



## Beyond the role of climate and soil conditions: Living and dead trees matter for soil biodiversity in mountain forests<sup>☆</sup>

Laureline Leclerc<sup>a</sup>, Irene Calderón-Sanou<sup>b</sup>, Camille Martinez-Almoyna<sup>b,a</sup>, Yoan Paillet<sup>a</sup>, Wilfried Thuiller<sup>b</sup>, Lucie Vincenot<sup>c</sup>, The Orchamp Consortium, Georges Kunstler<sup>a,\*</sup>

<sup>a</sup> Univ. Grenoble Alpes, LESSEM, INRAE, Grenoble, France

<sup>b</sup> Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Grenoble, France

<sup>c</sup> Univ. Rouen - Normandie, INRAE, ECODIV, Rouen, France

### ARTICLE INFO

#### Keywords:

Environmental DNA metabarcoding  
Soil biodiversity  
Trophic groups  
Mountain forest  
Dead wood  
French Alps

### ABSTRACT

While forests' contributions to people are intimately linked to their soil biodiversity, little is known about how forest soil biodiversity is structured and influenced by forest characteristics. Living and dead trees influence the quantity and the diversity of resources (e.g. litter content) and habitats (e.g. microclimate) available for soil organisms. In this study, we explored the effects of forest characteristics and their relative importance to regional climate and local soil conditions in explaining forest soil biodiversity.

We characterised forest quantity (abundance of living and dead trees, and dominant tree leaves C/N), and diversity characteristics (tree sizes, deadwood and tree species diversities). We assessed the response of the diversity of 34 soil trophic groups to climate, soil properties and forest characteristics using environmental DNA metabarcoding data along 16 elevational gradients in the French Alps.

Overall, we showed that climate and soil characteristics explained most of the diversity of soil trophic groups. For the diversity of some groups, however, forest characteristics were important drivers (e.g. ectomycorrhizal fungi). In general, forest diversity characteristics had a positive effect on the diversity of soil trophic groups, in agreement with the resource-heterogeneity hypothesis. We also found that the effects of forest characteristics can percolate to high trophic level groups or to groups that do not have a direct link with living or dead trees (e.g. fungivore mites).

Forest characteristics can have complex indirect effects that branch out throughout the whole soil food web. Even if mountain forests span large climatic gradients, forest structure and composition can be additional key drivers of soil biodiversity. Thus forest management, by driving forest structure and composition, can have important effects on soil biodiversity in managed forests.

### 1. Introduction

Forest ecosystems provide major nature contributions to people and are among the flagship tools to regulate climate change (IPBES, 2019). Yet, while it is well-recognized that their functioning and performance as a climate change regulator is intimately linked to the biodiversity of their soils (Schuldt et al., 2018; Bakker et al., 2019; Akinyede et al., 2022), little is known about how forest soil biodiversity is structured and influenced by soil characteristics, climate and forest characteristics themselves.

Soil biodiversity is abundant and organised in food webs composed of various trophic groups, from autotrophs that produce their own organic compounds, decomposers and detritivores that redistribute nutrients through the decomposition of organic matter, to predators in higher trophic levels (Potapov et al., 2022). A myriad of soil organisms also interact with plants through root herbivory, mutualistic and parasitic associations (Biere and Goverse, 2016; Genre et al., 2020). High species richness within these soil trophic groups is expected to enhance the ability of forest soils to withstand stresses and disturbances, since functional similarity (Eisenhauer et al., 2023) increases the likelihood

<sup>☆</sup> N.B. The institution where the author was located during the study is listed first and the present address is listed second if necessary.

\* Corresponding author. Univ. Grenoble Alpes, INRAE, Lessem, 2 rue de la Papeterie, BP76, 38402, Saint Martin d'Hères, France.

E-mail addresses: [leclerc.lrln@gmail.com](mailto:leclerc.lrln@gmail.com) (L. Leclerc), [irecalisa@gmail.com](mailto:irecalisa@gmail.com) (I. Calderón-Sanou), [cmartinezalm@gmail.com](mailto:cmartinezalm@gmail.com) (C. Martinez-Almoyna), [yoan.paillet@inrae.fr](mailto:yoan.paillet@inrae.fr) (Y. Paillet), [wilfried.thuiller@univ-grenoble-alpes.fr](mailto:wilfried.thuiller@univ-grenoble-alpes.fr) (W. Thuiller), [lucie.vincenot@univ-rouen.fr](mailto:lucie.vincenot@univ-rouen.fr) (L. Vincenot), [georges.kunstler@inrae.fr](mailto:georges.kunstler@inrae.fr) (G. Kunstler).

<https://doi.org/10.1016/j.soilbio.2023.109194>

Received 4 May 2023; Received in revised form 29 September 2023; Accepted 2 October 2023

Available online 4 October 2023

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that some species survive and maintain key functions such as primary production and soil carbon storage (Schuldt et al., 2018; Biggs et al., 2020). Understanding the drivers of soil biodiversity is thus critical to anticipate global change impacts on the functioning of forest ecosystems.

Climate and soil conditions have been relatively well studied as key drivers of soil biodiversity (e.g. Calderón-Sanou et al., 2022). Soil temperature and moisture affect the metabolism of soil organisms as well as their movement ability for nutrition or reproduction (Brown et al., 2004 in Robinson et al., 2018; Aupic-Samain et al., 2021). Soil characteristics, such as nitrogen availability, pH, and water retention capacity are also filters that select the taxa able to survive locally (Decaëns, 2010; Calderón-Sanou et al., 2022).

On top of climate and soil drivers, forest characteristics could also be another important determinant of soil biodiversity. Indeed, forest characteristics are related to the quantity and the diversity of habitats and resources available for soil biota. The quantity and diversity of both living and dead trees could influence soil biodiversity through multiple mechanisms.

Living trees are essential actors of forests functioning via their primary production, their links with biochemical cycles, the interfaces they represent with the regional climate and the many biotic interactions they support (Schwarz et al., 2016; Baldrian, 2017; De Frenne et al., 2021). Living trees shed large quantities of leaves forming the bulk of the litter and organic matter that is decomposed by soil biota. Litter chemical composition and diversity can be a driver of soil biodiversity through litter quality (Peng et al., 2022). For instance, C/N of tree leaves affect soil nitrogen availability, which could influence the diversity of decomposers and detritivores (Fierer et al., 2009; Ball et al., 2014). Indeed, if the dominant species have a low tree leaves C/N this might result in higher nitrogen availability (Dawud et al., 2017). Tree density can also affect the local microclimate (e.g. atmospheric humidity, temperature, light) experienced by the soil biota (De Frenne et al., 2021). Moreover, the diversity of tree species provides a variety of hosts for the establishment of symbiotic associations with soil micro-organisms, such as mycorrhizae (van der Linde et al., 2018) and nitrogen-fixing bacteria. However, the effect of living trees (i.e. tree density, diversity and litter input) on soil biodiversity is extremely variable between studies and taxonomic groups (sometimes negative, positive or absent, Bouget et al., 2014; Henneron et al., 2015; Tedersoo et al., 2016; Janssen et al., 2018), we thus do not know how general and important these effects are across soil food webs.

Dead trees are also essential for soil biodiversity, as they provide a source of habitat and of organic matter that is gradually returned to the soil, thus maintaining its fertility (Palviainen et al., 2010). Twenty to twenty five percent of forest-dwelling species are saproxylic (Speight, 1989; Schuck et al., 2004), i.e. organisms depending on deadwood as a habitat and feeding resource, but part of their life cycle can take place in the soil. Deadwood diversity, i.e. the diversity of species, moisture content, stage of decomposition and type - snag, stump or log - is related to saproxylic species diversity (Lassauce et al., 2011). The importance of deadwood quantity and diversity for saproxylic communities is widely documented (Brin et al., 2011; Lassauce et al., 2011; Bouget et al., 2014; Parisi et al., 2018; Moll et al., 2021), but its effect on the rest of the soil biota community is less known.

The number of studies exploring the link between forest soil biodiversity and quantity and diversity of trees, either living or dead, is limited and generally focused on few functional trophic groups and environmental conditions (e.g. van der Linde et al., 2018; Penone et al., 2019; Tinya et al., 2021). Thus, we have limited knowledge on the relative importance of quantity and diversity of living and dead trees on forest soil biodiversity compared to key abiotic filters (climate and soil). Moreover, we do not know how the importance and direction of these effects of forest characteristics on soil biodiversity vary across trophic levels. Soil biodiversity is expected to increase both with (i) the quantity of habitats and resources following the species-area relationship and the

species-energy theory (Wright, 1983), and (ii) with the diversity of habitats and resources following the resource-heterogeneity hypothesis (Tews et al., 2004; Stein et al., 2014). To progress on these questions, we need large scale studies that evaluate the relative importance of abiotic factors and forest features in controlling soil biodiversity.

Here, we explore this question by building on a large-scale observatory network across the French Alps (Orchamp, Spatio-temporal observatory of biodiversity and ecosystem functioning of mountain socio-ecosystems, Appendix 1). This network is built along elevation gradients in mountains and covers a large range of forest types, allowing to study the importance of climatic and forest effects over small distances. Our approach is based on environmental DNA (eDNA) metabarcoding (see Appendix A.2.3, Ruppert et al., 2019) that facilitates taxa recognition over a much larger sampling effort than what was possible with previous methods (Yoccoz et al., 2012; Zinger et al., 2016). We built our study on Calderón-Sanou et al. (2022) data, containing biodiversity metrics for 34 soil trophic groups from metabarcoding data on the Orchamp network distributed over 16 independent elevation gradients, and we focused our analyses on the 48 forest plots of the network. On these plots, we evaluated forest quantity characteristics as abundance of living and dead trees, and C/N of dominant tree leaves and forest diversity characteristics as tree sizes, deadwood and tree species diversities. Using these data we explored the following questions:

- (i) What is the relative importance of forest characteristics compared to climate and soil in explaining the diversity of soil trophic groups?
- (ii) Which factor, the quantity or diversity of forest resources, plays a more significant role in explaining the diversity of soil groups?
- (iii) Does forest quantity and forest diversity characteristics have positive effects on the diversity of all soil trophic groups as postulated by the species-energy theory and the resource-heterogeneity hypothesis presented above?

## 2. Material and methods

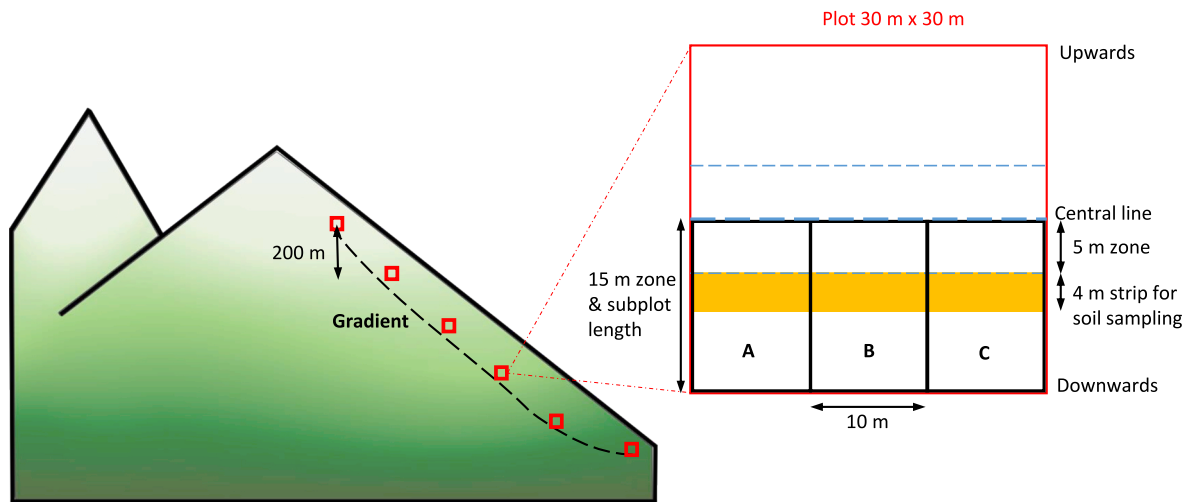
### 2.1. Study sites

We collected data between 2016 and 2022 along 16 elevational gradients of the long-term observatory Orchamp (<https://orchamp.os.ug.fr/>, Appendix 1). These gradients are distributed throughout the French Alps (ca. 40,500 km<sup>2</sup>) and encompass a variety of climatic, soil and forest conditions (see Table A.2.2 in Appendix 2). These plots encompassed a very broad range of forests type: broadleaves forests with Mediterranean influence at low elevation (with dominant species such as *Quercus pubescens* and *Acer monspessulanum*), mixed mountain forests at mid-elevation (with *Fagus sylvatica* and *Abies alba* in Northern Alps and *Pinus sylvestris* in Southern Alps) and conifers forests at high elevation (with dominant species such as *Pinus mugo*, *Picea abies*, and *Larix decidua*).

Each elevational gradient consisted of permanent plots of 30 × 30 m, with a homogeneous slope and aspect, and plots are separated by ca. 200 m in altitude (Fig. 1). We considered data from the 48 forest plots (3 plots per gradient on average) in this study, ranging from 280 to 2100 m in altitude. We used the BD Forêt® V2 cartography of the French National Institute for Geographic and Forestry Information (IGN, 2016) to select plots located in areas with a forest cover equal to or greater than 25%.

### 2.2. Experimental design and field measurements

Each 30 × 30m plot was divided into three 10 × 30m areas, and a central line delimited the upper and lower parts of the plot. In this study, we only used the 10 × 15m subplots corresponding to the half lower part of the plot (noted subplots A, B and C in Fig. 1). Thus, although forest characteristics were measured on the full 30 × 30m plots, for the



**Fig. 1.** A gradient of the experimental design of the Orchamp observatory network. A gradient is composed of 3 forest plots on average ranging from low to high altitude (280–2100 m). Subplots used in this study correspond to the 150 m<sup>2</sup> zones highlighted in black and named A, B and C.

analyses we estimated their value only for each subplot (see section 3 below). A wide strip in the lower part of the plots was dedicated to soil sampling.

### 2.2.1. Soil sampling

Soil sampling was carried out by the Orchamp consortium following the methods described in Calderón-Sanou et al. (2022). In each subplot, a 2 m × 2 m square was selected within the wide strip dedicated to soil sampling, and 10 soil cores of 5 cm diameter were taken from the top 16 cm of the soil in the square area (however, given mountain soils can be very shallow, some cores were smaller). The 10 soil cores were homogenised to obtain 1 composite sample per subplot (Fig. 1).

### 2.2.2. Tree measurements

**2.2.2.1. Livewood.** We identified species and measured the diameter of living trees at 1.30 m (Diameter at Breast Height - DBH). Living trees with a diameter larger than 30 cm were surveyed in the entire 30 × 30 m plot. Living trees with a DBH comprised between 7.5 cm and 30 cm were only surveyed in the area 5 m upwards and downwards of the central line.

**2.2.2.2. Deadwood.** We recorded three types of deadwood: fallen deadwood (logs), snags (standing deadwood, height ≥1.30 m) and stumps (height ≤1.30 m). Each piece of deadwood was identified to species level whenever possible and classified according to the degree of decay of the wood (hard, less than 50% rotten, more than 50% rotten) assessed by a knife penetration test (Larjavaara and Muller-Landau, 2010). All deadwood with a minimum diameter of 30 cm was measured on the whole plot (Fig. 1). Stumps and snags with a diameter between 7.5 cm and 30 cm (diameter at mid-height for stumps and diameter at 1.30 m for snags) were measured in the 5 m zone from the central line upwards and downwards (Fig. 1). Finally, along the central line (Fig. 1), logs intersecting the line and with a diameter between 7.5 cm and 30 cm, were measured.

## 2.3. Environmental variables

We defined four groups of explanatory variables related to local (i) climatic, (ii) soil, (iii) forest quantity and (iv) forest diversity characteristics (see below). We selected three variables for each group in order to best describe the climatic, soil and forest conditions encountered by soil organisms. We selected the variables based on knowledge of which variables are important drivers of the different ecological groups. To

avoid any collinearity, we also ensured that we retained 12 variables with a bivariate Pearson correlation coefficient lesser than 0.7 (Zuur et al., 2010) (see Appendix 2, Table A.2.1 for correlation coefficients between environmental variables and Table A.2.2 for information about environmental variables).

### 2.3.1. Climate characteristics

The climatic data averaged over a period of 10 years prior to the sampling of plots were extracted from the SAFRAN-Crocus models (Durand et al., 1993; Vernay et al., 2022). The three selected climatic variables were mean annual temperature, mean annual Freezing Degree Days (FDD) and mean annual Climatic Water Stress (CWS). FDD is the sum per year of the daily average temperature in the upper first cm of soil, when it is below 0 °C. The more negative the FDD, the greater the frost stress. The CWS is an adaptation of the climatic water deficit (CWD; Stephenson, 1998) to approximate the intensity of water stress. The CWS was calculated as the difference between the water supply from precipitation and snow melt and the potential evapotranspiration (PET) calculated according to the Penman-Monteith equation (Vannier and Braud, 2012). The lower the CWS values, the higher the potential water stress.

### 2.3.2. Soil characteristics

Soil physico-chemical properties were measured from soil samples as described in Calderón-Sanou et al. (2022) and Martínez-Almoyna et al. (2020). The soil pH, soil organic matter content and soil C/N ratio were measured from each soil sample sieved to 2 mm according to the method described by Martínez-Almoyna et al. (2020).

### 2.3.3. Forest quantity and diversity characteristics

The variables used to represent forest quantity and diversity characteristics were related to three key components of the forest structure: living trees, deadwood, and tree species composition. We quantified the forest characteristic variables for each 10 × 15 m subplot (A, B and C in Fig. 1) based on the living trees and deadwood measurements belonging to each subplot.

Living trees were characterised by their basal area (quantity feature) and their size diversity (diversity feature). Basal area (m<sup>2</sup>/ha) is the sum of the cross-sectional areas of the trunks at 1.30 m per hectare and characterises tree abundance and canopy cover. Tree diameters diversity was calculated as the Gini coefficient of basal area (Gini, 1921; see Bourdier et al., 2016 for an application to tree diameters). The Gini coefficient varies from 0 (all tree basal areas are identical) to 1 (maximum differentiation between tree basal areas) (Sterba, 2008).

Deadwood was characterised by the total volume (quantity feature) and diversity of deadwood pieces (diversity feature). The total volume of deadwood corresponds to the sum of the volumes of logs (diameter >30 cm), stumps and snags. These were obtained from the diameters and lengths or heights of each piece of deadwood and the value obtained from the deadwood on the ground surveyed on the central line (diameters between 7.5 cm and 30 cm) according to line intersect sampling equation [8] of Marshall et al. (2003) (see Appendix 2, A.2.4). Deadwood diversity was characterised by the number of different combinations of deadwood characteristics: tree species x deadwood types (log, snag or stump) x degree of decay (hard, less than 50% rotten, more than 50% rotten), resulting in 144 possible combinations.

Tree species composition was described by the community weighted mean (CWM) of tree leaves C/N (quantity feature) and tree species diversity (diversity feature). CWM was computed using mean C/N species values measured from field surveys by the Orchard consortium and species abundance estimated by their basal area. The CWM of tree leaves C/N is an indicator of the average quality of the litter produced. The higher the C/N ratio of tree leaves, the less easily the leaves decompose. It characterises the quantity of resource available for soil organisms in the litter and is thus considered as an abundance metric. Finally, tree species diversity was calculated as the exponential of the Shannon diversity index (Hill number with  $q = 1$ ), which gives the “effective number” of tree species (*i.e.* the number of equiprobable species giving the same diversity value as the observed distribution, Chao et al., 2014).

#### 2.4. Soil biodiversity and trophic groups

We used the data from Calderón-Sanou et al. (2022), obtained through eDNA metabarcoding, to get the diversity of 34 soil trophic groups across the forest plots. Briefly, 15 g of each fresh soil sample was used to extract eDNA. Six DNA markers, described in Taberlet et al. (2018), were used to quantify the overall soil diversity: euka02 for mites, nematodes and protist, bact01 for bacteria, fung02 for fungi, ins02 for insects, coll02 for springtails and olig01 for oligochaetes. A standardised bioinformatic pipeline, using the OBITools software (Boyer et al., 2016) and the R package ‘metabaR’ (Zinger et al., 2021), was used to remove contaminants and errors. Sequences were clustered into Molecular Operational Taxonomic Unit (MOTU) at 97% of similarity and MOTU was taxonomically assigned using SILVA (v.132) and EMBL (v.136) databases. Appendix A.2.3 gives more details on the method of eDNA analysis done in Calderón-Sanou et al. (2022).

To assign each MOTU to a trophic group, Calderón-Sanou et al. (2022) used reference databases and literature specific to different soil taxa (see list of references in Appendix 2, Table A.2.5). The obtained 34 trophic groups were distributed across 6 trophic levels - autotrophs, decomposers, detritivores, second consumers, tertiary consumers and plant symbionts - and comprised major soil taxonomic groups - fungi, protists, bacteria, insects, mites, springtails, nematodes and Enchytraeidae (Calderón-Sanou et al., 2021, 2022, Fig. 2, Appendix 2, Table A.2.5). While certain portion of the data may lack trophic group assignments (Appendix 2, Table A.2.3) due to limited taxonomic resolution or insufficient information in the reference databases, our study

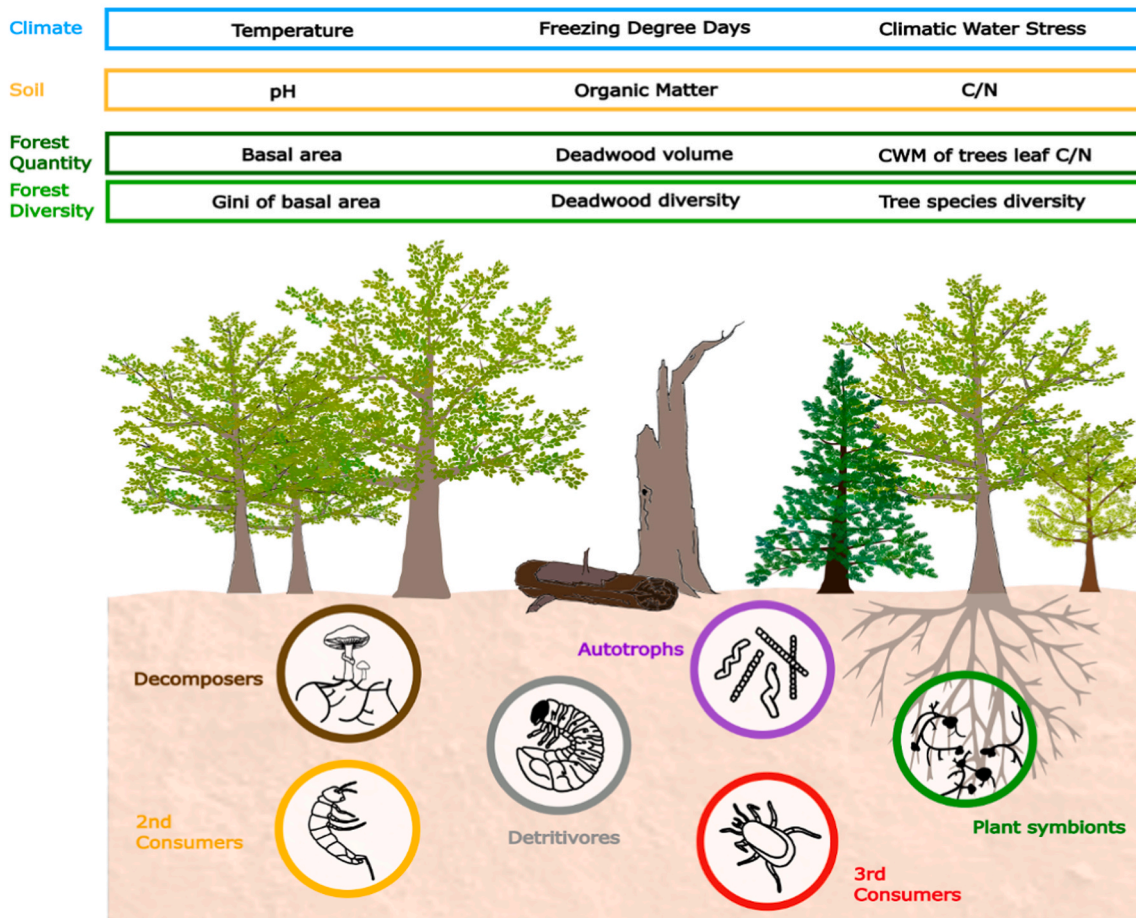


Fig. 2. Outline of the variables considered in this study belonging to the four groups of environmental variables among climate, soil, forest quantity and forest diversity characteristics (CWM: community weighted mean) as well as six examples of organisms representing the trophic levels studied.

prioritised analysing discernible functional groups. This approach allowed us to uncover valuable ecological insights by focusing on groups with known functions and their responses.

The MOTU diversity was calculated for each trophic group using the Shannon diversity index. This was done using the relative abundance of reads estimated per MOTU per subplot, to limit the contributions of MOTUs with low read counts, which may correspond to artefacts related to the eDNA extraction method (Calderón-Sanou et al., 2020). We also ensured that the metabarcoding sequencing was deep enough to estimate the diversity *i.e.* the accumulation curves of sequencing depth *vs.* the Shannon diversity index all reached a plateau.

### 2.5. Statistical analyses

We conducted all analyses in R (4.2.2 version, R Core Team, 2022). The pipeline of our analysis is schematised in supporting information (Appendix 2, Figure A.2.6). We modelled separately 34 response variables corresponding to the 34 Shannon diversity indexes (in MOTUs) of the soil trophic groups studied (hereafter referred to as trophic group diversities) as a function of environmental variables. We used linear mixed effects models with a nested random intercept accounting for plots nested in gradients. For each soil trophic group, we selected the most important variable among the full list of candidate variables separately, *i.e.* the 3 variables per group of environmental variables among climate, soil, forest quantity and forest diversity characteristics (Fig. 2). We also selected the best transformation for each variable to account for potential non-linear effects (linear, logarithmic or

polynomial of order 2). To do this, we used the “dredge” function of the “MuMin” package (Bartoń, 2022) to select from 0 (null model) to 3 variables per model and per group of environmental variables by imposing the choice of a single transformation per variable. Then, a full model was fitted per trophic group with the variable(s) previously selected for each group of variables (up to 12 variables, but the maximum obtained was 8 variables). Normality and homoscedasticity of residuals were checked graphically for each model.

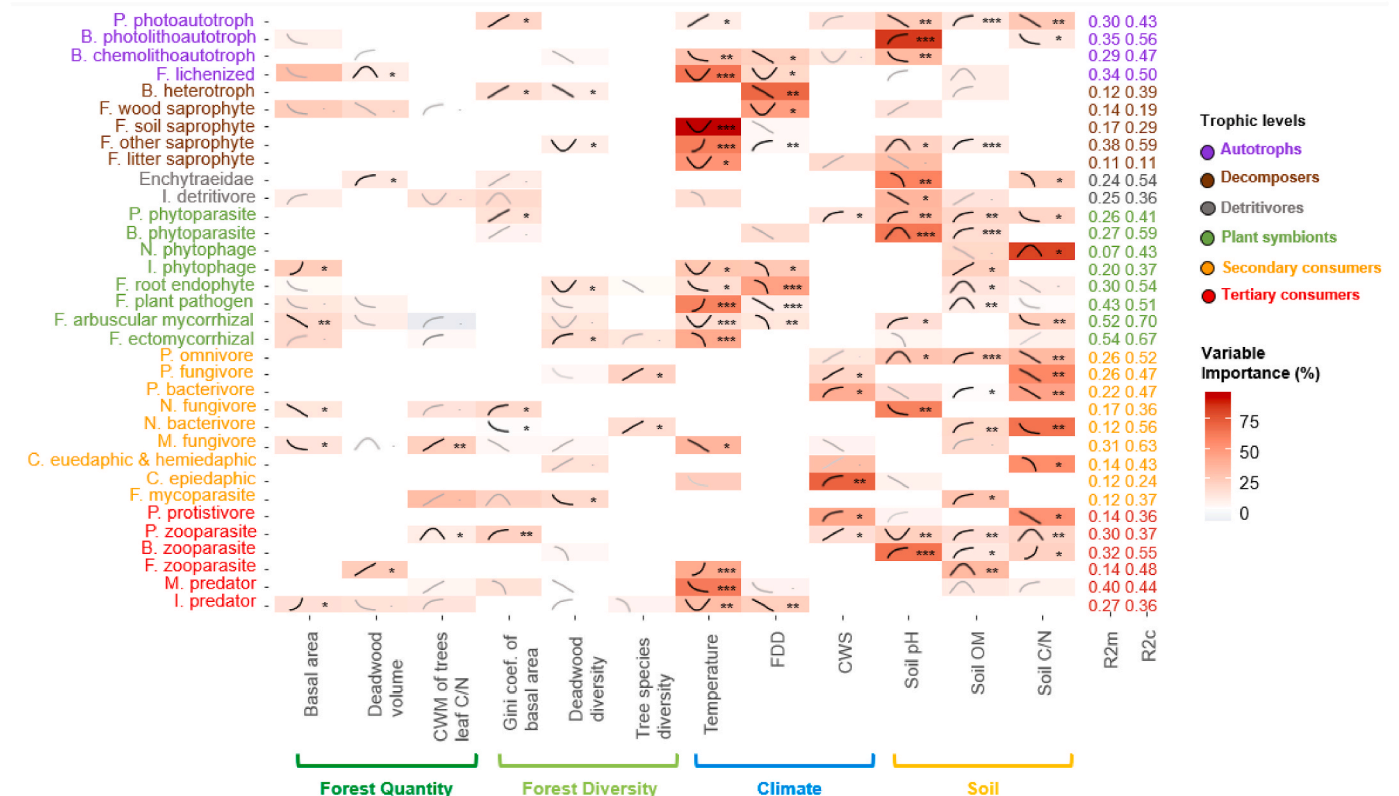
Then our objectives were to estimate 1) the relative importance of each group of variables relative to the total explanatory power of the full model and 2) the total variance explained. The relative importance must be considered in conjunction with the total explained variance for a trophic group in order to assess the explanatory power of the variable.

The relative importance of each of the four groups of variables were calculated using the “explain” function of the “DALEX” package and the “feature\_importance” function of the “ingredients” package (both packages from Biecek, 2018). These functions calculate the importance of a group of variables as the change in the Root Mean Square Error (RMSE) value with data permutation. The number of permutations was set to 499. Then the relative importance of a variable (or group of variables) was computed as the average of the 499 differences between the RMSE of the models fitted on permuted data and the RMSE of the model fitted on observed data (full model). In order to compare the relative importance of groups of variables across trophic groups, we expressed the relative importance as a percentage of the sum of the relative importances of all the variables of the full model.

To estimate the total variance explained for each of the 34 diversity

**Table 1**

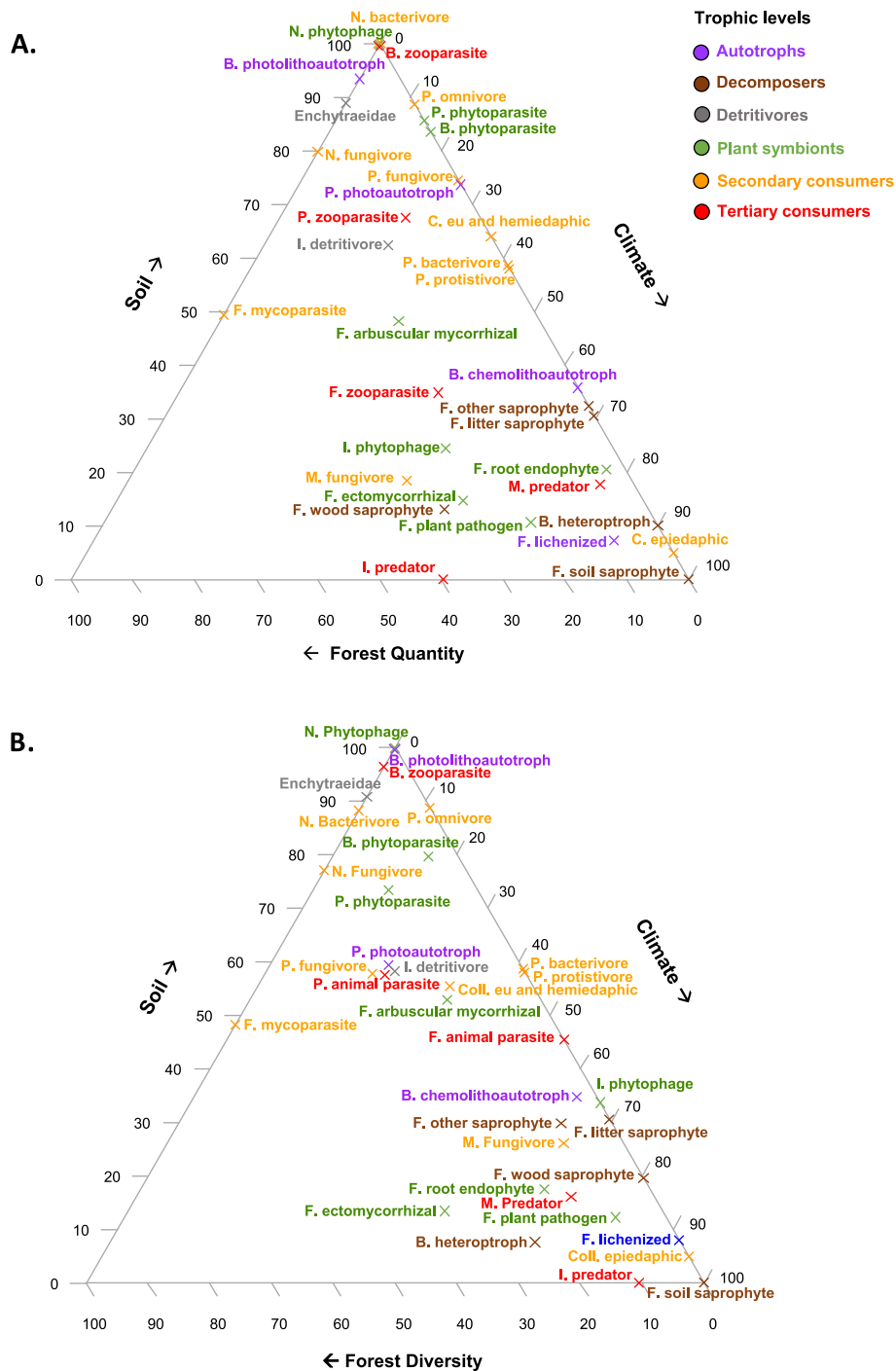
Effects of forest, climate and soil features on soil trophic groups diversities. Curves represent the type of relation between trophic groups and environmental variables (( / for positive or \ for negative linear, / for positive or \ for negative logarithmic and / \ or \ / for polynomial relations). Greys and black symbols means respectively non-significant and significant variables effects with associated p-values thresholds: ‘\*\*\*’ ≤ 0.001; ‘\*\*’ ≤ 0.01; ‘\*’ ≤ 0.05; ‘.’ ≤ 0.1; ‘.’ ≥ 0.1. The importance of each variable is represented with a red colour scale based on the contribution of the variable to the explanatory power of the full model (as the percentage of RMSE loss). The marginal r-squared (R2m) and the conditional r-squared (R2c) of the fitted model are given for each soil trophic group are given. Letters indicate broad taxonomic groups: Bacteria (B.), Fungi (F.), Protozoa (P.) and Metazoa *i.e.* Collembola (C.), Insects (I.), Mites (M.), Nematodes (N.).



models, we also calculated pseudo-R-squared for mixed-effect models ("MuMin" package, Bartoń, 2022): the marginal r-squared (R2m) takes into account only fixed effects while the conditional r-squared (R2c) takes into account both fixed and random effects. R2m gives the total variance explained by all the environmental explanatory variables in the model. The difference between these pseudo-R-squares reflects the role of spatial effects on diversity that were not explained by the environmental explanatory variables considered.

### 3. Results

The total variance explained by full models varied from 11% for litter saprophytes fungi to 70% for arbuscular mycorrhizal fungi when accounting for fixed and random effects (Table 1, R2c). Fixed effects explained from 7% of the variation in the diversity for phytophagous nematodes and up to 54% for ectomycorrhizal fungi (Table 1, R2m). The random gradient effect was overall low compared to the random plot effect. For some trophic groups, the observed variability in diversity was



**Fig. 3.** Importance of climate and soil characteristics compared to A. forest quantity features and B. forest diversity features in explaining soil trophic groups diversity. The relative importance values given here correspond to the importance of a group of variables (estimated as RMSE loss) expressed as percentages of the sum of importance of all variables and must be considered in conjunction with the total variance explained for a trophic group in order to assess the explanatory power of the group of variables (cf. R2m in Table 1). Letters indicate broad taxonomic groups: Bacteria (B.), Fungi (F.), Protozoa (P.) and Metazoa i.e. Collembola (C.), Insects (I.), Mites (M.), Nematodes (N.).

mainly due to the spatial structure of the sampling design, e.g. bacterivore nematodes, phytophage nematodes, zooparasite fungi and phytoparasite bacteria.

### 3.1. Relative importance of climate, soil vs. forest features

On average, climate and soil explained most of the variation in the diversity of the trophic groups, i.e. 39% and 42% respectively, while forest quantity and diversity features explained on average only 10% and 9% respectively (based on the percentage of RMSE loss, Appendix 3, Figure A.3.1). We observed differing responses between taxonomic groups. Mites, fungi and insects were more strongly affected by climatic than soil characteristics. Conversely, soil characteristics were more important than climatic features for protists, nematodes and Enchytraeidae. Furthermore, we observed differing responses between trophic levels. The diversities of decomposers were more influenced by climate than by soil features (Fig. 3). Conversely, soil was more important for detritivores diversity than climate (Fig. 3).

Forest characteristics had no effect on the biodiversity of 8 trophic groups: protistivore, omnivore and bacterivore protists, fungi saprophytic of soil and litter, epiedaphic springtails, phytophage nematodes and fungivore insects (Table 1). However, the importance of forest characteristics was rather high for some specific groups. For instance, based on the percentage of RMSE loss, forest quantity explained more than 20% of the diversity of predatory insects, fungivorous mites, ectomycorrhizal, arbuscular mycorrhizal and plant pathogenic fungi (Fig. 3A), while forest diversity explained more than 20% of the diversity of heterotrophic bacteria, fungivore and zooparasite protists, mycoparasite and ectomycorrhizal fungi (Fig. 3B).

Interestingly, forest quantity and diversity characteristics were not more important for soil trophic groups directly linked to living and dead trees (i.e. decomposers, detritivores and plant symbionts) than for other trophic levels (Table 1). For example, the relative importance of tree leaf C/N was greater for secondary and tertiary consumer groups than for other trophic levels (Table 1). The effects of forest quantity and diversity characteristics were, however, relevant in explaining finer trophic group diversities.

### 3.2. Relative importance of forest quantity vs. diversity characteristics

The relative importance of forest quantity and diversity characteristics for the diversity of soil trophic groups is overall similar, when considering the average effects across all groups. Yet, we showed that the relative importance of forest quantity vs. diversity characteristics depends on the trophic groups. For instance, while they have both similar importance for ectomycorrhizal and mycoparasite fungi (Fig. 3), forest quantity characteristics better explained the diversity of fungivore mites, and forest diversity characteristics were more important to explain the diversity of phytoparasite protists (Fig. 3).

### 3.3. Direction of the effects of forest features on trophic groups diversity

Forest quantity characteristics were significantly related to the diversity of ten soil trophic groups (Table 1). Some relationships were positive, in agreement with the area-species theory and its extension to the amount of energy. For example, the Shannon diversity of Enchytraeidae increased by 0.07 on average when the logarithm of the volume of deadwood increased by 1 and the Shannon diversity of fungivore mites increased by 0.01 when tree leaves C/N increased by 1. We also found negative relationships. For instance, the Shannon diversity of arbuscular mycorrhizal fungi and fungivore mites decreased respectively by 0.01 and 0.1 on average when basal area increased by 1 m<sup>2</sup>/ha (Fig. 4 A. and B.).

Forest diversity characteristics were significantly related to the diversity of thirteen trophic groups (Table 1). The diversity of most groups increased with the diversity of forest diversity characteristics (Table 1)

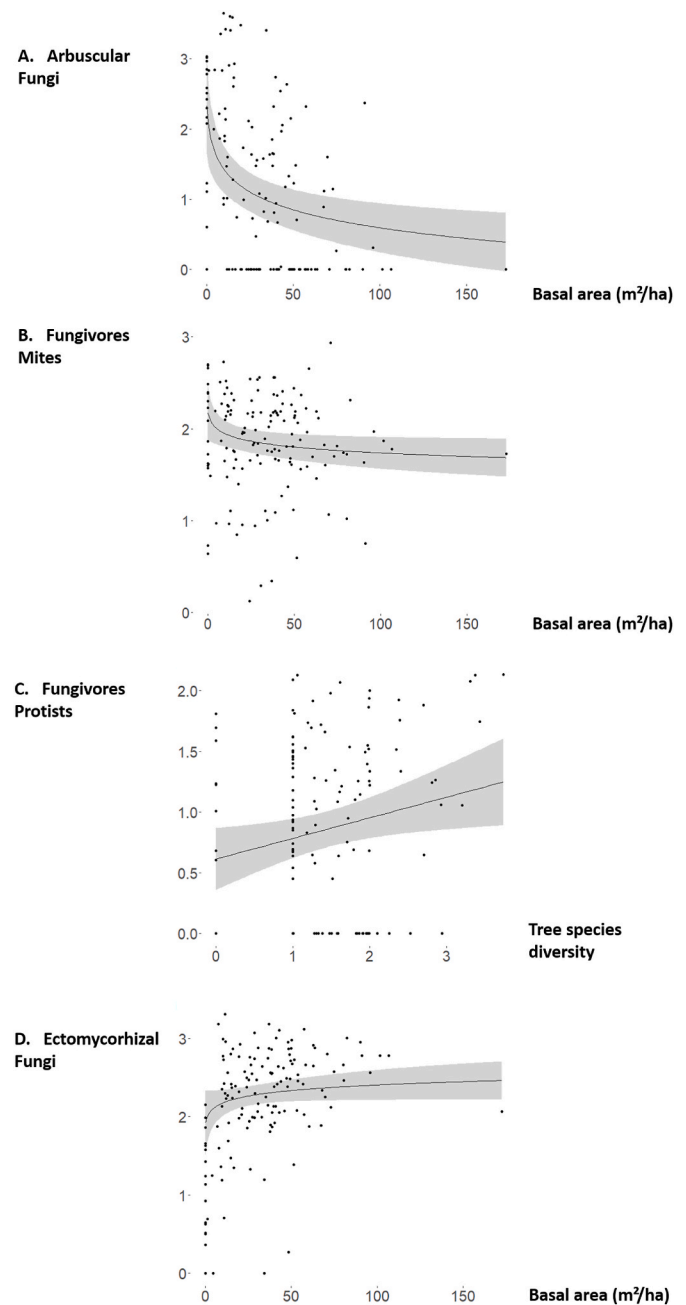


Fig. 4. Shannon diversity of A. arbuscular fungi, B. fungivore mites as a function of basal area (m<sup>2</sup>/ha) and C. fungivore protists as a function of tree species diversity. D. Shannon diversity of ectomycorrhizal fungi as a function of basal area (m<sup>2</sup>/ha). The plain line represents the values predicted by the full model when other explanatory variables are set to their mean. The grey area represents the 95% confidence interval.

in agreement with the resource-heterogeneity hypothesis. For instance, the Shannon diversity of fungivore protists (Fig. 4 C.) and bacterivore nematodes increased respectively by 0.17 and 0.14 on average when the effective number of tree species increases by 1. Unexpected significant negative relationships were found. For instance, the Shannon diversity of bacterivore nematodes decreased by 0.53 when the Gini coefficient of basal area increased by 0.1 unit, while the diversity of heterotrophic bacteria decreased by 0.04 when the diversity of deadwood increased by 1 additional combination.

#### 4. Discussion

We assessed the response of the diversity of 34 soil trophic groups to climate, soil properties and forest characteristics along elevational gradients in the French Alps. In general, we showed the great importance of climate and soil characteristics to explain the diversity of soil trophic groups. Forest quantity and diversity characteristics were less crucial in general, but with similar importance between the two characteristics. For some groups, however, forest characteristics were important drivers. In general, the diversity of forest resources and habitats showed positive effects on the diversity of soil trophic groups, in agreement with the resource-heterogeneity hypothesis (Tews et al., 2004; Stein et al., 2014; Calderón-Sanou et al., 2022). We also found that the effects of forest characteristics can percolate to high trophic level groups or to groups that do not have a direct link with living or dead trees. This shows that forest characteristics can have complex indirect effects that branch out throughout the whole soil food web.

##### 4.1. Relative importance of climate, soil vs. forest features

In mountain forests, we showed that forest quantity and diversity characteristics were generally less important than climatic and edaphic predictors in explaining soil biodiversity, which is consistent with previous studies (e.g. Janssen et al., 2018; Penone et al., 2019; Tinya et al., 2021). Indeed, thermal and hydric conditions exert strong ecological filters as they directly affect the metabolic functioning of organisms (Brown et al., 2004; Robinson et al., 2018). Moreover, soil organisms are distributed spatially according to their affinity for soil conditions, for instance in more or less acidic substrates (Siles and Margesin, 2016). Soil C/N was more important for soil biodiversity than leaf C/N of dominant trees in our study. Indeed, soil organic matter comes from trees but also from the herbaceous and shrubby vegetation as well as from animal faeces and necromass. More than just the trees, these different origins of soil organic matter as well as the nature of the soil, *i.e.* granulometry and parent rock (Roy et al., 2013), drive the nutrient quantity and quality of soil organisms resources.

The design of the Orchamp monitoring network, based on elevational gradients (from 280m to 3160m) located in several bioclimatic sectors across the French Alps, is particularly well suited to highlight the importance of climatic conditions for organisms. However, even over such broad environmental gradients, we showed that the importance of forest characteristics for soil biodiversity is significant and non-negligible for certain soil trophic groups (e.g. ectomycorrhizal and arbuscular mycorrhizal fungi, fungivore mites). Ectomycorrhizal and arbuscular mycorrhizal fungi were two of the trophic groups most influenced by forest characteristics in our study system (Fig. 2), which is in agreement with other studies (Martínez-García et al., 2015; van der Linde et al., 2018). First, ectomycorrhizal fungi are directly related to trees since ectomycorrhizae are formed almost exclusively between tree species and fungi (Genre et al., 2020). Tree species abundance and diversity in stands can also support ectomycorrhizal fungi diversity through the availability of multiple possible host tree species (Cavard et al., 2011; van der Linde et al., 2018, Fig. 4 D.). Second, understory plant community composition is driven by forest structure and composition (Guy et al., 2022), which may in turn influence arbuscular mycorrhizal fungi diversity through host availability (Martínez-García et al., 2015).

Our results also highlighted that forest characteristics are important for trophic groups that do not interact directly with vegetation. For instance, tree leaf C/N was important for the diversity of secondary and tertiary consumers. This is in agreement with Ganault et al. (2021) who showed that the proportion of conifers explains the proportion of predators in soil communities. Forest characteristics are related to litter habitat quality, quantity and structure (e.g. through tree species composition and their litter traits), which are important drivers of predators and their prey population dynamics. Indeed, prey abundance

is related to litter identity (Aupic-Samain et al., 2019) and both prey abundance and litter quantity as well as litter habitat structure are involved in the encounter probability between a predator and its prey (Kalinkat et al., 2013).

##### 4.2. Relative importance of forest quantity vs. diversity features

Overall, forest quantity and diversity characteristics were of similar importance in explaining the diversity of soil trophic groups. Both the quantity and the diversity of resources and habitats matter in explaining the diversity of soil organisms. Nonetheless, the relative importance of forest quantity compared to diversity differed between soil trophic groups.

Almost all forest diversity characteristics were generally positively associated with the diversity of soil trophic groups, contrary to forest quantity that exhibited both positive and negative relationships with soil diversity. Thus, our results support the resource-heterogeneity hypothesis (Tews et al., 2004; Stein et al., 2014), more than the species-area relationship and its extension to the amount of energy (Wright, 1983).

Furthermore, the resolution of our trophic groups did not allow a fine separation of species that interact directly with living and dead trees. Different resolutions of species grouping may result in different responses of organisms to environmental variables (Ohlmann et al., 2019; Ganault et al., 2021). The databases to assign species to trophic and functional groups have greatly improved over the last years (Potapov et al., 2022; Le Guillarme and Thuiller, 2023), but they remain too broad to accurately describe the individual species interacting with the trees.

For instance, in our study, saproxylic biodiversity was not well represented by the trophic groups defined, based on coarse resource types: deadwood-dependent taxa were divided into wood saprotroph fungi and detritivore insect groups, whose diversity was not explained by the volume and diversity of deadwood. The broad definition of these trophic groups can explain the low effect of deadwood volume and diversity. In addition, deadwood harbours a specific biodiversity that may not have been sampled by our soil sampling, which was not conducted directly on deadwood (Ranius and Jonsson, 2007). Finally, the low importance of deadwood volume and diversity can be due to the low gradient of deadwood volume encountered in the Orchamp network as the average volume of deadwood on plots was 10.82 m<sup>3</sup>/ha (Appendix 2, Table A.2.2). For instance, the peak diversity of saproxylic organisms is rather observed in mixed mountain forests with about 30–40 m<sup>3</sup>/ha of deadwood (Müller and Bütler, 2010). The significant number of forest plots at low elevations as well as very open forests in the subalpine range in the Orchamp network explain this rather low average of deadwood volume for mountain forests (e.g. Paillet et al., 2015).

##### 4.3. The different responses of trophic groups to forest features are linked to their ecological differences

###### 4.3.1. Effects of forest quantity characteristics on soil trophic groups

The diversity of arbuscular mycorrhizal fungi tended to be higher for low basal area levels and high C/N of tree leaves, which characterise a low canopy density that allows more light to reach the forest floor (Kovács et al., 2017) and favours the understory vegetation cover (Gao et al., 2014; see Appendix 3, Figure A.3.2 for the relationship between basal area and plant abundance in the forest plots studied). In European temperate forests, most trees do not form associations with arbuscular mycorrhizal fungi. Instead, shrub or herb species host this type of mycorrhizae (Genre et al., 2020). We suggest, as other studies tend to (Öpik et al., 2008; Scherber et al., 2010; Hiiesalu et al., 2014; Gerz et al., 2016; Guy et al., 2022), that the species richness of the understory could be positively related to the diversity of arbuscular mycorrhizal fungi.

We also observed this negative trend of basal area on diversity for several trophic groups (e.g. wood saprophyte fungi, fungivore nematodes and mites, Table 1). This agrees with results reported in other



studies for other taxa (e.g. saproxylic beetles in Bouget et al., 2014; fungi in Tedersoo et al., 2016). This trend might be related to light availability and the understorey plant diversity for trophic groups that rely on plants as host or resource such as plant pathogen fungi (Tedersoo et al., 2016).

By a bottom-up effect, the diversity of fungi could promote the diversity of fungivore trophic groups (Scherber et al., 2010). Indeed, we found similar relationships for the different groups of fungi mentioned above and fungivore nematodes as well as fungivore mites when considering the effect of basal area but also the effect of the C/N of tree leaves (Table 1, Fig. 4). Both variables are related to the quantity and nature of resources, conditioned by trees.

#### 4.3.2. Effects of forest diversity characteristics on soil trophic groups

The diversity of most trophic groups increased with increasing forest diversity (basal area Gini coefficient, deadwood diversity and tree species diversity), which is in agreement with the resource-heterogeneity hypothesis (Tews et al., 2004; Stein et al., 2014) and other studies (Penone et al., 2019). The diversity of forest could favour a multitude of microenvironmental conditions that could be related to a high ecological niche diversity (Frey et al., 2016; Kovács et al., 2017; Lindenmayer et al., 2022), which in turn favour soil biodiversity through niche partitioning.

Tree size diversity influences different aspects of forest microclimate such as temperature, humidity and light interception. Tree size diversity may hence have an influence on soil organisms but studies on this relationship are rare. Janssen et al. (2018) did not find, for instance, a link between the diversity of tree diameters and springtail diversity. However, some studies suggested that biodiversity can be higher in stands with heterogeneous tree diameters (Pach and Podlaski, 2015; Hilmers et al., 2018).

Deadwood diversity is a source of varied microclimates and microsites that support a high level of biodiversity (Seibold et al., 2016; Moll et al., 2021). As with living trees, deadwood may contain recalcitrant compounds that require specific decomposers and detritivores adaptations to be decomposed. Thus, different communities succeed one another on deadwood pieces to degrade lignins and cellulose down to simplest molecules (Kraus and Krumm, 2013). Moreover, deadwood diversity supports a variety of species through the different types of deadwood and their characteristics. Indeed, the biodiversity associated with lying deadwood is different from that associated with standing dead trees (Lassaue et al., 2011). This difference is, for instance, due to the higher moisture content of lying deadwood which, compared to standing dead trees, facilitates its colonisation by decomposers (Kraus and Krumm, 2013; Parisi et al., 2018).

Our results suggest that tree species diversity is of little importance for the diversity of soil trophic groups (Table 1). We showed a positive and significant effect of tree species diversity for fungivore protists and bacterivore nematodes (Fig. 4 C.; Table 1). This positive effect could be the result of complementarity effects, with different species providing different resources and functions that could affect the diversity of soil groups even at high trophic levels (Milcu et al., 2013; Gillespie et al., 2021). Previous studies reported, however, either no effect of tree species diversity on the diversity of fungal groups (Tinya et al., 2021), or even negative effect on saprotroph fungi diversity (Penone et al., 2019) and emphasised the importance of the stand/landscape heterogeneity in explaining forest biodiversity (Hilmers et al., 2018; Schall et al., 2018). When interpreting the magnitude of the species diversity effect, it is important to keep in mind that the level of diversity found in European forest is relatively low compared to other ecosystems such as tropical forests. The species diversity effect might thus vary depending on the ecosystem type.

#### 4.4. Perspectives and conclusion

To conclude, we have shown the importance of forest quantity and diversity characteristics for several soil trophic groups. High diversity of

forest conditions is generally associated with high soil trophic biodiversity. This study thus contributes to a better understanding of the direct effects of forest structure on soil biodiversity which arise on top of the dominant effects of abiotic variables - climate and soil conditions. The next step will be to evaluate the importance of indirect effects of forest structure mediated by a modification of local climatic and soil conditions. Indeed, forests have a profound influence on the local microclimate (De Frenne et al., 2021) and on soil conditions (Thoms et al., 2010; Hicks Pries et al., 2022).

In terms of forest management, these results mean that harvesting choices, especially tree density and tree species composition, may influence soil community. As such, forest management may, to a certain extent, counteract the negative effects of climate change for certain groups of species, like ectomycorrhizal and arbuscular mycorrhizal fungi. Forest management may hence help preserve some important ecosystem soil functions in managed forests.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Wilfried Thuiller reports financial support was provided by French National Research Agency through the GlobNet project (ANR-16-CE02-0009), and Montane project (OSUG@2020: ANR-10-LAB-56). Wilfried Thuiller reports financial support was provided by French Biodiversity Office. Wilfried Thuiller reports financial support was provided by Grenoble Alpes Metropole. Wilfried Thuiller reports financial support was provided by Department of Isere. Wilfried Thuiller reports financial support was provided by OSUG2020. Georges Kunstler reports financial support was provided by BIOSEFAIR MP INRAE.

#### Data availability

Environmental and soil biodiversity data are available at <https://datadryad.org/stash/dataset/doi:10.5061/dryad.q573n5tm6> Forest data are available at [https://shiny.osug.fr/app/orchamp\\_download](https://shiny.osug.fr/app/orchamp_download)

#### Acknowledgements

This project was possible thanks to the many people that participated in the field work and in the laboratory procedures, including students, interns, postdoctoral fellows, field assistants, park managers and rangers, and Amélie Saillard that manages to make this all work. Orchamp is a member of the Sentinelles des Alpes, a program led by the LTSEZ Zone Atelier Alpes belonging to the eLTER-Europe network. We thank Cindy Arnoldi for conducting the soil physicochemical analyses, Ludovic Gelly for the DNA extraction and PCRs, and Nicolas Le Guillarme and Clément Lionnet for support with the development of bioinformatic pipelines. We thank Sophie Labonne who, with the help of Pascal Tardif, has led the field work since 2016 to gather the dendrometric data. This research was funded by the French Biodiversity Office (OFB) to support Orchamp, and the French Agence Nationale de la Recherche (ANR) through the GlobNet project (ANR-16-CE02-0009), from the "Investissement d'Avenir" grants (Montane: OSUG@2020: ANR-10-LAB-56), the METRO Grenoble Alpes, the Isere department, and SICCCUB BIOSEFAIR-MP Inrae project. LL master was funded by SICCCUB BIOSEFAIR Inrae project.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2023.109194>.

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