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# Strong links between plant traits and microbial activities but different abiotic drivers in mountain grasslands

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## Abstract

**Aim:** Plant–soil interactions can be major driving forces of community responses to environmental changes in terrestrial ecosystems. These interactions can leave signals in aboveground plant functional traits and belowground microbial activities and these signals can manifest in observed covariations. However, we know little about how these plant–soil linkages vary in response to environmental conditions at biogeographic scales for which experiments are impossible. Here, we investigate patterns of direct and indirect linkages between plant functional traits, soil microbial activities and environmental conditions in mountain grasslands along elevational gradients.

**Location:** The French Alps.

**Taxon:** Vascular plants and soil microbiota.

**Methods:** We analysed observational grassland data sampled along 14 elevational gradients across the entire French Alps (between 1500 and 2800 m of elevation). Using Graphical Lasso, we inferred a partial correlation network to tease apart direct and indirect plant–soil linkages without defining the direction of interactions a priori.

**Results:** We found tight spatial associations of plant traits with microbial activities, climate driving the former and soil properties the latter. In these plant–soil linkages, the dominance of specific plant traits was more important than their diversity. We then showed that in sites with conservative plant traits and reduced organic matter quality, soil microbes invested strongly in nutrient acquisition.

**Main conclusions:** By investigating plant–soil linkages along elevational gradients in the French Alps, we showed that plant functional traits and belowground microbial activity are tightly linked and how they depend on environmental conditions. Overall, we demonstrated how soil functioning can be integrated in studies of ecosystem shifts under environmental change at large spatial scales.

KEYWORDS
elevational gradient, graphical lasso, ORCHAMP, partial correlation network, plant functional traits, plant–soil linkages, soil enzymatic activities

## 1 | INTRODUCTION

Plant–soil interactions are fundamental elements of ecosystem functioning and structure (Bardgett & Wardle, 2010; De Vries et al., 2013; Martinez-Almoyna et al., 2019; Wardle et al., 2004). Plants rely on soil microbial communities that drive the decomposition of detrital organic matter and the recycling of nutrients through their extracellular enzymatic activities (EEA; Burns & Dick, 2002; Burns et al., 2013; Schimel & Bennett, 2004). Conversely, the resource-acquisition strategy of soil microbes depends on the quantity and nutritional quality of plant litter inputs, and is reflected in the relative investment in extracellular enzymes that target C-, N- or P-rich compounds (Bardgett & Wardle, 2010; Bowman et al., 2004; Fanin et al., 2014; Legay et al., 2014; Piton, Legay, et al., 2020).

Observed correlations between components of plant communities and soil microbial communities, called plant–soil linkages in the following, can be the result of plants affecting soil, of soil affecting plants, or of both processes simultaneously (Figure 1). Concerning the effect of plants on soil ecosystem properties, there are two conflicting visions in the literature. Grime (1998; see also García-Palacios et al., 2017) proposed that plant species in a community control ecosystem functions, such as primary production, resistance and resilience to perturbations and nutrient cycling and storage, proportionally to their biomass. In other words, the traits of dominant plant species determine ecosystem properties more strongly than the traits of rare species ('mass-ratio-hypothesis'). The other vision suggested that functional diversity affects ecosystem functioning through the complementary use of resources ('diversity-function-hypothesis'; Hooper et al., 2005; Tilman et al., 1997). For example, diverse plant communities may increase rates of nitrogen (N) cycling by providing variable litter qualities that can be broken down at different rates, thus providing a more consistent supply of organic N (Laughlin, 2011). Since rare species can have keystone effects and strongly influence pathways of energy and material flows (see also Violle et al., 2017), the relative abundance of species is not always a good predictor of ecosystem-level importance of species. These hypotheses have mostly been tested at regional scales for individual ecosystem processes, and most studies supported the mass-ratio-hypothesis (Díaz et al., 2007; García-Palacios et al., 2017; Grigulis et al., 2013; Lavorel, 2013). However, we still lack knowledge about whether functional diversity or traits of dominant species are of greater importance in plant–soil linkages at biogeographic scales.

Soil functioning also impacts the plant community. On fertile soils with high nutrient availability, plant communities are often composed of exploitative plants (high leaf nitrogen content [LNC] and low leaf dry matter content [LDMC]) and are associated with bacteria-dominated belowground communities that quickly decompose the easily degradable litter (Fortunel et al., 2009; Quested et al., 2007; Wardle et al., 2004). On infertile soils with low nutrient availability, conservative plant communities with slow growth rates

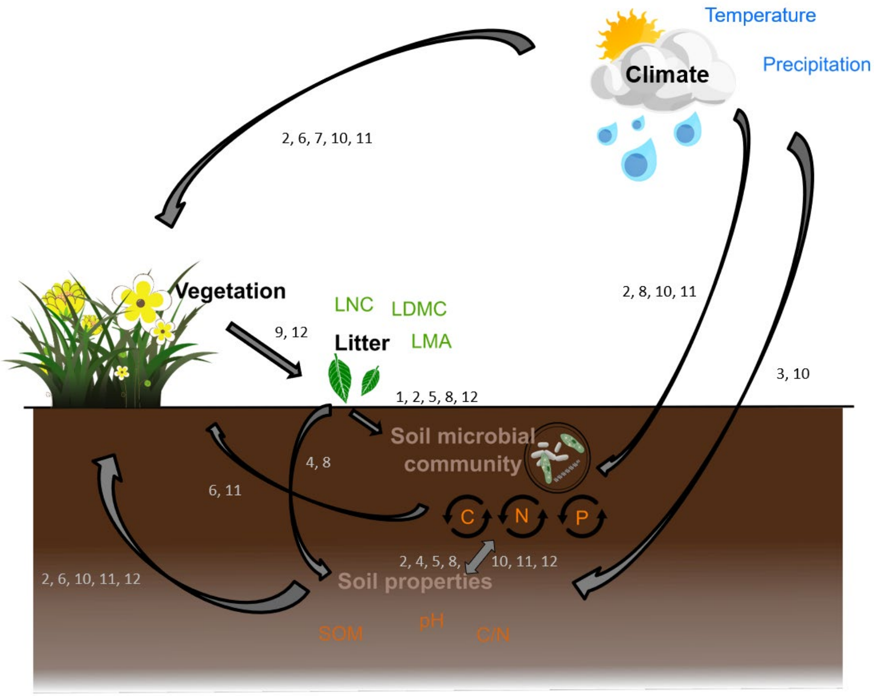

FIGURE 1 Linkages between aboveground plant communities and belowground microbial communities and abiotic factors affecting them. Variables defining the compartments plant community, soil properties and climate are written next to them: C/N, soil carbon nitrogen ratio; LDMC, leaf dry matter content; LMA, leaf mass per area; LNC, leaf nitrogen content; SOM, organic matter. References for the specific linkages are indicated by numbers: 1: Bowman et al. (2004); 2: De Vries et al. (2012); 3: Freppaz et al. (2007); 4: Grigulis et al. (2013); 5: Legay et al. (2014); 6: Martinez-Almoyna et al. (2020); 7: Mayor et al. (2017); 8: Piton, Legay, et al. (2020); 9: Quested et al. (2007); 10: Sundqvist et al. (2013), and references therein; 11: Van der Putten et al. (2016), and references therein; 12: Wardle et al. (2004), and references therein.

are often linked to fungi-dominated belowground communities with slower cycling rates but with the ability to decompose more recalcitrant material (Aerts, 1999; Bardgett & Wardle, 2010). Although these associations are well-known locally, at biogeographic scales it is rarely studied how the changes in nutrient and energy availability in soils influence the traits of plant communities along the exploitative to conservative plant spectrum (Piton, Legay, et al., 2020). EEAs of microbial communities are related to both nutrient availability and microbial growth, acting at the interface between aboveground and belowground communities. EEAs can be either directed towards nutrient (e.g. N or P) or energy (i.e. C) acquisition. Ratios of EEAs therefore reflect the equilibria between elemental composition of microbial biomass and soil organic matter (SOM; Sinsabaugh et al., 2009), and the shift between nutrient and energy flow associated with microbial community metabolism. Although EEAs might underlie plant–soil linkages through organic matter recycling, their relationship with plant traits have rarely been investigated.

On top of the plant–soil interactions, environmental conditions, that is, soil physicochemical properties and climate, also influence the plant and microbial communities differentially, and therefore modulate their observed linkages (Bonito et al., 2014; Van der Putten et al., 2016; Figure 1). In mountain systems, for instance, temperature and snow cover determine growing season length, solar radiation (SR) that plants are exposed to, soil moisture regime and soil pH. These environmental conditions might affect nutrient and energy availability which impacts soil microbial communities, EEAs, plant community composition, and associated litter quality, and in turn, nutrient availability. In particular, freezing cycles constitute a physiological stress which alters microbial demand and allocation of C and nutrients (Freppaz et al., 2007; Schimel et al., 2007). However, it is difficult to distinguish between direct and cascading effects of the environment on plant–soil linkages because of the multitude of interactions between all components of the system. This is why all components implicated in the complex system of plant–soil linkages have rarely been studied together in the past (e.g. Delgado-Baquerizo et al., 2019; Kulmatiski et al., 2008; Wardle et al., 2004).

At biogeographic scales, it is almost impossible to uncover and study interactions through experiments. But plant–soil interactions leave correlative signals in spatial patterns of aboveground functional traits and belowground activity that we can study with observational data (De Vries et al., 2012; Delgado-Baquerizo et al., 2018). We know, for instance, that at large scales aboveground plant properties (e.g. exploitative-conservative spectrum) are drivers of soil microbial community diversity and composition (Boeddinghaus et al., 2019; De Vries et al., 2012; Delgado-Baquerizo et al., 2018). However, such studies have focused on abundance weighted trait values and have rarely assessed plant functional diversity. Moreover, most models used in previous studies to infer patterns in aboveground-belowground linkages, such as structural equation models, assume causality and directionality. In particular, microbial community composition was mostly assumed to be the response variable (Boeddinghaus et al., 2019; De Vries et al., 2012; Delgado-Baquerizo et al., 2018; but see Martinez-Almoyna et al., 2020). However, aboveground-belowground linkages result from interactions and feedbacks. From observations alone, we can neither determine how the observed patterns were created nor the most prominent directions of the effects. They may result from plant traits influencing the soil community through litter quality, or from the soil community influencing the plant community through nutrient availability, or they may result from a combination of both. Also, we do not know where abiotic factors come into play and it is difficult to disentangle direct and indirect effects.

For these reasons, here, we used a graphical model approach to tease apart direct and indirect influences in plant–soil linkages without defining the direction of interactions a priori. Using a graphical lasso to infer a partial correlation network, we analyse interdependencies between aboveground plant functional traits, belowground enzymatic activities and abiotic conditions. We apply this method to grassland communities sampled along 14 elevational gradients from a large-scale observatory representative of the entire French Alps (ORCHAMP). Elevational gradients are associated with drastic abiotic gradients over short distances and are excellent systems to study ecosystem processes for a multitude of climatic and edaphic conditions, and to test how ecosystems respond to environmental variation (Martinez-Almoyna et al., 2019; Sundqvist et al., 2013). We focus on mountain grasslands because little is known about large scale patterns in aboveground-belowground linkages in these vulnerable ecosystems. In the context of unprecedented environmental changes, understanding the relevance of plant–soil linkages for biogeographic distributions of plant diversity and microbial activity, and measuring the effects of single components on overall plant–soil functioning is of tremendous importance (Hagedorn et al., 2019).

To better characterize plant–soil linkages along climatic and edaphic gradients in the French Alps, we ask three specific questions:

1. How do abiotic and biotic interdependencies between climate, abiotic soil conditions, and above- and belowground communities vary over biogeographic scales (focus on between-compartment correlations)?
2. Are plant–soil linkages better explained by plant functional diversity or by dominant trait values?
3. Which specific associations exist between extracellular enzyme activities and other specific variables involved in plant–soil linkages (focus on within-compartment correlations)?

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and the observatory ORCHAMP

ORCHAMP (Spatio-temporal observatory of biodiversity and ecosystem functioning of mountain socio-ecosystems, Supporting Information) is a long-term observation network covering the French Alps (Figure 2; Figure S1). It consists of multiple elevational gradients across the entire study area. For each gradient, 30 m × 30 m permanent plots were established every ~200 m of altitude. Characteristics

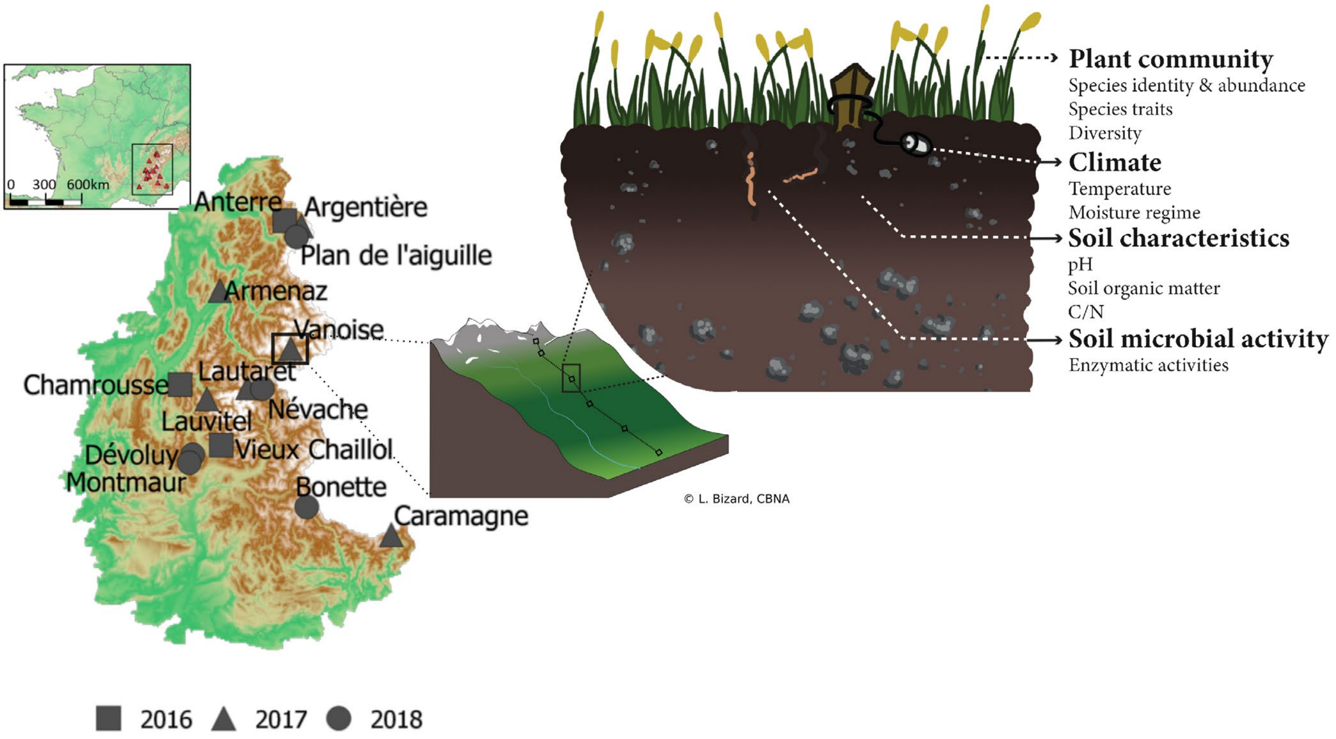

FIGURE 2 ORCHAMP observatory network in the French Alps (with years of sampling) and measurements that were taken on the plots of the individual elevational gradients

of plant communities (presence/absence and abundances), microbial activities, climatic conditions and soil properties were measured between 2016 and 2018 (Figure S2). For this study, we selected 41 plots in open habitat (including grasslands and few shrublands) along 14 elevational gradients on different metamorphic and sedimentary bedrock, such as schist, gneiss and limestone (Figure 2, complete sampling protocols and descriptions of the plots available on orchamp.osug.fr).

## 2.2 | Biotic plant–soil linkages—Aboveground community

In each plot, we recorded plant species abundances using a pin-point sampling along a 30 m transect parallel to the slope in the middle of the plot. Two measurements were taken every 20 cm: one measurement 25 cm upslope, the other 25 cm downslope from the transect. All individuals touching the pole that marked the two measure points per 20 cm increment were identified and counted. Furthermore, an additional dataset of presence/absences of all species along the same 30 m transect but of 3 m width was sampled to obtain a value of species richness representative of the whole plot. All plant species in the subplot were identified by professional botanists.

To test the mass-ratio-hypothesis (Grime, 1998), we calculated community-weighted means (CWMs) of plant traits (Garnier et al., 2004; Lavorel et al., 2008, Equation 1).

$$\mathrm{CWM} = \sum_{i=1}^{n} \left( p_i \times \mathrm{trait}_i \right), \tag{1}$$

where $p_i$ is the relative abundance of species $i$ in a plot, $\mathrm{trait}_i$ the trait value of species $i$ and $n$ the number of species.

We calculated the CWMs for the following traits: LNC, leaf carbon to nitrogen ratio (C/N), leaf dry mass per area (LMA), LDMC, plant height and root depth (RD). These traits were not measured on individuals on the Orchamp plots but in multiple populations across the whole French Alps to account for intra-specific variability (Albert, Thuiller, Yoccoz, Soudant, et al., 2010) between 2008 and 2018. More specifically, at least 20 individuals were measured for traits related to height (vegetative and reproductive plant height) and 10 for leaf traits (LNC, C/N, LMA and LDMC). The measurements were carried out according to the protocol developed by Cornelissen et al. (2003). We used Flora indicativa (Landolt et al., 2010) to complement missing data on vegetative and reproductive plant height, and to extract data on RD. Leaf carbon and nitrogen contents were measured with an elemental analyzer (Flash EA1112; Thermo Scientific). Mean trait values per species were then calculated.

In the 41 selected Orchamp plots, 484 different plant species were identified in total. On average, trait data was available for 82% of all individuals present in a given plot. They were transformed to approximate a normal distribution: a natural logarithm was applied to LNC and plant height, LDMC was square-root transformed and LMA, C/N and RD were log-transformed (basis 10).

To measure the overall functional diversity of the plot, we calculated three independent measures: Functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve; Villéger et al., 2008). FRic represents the multidimensional volume of traits (trait space) filled by the species present in the community. For a single trait, this is simply the range of trait values spanned by the species present in the community. FDiv describes the overall FDiv between species in the community. Low FDiv values mean that species within the community have similar combinations of traits, thought to be indicative of strong environmental filtering (Mouchet et al., 2010) but also asymmetric competition (Mayfield & Levine, 2010). Conversely, high FDiv values indicate that species in the community have a wide range of trait values, leading to a high degree of complementarity and resource use. FEve measures the evenness in the distribution of abundances in trait space. In other words, whether species' abundances tend to be more abundant on one side (low complementarity) or to be evenly distributed in the trait space indicating a high degree of complementarity or niche partitioning among coexisting species. We included all six traits presented above to calculate the diversity measures using the R package "FD" (Laliberté & Legendre, 2010; Laliberté et al., 2014). The traits were standardised (mean $\mu = 0$, standard deviation $\sigma = 1$) before calculating FRic, FDiv and FEve. Since FRic and species richness were correlated (Villéger et al., 2008; Pearson correlation between FRic and species richness $> 0.98$), we used a randomization process and calculated the standard effect size to remove the effect of richness (FRic_ses; Supporting Information, Pearson correlation between FRic_ses and species richness $< 0.5$).

The normalized difference vegetation index (NDVI) has been shown to be related to chlorophyll abundance and leaf area index (Myneni et al., 1995). We used the mean yearly sum of NDVI > 0.2 of the period 2000–2018 ($\text{NDVI}_{\text{int}}$) as a proxy of plant primary productivity. Estimates of the surface spectral reflectance at a resolution of 250 m were derived from MODIS (Moderate Resolution Imaging Spectroradiometer) bands 1 and 2; MOD09Q1: MODIS/Terra Surface Reflectance 8-Day L3 Global 250 m SIN Grid V006 satellite MODIS (Terra), available online: https://lpdaac.usgs.gov/products/mod09q1v006/. The preprocessing of NDVI time series followed the method described by Choler (2015).

## 2.3 | Biotic plant–soil linkages—Belowground community

At 5 m downside of the vegetation transect in each plot, soil samples were taken in three 2 m × 2 m sub-plots. In each subplot, an average of ten soil cores was taken from the top-soil (0–10 cm depth) and mixed to get around 1 kg of soil.

The collected composite samples were sieved at 5.6 mm, and 40–50 ml per sample were extracted and frozen at −20°C for subsequent analysis of microbial activities. The potential activities of seven different extracellular enzymes involved in carbon ($\alpha$-Glucosidase [AG], $\beta$-Glucosidase [BG], $\beta$-D-cellobiosidase [CB], $\beta$-Xylosidase [XYL]), nitrogen (Leucine aminopeptidase [LAP], N-acteyl-$\beta$-Glucosaminidase [NAG]) and phosphorus (Phosphatase [PHOS]) acquisition, were measured according to an adapted protocol of Bell et al. (2013; see Supporting Information). The sum of all measured potential enzymatic activities (total EEA) was used as an overall indicator for the potential of the soil to depolymerize and recycle organic compounds and is therefore an important component of plant–soil linkages (Piton, Legay, et al., 2020). Soil microbial community is the primary driver of this potential activity as microbes produce most of these enzymes. Then, abiotic factors (e.g. temperature) and processes (e.g. substrate diffusion and enzyme stabilization in the soil matrix) modulate potential and realized enzymatic activity in situ (Nannipieri et al., 2018; Piton, Foulquier, et al., 2020; Wallenstein & Weintraub, 2008).

Enzyme activity vectors have recently been shown to quantify simultaneous resource demands of the belowground community and the belowground community's relative investment in C, N and P acquisition (Chen et al., 2018; Fanin et al., 2016; Moorhead et al., 2016). The proportional activity of enzymes targeting carbon (AG, BG, CB and XYL) and nitrogen (LAP and NAG)—that is, (AG + BG + CB + XYL)/[(AG + BG + CB + XYL) + (LAP + NAG)]—was plotted against C versus P acquiring enzymes (PHOS)—that is, (AG + BG + CB + XYL)/[(AG + BG + CB + XYL) + (PHOS)]. In general, a relative increase in the activity of enzymes targeting a specific element indicates that this element is limited in the environment (Olander & Vitousek, 2000). The length of the vector created by each point in the plot and the origin quantifies therefore relative C versus nutrient limitation, with increasing vector length indicating increasing C limitation. The angle formed by the *x*-axis and the vector on the other hand quantifies the relative P versus N limitation (Figure S3). The three replicates of each plot were averaged, and a natural logarithm was applied to total EEA.

## 2.4 | Abiotic factors modulating plant–soil linkages—Soil physicochemical properties

Soil dry weight was measured by weighing soil samples after drying at 70°C for 48 h, and SOM was determined by loss on ignition using the previously dried samples (4 h at 550°C).

The rest of the composite samples was then dried, sieved at 2 mm and homogenized to obtain representative subsamples for the following analyses. We measured pH following the ISO 10390:2005 norm using a pH-meter (pH7110, inoLab) in a 1:5 soil/distilled water-solution. We used an Ultra Centrifugal Mill ZM 200 (Retsch ZM200) to grind part of the dried and sieved samples below 250 μm. Carbon and nitrogen contents were then determined using an elemental analyser (Flash EA1112; Thermo Scientific). The three replicates per plot were averaged and SOM and C/N log-transformed.

## 2.5 | Abiotic factors modulating plant–soil linkages—Climate variables

We characterized climate conditions at each plot using: Mean annual soil temperature (MAT), mean total annual precipitation (MAP), growing degree days (GDD), freezing degree days (FDD), climate water stress (CWS) and SR. To do this, we extracted for each plot meteorological time series of surface conditions from the SAFRAN-Crocus (S2M) reanalyses that are available at hourly resolution for the time period 1988–2018 (Durand, Giraud, et al., 2009; Durand, Laternser, et al., 2009; Vernay et al., 2019; Vionnet et al., 2012). S2M is a regional-scale reanalysis that takes topographical effects into account. Data are produced for 23 massifs of the French Alps as a function of elevation in 300 m increments, slope aspects and angles. The S2M reanalysis has been used for many real-time and climatological applications in the French mountain areas (e.g., Corona et al., 2019; Verfaillie et al., 2018; see also Figure S6). Rainfall and incoming shortwave radiation (direct + scattered) from the SAFRAN reanalysis were aggregated at a daily time resolution. The soil temperature values (temperature in the first centimetre of the soil column, variable TG1 in S2M datasets) were computed by the ISBA-Crocus model fed by meteorological information from SAFRAN.

Growing degree days correspond to daily average soil temperature sums (using data for the first centimetre of the soil column) above 0°C and were calculated based on the assumption that plant growth is more affected by cumulated heat than by mean temperature (Körner & Hiltbrunner, 2018). To capture frost intensity and length of frost episodes, FDD was calculated analogously to GDD (daily average ground temperature sums below 0°C) following Choler (2018). GDD was calculated over the growing season, the onset of which was defined by four consecutive days without snow and a soil temperature of at least 4°C in the simulations, and the offset of which was defined by the first day of the winter season with snow on at least four consecutive days. FDD was calculated over the whole year. Both variables were calculated on an annual timescale and then averaged over the whole time period (1988–2018). We log-transformed absolute values of yearly averaged FDD. We calculated the climatic variables over a 30-year time period. This was done as a compromise since plant communities in alpine systems are known to respond to medium-term climatic conditions rather than annual variations (Körner, 2003). Soil communities might instead be more affected by shorter climatic conditions but it has been suggested that soil communities might actually be very tolerant to climatic variations (Thakur, 2020; Thakur & Geisen, 2019; Thakur et al., 2020).

To quantify water stress and severity of summer drought, we used an approximation of climate water deficit (CWD). CWD is the difference between potential evapotranspiration and water availability in the soil (Stephenson, 1998) and usually accounts for actual evapotranspiration and local soil conditions. Since local soil conditions, and especially available water capacities, are poorly understood in the Alps, we approximated CWD by calculating CWS: daily CWS corresponds to the difference of daily potential evapotranspiration (calculated after Vannier & Braud, 2012 using the Penman-Monteith Equation, Allen et al., 1998) and daily precipitation. Water stress increases as values of CWS increase. In the case of precipitation exceeding evapotranspiration there is no water limitation in the soil compartment, therefore CWS values were set to zero (see Aragão et al., 2007). We calculated CWS sums over the growing season for each year between 1988 and 2018, and then averaged these sums to characterize mean water stress and severity of summer drought of the soil compartment.

We calculated cumulative SRs over the growing season, and then averaged the cumulative values over the whole period 1988—2018.

## 2.6 | The graphical lasso

Given that plant–soil linkages are by definition bi-directional and some of the potential relationships between variables are not clearly identified, we used Graphical Lasso (glasso, Friedman et al., 2007; Mazumder & Hastie, 2012). Glasso is a type of model that is able to decipher the partial correlations between all the variables across our 41 plots without imposing a directional structure, like it would be the case with a structural equation model. In glasso, the partial correlations between all variables are inferred from the inverse of the variance-covariance matrix. Similarly to the lasso regression (Least Absolute Shrinkage and Selection Operator, Tibshirani, 1996), glasso uses a regularization penalty to set all spurious partial correlations to zero. To do so, partial networks are estimated for different values of $\lambda$ (the penalty coefficient). We used the Extended Bayesian Information Criterion to select the optimal $\lambda$, as implemented in the package qgraph (Epskamp et al., 2012; see also Ohlmann et al., 2018). The optimal $\lambda$ depends on the number of variables and the strength of the partial correlations in the network; different sets of variables will therefore lead to different $\lambda$ being selected and different correlations being considered as spurious. The obtained regularized partial correlation network was then visualized using Gephi (Bastian et al., 2009). The network consisted of nodes representing the variables and edges which connect the nodes. Two variables were connected if they were conditionally dependent on each other, i.e. they were partially correlated given all other variables in the graph. Reciprocally, two unconnected variables are said to be conditionally independent (i.e. they cannot causally influence each other, Murphy, 2012). Within the glasso, we included several variables representing the different compartments implicated in plant–soil linkages: Plant community, belowground microbial community, physicochemical soil properties and climatic conditions (Figure 1; Table 1). To assess the importance of a variable within its own group and its importance for other groups, we extracted the degree of each variable (i.e. number of edges that are incident to a given node). We calculated two different measures: the probability of a node to form a connection within its own group (number of realized edges within group/number of possible edges within group), and the probability of a node to form an edge with a node not belonging to its own group (number of realized edges across groups/number of possible edges across groups).

Moreover, we analysed the weights of the edges to estimate the strength of a node (i.e. how important a variable was to the overall plant–soil linkages). The weight of the edges incident to a node corresponds to the strength of its partial correlations. We calculated the sum of absolute partial correlations incident to a node within its own group and the sum of absolute partial correlations incident to a node across groups. The sum of all absolute partial correlations of a node was divided by the number of realized edges to calculate the mean strength of partial correlations.

**TABLE 1** Overview of variable pool from which a selection was made to use in the graphical lasso

| Variable | Acronym | Unit | Data source | Mean (median) ± SD | [min, max] | Transfor-mation |
|---|---|---|---|---|---|---|
| Extracellular enzymatic activity (EEA) | | | | | | |
| Total EEA | Total EEA | nmol/(h·g dry mass) | ORCHAMP | 12,677 (12,174) ± 6520 | [3713, 29,858] | ln |
| Vector length (proportion carbon/nutrients) | EEC/EEN | ° | ORCHAMP | 0.79 (0.78) ± 0.08 | [0.63, 1.00] | — |
| Vector angle (proportion P/N) | EEN/EEP | — | ORCHAMP | 66.1 (65.7) ± 6.0 | [53.5, 79.1] | — |
| Physico–chemical soil properties | | | | | | |
| Soil organic matter | SOM | % | ORCHAMP | 25.1 (23.3) ± 11.1 | [8.5, 55.2] | log10 |
| Carbon to nitrogen ratio | Soil C/N | — | ORCHAMP | 14.68 (14.42) ± 2.59 | [10.96, 23.35] | log10 |
| pH | pH | — | ORCHAMP | 5.45 (5.43) ± 0.88 | [4.01, 7.38] | — |
| Vegetation variables | | | | | | |
| Leaf nitrogen content (CWM) | LNC | mg/g | | 21.4 (20.9) ± 3.3 | [13.6, 31.0] | ln |
| Leaf carbon to nitrogen ratio (CWM) | C/N | — | | 22.8 (22.4) ± 4.1 | [14.8, 38.2] | log10 |
| Leaf dry mass per area (CWM) | LMA | mg/$mm^2$ | | 0.068 (0.067) ± 0.014 | [0.033, 0.098] | log10 |
| Leaf dry matter content (CWM) | LDMC | mg/g | | 296 (291) ± 41 | [198, 400] | sqrt |
| Plant height (CWM) | | cm | | 26 (25) ± 11 | [10, 59] | ln |
| Root depth (CWM) | RD | — | Landolt et al. (2010) | 2.02 (2.00) ± 0.44 | [1.24, 3.04] | log10 |
| Species richness | spnm | Number of species | ORCHAMP | 55 (55) ± 13 | [32, 82] | — |
| Standard effect size of functional richness | $\text{FRic}_{\text{ses}}$ | — | | −0.08 (−0.08) ± 0.04 | [−0.15, −0.03] | — |
| Functional evenness | FEve | — | | 0.57 (0.57) ± 0.07 | [0.40, 0.70] | — |
| Functional divergence | FDiv | — | | 0.94 (0.95) ± 0.03 | [0.87, 0.98] | — |
| Integrated normalized difference vegetation index (proxy for biomass production) | $\text{NDVI}_{\text{int}}$ | — | Terra MODIS 2000–2018 | 80 (86) ± 38 | [7, 158] | — |
| Climatic variables | | | | | | |
| Mean annual temperature | MAT | °C | Safran-Crocus 1988–2018 | 3.10 (2.97) ± 0.77 | [1.75, 5.05] | — |
| Mean total annual precipitation | MAP | mm/year | Safran-Crocus 1988–2018 | 673 (650) ± 223 | [308, 1094] | — |
| Growing degree days (growing season) | GDD | °C/year | Safran-Crocus 1988–2018 | 1164 (1087) ± 289 | [660, 1881] | — |
| Freezing degree days (whole year) | FDD | °C/year | Safran-Crocus 1988–2018 | 42 (38) ± 21 | [16, 98] | ln on absolute values |
| Mean climate water stress (growing season) | CWS | mm/year | Safran-Crocus 1988–2018 | 276 (263) ± 46 | [179, 369] | — |
| Mean solar radiation (growing season) | SR | kJ/($m^2$·year) | Safran-Crocus 1988–2018 | 282,823 (280,069) ± 40,191 | [202,322, 367,770] | — |

Abbreviation: CWM, community-weighted mean.

To assess the importance of interactions between groups, we aggregated the results at the group level, that is, the probability to form connections as well as the mean partial correlations were calculated for all variables of one group (plant community, EEA, abiotic soil and climate) towards all variables of another group.

### 2.7 | Variable selection

From the initial pool of variables (Table 1), a pre-selection was made to avoid redundant information. To select those variables that explained most of the environmental variation while being weakly correlated with each other, we used a principal component analysis (PCA) on plant traits and on climatic variables, respectively. We identified MAT, MAP, SR, plant height and leaf C/N as variables with little additional information and thus removed them from further analysis.

The glasso was run two times. First, all variables in Table 1 except those eliminated in the PCA step were included (Figure S4). Then, nodes were excluded that were deemed of minor importance because they were completely unconnected or only connected to other variables in their own group. The network presented in this paper is the result of this process, and only includes five plant community variables (the CWMs LDMC, LMA, RD, LNC, and the canopy variable $\mathrm{NDVI}_{\mathrm{int}}$), three abiotic soil variables (C/N, SOM, pH), two climatic variables (GDD, CWS) and two EEA variables (total EEA, vector angle (P/N)). To test the robustness of the result, we ran a regression between the partial correlations from the network containing all variables and the network containing the selection of variables (Figure S5).

## 3 | RESULTS

### 3.1 | General linkages between biotic plant–soil components and abiotic factors

The probability of observing linkages (Figure 3a) between the plant community and abiotic components was twice as high for climate as for soil (0.40 and 0.20 respectively). The same pattern was observed for the mean strength of those links (0.44 and 0.26 respectively, Figure 3b). Enzymatic activity of the soil microbial community was strongly linked to abiotic soil variables (probability 0.67 and mean strength 0.42), but not to climate. There was neither a direct connection between climate and soil properties, nor between the plant community and the soil microbial community (Figure 3).

### 3.2 | Role of the different facets of the plant community in plant–soil linkages

Neither CWMs nor functional diversity indices were linked to microbial activities (Figure 4; Figure S4). However, functional diversity measures were completely isolated (spnm, FDiv, $\mathrm{FRic}_{\mathrm{ses}}$ and FEve, Figure S4) and thus removed from the final graph, whereas CWMs of several traits showed clear and strong links to the soil C/N ratio which was a focal variable linking the plant and microbial communities. We observed a partial correlation between RD and soil C/N of −0.24 and of 0.26 between LMA and soil C/N (Figure 4). $\mathrm{NDVI}_{\mathrm{int}}$ and soil C/N were positively correlated (0.27).

### 3.3 | Variables linked to soil enzymatic activities

We observed no direct linkages between plant traits and ratios of enzymatic activities. However, soil C/N was a focal variable linking plant traits to microbial activity, suggesting that the interaction between plant traits and enzymatic activities passes by litter quality. Soil C/N showed the highest probability to form edges across groups overall (0.44), albeit of medium strength (0.29, Table 2). Soil C/N showed a strong linkage to the conservative-exploitative plant continuum. Low soil C/N was associated with low LMA, which in turn was linked to high LNC, which was linked to low LDMC, thus representing a trait assemblage of an exploitative strategy with high investment in photosynthetic leaf area. This spectrum of conservative-exploitative species was indirectly related to soil enzymatic activities via soil C/N. Conservative species (high LMA) and high soil C/N were associated with a high vector angle, indicating that sites with conservative species were less nitrogen and more phosphorus limited than sites with more exploitative species.

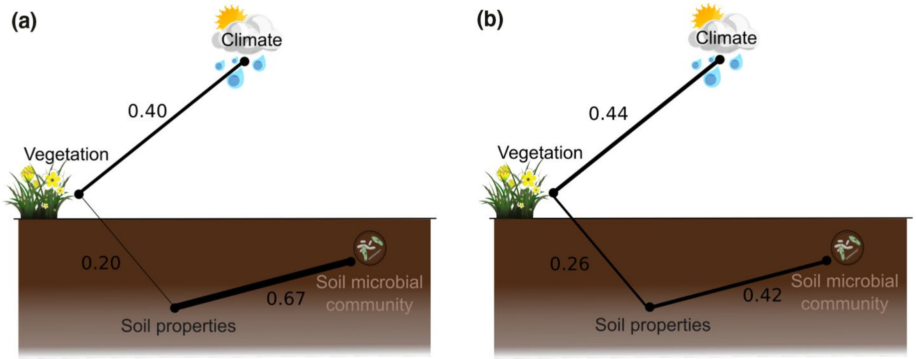

FIGURE 3 Probability of observing links between compartments (a) and mean strength of links between compartments (b)

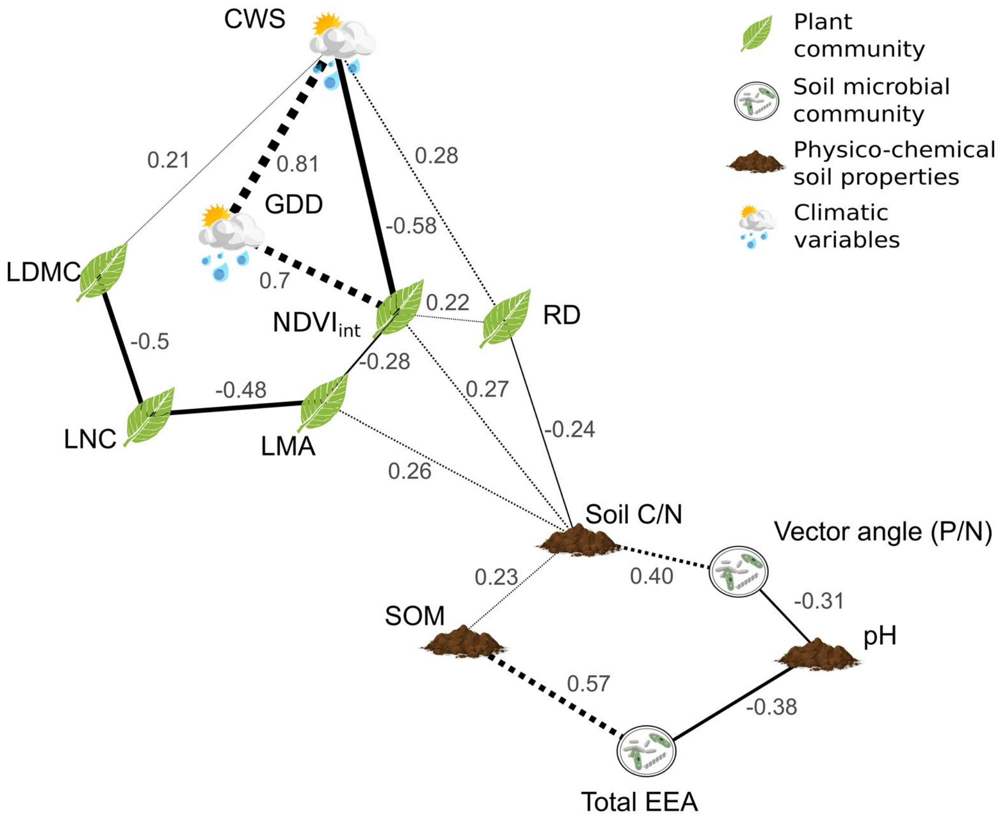

**FIGURE 4** Graph of a partial correlations network in alpine communities, including plant community weighted means, soil microbial enzymatic activities, climatic variables and physico-chemical soil properties. Positive partial correlations are represented by dotted edges, negative ones by continuous ones. The weight of the edges (thickness) corresponds to the absolute strength of their partial correlations. CWS, climate water stress; GDD, growing degree days; LDMC, leaf dry matter content; LMA, leaf mass per area; LNC, leaf nitrogen content; NDVI$_{int}$, integrated normalized difference vegetation index; RD, root depth; soil C/N, soil carbon to nitrogen ratio; SOM, soil organic matter content; total EEA, total extracellular enzymatic activity

**TABLE 2** Degree analysis of the partial correlations network presented in Figure 4. 'Edges within' corresponds to the probability to observe partial correlations between a given variable and other variables that belong to its own group. 'Mean strength within' corresponds to the mean sum of all absolute partial correlations that are realized within the group. 'Edges across' and 'Mean strength across' are analogous metrics to the ones cited before concerning partial correlations *across* groups

| Variable | Group | Edges within | Mean strength within | Edges across | Mean strength across |
|---|---|---|---|---|---|
| LNC | Vegetation | 0.50 | 0.49 | 0 | 0 |
| RD | Vegetation | 0.25 | 0.22 | 0.29 | 0.26 |
| LMA | Vegetation | 0.50 | 0.38 | 0.14 | 0.26 |
| LDMC | Vegetation | 0.25 | 0.50 | 0.14 | 0.21 |
| NDVI$_{int}$ | Vegetation | 0.50 | 0.25 | 0.43 | 0.52 |
| soil C/N | Soil | 0.50 | 0.23 | 0.44 | 0.29 |
| SOM | Soil | 0.50 | 0.23 | 0.11 | 0.57 |
| pH | Soil | 0 | 0 | 0.22 | 0.35 |
| GDD | Climate | 1 | 0.81 | 0.10 | 0.70 |
| CWS | Climate | 1 | 0.81 | 0.30 | 0.36 |
| Vector angle (proportion P/N) | Enzymatic activity | 0 | 0 | 0.20 | 0.36 |
| Total EEA | Enzymatic activity | 0 | 0 | 0.20 | 0.48 |

Abbreviations: CWS, climate water stress; GDD, growing degree days; LDMC, leaf dry matter content; LMA, leaf mass per area; LNC, leaf nitrogen content; NDVI$_{int}$, integrated normalized difference vegetation index; RD, root depth; soil C/N, soil carbon to nitrogen ratio; SOM, soil organic matter content; total EEA, total extracellular enzymatic activity.

Conservative species (high LDMC) were also associated with higher water stress (CWS, 0.21).

In addition to plant functional traits, primary productivity played an important role since $\mathrm{NDVI}_{\mathrm{int}}$ was the link between climate variables and soil C/N. It was positively correlated to GDD (0.7) and negatively to CWS (−0.58), indicating that higher temperatures increased biomass production but associated water stress limited it. $\mathrm{NDVI}_{\mathrm{int}}$ and soil C/N were positively correlated (0.27) suggesting an increased soil C/N in productive sites.

Soil abiotic characteristics were strongly linked to variables of enzymatic activities. SOM and total EEA showed a strong positive correlation indicating high enzymatic activity in organic matter rich sites, and pH was negatively correlated to both vector angle and total EEA (−0.31 and −0.38, respectively). This suggests strong phosphorus limitation and increased enzymatic activity in acidic soils. Vector length was not related to any other variables (Figure S4), suggesting that P versus N limitation is of more importance than carbon versus nutrient limitation in alpine open habitats.

# 4 | DISCUSSION

## 4.1 | Plant–soil linkages and environmental gradients

Studying for the first time the spatial interdependencies between plant functional composition and soil microbial enzymatic activities across grasslands in the French Alps, we found that plant functional composition was mostly associated with climatic variables, while microbial enzymatic activities were primarily related to soil properties. Abiotic factors thus dominate direct biotic linkages in our study system which confirms what has been proposed before: that abiotic factors are of primary importance in mountain systems (Körner, 2003; Neuwinger, 1970). Our results further revealed that an interdependency between plant traits and soil C/N links the aboveground community to the belowground community. This is congruent with the hypothesis that plant traits play a central role in plant–soil linkages through control of litter quality (Lau & Lennon, 2011; Schweitzer et al., 2008; Van der Putten et al., 2013). Moreover, our results showed that in alpine open habitats effects of climate propagate to the soil community through plant traits. This is in accordance with previous studies that demonstrated links between climate and plant traits (Mayor et al., 2017), as well as indirect effects of climate on the soil community via plant traits (Delgado-Baquerizo et al., 2018).

However, in contrast to previous studies (De Vries et al., 2012; Delgado-Baquerizo et al., 2018), we neither found a direct link between soil microbial community activity and plant functional CWMs, nor between soil microbial community activity and climatic variables. This might be due to the fact that the focus of our study was assessing the functioning of the microbial community through EEA (e.g. recycling of organic matter) rather than the composition of the microbial community itself. The link between microbial community composition and function is not necessarily straightforward. Potential changes in microbial community composition, resulting from changes in plant functional traits for example, that could occur here might not have had an impact if there is some level of functional redundancy in the microbial community for the EEA we measured (Louca et al., 2018). Future studies considering the diversity or composition of microbial communities along with their function could reveal more direct links with plant traits as observed in De Vries et al. (2012) and Delgado-Baquerizo et al. (2018), and help understand spatial interdependencies between below- and aboveground communities along large environmental gradients. An explanation for the missing link between soil microbial and climatic variables may be the 30-year time period over which the climatic variables were calculated. This period was chosen because plant communities in alpine systems are known to respond to medium-term climatic conditions rather than annual variations (Körner, 2003). While soil communities might instead be more affected by shorter climatic conditions it has also been suggested that soil communities might actually be very tolerant to climatic variations (Thakur, 2020; Thakur & Geisen, 2019; Thakur et al., 2020). The choice of the time period over which climatic variables are calculated is, in a large-scale ecosystem study, necessarily a compromise between the studied compartments (see Section 4.4).

## 4.2 | Role of the different facets of the plant community in plant–soil linkages

Contrasting the mass-ratio-hypothesis (Grime, 1998) with the diversity-function-hypothesis (Hooper et al., 2005; Tilman et al., 1997), we found that CWMs of plant traits were more important than diversity metrics, supporting the mass-ratio-hypothesis. CWMs showed clear and strong linkages to soil C/N, propagating on to microbial activities and SOM content, indicating a strong effect on organic matter decomposition and the recycling of nutrients (Fortunel et al., 2009; Garnier et al., 2004; 2013; Lavorel, 2013; Quested et al., 2007). These results are consistent with the growing body of evidence for the mass-ratio-hypothesis as a central mechanism controlling ecosystem functioning and services (Lavorel, 2013; Li et al., 2017). They also confirm that it is the linking mechanism between plants and the functional properties of microbial communities (Grigulis et al., 2013; Piton, Legay, et al., 2020).

The isolation of functional diversity indices in our analyses may be in part due to the mountain context of our study. Hooper et al. (2005) suggested that ecosystems might be less defined by functional diversity in challenging abiotic conditions. They also argued that species with different response traits to environmental changes are needed under increasing temporal and spatial variability in order to ensure a stable supply of ecosystem functions. Furthermore, it has been shown that mass ratio effects better explain individual functions, but that multifunctionality of ecosystems is more driven by diversity effects (Le Bagousse-Pinguet et al., 2019). Therefore, considering today's climate and land-use changes and biological invasions, even a system where the diversity-function-hypothesis does not play an important role under current conditions may depend on trait diversity if certain thresholds are crossed in the future. Thus, although our results confirm the importance of CWMs for ecosystem functioning (e.g. decomposition and nutrient recycling) their importance for ecosystem stability still needs further exploration (e.g. Piton, Legay, et al., 2020), especially in alpine systems where species' trait values may vary a lot depending on altitude due to high plasticity (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010).

## 4.3 | Variables linked to soil enzymatic activities

It is well understood that plant traits are linked to microbial community composition and functioning, directly and via plant litter quality (Fanin et al., 2014; Grigulis et al., 2013; Legay et al., 2014; Martinez-Almoyna et al., 2020). In our study, plant traits associated with the plant conservative-exploitative continuum (LMA, LNC and LDMC) were indirectly connected to SOM, as well as soil enzymatic activities, via a central link between plant traits and soil C/N. This supports at a biogeographic scale the hypothesis that litter quality rather than quantity plays a central role in microbial functions involved in aboveground-belowground linkages in grassland ecosystems, as has been shown previously also for soil microbial community composition and diversity in studies of temperate grasslands in England and Germany (De Vries et al., 2012; Delgado-Baquerizo et al., 2018).

Interestingly, our partial correlation network is consistent with the expected ecosystem functioning along a conservative-exploitative continuum (Bardgett & Wardle, 2010; Moore, 1988; Mulder et al., 2013). On the conservative side, reduced organic matter quality (high soil C/N) associated with conservative plant traits favours SOM accumulation, increasing total enzymatic activity. High soil C/N was also associated with an increased investment of microbial communities in P-acquisition relative to N-acquisition, suggesting that conservative plant traits and high soil C/N are also associated with a high N/P ratio of resources available for microbes. The link between soil C/N and microbial nutrient acquisition strategies might be central in the feedback from soil to plants. In infertile soils, microbial communities immobilize nutrients in their biomass, releasing less nutrients to the soil (Mooshammer et al., 2014; Zechmeister-Boltenstern et al., 2015). This creates a negative feedback-loop since a nutrient poor soil will result in a more conservative plant community which will then produce more recalcitrant litter increasing further SOM accumulation and the nutrient limitation of microbial communities (De Vries & Bardgett, 2012; Wardle et al., 2004).

Our network also showed soil C/N to be linked with plant community productivity ($NDVI_{int}$) and RD. High plant productivity was associated with a warm growing season, low water deficit and exploitative plant traits (low LMA). It was also positively associated with soil C/N, likely explained by higher plant-derived C input in the soil with higher productivity. On the contrary, high RD associated with high water deficit (stress resistance strategy) decreased soil C/N, possibly because a higher fraction of the plant-derived C was released deeper into the soil and thus could not be captured in our soil data from the upper horizon. Our results also suggest stronger microbial phosphorus than nitrogen limitation (high vector angle) and increased enzymatic activity in acidic soils, in accordance with Piton, Legay, et al. (2020). In acidic soils (mean pH of our sites was 5.5), leaching of acids towards the bedrock releases (Fe, Al or Mn) cations. These cations form compounds with bioavailable forms of phosphorus, such as $H_2PO_4^-$, and hence decrease P availability (Iqbal, 2012; Wild, 1950).

## 4.4 | Critical aspects and perspectives

Our study gives insights about linkages between plant and microbial soil communities in alpine habitats at large scales, and we show how abiotic climatic conditions and soil properties influence these linkages. However, our study is not without flaws. First, there may be a conflict of scales in our analysis. Plant and microbial soil communities have a very different temporal turnover, that is, composition and abundances may change faster in microbial than in plant communities, and microbial communities may hence respond faster to changes in environmental conditions (Bardgett & Wardle, 2010; but see Thakur & Geisen, 2019; Thakur, 2020; Thakur et al., 2020). They may thus be more determined by short-term fluctuations in abiotic conditions while plant communities may respond more to long-term changes. This may create a mismatch in temporal scales when analysing both components at the same time. For example, we calculated climatic variables like GDD over a period that could be considered more of a determinant of the plant community. To determine whether this temporal mismatch was truly an issue, we compared GDD calculated over a 30-year time period (as used here), with the GDD calculated over 10 years and over the year before sampling for all our 41 plots. All correlations were very high, demonstrating that the differences between plots remain relatively constant whatever the time-scale used to calculate GDD (Figures S7 and S8). We are thus confident that this should not influence the results and the conclusion of our paper. In addition to a temporal mismatch, there may also be a spatial one. The quantitative prediction of precipitation in mountainous areas can be biased because precipitation is a very local phenomenon that changes from one mountain massif to another (Quintana-Segui et al., 2008, 2017; Roe, 2005). Spatial variability in precipitation may therefore be difficult to capture with climate models if few observation stations are available (Hofstra et al., 2010). However, while SAFRAN is known to overestimate the number of precipitation days and underestimate high precipitation events (Quintana-Seguí et al., 2017), it is very likely that plot differences (i.e. the ranking between the plots) are relatively robust to these uncertainties and should thus not influence the Graphical lasso estimation.

Second, plant–soil linkages are complex and they may be affected by factors that we did not include in this study, such as herbivores and soil meso- and macrofauna. Furthermore, we did not include direct measures of diversity or composition of the microbial community but only variables related to their activities. Specifically, we did not use environmental DNA metabarcoding approaches because they do not provide reliable information on the biomass of different organisms (Calderón-Sanou et al., 2020; Taberlet et al., 2018). It would thus neither have been possible to calculate ratios of fungal and bacterial biomass, nor would we have had information about abundances of oligotrophic and copiotrophic groups. While we showed that functional diversity of the plant community did not play a role in our study system, we cannot exclude the possibility that diversity of the microbial community did. In addition, we showed in our study that litter quality may be a key determinant of microbial functions in alpine grassland ecosystems. We deduced this from measures of topsoil C/N content which we interpreted as a proxy of litter quality. In future studies, it may hence be of interest to include direct measures of litter quality.

Third, it is important to note that we quantified EEA in vitro and therefore used measures of potential enzymatic activity and not in situ activity. It has been argued that in vitro assays may be a limited proxy for EEA in real conditions since substrate diffusion and abundance, as well as soil type and temperature are not reflected in vitro assays (Bell et al., 2013; Wallenstein & Weintraub, 2008). However, in situ measurements provide only a snapshot of the belowground community's activity and may therefore not adequately represent longer-term linkages between the plant and the soil microbial communities.

Last, we chose to study plant–soil linkages with the graphical lasso because it is difficult or even impossible to uncover interactions through experiments at large scales. More importantly, we do not know if observed patterns result from the plant community influencing the soil community, or the other way around, or both influencing each other reciprocally. Hence, an undirected partial correlations network is a very well-suited method to disentangle direct and indirect effects between the plant and the soil microbial communities, and to look at biogeographic patterns. Nevertheless, experimental validation is necessary to determine causal pathways, which is especially important considering the potential effects of rising temperatures or changes in precipitation on plant–soil relationships.

## 5 | CONCLUSIONS

Studying the spatial interdependencies between the plant functional composition, soil microbial enzymatic activities and abiotic conditions across the French Alps, we found abiotic drivers to be key elements. Plant traits were more strongly controlled by climate, whereas enzymatic activities were more associated with soil abiotic properties. The connections between climate and soil biotic and abiotic properties were only indirect through plant trait association with soil C/N. At the same time, the links between microbial enzymatic activities and plant traits through soil C/N highlighted the role of plant–soil interdependencies in ecosystem responses to abiotic changes. The observed plant–soil linkages are well in accordance with the conservative-exploitative continuum with soil C/N as an important player. Our study is one of the first to identify a signal of the conservative-exploitative plant continuum and microbial nutrient acquisition strategies in patterns of co-distributions of plant functional traits and microbial activity on a biogeographic scale (the French Alps) in alpine ecosystems. It thus demonstrates how the soil functioning can be integrated in studies of ecosystem shifts under environmental change at large spatial scales.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data and the R code supporting the results are available on Dryad (https://doi.org/10.5061/dryad.cjsxksn63).

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## BIOSKETCH

**Sarah-Sophie Weil** is interested in large scale biogeographic patterns and the underlying mechanisms and processes. She is currently working on the role of traits in long-distance dispersal in the context of her joint PhD at the Laboratoire d'Ecologie Alpine (LECA, France) and the Biosciences Department in Swansea (Wales, UK). This work was part of her Master's thesis in the LECA.

**Author Contributions**: WT and TM conceived the ideas, field observations and lab measurements were carried out by the ORCHAMP consortium. WT, CMA and AS collected soil samples, GP, AS and AF analysed the enzymatic activities and LB performed the trait measurements. JR managed and maintained databases of traits, climatic variables and ORCHAMP field measurements, PC provided NDVI data, CMA calculated the climatic indices. SSW performed the modelling work and all subsequent analyses. GP, AF and JP gave additional perspectives to the paper. SSW wrote the first draft of the manuscript and all authors contributed substantially to revisions and gave final approval for publication.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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