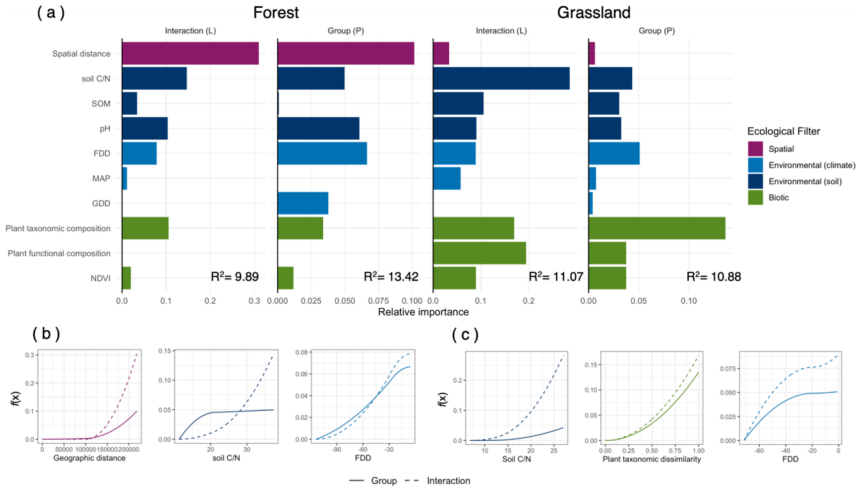

Figure 5. Main predictors of soil food web dissimilarity within forest and grassland habitats. The relative importance of each predictor was estimated using Generalised Dissimilarity Models (a). It is measured as the sum of the coefficients of the three I-splines of the focus predictor and represents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

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