Soil Biology and Biochemistry 172 (2022) 108771

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Differential effects of soil trophic networks on microbial decomposition activity in mountain ecosystems

Camille Martinez-Almoyna [a,*], Amélie Saillard [a], Lucie Zinger [b,c], Clément Lionnet [a], Cindy Arnoldi [a], Arnaud Foulquier [a], Ludovic Gielly [a], Gabin Piton [a,d], The Orchamp Consortium, Tamara Münkemüller [a], Wilfried Thuiller [a]

[a] Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, 38000, Grenoble, France
[b] Institut de Biologie de l'ENS (IBENS), Département de biologie, École normale supérieure, CNRS, INSERM, Université PSL, 75005, Paris, France
[c] Naturalis Biodiversity Center, PO Box 9517, 2300, RA, Leiden, the Netherlands
[d] Eco&Sols, INRAE-IRD-CIRAD-SupAgro, University Montpellier, Montpellier, France

ARTICLE INFO

Keywords:
Trophic regulation
Ecosystem functioning
Multitrophic communities
Soil food web
Structural equation models
Mountain ecosystems

ABSTRACT

Soil trophic networks are key to biogeochemical cycles, in particular decomposition. However, few studies have yet quantified how microbial decomposition activity along environmental gradients is jointly driven by bacteria, fungi, and their respective consumers. Here, we quantified these direct and indirect effects on decomposition and contrasted them between forests and open habitats using multiple elevational gradients in the French Alps.

While environmental control on microbial decomposition activity was comparable in the two habitats, the pathways and strengths of biotic predictors strongly differed. The fungal channel composition played a moderate role in forests, while the bacterial channel composition was critical in open habitats. Importantly, we found trophic regulation by consumers to be a key modulator of the direct environmental effects on decomposition in open habitats. These results highlight the need to integrate trophic regulation when predicting future ecosystem functioning.

1. Introduction

Soil biodiversity underpins a range of ecosystem functions and services crucial to human well-being, including carbon storage and litter decomposition (Bardgett and Putten, 2014; Smith et al., 2015). Predicting the consequences of environmental change on soil biodiversity and associated ecosystem functions is therefore crucial (Jansson and Hofmockel, 2020; Wall et al., 2010). To do so, we need to better understand the regulatory pathways that occur in soil trophic networks, and their changes along environmental gradients and habitats (Thakur and Geisen, 2019; Wardle et al., 1998).

Bacteria and fungi are key decomposers of organic matter (De Boer et al., 2005; Swift et al., 1979). Their activity is context-dependent and varies with climatic conditions, soil physico-chemistry and vegetation structure. In forests, the litter coming from the trees is of rather low quality, which generates rather acidic soils with high organic matter content. Recycling organic matter thus requires the ability to use complex forms of carbon immobilised in recalcitrant litter (Begon et al., 2006). This favours the dominance of many fungal species but also certain bacterial clades that represent the slow cycling of organic matter (López-Mondéjar et al., 2020; Wardle et al., 2004). In contrast, open habitats like grasslands, mineral surfaces and, to a lesser extent, heathlands have a higher availability of labile nutrients and a lower organic matter content (Fierer et al., 2007; Hagedorn et al., 2019). They are therefore more suitable for the dominance of many bacterial species but also certain groups of fungi representing the rapid cycling of organic matter (Ruess and Ferris, 2004; Wardle et al., 2004). Following this observation, many studies have used the fungi to bacteria biomass ratio to quantify the importance of primary decomposers (i.e. bacteria and fungi) in relation to the environment for decomposition (Maassen et al.,

* Corresponding author. LECA, UMR UGA-USMB-CNRS 5553, Université Grenoble Alpes, CS, 40700 38058, Grenoble cedex 9, France.
E-mail addresses: cmartinezalm@gmail.com (C. Martinez-Almoyna), amelie.saillard@univ-grenoble-alpes.fr (A. Saillard), lucie@zinger.fr (L. Zinger), clement.lionnet@univ-grenoble-alpes.fr (C. Lionnet), cindy.arnoldi@univ-grenoble-alpes.fr (C. Arnoldi), arnaud.foulquier@univ-grenoble-alpes.fr (A. Foulquier), ludovic.gielly@univ-grenoble-alpes.fr (L. Gielly), gabinpiton@gmail.com (G. Piton), munremut@univ-grenoble-alpes.fr (T. Münkemüller), wilfried.thuiller@univ-grenoble-alpes.fr (W. Thuiller).

https://doi.org/10.1016/j.soilbio.2022.108771
Received 14 February 2022; Received in revised form 20 April 2022; Accepted 29 June 2022
Available online 2 July 2022

2006; Malik et al., 2016). In contrast, far fewer studies have compared the relative importance of bacterial community composition, fungal community composition and the environment in forests and open habitats. Even fewer studies have integrated and quantified the role of higher trophic levels for decomposition (Thakur and Geisen, 2019).

Indeed, primary decomposers are part of a complex trophic network, which draws energy from the decomposition of soil organic matter, and which can also influence microbial decomposition activity. This trophic network is structured along two main channels and flows of energy (Moore et al., 2003; Moore and William Hunt, 1988; Wardle et al., 2004). On the one hand, the bacterial channel is based on bacterial communities and the organisms that feed on bacteria, i.e. protists, nematodes and some micro-arthropods, and on the other hand, the fungal channel is based on fungal communities and their consumers, i.e. micro-arthropods (e.g. springtails and mites) and some nematodes and protists (Moore et al., 2003; Thakur and Geisen, 2019; Wardle et al., 2004). Studies of trophic regulation on the biomass of primary decomposers have shown varied results with either important or negligible top-down regulation for both fungi and bacteria (Goncharov and Tiunov, 2014; Mikola and Setälä, 1998; Wardle et al., 1998). Moreover, the direct effects of this trophic regulation on the composition and diversity of primary decomposer communities are poorly understood, as are the indirect effects on microbial decomposition activity and the differences between channels (Thakur and Geisen, 2019). The composition of consumer communities can be expected to influence the composition of primary decomposer communities, for example when consumers preferentially feed on certain groups of bacteria or fungi (A'Bear et al., 2014; reported for nematodes, springtails and mites feeding on bacteria and fungi, Ruess et al., 2000; Schneider and Maraun, 2005). Preferential feeding has the effect of relieving consumer pressure on the non-preferred taxa of primary decomposers, which indirectly influences microbial decomposition activity (Crowther et al., 2012; Thakur and Geisen, 2019; Trap et al., 2016). The effect of indirect regulation by the consumers of bacteria and fungi may even be stronger than their direct effects on ecosystem functions (Hättenschwiler et al., 2005). However, so far, we still know little about how these trophic regulations influence microbial decomposition activity, and even less about how this influence varies between habitats dominated by different channels, such as forests or open habitats.

Finally, the existence of this trophic regulation could modulate the direct effects of the environment on microbial decomposition activity. Indeed, since consumers are also structured by the environment, their response could feed through to the composition of primary producers (Xiong et al., 2021). So far, these indirect environmental effects have never been quantified along varying environmental conditions and habitat types.

Here, we quantified the direct and indirect effects of the environment, primary decomposers, and their respective consumers on decomposition along elevational gradients in both forests and open habitats. We used extracellular enzymes to estimate microbial decomposition activity and environmental DNA (*eDNA*) extracted from the same soil samples to describe local compositions in fungi and bacteria, and their respective consumers among protists, nematodes and arthropods. We then built structural equation models (*SEMs*) to answer the following questions:

1 What are the main direct biotic and abiotic drivers of microbial decomposition activity and how does their importance vary between habitats?
2 Is there a trophic regulation of microbial decomposition activity via the composition of fungal and/or bacterial channels in both habitats?
3 Does the composition of the soil trophic network modulate the direct effect of the environment on microbial decomposition activity?

2. Material & methods

2.1. Study sites: Alpine elevation gradients characterised by two habitats

We studied the composition of soil communities in the French Alps along 18 elevational gradients of the ORCHAMP observatory (www.orchamp. osug.fr, Appendix S1). The gradients were continuous from about 900 m to 3000 m, had a homogeneous exposure and slope, and were representative of the environmental and topographic variability of the French Alps. Between 2016 and 2018, at least five sampling plots (30*30 m, see Fig. S1 for details) were placed along each gradient, with an altitude difference of 200 m, resulting in a total of 37 forest sites and 64 open habitat sites (such as meadows or heaths, see Fig. S2 for details).

2.2. Climatic data

In mountain ecosystems, the presence of snow determines the start and length of the vegetation growing season. During this growing season, heat accumulation (i.e. energy available for growth) and soil exposure to frost (i.e. physiological limit of most metabolic processes) shape the composition of plant and microbial communities (Choler, 2005; Edwards et al., 2007; Zinger et al., 2009). In each plot, we calculated growing degree days (GDD) to characterise heat accumulation, and freezing degree days (FDD) to characterise the intensity of freezing events during the growing season (Fig. S3). They are the sum of average daily degrees above (GDD) and below (FDD) zero accumulated over the growing season each year, averaged over the period 1988–2018, and modelled in the first soil horizon (up to 10 cm depth, see Martinez-Almoyna et al. (2020), Table 1 for details). As FDD is a sum of negative degrees, the lowest FDD values correspond to the plots with the most frequent and intense frost stress events. GDD and FDD were calculated from the SAFRAN- SURFEX/ISBA-Crocus-MEPRA re-analysis (Durand et al., 2009), a model that deals with weather and snow conditions in mountainous regions based on large-scale topographic features.

2.3. Sampling, physicochemical properties and total potential extracellular enzyme activity of the soil

In each plot, we sampled soil in three 2 × 2 m subplots with homogeneous vegetation, separated by a distance of 2–12 m (Fig. S1), taking particular care to avoid sample contamination. In each sub-plot, we took about ten 5-cm-diameter cores of superficial soil (ca. 1–8 cm deep) and deeper soil (ca. 8–16 cm), in order to properly describe the first soil horizons. The superficial soil cores were pooled and homogenised separately from the deeper soil cores, resulting in two composite soil samples per subplot. In total, we collected 606 soil samples over the three years, 222 in forest and 384 in open habitats.

We immediately recovered 15 g per soil sample for subsequent eDNA extractions, and sieved the remaining parts to 5.6 mm. Then, we froze 2.75 g of the sieved sample for subsequent analyses of extracellular enzyme activities, 5 g to quantify water content, and sieved the remainder to 2 mm for analyses of the soil physico-chemistry (soil pH, soil organic matter (SOM) and soil C/N as described in Martinez-Almoyna et al. (2020); Appendix S2).

We estimated the potential extracellular enzyme activity of six extracellular enzymes involved in the decomposition of C-rich substrates (α-Glucosidase (AG, EC 3.2.1.20), β-1,4-Glucosidase (BG, EC 3.2.1.21), β-D-Cellobiosidase (CB, EC 3.2.1.91) and β-Xylosidase (XYL, EC 3.2.1.37)) and N-rich substrates (β-1,4-N-acetylglucosaminidase (NAG, EC 3.2.1.30) and leucine aminopeptidase (LAP, EC 3.4.11.1)) using standardised fluorimetric techniques (Bell et al., 2013; see also Martinez-Almoyna et al., 2020 for more experimental details). We calculated the total potential extracellular enzyme activity (*total EAA*) as the sum of the raw potential activity values of the six extracellular enzymes, which had comparable levels of potential activity (Fig. S4). We then

standardized total EEA by soil organic matter (*SOM*) to capture difference of SOM turnover between sites (German et al., 2011). SOM-standardisation also has the advantage of limiting confounding effects due to the correlation between total EEA and microbial biomass (Crowther et al., 2019; Piton et al., 2020). Hereafter, we refer to this variable as *microbial decomposition activity*, as extracellular enzymes are the functional tools by which microbes break down organic matter (Burns et al., 2013). Specifically, we address the enzymatic potential for depolymerization and recycling of specific C- and N-rich substrates that dominate plant and microbial necromass (e.g., cellulose, hemicellulose, proteins, chitin and peptidoglycan, German et al., 2011). Note that investigating the whole decomposition process would require considering the action of other drivers (e.g. mechanical action of other soil species, action of other enzymes), and is not directly the subject of this article.

2.4. Soil eDNA extraction, amplification, sequencing and curation

From the 15 g per soil sample, we conducted the extraction of soil eDNA immediately in the field following the protocol of Taberlet et al. (2012). This method was used due to its easiness of implementation for large-scale samplings, and also because it produces ecological patterns that are similar to those obtained with total DNA, although it may under-sample rare taxa (Zinger et al., 2016). For eDNA amplification, we targeted Eukaryotes, Fungi and Bacteria using the DNA markers Euka02 (18S rRNA), Fung02 (ITS) and Bact01 (16S rRNA) described in Taberlet et al. (2018). We added unique eight-base long tags to the 5′ end of each primer in order to be able to find the original sample of each sequencing read after sequencing. PCR reactions were conducted in quadruplicates for each DNA extract and control. Finally, the PCR samples were pooled and purified prior to sequencing. We built one library per marker in 2016 and 2018 and two libraries per marker in 2017, using the METAFAST protocol. Sequencing was performed with pair-end sequencing technology on the Illumina platform at Fasteris, Geneva, Switzerland (2*125, Hiseq 2000, for Euka02, and 2*250 miseq, for Bact01 and Fung02).

We curated the sequencing reads using the obitools package (Boyer et al., 2016) and the R metabaR package (Zinger et al., 2021, Fig. S5). For each sequencing library, paired-end reads were assembled, assigned to their original samples and markers, and dereplicated with the OBITools package. We then removed PCR errors and grouped the remaining sequences into molecular operational taxonomic units (MOTUs). MOTUs were assigned a taxonomy using different databases depending on the marker. Cross-samples, reagents, sequencing contaminants, dysfunctional PCRs and other artefacts were eliminated using metabaR using conservative quality criteria (Zinger et al., 2021). Next, we excluded samples for which only two or fewer PCR replicates remained. 562 samples remained after this curation procedure, of which 212 were from forest soils and 350 from open habitats. We finally performed a final clustering step to unify the MOTUs across the libraries for each marker. For more details, see Appendix S3 (1, Fig. S5 and Tables S1 and S2)

2.5. Trophic classes and groups of MOTUs

In order to assess the importance of trophic regulation, we only considered organisms directly involved in decomposition (i.e. fungi and bacteria) and their consumers. Finally, we grouped them following their known role in the soil trophic network (i.e. according to their resources and predators, Elton, 1927; Gauzens et al., 2015) and according to their function in the ecosystem. MOTUs were therefore aggregated at two levels: first, at the level of their *trophic class* (e.g. fungi), and second, at the level of a subgroup of this trophic class, which we call a *trophic group* for simplicity (e.g. saprophytic fungi).

2.5.1. At trophic class level

We separated bacterial MOTUs and fungal MOTUs into two different trophic classes, which respectively form the basis of bacterial and fungal channels (Wardle et al., 2004). We referred to the trophic classes of bacteria and fungi together as *primary decomposers*.

We then separated MOTUs feeding on bacteria from those feeding on fungi in two different trophic classes, using literature, expert knowledge and databases (Fig. S6). Among the bacterivores, we found mainly protists and nematodes, while among the fungivores, we found mainly mites and springtails. We removed the MOTUs referenced as feeding on both bacteria and fungi as they were very rare (~15 MOTUs and less 1% of reads in forests and open habitats). This classification represents the knowledge we have been able to extract from the current literature and databases. We are aware that it may only represent the preferred diet (and not obligate, Geisen, 2016). Details on the number of MOTUs within each trophic class are in Appendix S3 (Table S3).

2.5.2. At the trophic group level

We assigned MOTUs within each trophic class to more resolved trophic groups, to facilitate interpretation of compositional variation within trophic classes. For fungi, we used FUNGuild (Nguyen et al., 2016), FungalTraits (Põlme et al., 2020) and Tedersoo et al. (2014) to divide the MOTUs into eleven trophic groups (Table S3). For bacteria, we used FAPROTAX combined with expert knowledge to derive six trophic groups (Louca et al., 2016; Sansupa et al., 2021, Table S3). Then, for the two consumer trophic classes, bacterivores and fungivores, we used taxonomy to assign MOTUs to more resolved trophic groups, as closely related taxa exhibit similar functions (Potapov et al., 2016; Schaefer and Caruso, 2019; Wiens et al., 2010). Details on the number of MOTUs within each trophic group are in Appendix S3 (Table S3).

2.6. Statistical analyses

To quantify the direct and indirect effects of the environment and the compositions of the four trophic classes on microbial decomposition activity, we first constructed variables representing the composition of each trophic class, and integrated these variables into a SEM. This was done for both forest and open habitats independently to highlight differences in decomposition regulation in the two habitats.

2.6.1. First step: composition of each trophic class

2.6.1.1. Variables construction. To summarise the main variation of composition of a trophic class between samples of a given habitat, we performed a correspondence analysis (CA) for each trophic class for each habitat, using the *dudi.coa* function of the *ade4* package in R (R version 3.6.1., Core Development Core Team, 2020; Dray and Dufour, 2007), and we kept the first axis. Two samples with similar coordinates on the first axis had similar compositions of the trophic class considered. To describe the composition of a trophic class in a sample, we therefore used its coordinate on the first axis of the corresponding CA. CA is based on the chi2 distance, which is hardly sensitive to sampling depth, allowing it to be performed directly on the numbers of reads (Appendix S4, Figs. S7 and S8).

2.6.1.2. Interpretation of the compositional CA axes. For each trophic class, we then used the more resolved information of the trophic groups to facilitate the interpretation, the aim being to visualise which compositional variations structure the position of the samples on the first CA axes. First, for each sample, we calculated the relative abundance of each trophic group within each trophic class as the sum of the number of reads of all MOTUs belonging to that trophic group standardised by the total sum of the number of reads of all MOTUs in the same trophic class. We then fitted generalised linear models to visualise the relative abundance of each trophic group as a function of the sample

coordinates on the first CA axis (Appendix S5, Figs. S9 and S10). Second, for each trophic class, we also used the variations in trophic diversity to interpret the compositional variations represented by the first CA axes. To do this, we calculated the trophic diversity of each trophic class in each sample, via the Shannon index applied to the relative abundances of trophic groups (Figs. 1 and 2).

2.6.2. Second step: structural equation models

2.6.2.1. Construction of the SEMs and evaluation of path coefficients. For each habitat, we built a SEM to explain microbial decomposition activity. In this SEM, we used the first CA axes to describe the compositions of the different trophic classes and tested the existence of a trophic regulation of decomposition, through cascading links between the compositions of the different trophic classes (i.e. representing their trophic interactions). The SEM also allowed us to consider the direct effects of the environment on the composition of the trophic classes and on decomposition (see Appendix S6 for the *a priori* model).

We first tested the structure of the *a priori* model using the *sem* function in R (Lefcheck, 2016). This function locally estimates the path coefficients and then assesses the fit between the *a priori* model and the data by testing the conditional independence of variables that are not linked by a path (Shipley, 2000). Then, where necessary, we added some of the missing paths based on their ecological relevance to our model (Grace et al., 2010). Finally, we optimised the model structure through a stepwise procedure using the BIC criterium (Hertzog, 2018).

2.6.2.2. Interpretation of the SEM in each habitat. For interpretations, we used the standardised coefficients extracted from the most parsimonious model (Grace et al., 2010). We also used the information on relative abundances of trophic groups and trophic diversity within each trophic class to better understand the direction of the effects of the composition of each trophic class on microbial decomposition activity.

3. Results

3.1. The direct effects of abiotic and biotic predictors on microbial decomposition activity varied between habitats

The two SEMs for forest and open habitats explained a very similar percentage of the total variation in microbial decomposition activity (R^2 = 0.16). Interestingly, although close in terms of explained variance, the pathway strengths differed strongly between forests and open habitats (Figs. 1 and 2). In forests, microbial decomposition activity was strongly influenced by a direct and negative effect of GDD and FDD, to a lesser extent by a direct and negative effect of soil C–N ratio, and less, but still significantly, by the composition of the fungal class (Fig. 1). In contrast, for open habitats, the composition of the trophic class of bacteria was the main factor controlling microbial decomposition activity, while climate and soil played a similar direct role as in forests, but to a lesser extent (Fig. 2).

3.2. Different roles of biotic channels in decomposition activity in the two habitats

To quantify the overall influence of fungal vs. bacterial channels, we extracted from the SEMs the standardised direct and indirect effects through both the bacterial channel (i.e., bacterivores and bacteria), and

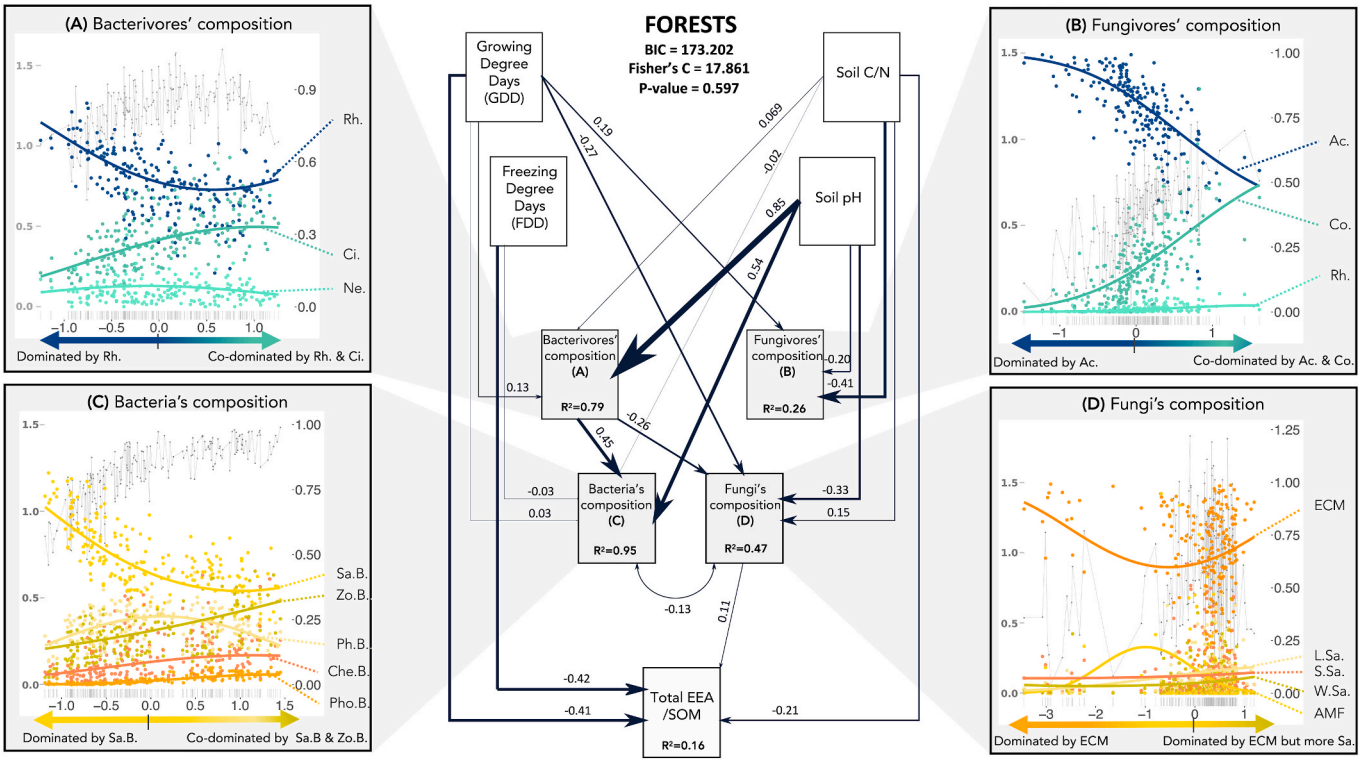

Fig. 1. SEM of the effects of environment and composition of the soil trophic network on microbial decomposition activity in forests. Arrow sizes are proportional to the associated path coefficients. Paths with double arrows represent correlations. The external panels represent the trophic diversity of each trophic class (grey points, left-hand y-axis) and the relative proportion of each trophic group within each trophic class (colored curves, right-hand y-axis) as a function of the position of the samples along the first axis of the CA (x-axis). We represented only the most abundant trophic groups, and more detailed plots are provided in Fig. S9. For example, for Bacteria-consumers, only the variations of Rh. (Rhizaria), Ci. (Ciliophora) and Ne. (Nematoda) are represented. Other abbreviations are ii) Ac. (Acari), Co. (Collembola), iii) Sa. B. (saprophytic bacteria), Che.B. (chemolitoautotrophic bacteria), Zo. B. (zooparasitic bacteria), Ph.B. (phytoparasitic bacteria), Pho. B. (photoautotrophic bacteria), iv) S.Sa (soil saprotrophic fungi), L.Sa (litter saprotrophic fungi), W.Sa (wood saprotrophic fungi), ECM (ectomycorrhizal fungi), AMF (arbuscular mycorrhiza fungi).

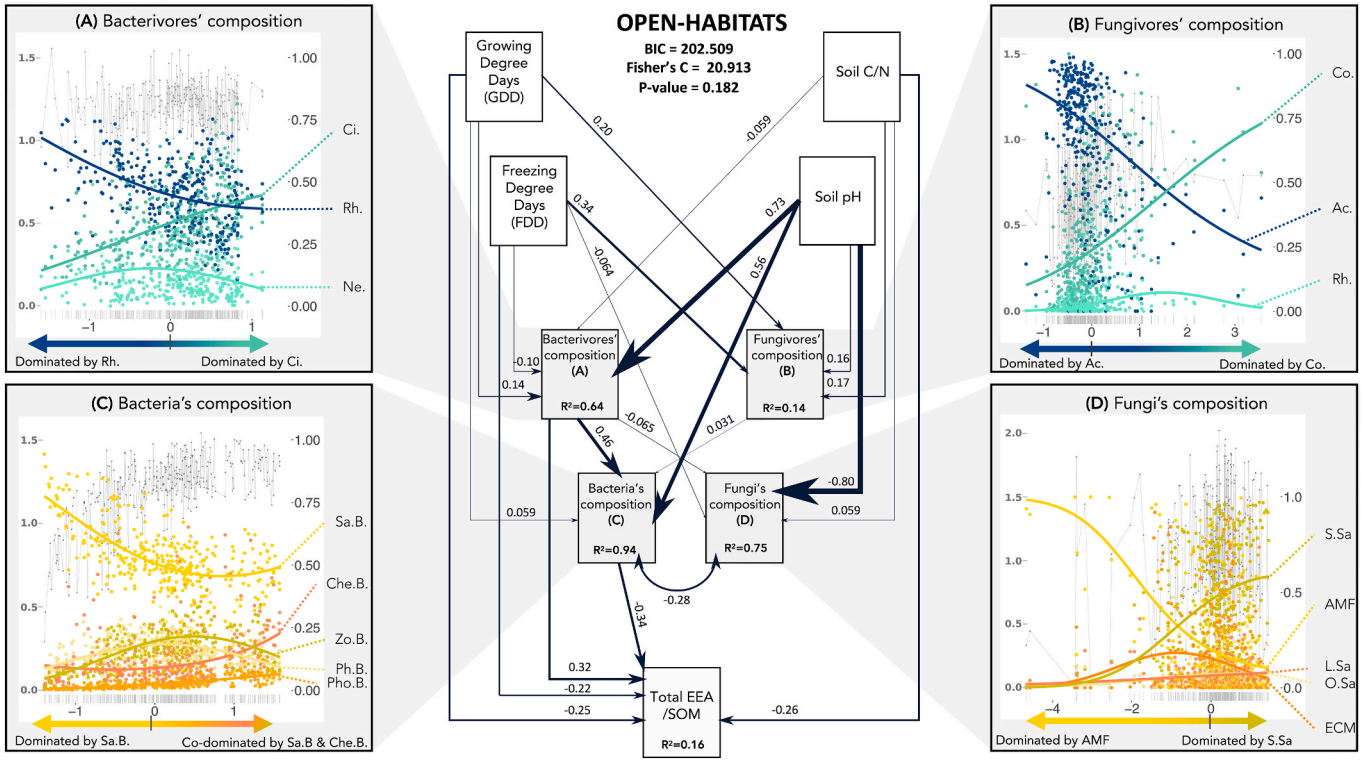

Fig. 2. SEM of the effects of environment and composition of the soil trophic network on microbial decomposition activity in open-habitats. Arrow sizes are proportional to the associated path coefficients. Paths with double arrows represent correlations. The external panels represent the trophic diversity of each trophic class (grey points, left-hand y-axis) and the relative proportion of each trophic group within each trophic class (colored curves, right-hand y-axis) as a function of the position of the samples along the first axis of the CA (x-axis). We represented only the most abundant trophic groups, and more detailed plots are provided in Fig. S10. For example, for Bacteria-consumers, only the variations of Rh. (Rhizaria), Ci. (Ciliophora) and Ne. (Nematoda) are represented. Other abbreviations are ii) Ac. (Acari), Co. (Collembola), iii) Sa. B. (saprophytic bacteria), Che.B. (chemolitoautotrophic bacteria), Zo. B. (zooparasitic bacteria), Ph.B. (phytoparasitic bacteria), Pho. B. (photoautotrophic bacteria), iv) S.Sa (soil saprotrophic fungi), L.Sa (litter saprotrophic fungi), O.Sa (other saprotrophic fungi), ECM (ectomycorrhizal fungi), AMF (arbuscular mycorrhiza fungi).

the fungal channel (i.e., fungivores and fungi, Fig. 3). Contrasting forests and open habitats, we found that the biotic effect on microbial decomposition activity was due to different channels. In forests, it was the composition of the fungi channel that influenced microbial decomposition activity, with a weak influence of primary decomposers (i.e., fungi) and no trophic regulation by fungivores. In contrast, in open habitats, the bacterial channel strongly influenced microbial decomposition activity, with a strong effect of the compositions of the trophic classes of bacteria and bacterivores, but also through strong trophic regulation, i.e. a strong indirect effect of bacterivores (Fig. 3).

3.3. *The composition of the trophic classes of primary decomposers and trophic regulation modulate the effects of the environment on microbial decomposition activity*

Based on SEMs, we calculated the standardised indirect effects of the environment on microbial decomposition activity through its direct effect on the composition of primary decomposers, but also through its

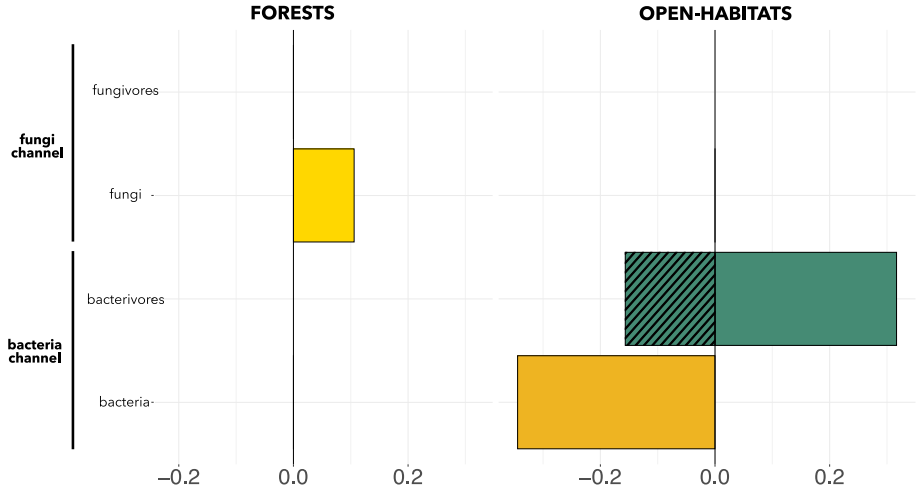

Fig. 3. Comparison of direct and indirect standardized effects of soil trophic network on microbial decomposition activity, extracted from the SEMs (Figs. 1 and 2). Indirect effects (hatched boxes) correspond to the sum of the effects for each indirect path, where the effect for each indirect path is computed as the product of the standardized path coefficients along the path. The sum of the direct and indirect effect is the total effect of a variable. To meet the definition of *channel*, we considered for this figure only the mediation via bacteria for bacteria-channel and via fungi for fungi-channel.

direct effect on the composition of consumers, which then cascades indirectly on primary decomposers (i.e. trophic regulation (Fig. 4),). The indirect influence of the environment on microbial decomposition activity was much lower in forests than in open habitats. This highlighted that the modulation of environmental effects by the soil trophic network depended on the habitat type (Figs. 3 and 4).

In forests, we found a weak indirect effect of the environment on decomposition through its effect on the composition of primary decomposers. Acidic, rather cold soils with poor organic matter slightly enhanced the presence of different groups of saprophytic fungi (i.e. wood, soil and litter saprotrophs) compared to ectomycorrhizal fungi (*ECM*) in the fungal composition (Fig. 1 (D)), which slightly increased the microbial decomposition activity. On the other hand, the indirect effect of the environment via its effect on the composition of consumers was minor in forests (Fig. 4), although the environment explained the composition of consumers well ($R^2_{\text{bacterivores}} = 0.79$, $R^2_{\text{fungivores}} = 0.26$). The composition of fungivores was mainly determined by the quality of soil organic matter, with a dominance of mites on low fertility soils (i.e. high C/N ratio) and a co-dominance of mites and springtails on soils where organic matter was of better quality (Fig. 1 (B), S9 (B)). However, fungivore composition was not directly related to fungi composition, which negated the indirect effect of the environment via fungivores. In addition, soil pH was the main predictor of the composition of bacterivores, with Rhizaria-dominated communities occurring in acidic soils, and communities with a co-dominance of Rhizaria and Ciliophora found in less acidic conditions (Fig. 1 (A), S9 (A)). The indirect effect of the environment on microbial decomposition activity in forests was only modulated via bacterivores and their weak effect on fungal composition.

In open habitats, however, we found a strong indirect effect of the environment, both through primary decomposers and their consumers (Fig. 4). Acidic soils favoured the dominance of saprophytic bacteria, which clearly increased microbial decomposition activity (Fig. 2 (C), 4). In contrast, the strong effect of pH on fungal composition resulted in a dominance of soil saprophytes on acidic soils and arbuscular mycorrhizal fungi (*AMF*) under less acidic conditions, but did not affect decomposition (Fig. 2 (D)). The indirect effect of the environment via the consumers was explained on the one hand by the strong influence of bacterivores on microbial decomposition activity and on the other hand by trophic regulation. As in forests, the environment explained the composition of the consumer classes fairly well ($R^2_{\text{bacterivores}} = 0.64$, $R^2_{\text{fungivores}} = 0.14$). In particular, pH was the main predictor of bacterivore composition, leading to the same compositional trends as in forests (Fig. 2 (A), S10 (A)). This effect cascaded to microbial decomposition activity, firstly because bacterivore communities with a greater trophic diversity were themselves strongly associated with higher microbial decomposition activity. On the other hand, the indirect effect of pH was moderated by the effect of trophic regulation (Figs. 3 and 4). In acidic soils, Rhizaria-dominated bacterivore communities were associated with communities of bacteria dominated by saprophytic bacteria and with increased microbial decomposition activity. In less acidic soils, where bacterivore communities were more trophically diverse, bacterial communities were also characterised by greater trophic diversity and associated with decreased decomposition activity (Fig. 2 (A, C), S10 (A, C), 4).

4. Discussion

While the importance of soil decomposers in ecosystem functioning is increasingly acknowledged, the regulating effects of other trophic soil classes on microbial decomposition remain poorly understood, as does their dependence on habitat (Thakur and Geisen, 2019). Here, we compared the role of four environmental variables and of the consumers of primary decomposers in structuring the composition and activity of primary decomposers in two different habitats. In respect to our three initial questions, we found that (i) the environment, in particular climate, have a stronger effect on microbial decomposition activity in forests than in open habitats, where the biotic effect is more important. (ii) In forests, the composition of the soil network, and primarily of fungal communities, was moderately linked to microbial decomposition activity, whereas in open habitats the effects were much stronger, driven by bacteria, but also strongly influenced by bacterivores. (iii) The environment influences the composition of the different trophic classes, which indirectly influences the microbial decomposition activity through trophic interactions.

Climate, much more than soil physico-chemistry, was an important direct driver of microbial decomposition activity in both habitats. The negative relationships between GDD, FDD and microbial decomposition activity showed that the investment of microbes in extracellular enzyme production was favoured in difficult climatic conditions during the vegetation season, i.e. low heat energy input (i.e. low GDD) and frequent

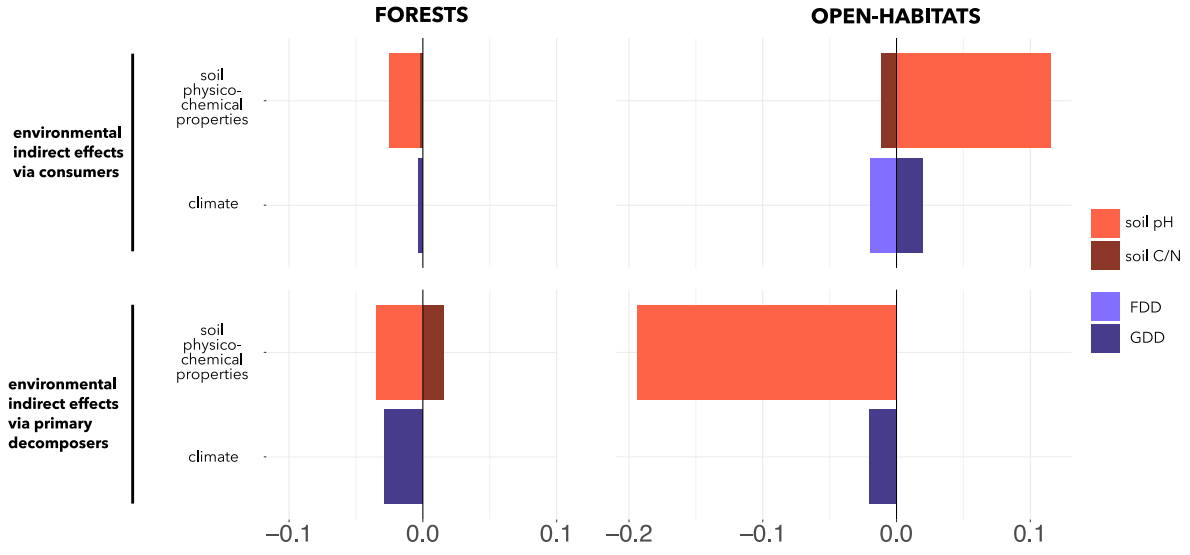

Fig. 4. Comparison of the indirect standardized effects of the environment (soil physico-chemical properties and climatic variables) via consumers and primary decomposers on decomposition activity, extracted from the SEMs (Figs. 1 and 2). *Environmental indirect effects via consumers* correspond to the sum of the effects of each indirect path, which includes the composition of a trophic group of consumers. By contrast, *environmental indirect effects via primary decomposers* correspond to the sum of the effects of each indirect path, which does not include the composition of a trophic class of consumers. The effect of each indirect path is computed as the product of the standardized path coefficients along the path.

and/or intense frost events (i.e. low FDD). Lower (or more frequently negative) average temperatures can indeed reduce (or even stop) extracellular enzyme activity *in situ* (Steinweg et al., 2012), thus increasing the amount of extracellular enzymes needed to capture the same amount of resource (Allison et al., 2010).

This study corroborates the hypotheses of Wardle et al. (2004) on a large scale, with a complete shift from a moderate direct effect of the composition of fungi in forests to a strong direct effect of the composition of bacteria in open habitats. In forests, our results are supported by the work of Schneider et al. (2012, 2010), who showed that fungi produce most extracellular enzymes in forest soils. Indeed, some trophic groups of fungi are key to forest decomposition, because they open access to organic compounds, such as cellulose, blocked in recalcitrant plant debris (e.g. wood and litter saprotrophs, De Boer et al., 2005). This could explain why the increase in the relative abundance of saprophytic fungal groups compared to ECM is associated with an increase in microbial decomposition activity in our study (Fig. 1). In contrast, open habitats are characterised by plants with fewer recalcitrant compounds, generally associated with less acidic soils (Appendix S2, Fig. S3). This could relieve bacteria from the aforementioned constraints and a pH-related environmental stress, and make them more competitive and active in open habitats overall (Rousk et al., 2010b). The increase in relative abundance of parasitic and autotrophic bacterial groups (Fig. 1 (C), S9 (C)) is likely driven by the presence of a mineral nutrient availability gradient in the mountainous open habitats of our study (Fierer et al., 2007; Guo et al., 2015), and could explain the association of the composition of bacteria with a decrease in microbial decomposition activity.

We also demonstrated the importance of a top-down regulation of the composition of the consumer trophic classes on microbial decomposition activity. In particular, in line with Xiong et al. (2021), the link between the composition of bacterivores and bacteria was central in our two habitats (Figs. 1 and 2). This can arise from the high degree of specificity of bacterivores, which had already been observed for bacterivorous protists, dominant in our study (Adl and Gupta, 2006; Trap et al., 2016). More generally, it is known that the presence of specific groups of protists and nematodes influences the composition of primary decomposer classes (Gao et al., 2019; Geisen et al., 2018; Griffiths et al., 1999). Furthermore, we found a fairly strong link between the composition of bacterivores and fungi in forest habitats, possibly due to the quite generalist feeding behaviour of some groups of protists (Geisen, 2016). In the forests of our study, for example, Rhizaria-dominated bacterivore communities seemed to favour the presence of saprophytic fungi over ECMs (Fig. 1). In contrast, the effect of fungivore community composition on fungal community composition and function was less clear in both habitats (Figs. 1–3). This lack of signal could be caused by a biased representation of specific animal organisms in eDNA data, because it includes not only signal from current communities, but also to a lesser extent, from those from the recent past. For example, fungivores with stable bodies (e.g. mites) might be decomposed more slowly and thus be slightly over-represented in fungivore communities (Table S3). However, the literature also reports more contrasting effects of fungivores, suggesting that fungivores are less specific (Crowther et al., 2012; Hanlon and Anderson, 1979; Maraun et al., 2003). The weak links we found between the compositions of fungivores and fungi could also be explained by the length and spatial extent of mycelia, which makes the effect of grazing by fungivores less drastic. Up to a certain grazing pressure, fungivores do not suppress the whole individual, which makes the trophic interaction less likely to influence the composition of the fungal community (Crowther et al., 2012; Hanlon and Anderson, 1979).

Moreover, we provided new information on environmental drivers of the composition of multi-trophic soil assemblages, and how environmentally induced compositional changes can affect microbial decomposition activity. Soil physico-chemical properties had a stronger effect on the composition of four soil trophic classes than climatic variables. In particular, soil pH was a key predictor of the composition of bacteria, fungi and bacterivores (Figs. 1 and 2). This result is known for bacteria and fungi (Donhauser and Frey, 2018; Fierer and Jackson, 2006; Griffiths et al., 2011; Looby and Martin, 2020; Rousk et al., 2010a; Tedersoo et al., 2014), but is more surprising for bacterivores, which are mainly protists in our study. Indeed, studies on protist biogeography suggest that protist community composition is mainly determined by climatic and topographic factors (Bates et al., 2013; Seppey et al., 2020). However, most of the bacterivorous protists in our study belong to the Ciliophora and Rhizaria clades that have recently been shown to be strongly affected by soil pH (Oliverio et al., 2020).

Finally, we showed that the environment has a top-down influence on trophic network composition that cascades down to microbial decomposition activity. This effect was rather moderate within both habitats (Fig. 4), but our study suggests that larger long-term climate changes, i.e. causing a habitat switch, would induce a radical change in decomposition regulation. Moreover, our results imply that more abrupt compositional changes in the trophic network, especially in consumer classes that are particularly sensitive to anthropogenic effects (Xiong et al., 2021), could induce greater indirect environmental effects (O'Neill, 1994; Wardle et al., 1998).

5. Conclusions

Our comparison of the regulation of microbial decomposition activity in forests vs. open habitats demonstrates the complexity of direct and indirect environmental effects on an ecosystem function. By hierarchically integrating the environment and soil trophic network, we showed how top-down regulation through the soil trophic network can affect the outcome of decomposition, and modulate the direct effects of the environment. Experimental studies testing the trophic pathways identified here will help further understanding the biological mechanisms involved in our observations. Moreover, predictive models are needed to predict the cascading effects of future environmental and biodiversity changes on ecosystem functioning and multifunctionality.

Author statement

CMA, TM and WT conceptualized the overall study and methodology. WT, AS, CMA, TM and the ORCHAMP Consortium collected the soil data. LG, GP and AS carried out the lab work for eDNA extractions, PCRs and measures of extracellular enzyme activities and soil properties. CL and CMA run the bioinformatic pipelines. LZ helped with the trophic assignment and bioinformatic pipelines. CMA run all statistical analyses. CMA, TM and WT led the interpretation of the results. CMA drafted the initial draft of the paper together with WT and TM. All authors contributed to editing and finalizing the paper.

Funding

Part of the funding came from the French Agence Nationale de la Recherche (ANR) through the GlobNets (ANR-16-CE02-0009), from two 'Investissement d'Avenir' grants (Trajectories: ANR-15-IDEX-02; Montane: OSUG@2020: ANR-10-LAB-56) and the METRO Grenoble Alpes and the Isere department. We also received support from the Lautaret Garden-UMS 3370 (Univ. Grenoble Alpes, CNRS, SAJF, 38,000 Grenoble, France), member of AnaEE-France (ANR-11-INBS-0001AnaEE-Services, Investissements d'Avenir frame) and of the LTSER Zone Atelier Alpes, a member of the eLTER-Europe network.

Data accessibility statement

The data supporting the results will be archived in an appropriate public repository and the data DOI will be included at the end of the article should the manuscript be accepted.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The research presented here belongs to the ORCHAMP monitoring program. We thank the few dozens of interns, field assistants, park managers and rangers for their help conducting the field observations and the lab measurements. In particular, we thank Cindy Arnoldi for her help with the laboratory work on the AEEM technical platform. The S2M data were provided by Météo-France – CNRS, CNRM Centre d'Etudes de la Neige, through AERIS.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108771.

References

Adl, M.S., Gupta, V.V.S.R., 2006. Protists in soil ecology and forest nutrient cycling. Canadian Journal of Forest Research 36, 1805–1817. https://doi.org/10.1139/X06-056.

Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3, 336–340. https://doi.org/10.1038/ngeo846.

A'Bear, A.D., Jones, T.H., Boddy, L., 2014. Size matters: what have we learnt from microcosm studies ofdecomposer fungus-invertebrate interactions? Soil Biology and Biochemistry. https://doi.org/10.1016/j.soilbio.2014.08.009.

Bardgett, R.D., Putten, W.H. Van Der, 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511. https://doi.org/10.1038/nature13855.

Bates, S.T., Clemente, J.C., Flores, G.E., Walters, W.A., Parfrey, L.W., Knight, R., Fierer, N., 2013. Global biogeography of highly diverse protistan communities in soil. ISME Journal 7, 652–659. https://doi.org/10.1038/ismej.2012.147.

Begon, M., Townsend, C.R., Harper, J.L., 2006. Ecology. From Individuals to Ecosystems. Blackwell Publishing.

Bell, C.W., Fricks, B.E., Rocca, J.D., Steinweg, J.M., McMahon, S.K., Wallenstein, M.D., 2013. High-throughput fluorometric measurement of potential soil extracellular enzyme activities. Journal of Visualized Experiments 9, 223–230. https://doi.org/10.3791/50961.

Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P., Coissac, E., 2016. obitools: a unix-inspired software package for DNA metabarcoding. Molecular Ecology Resources 16, 176–182. https://doi.org/10.1111/1755-0998.12428.

Burns, R.G., DeForest, J.L., Marxsen, J., Sinsabaugh, R.L., Stromberger, M.E., Wallenstein, M.D., Weintraub, M.N., Zoppini, A., 2013. Soil enzymes in a changing environment: current knowledge and future directions. Soil Biology and Biochemistry 58, 216–234. https://doi.org/10.1016/j.soilbio.2012.11.009.

Choler, P., 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. Arctic, Antarctic, and Alpine Research 37, 444–453. https://doi.org/10.1657/1523-0430(2005)037[0444:CSIAPT]2.0.CO;2.

Core Team, R., 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.

Crowther, T.W., Boddy, L., Hefin Jones, T., 2012. Functional and ecological consequences of saprotrophic fungus-grazer interactions. ISME Journal 6, 1992–2001. https://doi.org/10.1038/ismej.2012.53.

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science 365. https://doi.org/10.1126/science.aav0550.

De Boer, W., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiology Reviews 29, 795–811. https://doi.org/10.1016/j.femsre.2004.11.005.

Donhauser, J., Frey, B., 2018. Alpine soil microbial ecology in a changing world. FEMS Microbiology Ecology 94, 1–11. https://doi.org/10.1093/femsec/fiy099.

Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22, 1–20. https://doi.org/10.18637/jss.v022.i04.

Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., Mérindol, L., 2009. Reanalysis of 44 yr of climate in the French Alps (1958-2002): methodology, model validation, climatology, and trends for air temperature and precipitation. Journal of Applied Meteorology and Climatology 48, 429–449. https://doi.org/10.1175/2008JAMC1808.1.

Edwards, A.C., Scalenghe, R., Freppaz, M., 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. Quaternary International 162–163, 172–181. https://doi.org/10.1016/j.quaint.2006.10.027.

Elton, C.S., 1927. Animal Ecology. University of Chicago Press.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America 103, 626–631. https://doi.org/10.1073/pnas.0507535103.

Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. Ecology 88, 1354–1364. https://doi.org/10.1890/05-1839.

Gao, Z., Karlsson, I., Geisen, S., Kowalchuk, G., Jousset, A., 2019. Protists: puppet masters of the rhizosphere microbiome. Trends in Plant Science. https://doi.org/10.1016/j.tplants.2018.10.011.

Gauzens, B., Thébault, E., Lacroix, G., Legendre, S., 2015. Trophic groups and modules: two levels of group detection in food webs. Journal of the Royal Society Interface 12. https://doi.org/10.1098/rsif.2014.1176.

Geisen, S., 2016. The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. Soil Biology and Biochemistry 102, 22–25. https://doi.org/10.1016/j.soilbio.2016.06.013.

Geisen, S., Mitchell, E.A.D., Adl, S., Bonkowski, M., Dunthorn, M., Ekelund, F., Fernández, L.D., Jousset, A., Krashevska, V., Singer, D., Spiegel, F.W., Walochnik, J., Lara, E., 2018. Soil protists: a fertile frontier in soil biology research. FEMS Microbiology Reviews 42, 293–323. https://doi.org/10.1093/femsre/fuy006.

German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L., Allison, S.D., 2011. Soil Biology & Biochemistry Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. Soil Biology and Biochemistry 43, 1387–1397. https://doi.org/10.1016/j.soilbio.2011.03.017.

Goncharov, A.A., Tiunov, A.V., 2014. Trophic chains in the soil. Biology Bulletin Reviews 4, 393–403. https://doi.org/10.1134/S207908641405003X.

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. Ecological Monographs 80, 67–87. https://doi.org/10.1890/09-0464.1.

Griffiths, B.S., Bonkowski, M., Dobson, G., Caul, S., 1999. Changes in soil microbial community structure in the presence of microbial-feeding nematodes and protozoa. Pedobiologia 43, 297–304.

Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., Whiteley, A.S., 2011. The bacterial biogeography of British soils. Environmental Microbiology 13, 1642–1654. https://doi.org/10.1111/j.1462-2920.2011.02480.x.

Guo, G., Kong, W., Liu, J., Zhao, J., Du, H., Zhang, X., Xia, P., 2015. Diversity and distribution of autotrophic microbial community along environmental gradients in grassland soils on the Tibetan Plateau. Applied Microbiology and Biotechnology 99, 8765–8776. https://doi.org/10.1007/s00253-015-6723-x.

Hagedorn, F., Gavazov, K., Alexander, J.M., 2019. Above- and belowground linkages shape responses of mountain vegetation to climate change. Science 1123, 1119–1123.

Hanlon, R.D.G., Anderson, J.M., 1979. The effects of collembola grazing on microbial activity in decomposing leaf litter. Oecologia 38, 93–99. https://doi.org/10.1007/BF00347827.

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932.

Hertzog, L.R., 2018. How robust are Structural Equation Models to model miss-specification? A simulation study 1–24.

Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. Nature Reviews Microbiology. https://doi.org/10.1038/s41579-019-0265-7.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7, 573–579. https://doi.org/10.1111/2041-210X.12512.

Looby, C.I., Martin, P.H., 2020. Diversity and function of soil microbes on montane gradients: the state of knowledge in a changing world. FEMS Microbiology Ecology 96, 1–13. https://doi.org/10.1093/femsec/fiaa122.

López-Mondéjar, R., Tláskal, V., Větrovský, T., Štursová, M., Toscan, R., Nunes da Rocha, U., Baldrian, P., 2020. Metagenomics and stable isotope probing reveal the complementary contribution of fungal and bacterial communities in the recycling of dead biomass in forest soil. Soil Biology and Biochemistry 148, 107875. https://doi.org/10.1016/j.soilbio.2020.107875.

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

Maassen, S., Fritze, H., Wirth, S., 2006. Response of Soil Microbial Biomass , Activities , and Community Structure at a Pine Stand in Northeastern Germany 5 Years after Thinning, vol. 1434, pp. 1427–1434. https://doi.org/10.1139/X06-039.

Malik, A.A., Chowdhury, S., Schlager, V., Oliver, A., Puissant, J., Vazquez, P.G.M., Jehmlich, N., von Bergen, M., Griffiths, R.I., Gleixner, G., 2016. Soil fungal:bacterial ratios are linked to altered carbon cycling. Frontiers in Microbiology 7, 1–11. https://doi.org/10.3389/fmicb.2016.01247.

Maraun, M., Martens, H., Migge, S., Theenhaus, A., Scheu, S., 2003. Adding to "the enigma of soil animal diversity": fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology. https://doi.org/10.1016/S1164-5563(03)00006-2.

Martinez-Almoyna, C., Piton, G., Abdulhak, S., Boulangeat, L., Choler, P., Delahaye, T., Dentant, C., Foulquier, A., Poulenard, J., Noble, V., Renaud, J., Rome, M., Saillard, A., Thuiller, W., Münkemüller, T., 2020. Climate, soil resources and microbial activity shape the distributions of mountain plants based on their functional traits. Ecography 43, 1550–1559. https://doi.org/10.1111/ecog.05269.

Mikola, J., Setälä, H., 1998. NO evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79, 153–164. https://doi.org/10.1890/0012-9658(1998)079[0153:NEOTCI]2.0.CO;2.

Moore, J.C., William Hunt, H., 1988. Resource compartmentation and the stability of real ecosystems. Nature 333, 261–263.

Moore, J.C., McCann, K., Setälä, H., De Ruiter, P.C., 2003. TOP-DOWN IS bottom-up: does predation in the rhizosphere regulate aboveground dynamics? Ecology 84, 846–857. https://doi.org/10.1890/0012-9658(2003)084[0846:TIBDPI]2.0.CO;2.

Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.

Oliverio, A.M., Geisen, S., Delgado-Baquerizo, M., Maestre, F.T., Turner, B.L., Fierer, N., 2020. The global-scale distributions of soil protists and their contributions to belowground systems. Science Advances 6, eaax8787. https://doi.org/10.1126/sciadv.aax8787.

O'Neill, E.G., 1994. Responses of soil biota to elevated atmospheric carbon dioxide. Plant and Soil 165, 55–65.

Piton, G., Foulquier, A., Martínez-García, L.B., Legay, N., Hedlund, K., Martins da Silva, P., Nascimento, E., Reis, F., Sousa, J.P., De Deyn, G.B., Clement, J.C., 2020. Disentangling drivers of soil microbial potential enzyme activity across rain regimes: an approach based on the functional trait framework. Soil Biology and Biochemistry 148. https://doi.org/10.1016/j.soilbio.2020.107881.

Põlme, S., Abarenkov, K., Nilsson, R.H., Lindahl, B.D., Clemmensen, K.E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S.T., Baldrian, P., Frøslev, T.G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H., Järv, H., Madrid, H., Nordén, J., Liu, J., Pawlowska, J., Põldmaa, K., Pärtel, K., Runnel, K., Hansen, K., Larsson, K., Hyde, K. D., Sandoval-denis, M., Smith, M.E., Toome-heller, M., Wijayawardene, N.N., Menolli, N., Reynolds, N.K., Drenkhan, R., Maharachchikumbura, S.S.N., Gibertoni, T.B., Læssøe, T., Davis, W., Tokarev, Y., Corrales, A., Soares, A.M., Agan, A., Machado, A.R., Argüelles-moyao, A., Detheridge, A., Meiras-ottoni, A. De, Verbeken, A., Dutta, A.K., Cui, B., Pradeep, C.K., Marín, C., Stanton, D., Gohar, D., Wanasinghe, D.N., Otsing, E., Aslani, F., Griffith, G.W., Lumbsch, T.H., Grossart, H., Masigol, H., Timling, I., Hiiesalu, I., Oja, J., Kupagme, J.Y., Geml, J., Alvarez-manjarrez, J., Ilves, K., Loit, K., Adamson, K., Nara, K., Küngas, K., Rojas-jimenez, K., Bitenieks, K., Irinyi, L., Nagy, L.L., Soonvald, L., Zhou, L., Wagner, L., Aime, M.C., Öpik, M., Mujica, M.I., Metsoja, M., Ryberg, M., Vasar, M., Murata, M., Nelsen, M.P., Cleary, M., Samarakoon, M.C., Doilom, M., Bahram, M., Hagh-doust, N., Dulya, O., Johnston, P., Kohout, P., Chen, Q., Tian, Q., Nandi, R., Amiri, R., Perera, R.H., Chikowski, S., Mendes-alvarenga, R.L., Garibay-orijel, R., Gielen, R., Phookamsak, R., Jayawardena, R.S., Rahimlou, S., Karunarathna, S.C., Tibpromma, S., Brown, S.P., Sepp, S., Mundra, S., Luo, Z., Bose, T., Vahter, T., Netherway, T., Yang, T., May, T., Varga, T., Li, W., Rafael, V., Coimbra, M., Rodrigo, V., Oliveira, T. De, Lima, V.X.De, Mikryukov, V.S., Lu, Y., Matsuda, Y., Miyamoto, Y., Kõljalg, U., Tedersoo, L., 2020. FungalTraits : a user - friendly traits database of fungi and fungus - like stramenopiles. Fungal Diversity. https://doi.org/10.1007/s13225-020-00466-2.

Potapov, A.A., Semenina, E.E., Korotkevich, A.Y., Kuznetsova, N.A., Tiunov, A.V., 2016. Connecting taxonomy and ecology: trophic niches of collembolans as related to taxonomic identity and life forms. Soil Biology and Biochemistry 101, 20–31. https://doi.org/10.1016/j.soilbio.2016.07.002.

Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010a. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME Journal 4, 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Rousk, J., Brookes, P.C., Bååth, E., 2010b. Investigating the mechanisms for the opposing pH relationships of fungal and bacterial growth in soil. Soil Biology and Biochemistry 42, 926–934. https://doi.org/10.1016/j.soilbio.2010.02.009.

Ruess, L., Ferris, H., 2004. Decomposition pathways and successional changes. Nematology Monographs & Perspectives 2, 547–556.

Ruess, L., Garcia Zapata, E.J., Dighton, J., 2000. Food preferences of a fungal-feeding Aphelenchoides species. Nematology 2, 223–230. https://doi.org/10.1163/156854100508962.

Sansupa, C., Wahdan, S.F.M., Hossen, S., Disayathanoowat, T., Wubet, T., Purahong, W., 2021. Can we use functional annotation of prokaryotic taxa (Faprotax) to assign the ecological functions of soil bacteria? Applied Sciences (Switzerland) 11, 1–17. https://doi.org/10.3390/app11020688.

Schaefer, I., Caruso, T., 2019. Oribatid mites show that soil food web complexity and close aboveground-belowground linkages emerged in the early Paleozoic. Communications Biology 2, 1–8. https://doi.org/10.1038/s42003-019-0628-7.

Schneider, K., Maraun, M., 2005. Feeding preferences among dark pigmented fungal taxa (" Dematiacea") indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). Pedobiologia 49, 61–67. https://doi.org/10.1016/j.pedobi.2004.07.010.

Schneider, T., Gerrits, B., Gassmann, R., Schmid, E., Gessner, M.O., Richter, A., Battin, T., Eberl, L., Riedel, K., 2010. Proteome analysis of fungal and bacterial involvement in leaf litter decomposition. Proteomics 10, 1819–1830. https://doi.org/10.1002/pmic.200900691.

Schneider, T., Keiblinger, K.M., Schmid, E., Sterflinger-Gleixner, K., Ellersdorfer, G., Roschitzki, B., Richter, A., Eberl, L., Zechmeister-Boltenstern, S., Riedel, K., 2012. Who is who in litter decomposition Metaproteomics reveals major microbial players and their biogeochemical functions. ISME Journal 6, 1749–1762. https://doi.org/10.1038/ismej.2012.11.

Seppey, C.V.W., Broennimann, O., Buri, A., Yashiro, E., Pinto-Figueroa, E., Singer, D., Blandenier, Q., Mitchell, E.A.D., Niculita-Hirzel, H., Guisan, A., Lara, E., 2020. Soil protist diversity in the Swiss western Alps is better predicted by topo-climatic than by edaphic variables. Journal of Biogeography 47, 866–878. https://doi.org/10.1111/jbi.13755.

Shipley, B., 2000. A new inferential test for path models based on directed acyclic graphs. Structural Equation Modeling 7, 206–218. https://doi.org/10.1207/S15328007SEM0702_4.

Smith, P., Cotrufo, M.F., Rumpel, C., Paustian, K., Kuikman, P.J., Elliott, J.A., Mcdowell, R., 2015. Biogeochemical Cycles and Biodiversity as Key Drivers of 665–685. https://doi.org/10.5194/soil-1-665-2015.

Steinweg, J.M., Dukes, J.S., Wallenstein, M.D., 2012. Modeling the effects of temperature and moisture on soil enzyme activity: linking laboratory assays to continuous field data. Soil Biology and Biochemistry 55, 85–92. https://doi.org/10.1016/j.soilbio.2012.06.015.

Swift, M. J., Heal, O. W., Anderson, J. M., & Anderson, J. M., 1979. Decomposition in Terrestrial Ecosystems. Univ of California Press.

Taberlet, P., Prud'Homme, S.M., Campione, E., Roy, J., Miquel, C., Shehzad, W., Gielly, L., Rioux, D., Choler, P., Clément, J.C., Melodelima, C., Pompanon, F., Coissac, E., 2012. Soil sampling and isolation of extracellular DNA from large amount of starting material suitable for metabarcoding studies. Molecular Ecology 21, 1816–1820. https://doi.org/10.1111/j.1365-294X.2011.05317.x.

Taberlet, P., Bonin, A., Zinger, L., Coissac, E., 2018. Environmental DNA: for biodiversity research and monitoring. Environmental DNA: For Biodiversity Research and Monitoring 1–253. https://doi.org/10.1093/oso/9780198767220.001.0001.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S., Larsson, K.H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L.D., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346. https://doi.org/10.1126/science.1256688.

Thakur, M.P., Geisen, S., 2019. Trophic regulations of the soil microbiome. Trends in Microbiology 27, 771–780. https://doi.org/10.1016/j.tim.2019.04.008.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2016. Ecological importance of soil bacterivores for ecosystem functions. Plant and Soil. https://doi.org/10.1007/s11104-015-2671-6.

Wall, D.H., Bardgett, R.D., Kelly, E., 2010. Biodiversity in the dark. Nature Geoscience 3, 297–298. https://doi.org/10.1038/ngeo860.

Wardle, D.A., Verhoef, H.A., Clarholm, M., 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. Global Change Biology 4, 713–727. https://doi.org/10.1046/j.1365-2486.1998.00206.x.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D. H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633. https://doi.org/10.1126/science.1094875.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13, 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x.

Xiong, W., Jousset, A., Li, R., Delgado-Baquerizo, M., Bahram, M., Logares, R., Wilden, B., de Groot, G.A., Amacker, N., Kowalchuk, G.A., Shen, Q., Geisen, S., 2021. A global overview of the trophic structure within microbiomes across ecosystems. Environment International 151, 106438. https://doi.org/10.1016/j.envint.2021.106438.

Zinger, L., Shahnavaz, B., Baptist, F., Geremia, R.A., Choler, P., 2009. Microbial diversity in alpine tundra soils correlates with snow cover dynamics. ISME Journal 3, 850–859. https://doi.org/10.1038/ismej.2009.20.

Zinger, L., Chave, J., Coissac, E., Iribar, A., Louisanna, E., Manzi, S., Schilling, V., Schimann, H., Sommeria-Klein, G., Taberlet, P., 2016. Extracellular DNA extraction is a fast, cheap and reliable alternative for multi-taxa surveys based on soil DNA. Soil Biology and Biochemistry 96, 16–19. https://doi.org/10.1016/j.soilbio.2016.01.008.

Zinger, L., Lionnet, C., Benoiston, A.S., Donald, J., Mercier, C., Boyer, F., 2021. metabaR: an r package for the evaluation and improvement of DNA metabarcoding data quality. Methods in Ecology and Evolution 2021, 586–592. https://doi.org/10.1111/2041-210X.13552.