Vegetation creates microenvironments that influence soil microbial activity and functional diversity along an elevation gradient

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Vegetation alters how soil properties and climate influence microbial activity and functional diversity in rhizosphere and bulk soil along an elevation gradient

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Highlights

Soil physical and chemical properties were the main drivers of microbial activity.

Microbial activity converged in bulk and rhizospheric soils at higher elevations.

Plant species identity refined relationships with microbial activity and abiotic factors.

Abstract

Microbial communities strongly influence ecological processes across space and time. However, the influence of abiotic and biotic factors on microbial functioning in a complex, heterogeneous soil environment is still poorly understood, especially in montane plant communities. Here, we ask if microbial activity and functional diversity can be influenced by plant species identity and diversity and associated root system morphological and chemical traits that also influence soil properties. We investigated microbial global catabolic activity (i.e. microbial activity) and catabolic diversity (i.e. functional diversity) in bulk and rhizospheric soil beneath three plant species (*Vaccinium myrtillus*, *Juniperus communis* and *Picea abies*) that shape local plant communities. To do this, we measured soil physical and chemical properties, and plant diversity along an elevational gradient (1400 - 2400 m a.s.l.) in the French Alps. Microbial global catabolic activity and diversity were assessed using multiple substrate-induced respiration. Morphological and chemical traits of roots in bulk soil ('*community*' level traits, where several plant species were pooled together) and of individual plants ('*species*' level, where roots of single species were excavated) were measured. Results showed that at lower elevations, global catabolic activity in the

rhizosphere was higher than in bulk soil, but converged in the nutrient-poor, colder soils found at higher elevations, although changes in catabolic diversity were negligible. Variations in soil physical and chemical properties were the main drivers of global catabolic activity, especially texture, cation exchange capacity, carbon and nitrogen content and pH, but their effects on catabolic diversity were minimalPlant root traits at the *community* level in bulk soil had less effect on global catabolic activity than abiotic factors, with thicker roots, high root lignin content and low cellulose content influencing microbial activity, but not altering catabolic diversity. At the *species* level, more dense root tissue decreased global catabolic activity, reflecting changes in chemical composition. Our results show that relationships between catabolic activity, mean annual temperature and soil properties differed between plant species

1. Introduction

Mountainous regions are characterised by abrupt changes in physical, edaphic and biotic environments over short geographic distances because of the presence of elevational gradients. These gradients create a variety of ecological habitats (Körner et al., 2011; Abbott and Brennan, 2014; Hofmann et al., 2016), which makes them ideal for studying biodiversity patterns and their drivers. Several studies have emphasised the importance of investigating soil microbial community structure and function along elevation gradients, as soil microorganisms are often more responsive to environmental changes than other organisms (Shen et al., 2015; Cui et al., 2019; Bardgett and Caruso 2020). Soil microorganisms play a key role in a wide range of ecosystem processes, such as decomposition of organic matter, nutrient cycling, erosion control through their action on soil aggregate stability, regulation of water supply, soil development and maintenance of structure (Prosser et al., 2007; Maron et

al., 2011; Aislabie et al., 2013; Xu et al., 2019; Merino-Martín et al., 2021). As recently emphasised by several studies, there is a crucial need to consider belowground processes and integrate them with vegetation data in order to better predict soil dynamics and response to climate change (Cavicchioli et al., 2019; Hagedorn et al., 2019; D´Alò et al., 2021). We ask therefore, if it is possible to determine how climatic factors alter microbial activity and functional diversity, depending on soil and vegetation type, in a complex mountainous environment.

In temperate latitudes, (sub)alpine soils are very heterogeneous and are typically rocky, acidic and shallow with poorly developed horizons (Price and Harden, 2013). As elevation increases, plant growth and cover are mainly limited by climatic conditions and a shorter growing season, causing a reduction of organic matter content in soils at higher elevations and making soils nutrient-limited for plant growth (Zhou et al., 2002; Donhauser and Frey, 2018; Möhl et al., 2018; Stokes et al., 2021). Microclimatic conditions strongly influence soil microbial communities (Donhauser and Frey, 2018, Collins et al., 2020) and therefore microbial activity and functional diversity. Here, we define microbial activity as the global catabolic activity, an indicator of the functional capacity of microbial communities to decompose organic matter. Aditionally, we define microbial functional diversity as the catabolic diversity, i.e. the capacity of a microbial community to use different substrates for respiration, as measured through catabolic response profiles (Degens and Harris, 1997; Degens et al., 2001). Catabolic activity and diversity are strongly influenced by soil variables, especially pH (Moscatelli et al. 2018) and total and labile organic carbon (C) contents, assessed mainly through studies of increased fertilisation by organic amendments across a wide range of land uses (Degens et al., 2000; Margesin et al., 2009; Tian et al., 2015;

Bongiorno et al., 2020). Moreover, catabolic activity and diversity to increase with warmer temperatures in different grasslands (Grayston et al., 2001; Papatheodorou et al., 2004) and alpine climates (D´Alò et al., 2021). As climatic conditions are also determined by topography, they further influence variables such as soil nutrient availability and the quantity of litter input to the soil; altogether, these environmental variables are key to controlling the catabolic activity of soil microorganisms (Kang et al., 2009). However, the linkages between catabolic activity, diversity and soil properties are not yet fully elucidated, particularly in a complex, heterogeneous landscape, where soil type, climate and vegetation all interact to modify microbial community structure and function.

Vegetation can alter global catabolic activity and diversity either at the community level or through specific species effects. Several studies have shown that catabolic diversity increased with higher levels of plant diversity e.g., along a longitudinal gradient in temperate grasslands (Liu et al., 2008) and along an elevational gradient in temperate forests (Klimek et al., 2015). These effects were mainly attributed to increases in plant biomass and mediated by soil factors. The influence of increased plant diversity on microbial catabolic activity and diversity is likely through an increase in the variety of C sources, promoting a heterogeneous distribution of soil properties (Reverchon et al., 2015). However, individual plant species also alter the structure and function of soil microbial communities, through (i) shoot and root litter production (Xu et al., 2018), (ii) root exudation patterns (Williams et al., 2021) and (iii) above- and below- ground functional traits (Spitzer et al., 2021; Sweeny et al., 2021). Microbial activity and functional diversity are enhanced in litter-rich soil because of the large amount of C available as substrate for decomposers (Nsabimana et al., 2004; Nuccio et al., 2020), although the quality of litter, especially its content in soluble C, also has a determining

effect on microbial catabolic activity (Fanin et al., 2014). In particular, root nitrogen (N) and C content should increase microbial respiration and decomposition of soil organic matter (Han et al., 2020), whereas roots that are rich in more recalcitrant compounds such as lignin and cellulose could limit microbial activity (Poirier et al., 2018).

Within bulk soil, microbial processes can be altered by the proximity of plant roots. Plant roots release organic compounds that modify microbial catabolic activity and functional diversity, since many microorganisms use these root exudates and mucilage as their main energy source (Liu et al., 2008; Hobbie and Hobbie, 2013). These interactions take place with a greater intensity in the rhizosphere, a narrow zone around the root with high concentrations of easily degradable carbon sources, leading to an inflated rate of microbial activity and a greater functional diversity compared to bulk soil (Baudoin et al., 2002; Yang et al., 2013; Kuzyakov and Razavi, 2019; Nuccio et al., 2020). Therefore, plant root traits that promote rhizosphere dimensions, e.g., long, thin roots that have a large surface area, should also enhance microbial catabolic activity and diversity. Woody root traits that have the strongest effect on microbial catabolic activity and biomass include specific root length (SRL: length / mass ratio), root branching intensity and root diameter, whereas root chemical composition (C, phosphorus, calcium and magnesium content) has been found to have less effect (Khlifa et al., 2017; Sweeny et al., 2021). Thicker roots increase the volume of cortex available for mycorrhizal fungi colonisation, which would enhance nutrient uptake and soil nutrient cycling (Burke et al., 2011; Xiao et al., 2019; McCormack and Iversen, 2019), hence potentially promoting microbial activity in the rhizosphere (Chen et al., 2018). However, although root exudation is positively correlated to root diameter in grassland species (Williams et al., 2020), it is negatively related to root diameter in trees (Han et al., 2020). We

therefore expect that rhizospheric microbial communities relying on root exudates as a substrate should be less active around thicker woody roots with relatively small rhizosphere dimensions compared to highly branched roots or roots with a high SRL.

We aimed to unravel the effect that biotic and abiotic factors exert on global catabolic activity and diversity in bulk and rhizospheric soils in a heterogeneous environment. To do this, we examined changes in climatic parameters, soil properties, plant species diversity and root traits along an elevation gradient (without considering microtopography), and their relationships with global catabolic activity and diversity. We investigated the global catabolic activity and diversity in soils beneath three different plant species, in both rhizospheric soil andalso bulk soil where a mixture of roots from other plant species would be present. . We hypothesized that microbial catabolic activity and diversity would : (H1) decrease in colder and nutrient-poor soils from higher elevations, where reduced plant growth limits organic matter supply to soil, compared to soils at lower altitudes; (H2) increase at higher levels of plant diversity, especially in bulk soils, because of the more broad variety of C sources available from litter and root exudates, and (H3) increase around roots possessing traits that enlarge rhizospheric dimensions i.e. longer, thinner roots, that have large exchange surface areas and potentially more available exudates. However, roots that are rich in lignin and cellulose, could limit microbial activity, because these compounds are highly recalcitrant.

2. Material and Methods

2.1 Study site and plant species under study

Fieldwork was conducted along an 8 km elevational gradient located in the Belledonne massif in the French Alps (France, N 45° 7' 1" E 5° 53' 35', Table 1). The elevation gradient

that we used comprised six altimetric bands, each 200 m, and ranged from 1400 to 2400 m a.s.l. The current thermal treeline is situated between 2000 - 2100 m (Wang et al., 2018). Below the treeline, the dominant trees shifted along the gradient from mixed forest of *Fagus sylvatica*, *Pinus sylvestris* and *Abies alba* in the montane belt to mixed forests of *Picea abies*, *Pinus uncinata* and *Pinus cembra* in the subalpine belt. Above the treeline, the vegetation was dominated by (sub)alpine heaths of Ericaceae (*Vaccinium* spp, *Rhododendron ferrugineum*, *Loiseleuria procumbens* (L.) Loisel.) and *Juniperus communis* subsp. *nana* and grasslands dominated by graminoid species (*Nardus stricta*, *Carex sempervirens*, *Festuca* spp). Mean annual temperature (MAT), mean annual precipitation (MAP) and mean annual solar radiation (MAR) were calculated using the meteorological AURELHY model (Piedallu et al., 2013, 2016) during a ten year period (2004-2014) at each elevation (Stokes et al., 2021, Table 1). MAT decreased from 8.5 ± 0.2 °C to 5.7 ± 0.2 °C up the elevation gradient, while MAP increased from 1024 ± 41 mm to 1187 ± 40 mm. MAR varied from 4204 MJ/m^2 to 4339 MJ/m^2 up along the elevation gradient (Table 1, Fig. S1).

Five plots (20 x 20 m) were selected within each altitudinal band, with a lateral distance of at least 100 m between each plot (Fig. 1, a and b) in June 2018. Plots were selected if they included three species: *P. abies*, a tall evergreen tree; *Juniperus communis* L., a prostrate evergreen shrub and *Vaccinium myrtillus* L., a small deciduous shrub (if these species were present at that elevational band, Table S1). These three plant species were selected because of their different growth forms and occupation of different ecological niches along the elevational gradient. *P. abies* was the dominant tree species below the tree line; *J. communis* was abundant locally and *V. myrtillus* was one of the most frequent species above the treeline, as well as being present in all six elevational bands. *P. abies* and *V. myrtillus* are both

keystone species (Bjune et al., 2009; Nybakken et al., 2013) and although *J. communis* is not classed as a keystone species, its abundance above the treeline makes it an important species that structures plant communities. Therefore, these three species contribute to shaping the structure of the plant communities in which they are present, and we term them 'structuring species'.

Within each plot, one well-developed individual of each structuring species was selected and at the limit of its canopy, on the downslope side, a 1.0 × 1.0 m quadrat was located for further plant and soil sampling. A botanical survey was first performed in each quadrat (data are provided in Stokes et al., 2021). Plants were identified using two floras (*Flore Forestière Française*, Montagnes, Rameau et al., 1999 and *Flora Helvetica*, Laufen et al., 2001) and their abundance was estimated making a visual assessment of the relative area covered by different plant species in each quadrat. Simpson diversity index (*S*) was calculated as following:

$$S = 1 - \frac{\sum n(n-1)}{N(N-1)} \quad (1)$$

where *n* is the number of individuals of each species and *N* the total number of individuals of all species.

2.2 Bulk and rhizospheric soil sampling

At the center of each 1 x 1 m quadrat, a soil monolith (0.25 × 0.25 × 0.15 m) was excavated using a metal frame (Fig. 1, c). Bulk soil was collected from the monolith´s four lateral faces, sieved at 2 mm, air-dried and stored at room temperature before further analyses. These analyses comprised the assessment of soil physical and chemical properties and catabolic

activity and diversity (Stokes et al., 2021). A total number of 70 bulk soil samples were taken (six elevations × five plots × two to three plant species).

To obtain rhizospheric soil, further soil samples were obtained beneath plants in the same plots and close to the monoliths, using gloves and ethanol sterilized material. Individuals of *V. myrtillus* were identified and root systems extracted manually. Soil attached to the youngest roots (comprising the root apices) was sampled by gently shaking the roots inside paper bags whilst still in the field. In the case of *J. communis* and *P. abies*, whole individuals were not harvested. Instead, a large root was followed from the base of the trunk to a distance of about 0.5 m from the trunk, and fine roots (roots with a diameter ≤2 mm, whose primary function is resource uptake (Freschet and Roumet, 2017)), attached to this large root were collected and then shaken in paper bags. All 70 rhizospheric soil samples were taken to the laboratory and were air-dried for at least one week and stored at room temperature prior to catabolic activity and diversity analyses. We air-dried our soil samples to avoid logistical constraints linked to sampling, transport and storage (Gillespie et al., 2021).

2.3 Soil physical and chemical properties

Soil physical and chemical properties were measured in the same monoliths where we sampled bulk soil (Stokes et al., 2021). Analyses were performed on three replicates of 60-80 g of soil at the Laboratoire d'Analyses des Sols (INRAE, Arras, France), and included texture (clay, silt and sand content; pipette method, NF X 31-107), cation exchange capacity (CEC; Metson method, NF X 31-130), total soil organic C (SOC; dry combustion, NF ISO 10694), total N content (TN; dry combustion, NF ISO 13878), available phosphorus (P; Olsen method, NF ISO 11263) and pH (NF ISO 10390). Nitrate (NO_3^-) and ammonium

(NH_4^+) were measured by extraction with potassium chloride solution on bulk soil samples (NF ISO 14256, CIRAD Montpellier, France). Aggregate stability, expressed by mean weight diameter (MWD), was determined on bulk soil samples taken from two depths (topsoil [MWD_{top}] at a depth of 0-0.25 m and subsoil [MWD_{sub}] at a depth of 0.25-0.50 m), using the fast wetting standard method (Le Bissonnais, 1996; ISO/CD 10930). Infiltration tests were carried out to measure soil hydraulic conductivity (Kfs), using a quasi-steady infiltration rate in a single ring infiltrometer (Marín-Castro et al., 2016; Wu et al., 1999) and the soil water volumetric content at a depth of 0.05 - 0.10 m beneath the soil surface was measured with soil moisture meter TDR100 (6440FS, from Fieldscout – Spectrum technologies).

2.4 Microbial global catabolic activity and diversity of soil microbiota: multiple substrate-induced respiration (MSIR; MicroResp™ analysis)

Multiple substrate-induced respiration (MSIR) is a method for characterising and assessing the activity and functional diversity of soil microbiota. This method is used to assess the soil microbial functional capacity in C cycling (Creamer et al., 2016; Fromin et al., 2020) and is therefore used as a proxy for global catabolic activity and diversity of soil microbial communities (i.e., the mineralization of organic C into carbon dioxide (CO_2), Beare et al., 1990 and Nannipieri et al., 1990). Here, we used the MicroResp™ system (Macaulay Scientific Consulting, Aberdeen, UK) to characterize the community level physiological profiles of the soil microbial communities and assess the capacity to use multiple substrates for respiration (i.e. catabolic diversity). Since the production of CO_2 is measured within 6 hours after inducing respiration with the addition of substrates (Chapman et al., 2007), the advantage of this technique is that it gives immediate responses to C substrate decay instead

of relying on microbial growth. Briefly, both bulk and rhizospheric soil samples were adjusted to 80 % of their maximum water holding capacity and pre-incubated for one week at 25 °C in deepwell plates, that holds approximately 0.45 g $well^{-1}$ of soil (Baratella and Pinzari, 2019), before applying aqueous solutions of the different C substrates and assembling the deepwell-detection plate system. In this study, we used twelve substrates (with four replicates per substrate) of the three main families of organic compounds found in soil and root exudates; sugars (D-glucose, arabinose, N-acetyl-glucosamine), amino acids (L-alanine, L-lysine, L-asparagine, L-glycine) and organic acids (oxalic acid, malic acid, citric acid, vanillic acid) (Badri and Vivanco, 2009). Sugars and amino acids represent a main source of litterfall- and root- derived C compounds in the soil (Jones and Murphy, 2007) while organic acids are predominantly liberated in the form of root exudates (Farrar et al., 2003). All substrates were added at a concentration of 100 g L^{-1} except for L-asparagine (50 g L^{-1}) and vanillic acid (10 g L^{-1}) due to their low solubility. Additionally, water was used as a control to measure soil basal respiration that is defined as the steady rate of respiration in soil from the mineralization of organic matter. CO_2 emission was estimated using a colorimetric method. Detection plates containing 12.5 µg g^{-1} cresol red, 150 mM KCl and 2.5 mM $NaHCO_3$ set in 1 % Noble agar were prepared and 150 µl of the solution were distributed per well. After pre-incubation in the dark, each deepwell plate was covered with a detection plate using a silicon seal. The system was secured with a clamp and incubated for six hours at 28 °C. The optical density of each plate was determined using a microplate reader (Victor3 1420 Multilabel Counter, Perkin Elmer, MA, USA) at 570 nm before and after incubation. The optical density was normalized and converted to multiple substrate induced respiration rates (MSIR) expressed in µg CO_2 g^{-1} dry soil h^{-1} (Fromin et al., 2020). The respiration rates for the different C compounds were summed across all substrates as a proxy

of the global catabolic activity. The catabolic diversity index (Shannon index, *H'*), an indicator of the soil microbial functional diversity (Sparling et al., 2000), was calculated for each sample using Equation 2:

$$H' = -\sum_{i=1}^{12} \quad p_i * ln(p_i) \quad \text{..... (2)}$$

where p_i was the respiration rate for a given substrate divided by the sum of the total respiration rates of that particular substrate.

2.5 Measurements of *community*- and *species*- level root traits

2.5.1 *Community* level root traits

After the monoliths were extracted, the depth of the litter layer was noted and the litter removed. Half of the monolith was dissected to extract all roots (hereafter *community* level), that represented a mix of roots from one of the structuring species and from different plant species growing in the monoliths. This *community* level mixture of roots therefore comprised a large proportion of roots from one of the three structuring species. Within 1 day but sometimes up to 2 days after sampling, roots from the *community* level were sorted and fine, undamaged roots with a diameter < 2 mm were removed and washed. Absorptive roots are lower root orders, typically the first, second and third root orders (defined as the most distal root orders) (Pregitzer 2002; Freschet & Roumet, 2017). A subsample of absorptive roots were selected, scanned (Epson Expression 1680, Canada) in a tray of water and analysed (Winrhizo Pro version 2019, Regent Instruments, Canada), following Roumet et al. (2016). At the *community* level, root length (L_{com}), mean root diameter (RD_{com}), and root volume (V_{com}) were estimated in different diameter classes (from 0 to 2 mm diameter with a 0.1 mm

bin size). After scanning, root fresh mass (RFM_{com}) and root dry mass (RDM_{com}) (60°C for 72h) were determined. Specific root length (SRL_{com}) as the ratio between L_{com} and RDM_{com}, root tissue density (RTD_{com}) as the ratio between RDM_{com} and V_{com}, root dry mass content ($RDMC_{com}$) as the ratio between RDM_{com} and RFM_{com}, root length density (RLD_{com}) and root mass density (RMD_{com}) were calculated for roots at the *community* level (Table S2). Root nitrogen (RNC_{com}) and carbon (RCC_{com}) content were measured on absorptive roots using an elemental analyser (CHN model EA 1108; Carlo Erba Instruments, Italy). The content of water-soluble compounds, cellulose, hemicellulose and lignin in absorptive *community* level roots was determined using the Van Soest method (Van Soest, 1990) in a fiber analyser (Fibersac 24; Ankom, Macedon, NJ, USA).

2.5.2. Species level root traits

Species level root trait data were obtained from a separate study by Weemstra et al., (2021) who examined root traits of 11 individual plant species in the same plots and at the same dates, including the three structuring species that we examined, along the same elevational gradient. In their study, roots from the three structuring plant species (*P. abies*, *V. myrtillus* and *J. communis*) were carefully dug out from the top 0.15 m soil horizon and below the litter layer. Approximately 3 to 5 different roots were dug up from 0.5 – 1.5 m from the base of the stem and traced back to the stem to verify that they belonged to the chosen plant individuals. Roots were stored in moist plastic bags and kept refrigerated until analysed in the laboratory. Within 1 day but sometimes up to 2 days after sampling, roots were washed and undamaged absorptive roots were scanned and SRL_{sp}, $RDMC_{sp}$, RTD_{sp} at the *species* level were calculated as described above for roots harvested at the *community* level.

2.6 Data analysis

We examined the variations in global catabolic activity and catabolic diversity (*H′*) in bulk and rhizospheric soils with regard to elevation and structuring plant species.

Soil physical and chemical properties, *community*- and *species*- level root traits and global catabolic activity and diversity along the elevational gradient, were analyzed as a function of elevational band using one-way analysis of variance (ANOVA) and Tukey's HSD to test significant differences among elevational bands. Unbalanced two-way ANOVA (Type-III sums of squares) was performed to assess the effect of elevation, plant species and their interaction on the different soil physical and chemical properties and *community*- and *species*- level root traits.

Spearman's correlation coefficients were assessed tostudy the relationships between catabolic activity and diversity and climatic data, soil properties, plant diversity and *community*- and *species*- level root traits, along the elevational gradient for each one of the three structuring species.

Dissimilarity in global catabolic activity between bulk and rhizospheric soils, among elevation bands and structuring plant species was examined using non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis distance. Permutational multivariate analysis of variance (PERMANOVA), implemented with the *adonis* function from the vegan R package, was used to assess the significance of the observed NMDS differences.

Distance-based redundancy analysis (db-RDA) for constrained ordination based on the Bray–Curtis distance (*capscale* function of vegan R package) was carried out to determine the

extent to which variations in global catabolic activity can be explained by environmental variables along the elevational gradient, followed by a stepwise model selection using Generalized Akaike Information Criterion (AIC, *ordistep* function of vegan R package with forward and backward direction). Finally, db-RDA analysis was performed only for the variables obtained from the model selection.

Variation partitioning analysis, using the function *varpart* of the R vegan package, was performed to determine the relative importance of the environmental variables (soil physical and chemical properties, *community*- and *species*- level root traits and climatic data), and their contribution to catabolic activity, which was later identified by partial redundancy analysis in Hellinger transformed data.

3. Results

3.1 Changes in soil physical and chemical properties along the elevation gradient

Beneath *V. myrtillus* and *P. abies*, soil nutrient content (SOC, TN and P), CEC and C/N ratio varied little along the elevational gradient except at 1600 m where they were significantly higher than at all other elevations (Table S3). Beneath *J. communis*, changes in these properties were negligible along the gradient (Table S3). In bulk soil beneath *P. abies*, NH_4^+ content was significantly higher at 1600 m than at all other elevations, but under *V. myrtillus* and *J. communis*, there were no significant differences among elevational bands (Table S3). With regard to NO_3^- content, there were no significant changes along the gradient beneath any structuring species (Table S3). Litter depth beneath *P. abies* decreased significantly from 1400 m to 2000 m while under *V. myrtillus* the main change was between 1400 and 1600 m. No trends beneath *J. communis* occurred along the gradient (Table S3). Soils beneath all

three plant species along the gradient were acidic with a pH ranging from 4.40 to 5.60, and the percentage of soil water content was significantly lower at 1400 - 1600 m than at 1800 - 2400 m (Table S3). Both elevation and structuring plant species were not significantly related to changes in the majority of soil physical and chemical properties (ANOVA analysis, Tables S4). However, elevation had a significant influence on silt and sand content ($p<0.001$) and structuring species had a significant impact on MWD_{top} and soil water content ($p<0.001$; Table S4).

3.2 Global catabolic activity and diversity (*H'*) in bulk and rhizosphere soil along the elevation gradient

No significant differences were found between basal respiration and global catabolic activity, therefore, to simplify results, we present values for global catabolic activity only (Table S5).

In bulk soil beneath *V. myrtillus* and *P. abies*, global catabolic activity fluctuated along the gradient with a significant peak (pairwise comparisons between elevational bands, $p < 0.05$; Table S6) at 1600 m (Fig. 2 a,b). No changes in bulk soil catabolic activity under *J. communis* occurred between elevation bands (Fig. 2 c; Table S6). Global catabolic activity in rhizospheric soil beneath *V. myrtillus* and *P. abies* gradually decreased with increasing elevation and had significantly greater values at 1400 – 1600 m compared to those at higher elevations (Fig 2 a,b; Table S6). However, global catabolic activity in rhizospheric soil of *J. communis* did not show any significant differences amongelevation bands (Fig. 2 c; Table S6).

Global catabolic activity in rhizospheric soil from *V. myrtillus* and *P. abies* at 1400, 1600 and 1800 m was higher compared to bulk soil (Fig 2 a, b). Above 1800 m, bulk and

rhizospheric catabolic activity values from *V. myrtillus* and *P. abies* converged and were not significantly different (Fig. 2 a,b; Table S6). In samples from beneath *J. communis*, although catabolic activity in rhizospheric soil was generally higher than in bulk soil, differences were not significant (Fig. 2 c; Table S6). The mean catabolic diversity index (H′) of both bulk and rhizospheric soils was 2.4 and no significant differences were found (data not shown) either in bulk or rhizospheric soil, among plant species or along the elevation gradient.

No clear trend between global microbial catabolic activity and elevational bands in bulk and rhizospheric soil (NMDS plot, -Fig. S3), however the PERMANOVA test showed that elevation explained the majority of variation in catabolic activity in both rhizospheric soil ($p<0.001$, $R^2=0.36$; Table 2) and bulk soil ($p=0.01$, $R^2=0.10$; Table 2). In contrast, the variation in catabolic activity not explained by elevation was greater in bulk soil (residuals=0.87; Table 2) than in rhizosphere soil (residuals=0.52; Table 2). In addition, there was a significant influence of the interaction between plant species and elevation ($p=0.006$, $R^2=0.08$) and of plant species ($p=0.03$, $R^2=0.05$) on catabolic activity in rhizospheric soil. Finally, there was no significant influence of plant species ($p=0.43$, $R^2=0.02$) nor of the interaction between plant species and elevation ($p=0.87$, $R^2=0.01$; Table 2) on catabolic activity in bulk soil.

3.3 Relationships between abiotic factors and global catabolic activity and diversity (*H'*) in bulk and rhizospheric soil

Climatic data did not explain global catabolic activity in either bulk ($p=0.40$, adjusted $R^2=0.01$; Table 3) and rhizospheric soil ($p=0.11$, adjusted $R^2=0.04$; Table 3).. Nor were any significant relationships were found between either MAP, MAT or MAR and catabolic

activity or *H'* beneath *P. abies* or *J. communis* in bulk soil (Spearman correlation coefficients, Table 4) However, MAT was positively correlated with catabolic activity beneath *V. myrtillus*, whereas both MAP and MAR were negatively correlated (Table 4; Fig. S3). Bulk soil *H'* under *V. myrtillus* was negatively correlated with MAP (Table 4). In the rhizosphere of *V. myrtillus*, MAP and MAR were negatively and significantly correlated while MAT was significantly and positively correlated with catabolic activity (Table 4; Fig. S3). In the rhizosphere of *P. abies,* MAR was negatively and significantly correlated with catabolic activity (Table 4; Fig. S4). No climatic parameters were significantly correlated to global catabolic activity in the rhizospheric soil of *J. communis*.

The only significant relationships between *H'* and climatic variables were with MAP and MAT in the rhizosphere of *V. myrtillus*. MAP was positively correlated while MAT was negatively correlated with rhizospheric catabolic diversity (Table 4).

Along the elevation gradient, variations in soil physical and chemical properties were the main drivers explaining global catabolic activity in bulk soil even though the proportion of the variance was still limited ($p=0.01$, adjusted $R^2=0.09$; Table 3). Soil texture, C, P and N contents, cation exchange capacity and pH were particularly important since catabolic activity was strongly and positively related to bulk soil SOC, soil TN, P, CEC and clay content but decreased with higher pH and sand content (Fig. 3, Table S7). Regarding catabolic diversity, it was significantly and positively correlated with silt content in bulk soil beneath *V. myrtillus* and *P. abies* (Table S7) but no relationships were found beneath *J. communis* (Table S7).

According to the partition of variance analysis, global catabolic activity in rhizospheric soil was not significantly explained by soil physical and chemical properties ($p=0.71$, adjusted

R^2=0.02; Table 3). However, when examining plant species individually, rhizospheric soil global catabolic activity was, to a lesser extent than bulk soil, positively related to SOC, TN, P, CEC and clay content, but decreased at higher pH and sand content, mostly in the rhizosphere of *V. myrtillus* (Table S7). Underneath *P. abies*, pH was the only soil property to be negatively and significantly correlated to rhizospheric soil catabolic activity (Table S7). Changes in *H'* were few, but occurred mostly in the rhizosphere of *V. myrtillus*, where they were strongly related to litter depth, soil water content, topsoil aggregate stability and ammonium content (Table S7).

3.4 Relationships between plant diversity and global catabolic activity and diversity (*H'*) in bulk and rhizospheric soil

Vegetation cover varied along the elevational gradient (Table S8). Vegetation cover and trees decreased with elevation while shrub cover increased (Stokes et al., 2021; Weemstra et al., 2021). Graminoid and forb covers were greater at 1800 m – 2000 m. Simpson diversity in the quadrats containing *V. myrtillus* and *P. abies* changed significantly with elevation. At mid-elevations (1800 m – 2000 m), plant diversity peaked and slowly decreased at 2200 m – 2400 m (Table S8). However, plant diversity in the quadrats containing *J. communis* did not vary along the elevation gradient (Table S8).

Catabolic activity was negatively correlated with plant diversity in rhizospheric soil beneath *V. myrtillus* and bulk soil beneath *P. abies*, with no other significant relationships found among structuring plant species (Table S9). No significant relationships were found between *H'* and plant diversity in either bulk or rhizospheric soil (Table S9).

3.5 Relationships between plant root traits (*community*- and *species*-) and global catabolic activity and diversity (*H'*) in bulk and rhizospheric soil

Overall, global catabolic activity was best explained by RD_{com}, SOC, MAT, MWD_{top} and RNC_{com} (db-RDA, Fig 4)

In bulk soil, catabolic activity was best explained by *community* level root traits (partition of variance analysis: p=0.02, adjusted R^2=0.11; Table 3) and to a lesser extent by *species* level root traits (p=0.06, adjusted R^2=0.04; Table 3) although in both cases the proportion of variance was low.

Spearman correlation coefficients using *community* level root traits showed that *RD* and lignin content were always significantly and positively correlated with catabolic activity in bulk soil beneath all three plant species, whereas cellulose content was always negatively correlated (Fig. 5; Table S9). Hemicellulose was significantly and negatively correlated with bulk soil catabolic activity beneath *J. communis* only. SRL_{com} and RLD_{com} were both significantly and negatively correlated with bulk soil catabolic activity beneath *V. myrtillus* only (Table S9). With regard to *H'* in bulk soil, the only relationships between *community* level root traits were beneath *V. myrtillus*, whereby RNC_{com} was positively correlated and $RC{:}N_{com}$ was negatively correlated (Table S9).

At the *species* level, the only root trait that was significantly related to global catabolic activity in bulk soil was $RDMC_{sp}$ that was negatively correlated beneath *P. abies* only (Table S9). There were no other significant relationships between *H'* and root traits at the *species* level in bulk soil beneath all three plant species (Table S9).

Global catabolic activity in rhizospheric soil was not significantly explained by either *community*- (partition of variance analysis: p=0.64, adjusted R^2= −0.07; Table 3) or species- (p=0.24, adjusted R^2= −0.03; Table 3) level root traits.

In the rhizosphere, there were few significant relationships between global catabolic activity and *community* level root traits across the structuring species. Root *N* content was positively and significantly correlated with catabolic activity beneath *V. myrtillus* (Table S9) and $RC{:}N_{com}$ was negatively correlated beneath *P. abies* and *V. myrtillus* (Table S9). As in the bulk soil, root cellulose content was negatively correlated with catabolic activity, but in the rhizosphere of *V. myrtillus* only (Table S9). RLD_{com} was also negatively and significantly correlated with catabolic activity in the rhizosphere of *V. myrtillus* (Table S9). The only significant relationship between *H'* in the rhizosphere and *community* level root traits was beneath *V. myrtillus* and in contrast to that found in the bulk soil, RNC_{com} was negatively correlated with *H'* in the rhizosphere (Table S9).

With regard to *species*- level root traits, as in bulk soil, $RDMC_{sp}$ was negatively and significantly correlated with catabolic activity beneath *P. abies* only (Table S9). RTD_{sp} was negatively correlated with catabolic activity in the rhizosphere of *V. myrtillus* only (Table S9). However, no significant relationships were found between *H'* and *species* level root traits in the rhizosphere of any plant species.

4. Discussion

In agreement with our first hypothesis (H1), catabolic activity decreased at higher elevations (above 1800 m in the case of rhizospheric soil from *P. abies* and *V. myrtillus*). Along the elevation gradient, variations in soil physical and chemical properties were the main drivers

of catabolic activity, especially texture,pH, cation exchange capacity, carbon and nitrogen content Changes in catabolic diversity were few, but occurred mostly in the rhizosphere of *V. myrtillus*, where they were strongly related to litter depth and topsoil aggregate stability. Contrary to our H2, catabolic activity was negatively correlated with plant diversity in rhizospheric soil beneath *V. myrtillus* and bulk soil beneath *P. abies*, with no other significant relationships found among plant species. Also refuting our H2, we found no relationships between plant diversity and catabolic diversity in either bulk or rhizospheric soil. With regard to root traits, our H3 was not corroborated in that root traits that enhanced rhizospheric dimensions had little effect on global catabolic activity or diversity in the rhizosphere. Also contrary to our H3, we found that at the *community* level, root diameter (for *V. myrtillus* and *J. communis*) and lignin content (for *V. myrtillus*) were positively correlated with catabolic activity in bulk soil only, and had no effect on diversity. Also, root nitrogen and carbon contents had a negligible effect on catabolic activity and diversity, except for roots from *V. myrtillus*. Root cellulose content was negatively related to catabolic activity in bulk soil beneath all plant species and rhizospheric soil from *V. myrtillus* only, and had no effect on catabolic diversity. Trends in catabolic activity with root traits measured at the *species* level were only found for rhizospheric soil beneath *P. abies* and *V. myrtillus*, where more dense root tissue decreased catabolic activity, but had no effect on functional diversity.

4.1 Changes in catabolic activity and diversity along the elevation gradient and relationship with climatic factors

At elevations below 1800 mglobal catabolic activity in the rhizosphere was 2-3 times greater than in bulk soil for *P. abies* and *V. myrtillus*, converging beyond 1800 m. *Juniperus communis* was not present at lower elevations, therefore biasing results for this species. As

sampling was performed in early June, vegetation at lower elevations would have already commenced growth and photosynthesis several weeks previously (Wang et al., 2018), thus stimulating the production of exudates during root elongation. At higher elevations, the growing season was only just beginning, and plants were commencing physiological processes after winter dormancy. Therefore, root exudate production and microbial activity in the rhizosphere would be less than at lower elevations. In line with this, changes in climate also partially explained trends in catabolic activity in the rhizosphere: increased MAP and MAR decreased catabolic activity in the rhizosphere of *V. myrtillus*, but activity increased with higher MAT. Similar relationships were found in bulk soil beneath this structuring species, but were less distinct. The only relationship found between a climatic variable and catabolic activity for another structuring species, was in the rhizosphere beneath *P. abies*, where, as for *V. myrtillus*, high MAR decreased catabolic activity. Incident solar radiation can reach very high levels with increasing altitude, and causes photodegradation of plant litter (through the production of volatile compounds via photochemical mineralization) and photofacilitation (stimulation of biotic activity due to changes in litter chemistry) (Méndez et al., 2019). Therefore, at the treeline, where tree density is very sparse (stand basal area was only 18 m^2 ha^{-1} at our treeline site, Mao et al. (2015)), aboveground C input to mineral soil would be reduced via the biotic acceleration of C turnover in the litter layer (Méndez et al., 2019).

Unlike the study by Esch et al. (2017), where manipulated rainfall increased soil microbial activity, we found that high MAP decreased catabolic activity beneath *V. myrtillus* along the elevation gradient. As this species is an understory herb, with minimal buffering of precipitation by a large canopy, the effects of rainfall will be accentuated as precipitation

reaches the soil surface directly. Similar results were found by Shi et al. (2018), who performed a rainfall manipulation experiment in a moist, temperate deciduous forest. In their study, increased precipitation rapidly decreased fungal biomass but with no effect on bacterial biomass, and it was suggested that high rainfall reduced sodium concentrations in the soil with a detrimental effect on fungal activity. However, it seems more likely that high MAP will impact photosynthesis via stomatal closure (Zhang et al, 2017, Li et al, 2019), decreasing the flow of photoassimilates and the subsequent production of C-rich root exudates into the rhizosphere. Also, heterotrophic respiration can be suppressed in extremely moist conditions (Horz et al, 2004; Zhao et al 2016).

We also found a positive relationship between MAT and global catabolic activity in the rhizosphere of *V. myrtillus*, as several studies have shown that soil warming increases microbial activity (Grayston et al., 2001; Papatheodorou et al., 2004). Adamczyk et al. (2020) showed that increased microbial respiration rates at higher temperatures may be explained by additional C input to cold, nutrient-poor soils that are becoming warmer as a result of climate change. Additionally, increases in temperature stimulate microbial metabolism through changes in physiology or enzyme functioning involved in organic matter decomposition (Tang et al., 2018; Nottingham et al., 2019). Warmer temperatures also increase plant growth and biomass, stimulating photosynthesis and hence the production of C rich root exudates (Rossi et al., 2020). Enhanced root exudation with warmer temperatures has also been shown to increase microbial catabolic diversity (Papatheodorou et al., 2004). Nevertheless, Klimek et al. (2020) found a decrease in catabolic diversity at higher temperatures because less functionally diverse microbial communities were unable to effectively degrade various organic substrates. Our results show that catabolic diversity

decreased with higher MAT in rhizospheric soil, possibly indicating that colder temperatures lead to specialised microorganisms in these alpine soils (Donhauser and Frey, 2018; Collins et al., 2020).

4.2 Changes in catabolic activity and diversity along the elevation gradient and relationship with soil physical and chemical properties

Along the elevation gradient, bulk soil physical and chemical properties were major drivers of catabolic activity and to a lesser extent, catabolic diversity., SOC, TN, P, CEC, NH_4^+, sand and clay content were all strongly related to each other and generally decreased at higher altitudes (except for sand content that increased). Several authors report similar findings regardless of climate type (e.g., Xu et al.,2014; Kotas et al., 2018; Hofmann et al., 2016; Praeg et al., 2019). Therefore, we show that along an elevation gradient, nutrient content and texture had a greater influence on microbial activity in bulk soil than climate and vegetation.

The influence of soil properties on catabolic activity in the rhizosphere was less evident. Soil water content and pH had the strongest influence on catabolic activity in rhizospheric soil of *V. myrtillus*, with most activity in drier, acidic soils. Catabolic activity in the rhizosphere of *P. abies* was also greatest in the most acidic soils, suggesting that they were dominated by acid-tolerant microbial species (Shen et al., 2013). The respiratory activity of fungi increases under acidic conditions while that of bacteria decreases (Blagodatskaya and Anderson 1998). Therefore, if soil pH increases, the fungal contribution to respiration and decreasing overall catabolic activity could decrease, as observed in our results. A strong negative relationship did exist between catabolic diversity, litter depth and NH_4^+ in the rhizosphere of *V. myrtillus*. NH_4^+ is the nitrogen source on which *V. myrtillus* typically relies (Roth et al., 2021) but

Morvan et al., (2020) found a high proportion of di-nitrogen (N_2) fixers (Rhizobiales) in the rhizosphere of *Vaccinium angustifolium*. Therefore, the availability of NH_4^+ in soil beneath *Vaccinium* sp. could reduce catabolic diversity if N_2-fixing bacteria dominate the rhizosphere, reflected in the negative relationship that we found between root nitrogen content and catabolic diversity in the rhizosphere of *V. myrtillus*. Alternatively, nutrient-poor soils could moderate competition among microbial species. Eldridge et al., (2017) found that altered levels of soil carbon changed the competitive abilities of different microbial phyla, with reduced carbon promoting bacterial diversity, but decreasing fungal diversity. Carbon input to soil and litter depth are strongly associated, therefore, although litter depth increases catabolic activity in the rhizosphere of *V. myrtillus*, competition between microbial phyla may be increased, leading to less catabolic diversity with increasing litter depth.

An increase in aggregate stability in topsoil was negatively related to catabolic activity in the rhizosphere of *V. myrtillus*, but catabolic diversity increased. However, catabolic activity increased in the more stable subsoil aggregates. The decrease of catabolic activity with soil aggregate stability is likely due to physical protection of carbon in more stable aggregates (Chevalier, 2011), that may induce a reduction of catabolic activity. Many studies have highlighted the prominent role of microbial communities promoting aggregate stability (e.g. Bossuyt et al., 2001; Cosentino et al., 2006). Therefore, although Aspiras et al. (1971) postulated that the status of soil aggregation is determined by the cumulated effects of synthesis and degradation of binding materials by microbial populations, rather than the activity of specific microorganisms, our results suggest that species-specific microbial activity can have diverse effects on aggregate stability .

4.3 Relationships between plant diversity and catabolic activity and diversity

Generally,the more diverse a plant species assemblage, the more diverse the chemistry of the root exudates and litter produced (Klimek et al., 2015). Therefore, when plant diversity indices are high, more ecological niches should be available for soil microorganisms, as the spatial heterogeneity of soil resources and increased availability of labile carbon sources should promote catabolic activity (Creamer et al., 2016; Bongiorno et al., 2020). However, the relationship between species assemblage and the microbial communities of any given plant species is not necessarily direct. Individual plant species may be positively or negatively affected by increased plant diversity (Losapio et al.,2021)), also affecting the production of root exudates and microbial communities closely related to them. Here, we found that contrary to our second hypothesis, catabolic activity was negatively correlated with plant diversity in rhizospheric soil of *V. myrtillus* and bulk soil beneath *P. abies*, with no other significant relationships found among structuring species or sampling location. Unlike Klimek et al. (2015), we did not discriminate between bacterial and fungal catabolic diversity in our study. It is therefore possible that the relative contribution of fungi and bacteria to global catabolic activity varied depending on the soil under study. The presence of various exudates may also impact catabolic activity differently, for example, Yuan et al. (2017) found that the addition of three common components of root exudates (oxalic acid, glucose and glycine) altered considerably microbial communities, activities and related processes. Hence, this disparity could explain the observed lower catabolic diversity in the rhizosphere of *V. myrtillus* and in the bulk soil under *P. abies*.

4.4 Influence of plant root traits on catabolic activity and diversity

Along this complex environmental gradient, where multiple properties simultaneously change, root traits of different species varied in diverse ways, leading to species-specific

patterns in intraspecific root trait variation (described in detail by Weemstra et al., 2021) and associated microbial responses. We expected that in bulk soil, where litter is a major carbon source and microbial decomposers dominate, an increase in root nitrogen and carbon content should enhance global catabolic activity and diversity, but this hypothesis was only true for *V. myrtillus*, where catabolic diversity was positively related to root nitrogen content. Additionally, our hypothesis that plant root traits that increase rhizosphere dimensions or fungal colonisation (e.g., longer, thinner roots with large exchange surface areas), would increase global catabolic activity and diversity was not corroborated in either bulk or rhizospheric soil. However, at the *community* level, thicker roots did increase catabolic activity in bulk soil beneath *V. myrtillus* and *J. communis*. Root thickness is partially linked to root age, and so reflects chemical composition. Thin, woody roots are usually young and possess a greater quantity of cellulose (Genet et al., 2005; Hales et al., 2009), that is negatively related to lignin content (Thomas et al., 2014). Our results showed that at the community level, root diameter and cellulose content were negatively related in *P. abies* and *V. myrtillus*, and lignin content was positively correlated with root diameter beneath all three plant species (Figure S4). Therefore, relationships between catabolic activity and root diameter may not be causal, but rather due to root age and chemical composition. We found a strong positive relationship between catabolic activity and root lignin content (at the *community* level) in all bulk soils. Lignin is considered difficult to degrade (Roumet et al., 2016; Poirier et al., 2018), but within microbial fungal and bacterial phyla, diverse strategies exist to facilitate the decomposition of lignin, allowing microbial specialists to thrive in different ecological niches (Janusz et al., 2017). Therefore, lignin-degrading fungal and bacterial specialists are likely to be dominant in these root- and leaf-litter rich soils.

Trends in catabolic activity with root traits measured at the *species* level were only found for rhizospheric soil beneath *P. abies* and *V. myrtillus*, where more dense root tissue decreased catabolic activity. The changes in root chemical composition that we observed will be reflected in tissue density: cellulose increases wood density and lignin decreases density (Nuopponen et al., 2006), thus explaining why dense tissue decreases catabolic activity.

Our results demonstrate that relationships between microbial functioning and abiotic and biotic variables are complex in a highly heterogeneous environment. Nevertheless, we show that the main drivers of microbial activity and functioning are mean annual temperature and soil physicochemical properties but the presence of vegetation enhances these relationships through belowground characteristics such as root exudation, root chemical composition and changes in litter production that affect soil carbon. Therefore, in this environment, shifts in functional diversity of soil microbes under future climate scenarios could be mediated primarily by plant species, because soil properties will be slower to change. To better understand these relationships, future studies should examine temporal fungal and bacterial community taxonomic diversity and functioning, and how they relate to plant growth and root demography in a wide range of plant species.

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Tables

Table 1. Main characteristics of the elevation gradient. Mean values and standard deviation in brackets for climatic data, elevation and GPS coordinates measured in each of the five plots (further detail on the data description available in the data paper Stokes et al., 2021 and raw data available at https://data.inrae.fr/dataverse/ecopics).

Elevational band (m)	Elevation (m.asl.)	GPS coordinates	MAT (°C)	MAP (mm)	MAR (MJ/m^2)	Life zone
1400	1366 (15)	N 45°08′15″ E 5°85′79″	8.5 (0.2)	1024 (41)	4204 (0)	Montane
1600	1601 (12)	N 45°09′25″ E 5°86′91″	7.3 (0.7)	1066 (20)	4181 (0)	Subalpine
1800	1799 (20)	N 45°10′83″ E 5°89 ′ 27 ″	8.1 (0.5)	1110 (7)	4575 (102)	Subalpine
2000	1971 (11)	N 45°11′73″ E 5°90′28″	5.7 (0.7)	1155 (12)	4463 (0)	Subalpine
2200	2208 (19)	N 45°12′73 ″ E 5°92′29″	3.8 (0.1)	1205 (20)	4339 (0)	Alpine
2400	2405 (17)	N 45°12′95″ E 5°93′03″	5.7 (0.2)	1187 (40)	4339 (0)	Alpine

MAT: Mean annual temperature, MAP: Mean annual precipitation, MAR: Mean annual solar radiation

Table 2. Effect of structuring plant species and elevation on microbial global catabolic activity in bulk and rhizospheric soil assessed with PERMANOVA.

	Bulk soil						Rhizospheric soil					
Factors	**Df**	**Sums of Sqs**	**Means sqs**	**F**	**R^2**	**P(>F)**	**Df**	**Sums of Sqs**	**Means sqs**	**F**	**R^2**	**P(>F)**
Plant species	2	0.05	0.02	0.84	0.02	0.43	2	0.19	0.09	3.20	0.05	0.03
Elevation	1	0.210	0.21	7.35	0.1	0.01	1	1.29	1.29	44.01	0.36	0.001
Plant species*Elevation	2	0.01	0.006	0.02	0.005	0.87	2	0.28	0.14	4.72	0.08	0.006
Residuals	64	1.83	0.03		0.87		64	1.87	0.03		0.52	
Total	69	2.11			1.0		69	3.63			1.0	

Table 3. Partition of variance in constrained ordination distance-based redundancy analysis (db-RDA) for four environmental variables (soil physical and chemical properties, *community*- and *species*- level root traits and climatic data) influencing microbial catabolic activity and diversity for bulk and rhizospheric soil samples.

	Bulk soil				Rhizospheric soil			
	Df	**R^2**	**R^2 adjusted**	**P**	**Df**	**R^2**	**R^2 adjusted**	**P**
Climate	3	0.05	0.01	0.40	3	0.08	0.04	0.11
Soil properties	15	0.29	0.09	**0.01**	15	0.23	0.02	0.71
***Community* level root traits**	12	0.26	0.11	**0.02**	12	0.11	-0.07	0.64
***Species* level root traits**	3	0.08	0.04	*0.06*	3	0.02	-0.03	0.24

Values in bold are significant at p<0.05; values in italics are significant at p<0.1

Table 4. Spearman correlations between global microbial catabolic activity and diversity (H') and climatic data of the three structuring plant species along the elevational gradient (significance levels p < 0.0001 ****; p < 0.001 ***, p < 0.01 **, p < 0.05 *)**.**

	Bulk soil						Rhizospheric soil					
	Vaccinium myrtillus		***Picea abies***		***Juniperus communis***		***Vaccinium myrtillus***		***Picea abies***		***Juniperus communis***	
Climate	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'
MAT	0.48**	0.25	-0.33	0.3	-0.16	-0.33	0.85****	-0.44*	0.41	0.21	0.04	-0.21
MAP	-0.44*	-0.37*	0.33	-0.3	0.16	0.33	-0.79****	0.38*	-0.41	-0.21	-0.04	0.21
MAR	-0.36*	0.07	-0.4	0.01	0.18	0.37	-0.60***	0.35	-0.59**	-0.37	0.01	0.2

MAT is mean annual temperature; MAP is mean annual precipitation; MAR is mean annual solar radiation.

1.1 Supplementary materials (tables)

Table S1. Ecology and habitat type for each of the three structuring plant species used in this study

Species	Family	Life form	Light requirements	Soil preference	Mycorrhizal association	Root type	References
Picea abies L.	Pinaeceae	Coniferous tree	Shade-tolerant, it can survive under a closed canopy	Most common and widespread on acidic soils, preferring nutritious deep soils with enough fresh moisture	Ectomycorrhizal (ECM)	Shallow root system with several lateral roots and no taproot	Caudullo et al., (2016) Plants For A Future database (https://pfaf.org)
Juniperus communis L.	Cupressaceae	Prostrate evergreen shrub	Intolerant of heavy shade	Found on free-draining and nutrient-deficient soils Tolerates soil pH range of 4-8	Arbuscular mycorrhiza (AMF)	Shallow, extensive root system	Thomas et al., (2007) Enescu et al., (2016) Brundrett and Tedersoo (2020) Plants For A Future database (https://pfaf.org)
Vaccinium myrtillus L.	Ericaceae	Low growing deciduous shrub	Moderate shade tolerance	Commonly found on sandy and loamy soils. Prefers well-drained soil. Can grow in very acid soils.	Ericoid mycorrhiza (ErM)	Shallow root system. Numerous fine adventitious roots	Heath et al., (1938) Ritchie (1956) Plants For A Future database (https://pfaf.org)

Table S2. Definitions, equations used and functional significance of *community*- and *species*- level root traits.

Root trait	Equation	Functional Significance	References
Specific root length (*SRL*)	$SRL = \frac{L}{RDM}$	Indicator of resource investment	Freschet et al., (2021)
Root tissue density (RTD)	$RTD = \frac{RDM}{V}$	Indicator of plant species' resource use strategy	Birouste et al., (2014)
Root dry mass content (*RDMC*)	$RDMC = \frac{RDM}{RFM}$	Indicator of root tissue density	Birouste et al., (2014)
Root mass density (*RMD*)	$RMD = \frac{RDM}{Soil\ volume}$	Estimation of soil volume explored by a root system	Barber, (1971)
Root length density (*RLD*)	$RLD = RMD\ x\ SRL$	Estimation of soil volume explored by a root system	Barber, (1971)

L is root length (mm); V is root volume (cm^3); RDM is root dry mass (g); RFM is root fresh mass (g); SRL is specific root length (m/g^{-1}), RTD is root tissue density (g/cm^{-3}); RDMC is root dry mass content (mg/g^{-1}); RMD is root mass density (g/cm^{-3}); RLD is root length density (m/cm^{-3}); Soil volume (cm^{-3}) where roots were sorted.

Table S3. Mean values of soil physical and chemical properties along the elevation gradient beneath *Vaccinium myrtillus*, *Juniperus communis* and *Picea abies*. Standard deviation is shown in brackets. Different lowercase letters indicate significant differences (Tukey´s HSD test; $p<0.05$) between elevational bands following a one-way ANOVA.

Plant species	***Vaccinium myrtillus***							***Juniperus communis***					***Picea abies***			
Elevation (m)	1400	1600	1800	2000	2200	2400		1800	2000	2200	2400		1400	1600	1800	2000
SOC (g/kg)	127.5 (66.5) b	313.7 (126.1) a	140.9 (55.36) b	107.3 (39.1) b	183.8 (65.2) ab	93.1 (26.5) b		178.1 (111.1) a	86.4 (31.9) a	209 (86.9) a	104.3 (39.2) a		169.0 (71.9) b	336.4 (136.9) a	136.6 (24.2) b	145.4 (62.0) b
TN (g/kg)	6.3 (2.0) b	13.8 (5.6) a	7.4 (1.3) b	7.2 (2.5) b	9.8 (3.0) ab	6.1 (1.2) b		9.1 (4.5) a	6.2 (2.1) a	11.9 (5.9) a	6.6 (2.2) a		7.6 (1.7) b	13.3 (4.2) a	7.7 (1.0) b	8.8 (1.1) b
P (g/kg)	0.021 (0.011) b	0.061 (0.032) a	0.028 (0.012) ab	0.031 (0.018) ab	0.028 (0.011) ab	0.016 (0.005) b		0.028 (0.012) a	0.023 (0.017) a	0.027 (0.011) a	0.017 (0.006) a		0.024 (0.008) b	0.079 (0.05) a	0.020 (0.004) b	0.039 (0.014) ab
NH_4 (mg/kg)	36.05 (34.27) a	45.84 (24.02) a	33.98 (11.21) a	29.34 (11.82) a	13.30 (4.36) a	10.62 (7.40) a		37.83 (15.57) a	23.80 (12.70) a	25.93 (25.42) a	10.80 (2.54) a		31.70 (8.56) b	77.34 (52.54) a	48.59 (10.56) b	27.15 (18.29) b
NO_3 (mg/kg)	0.58 (0.70) a	0.31 (0.23) a	0.34 (0.48) a	1.04 (1.47) a	0.15 (0.004) a	0.15 (0.00) a		1.04 (1.43) a	0.27 (0.14) a	0.80 (1.43) a	0.28 (0.28) a		0.36 (0.26) a	0.28 (0.13) a	1.43 (1.37) a	1.18 (2.23) a
C/N	19.2 (5.0) ab	22.5 (2.4) a	18.4 (4.2) ab	14.7 (0.7) b	18.4 (1.2) ab	15.04 (1.8) b		18.7 (3.3) b	13.7 (0.8) a	18.3 (2.4) b	15.6 (1.6) ab		21.2 (4.7) a	24.4 (4.1) a	17.8 (3.5) a	16.4 (6.4) a
CEC ($cmol^+/kg$)	12.95 (6.67) b	31.80 (15.62) a	16.96 (6.27) ab	14.83 (3.54) b	13.92 (4.08) b	8.83 (3.13) b		21.78 (13.32) a	14.47 (3.54) a	16.25 (6.97) a	9.08 (3.0) a		17.84 (5.72) a	36.62 (17.59) a	18.74 (4.97) a	19.86 (8.19) a
pH	4.50 (0.24) ac	4.37 (0.43) a	4.9 (0.51)abc	5.35 (0.39) b	4.58 (0.10) ac	5.17 (0.19) bc		4.98 (0.60) ab	5.58 (0.42) a	4.75 (0.39) b	5.13 (0.35) ab		4.51 (0.30) a	4.63 (0.28) a	5.06 (0.51) a	5.08 (0.29) a

Clay (g/kg)	295 (48.0) ab	431.8 (160.7) a	342.4 (25.6) ab	346.2 (54.0) ab	373.4 (58.2) ab	238.4 (54.1) b		359 (63.4) a	319.8 (75.0) a	352.2 (104.4) a	254.2 (89.0) a		323.6 (31.1) b	488 (151.9) a	368.6 (21.7) ab	366.2 (56.5) ab
Silt (g/kg)	215.9 (15.2) a	211.4 (71.3) ab	225.9 (18.1) a	200.1 (30.3) ab	195.5 (28.4) ab	161.2 (14.2) b		232 (29.2) b	198.9 (41.0) ab	207.1 (60.6) ab	159.7 (28.4) a		224.6 (23.9) a	192.1 (43.3) a	218.3 (16.2) a	191.1 (37.9) a
Sand (g/kg)	136.6 (29.6) ab	72.7 (89.4) a	102.9 (25.4) a	126.8 (60.8) ab	117.8 (44.2) a	219.6 (84.0) b		88.5 (33.5) b	141.2 (75.6) ab	116.8 (45.3) ab	213.2 (74.2) a		113.6 (24.0) a	63.9 (80.4) a	97.4 (15.9) a	125.8 (69.3) a
Litter Depth (cm)	8.30 (3.46) a	3.10 (1.95) b	2.80 (0.27) b	1.40 (1.04) b	3.40 (0.55) b	1.20 (0.84) b		4.0 (1.46) b	1.30 (0.76) a	3.80 (1.68) b	1.10 (0.22) a		8.20 (3.49) b	5.80 (2.80) ab	5.30 (1.86) ab	1.80 (0.91) a
Kfs (cm/h)	9.57 (5.69) a	9.97 (2.88) a	8.02 (6.73) a	6.11 (6.94) a	4.22 (3.18) a	4.18 (4.52) a		6.38 (5.17)a	11.43 (10.62) a	7.02 (7.89) a	6.21 (5.56) a		10.09 (4.76) a	19.04 (11.32) a	8.85 (8.65) a	12.73 (9.95) a
MWD_{sub} (mm)	3.11 (0.08) a	2.95 (0.32) a	3.14 (0.14) a	2.55 (0.81) a	2.92 (0.20) a	2.33 (0.63) a		3.06 (0.31) a	2.49 (0.87) a	2.91 (0.35) a	2.69 (0.39) a		3.16 (0.12) a	2.94 (0.27) a	3.12 (0.22) a	2.95 (0.21) a
MWD_{top} (mm)	0 (0) b	2.98 (0.44) a	3.18 (0.09) a	2.87 (0.41) a	3.05 (0.24) a	2.53 (0.69) a		3.01 (0.10) a	2.89 (0.33) a	2.50 (1.41) a	2.68 (0.29) a		0 (0) b	2.92 (0.23) a	2.99 (0.24) a	2.90 (0.43) a
Water content (%)	10.16 (0.18) a	10.18 (0.15) a	43.59 (19.46) b	40.43 (12.02) b	56.37 (12.52) b	42.38 (5.12) b		44.68 (20.66) a	38.34 (6.69) a	58.66 (11.37) a	39.69 (9.36) a		9.98 (0.19) a	10.17 (0.38) a	45.31 (20.87) b	39.13 (23.27) b

SOC is soil organic carbon; TN is total nitrogen; C/N is soil carbon-nitrogen ratio; CEC is cation exchange capacity; Kfs is soil hydraulic conductivity; MWD_{sub} is mean weight diameter of subsoil aggregates; MWD_{top} is mean weight diameter of topsoil aggregates

Table S4. Effect of structuring plant species and elevation on soil physical and chemical properties along the elevation gradient tested with unbalanced two-way ANOVA (Type-III sums of squares). Bold values show a significant effect ($p<0.05$).

	Two-way ANOVA		
Factor	Elevation	Plant Species	Elevation * Plant Species
SOC (g/kg)	0.620	0.787	0.825
TN (g/kg)	0.796	0.986	0.972
P (g/kg)	0.557	0.965	0.931
NH_4 (mg/kg)	0.090	0.918	0.846
NO_3 (mg/kg)	0.379	0.165	0.118
C/N	0.513	0.227	0.323
CEC ($cmol^+$/kg)	0.078	0.745	0.691
pH	0.668	0.132	0.150
Clay (g/kg)	0.137	0.646	0.551
Silt (g/kg)	**<0.001**	0.139	0.190
Sand (g/kg)	**0.005**	0.251	0.245
Litter Depth (cm)	0.157	0.060	0.077
Water Content (%)	0.863	**0.021**	**0.025**
Kfs (cm/h)	0.734	0.895	0.748
MWD_{sub} (mm)	0.437	0.701	0.622
MWD_{top} (mm)	0.443	**<0.001**	**<0.001**

SOC is soil organic carbon; TN is total nitrogen; C/N is soil carbon-nitrogen ratio; CEC is cation exchange capacity; Kfs is soil hydraulic conductivity; MWD_{sub} is mean weight diameter of subsoil aggregates; MWD_{top} is mean weight diameter of topsoil aggregates

Table S5. Mean comparison of bulk and rhizospheric soil basal respiration and global catabolic activity for the three structuring species (*V. myrtillus*, *P. abies* and *J. communis*) along the elevational gradient using a two tailed t-test ($p < 0.05$).

		Bulk soil					Rhizospheric soil				
		Basal Respiration		Global catabolic activity			Basal Respiration		Global catabolic activity		
Elevational band	Structuring Species	Mean	SD	Mean	SD	p-value	Mean	SD	Mean	SD	p-value
1400	*Vaccinum myrtillus*	3.14	0.44	3.31	0.62	0.21	9.35	3.08	10.77	3.38	0.51
1600	*Vaccinum myrtillus*	6.45	2.52	6.08	2.82	0.25	8.47	1.99	8.96	1.84	0.70
1800	*Vaccinum myrtillus*	3.63	0.40	3.62	0.40	0.95	4.74	1.55	4.96	1.58	0.15
2000	*Vaccinum myrtillus*	2.44	0.31	2.42	0.33	0.66	2.89	0.92	2.97	1.02	0.26
2200	*Vaccinum myrtillus*	3.23	0.81	3.20	0.72	0.70	3.76	0.85	3.93	0.71	0.74
2400	*Vaccinum myrtillus*	2.68	0.93	2.95	0.87	0.21	3.24	1.03	3.15	0.86	0.56
1400	*Picea abies*	2.96	0.69	3.06	0.74	0.14	6.87	2.20	7.56	2.10	0.17
1600	*Picea abies*	5.49	1.25	5.83	1.49	0.14	6.22	1.69	7.21	2.67	0.14
1800	*Picea abies*	3.60	0.39	3.67	0.32	0.47	4.98	2.00	5.16	2.38	0.58
2000	*Picea abies*	2.78	0.47	2.86	0.68	0.48	2.79	0.33	2.86	0.66	0.68
1800	*Juniperus communis*	4.88	2.21	5.17	2.75	0.32	3.57	1.30	3.83	1.53	0.11
2000	*Juniperus communis*	2.48	0.44	2.46	0.45	0.43	4.05	1.14	4.40	1.86	0.63
2200	*Juniperus communis*	3.64	1.57	3.62	1.49	0.77	4.74	1.09	5.12	2.02	0.59
2400	*Juniperus communis*	2.53	0.96	2.87	1.19	0.71	3.31	0.58	3.27	0.68	0.81

Table S6. Tukey's HSD pairwise comparisons for global catabolic activity in bulk and rhizospheric soils along the elevation gradient. Bold values show significant different groups at $p < 0.05$.

		Bulk soil			Rhizospheric soil		
Elevation		***V. myrtillus***	***P. abies***	***J. communis***	***V. myrtillus***	***P. abies***	***J. communis***
		p-value	p-value	p-value	p-value	p-value	p-value
1400	1600	**0.01**	**0.0008**	–	0.62	0.99	–
	1800	0.99	0.69	–	**0.0004**	0.30	–
	2000	0.89	0.99	–	**<0.0001**	**0.01**	–
	2200	0.99	–	–	**0.00004**	–	–
	2400	0.99	–	–	**<0.0001**	–	–
1600	1800	**0.04**	**0.008**	–	**0.02**	0.47	–
	2000	**0.001**	**0.0004**	–	**<0.0001**	**0.02**	–
	2200	**0.01**	–	–	**0.002**	–	–
	2400	**0.004**	–	–	**0.0005**	–	–
1800	2000	0.66	0.49	0.09	0.51	0.30	0.93
	2200	0.99	–	0.50	0.93	–	0.51
	2400	0.93	–	0.15	0.63	–	0.95
2000	2200	0.92	–	0.68	0.96	–	0.86
	2400	0.99	–	0.99	0.99	–	0.66
2200	2400	0.99	–	0.85	0.99	–	0.25

Table S7. Spearman correlations between bulk and rhizospheric global microbial catabolic activity and diversity (H') and soil physical and chemical properties of the three structuring plant species along the elevation gradient (significance levels $p < 0.0001$ ****; $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *).

Soil properties	Bulk soil						Rhizospheric soil					
	Vaccinium myrtillus		***Picea abies***		***Juniperus communis***		***Vaccinium myrtillus***		***Picea abies***		***Juniperus communis***	
	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'
SOC	0.64***	0.25	0.65**	-0.15	0.68***	-0.13	0.38*	-0.04	0.3	-0.07	0.33	0.22
TN	0.61***	0.21	0.60**	0.07	0.59**	-0.18	0.26	0.03	0.12	-0.01	0.26	0.22
C/N	0.44*	0.3	0.54*	-0.44	0.54*	0.03	0.50**	-0.21	0.45*	-0.1	0.38	0.07
pH	-0.38*	-0.12	-0.27	0.07	-0.47*	0.24	-0.65****	0.14	-0.54*	-0.17	-0.34	-0.16
P	0.44*	0.23	0.52*	-0.08	0.52*	-0.09	0.29	0.04	0.07	-0.06	0.37	0.19
CEC	0.77****	0.29	0.48*	-0.1	0.66**	0.11	0.36*	-0.1	0.2	-0.15	0.28	0.24
Water content	-0.31	-0.19	-0.22	-0.27	0.48*	-0.09	-0.62***	0.37*	-0.26	-0.31	0.39	0.09
NH_4	0.19	0.34	0.69***	-0.09	0.54*	0.05	0.24	-0.53**	0.16	-0.11	0.11	0.25
NO_3	-0.10	-0.01	-0.28	-0.01	0.2	0.1	0.05	0.06	-0.33	-0.36	0	0.26
Clay	0.54**	0.21	0.50*	0.02	0.46*	-0.15	0.22	0.05	-0.03	-0.17	0.22	0.42
Silt	0.17	0.39*	-0.39	0.66**	0.36	0	0.36*	-0.03	0.31	0.02	-0.05	0.37
Sand	-0.48**	-0.35	-0.28	-0.34	-0.45*	0.09	-0.34	-0.02	-0.12	0.15	-0.1	-0.43
Litter Depth	0.06	0.17	0.13	0.12	0.24	0.19	0.50**	-0.68****	0.33	-0.17	0.22	0.26
Kfs	0.25	0.31	0.37	0.04	0.17	0.12	0.40*	-0.3	0.09	0.15	0.12	-0.24
MWD_{sub}	0.18	0.28	-0.12	0.11	0.29	0.16	0.47**	-0.14	-0.33	-0.02	0.06	0.03
MWD_{top}	0.10	0	0.29	-0.2	-0.22	0.17	-0.53**	0.59***	-0.42	-0.14	0.17	-0.16

SOC is soil organic carbon; TN is total nitrogen; C/N is soil carbon-nitrogen ratio; CEC is cation exchange capacity; Kfs is soil hydraulic conductivity; MWD_{sub} is mean weight diameter of subsoil aggregates; MWD_{top} is mean weight diameter of topsoil aggregates.

Table S8. Mean values of Simpson vegetation diversity index in quadrats containing the structuring plant species, *V. myrtillus*, *P. abies* and *J. communis,* along the elevational gradient**.** Standard deviation is shown in brackets. Different lowercase letters indicate significant differences (Tukey´s HSD test; $p<0.05$) between elevational bands. (Data from Stokes et al., 2021).

Elevation	**Structuring Plant Species**	**Simpson diversity index**
1400	*Vaccinium myrtillus*	0.21 (0.20) b
1600	*Vaccinium myrtillus*	0.37 (0.16) ab
1800	*Vaccinium myrtillus*	0.70 (0.14) c
2000	*Vaccinium myrtillus*	0.66 (0.11) c
2200	*Vaccinium myrtillus*	0.61 (0.14) ac
2400	*Vaccinium myrtillus*	0.67 (0.12) c
1400	*Picea abies*	0.44 (0.27) ab
1600	*Picea abies*	0.24 (0.30) a
1800	*Picea abies*	0.70 (0.08) b
2000	*Picea abies*	0.54 (0.29) ab
1800	*Juniperus communis*	0.60 (0.15) a
2000	*Juniperus communis*	0.50 (0.19) a
2200	*Juniperus communis*	0.47 (0.19) a
2400	*Juniperus communis*	0.32 (0.17) a

Table S9. Spearman correlations between bulk and rhizospheric microbial global catabolic activity and diversity (H'), absorptive *community*- and *species*- level root traits and plant diversity for the three structuring plant species along the elevational gradient (significance levels $p < 0.0001$ ****; $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *).

	Bulk soil						Rhizospheric soil					
***Community*-level root traits**	***Vaccinium myrtillus***		***Picea abies***		***Juniperus communis***		***Vaccinium myrtillus***		***Picea abies***		***Juniperus communis***	
	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'	Catabolic Activity	H'
RD_{com}	0.48**	0.31	0.44	0.18	0.61**	0.19	0.14	0.08	-0.22	-0.12	0.19	0.01
$RDMC_{com}$	-0.13	-0.17	0.03	-0.15	-0.39	0.21	-0.31	0.22	-0.18	0.35	0.19	-0.36
SRL_{com}	-0.44*	-0.34	-0.35	-0.22	-0.36	-0.43	-0.11	-0.11	0.33	0	-0.2	0.24
RTD_{com}	-0.18	-0.08	-0.16	0.03	-0.15	0.12	-0.1	0.26	-0.04	0.34	0.29	-0.22
RNC_{com}	0.08	0.38*	0.06	0.07	0.36	-0.41	0.40*	-0.36*	0.43	-0.33	-0.22	0.28
RCC_{com}	0.12	0.13	0.21	-0.19	0.31	0.22	0.05	0.1	-0.08	-0.08	0.28	-0.22
$RC:N_{com}$	-0.11	-0.38*	-0.1	-0.17	-0.4	0.35	-0.40*	0.35	-0.46*	0.29	0.26	-0.42
RMD_{com}	-0.15	0.17	-0.03	0.4	0	0.19	-0.3	0.12	-0.32	-0.2	0.23	-0.31
RLD_{com}	-0.40*	-0.1	-0.36	0.13	-0.22	0.04	-0.37*	-0.07	-0.07	-0.2	0.08	-0.17
$Hemicellulose_{com}$	-0.3	-0.25	-0.25	-0.06	-0.48*	-0.3	0.16	-0.1	0.14	-0.23	-0.42	0.22
$Cellulose_{com}$	-0.54**	0.02	-0.55*	0.35	-0.57**	-0.07	-0.59***	0.13	-0.3	0.15	0.42	-0.1
$Lignin_{com}$	0.44*	0.18	0.50*	-0.19	0.67**	0.24	0.28	0.02	0.19	0.27	0.22	-0.24
***Species*- level root traits**												
SRL_{sp}	0.27	-0.02	0.29	0.13	-0.25	0.19	0.3	-0.09	0.09	0.21	-0.03	-0.29
$RDMC_{sp}$	-0.17	-0.28	-0.65**	0.25	-0.21	-0.38	-0.1	-0.24	-0.45*	-0.05	-0.02	0.17
RTD_{sp}	-0.24	-0.33	-0.3	0.27	-0.31	-0.44	-0.44*	0.16	-0.19	0.02	-0.35	-0.03
Plant diversity												
Simpson index	-0.19	-0.21	-0.53*	0.14	0.14	0.22	-0.82****	0.27	-0.26	-0.12	0.11	0.17

RD is root diameter; RDMC is root dry mass content; SRL is specific root length; RTD is root tissue density; RMD is root mass density; RLD is root length density; RNC is root nitrogen content; RCC is root carbon content, RC:N is root carbon to nitrogen ratio; subscript$_{com}$ denotes *community* level root traits and subscript$_{sp}$ denote *species* level root traits.

2. Figures

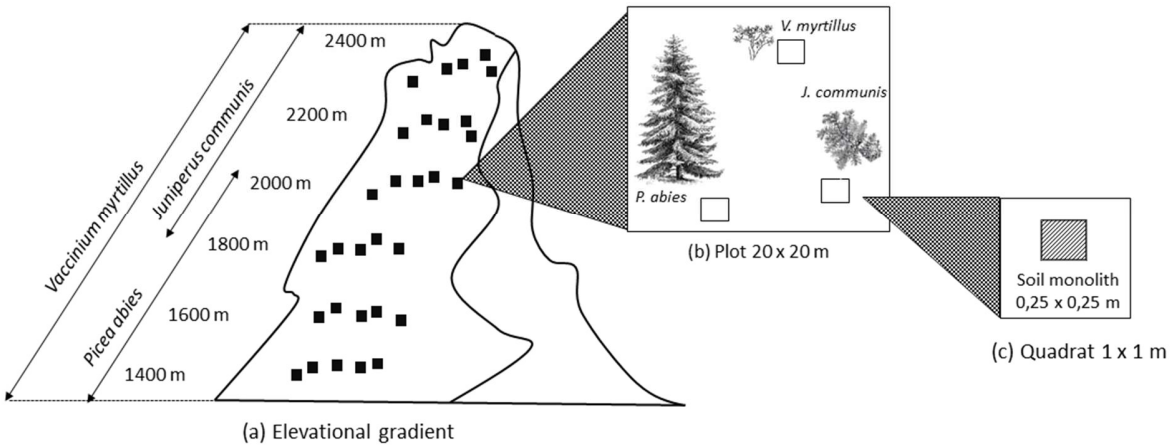


Figure 1. Sampling design along the elevational gradient. (a) Six elevational bands, situated at 200 m from each other, were located along the gradient, ranging from 1400 m to 2400 m. Five plots (20 m x 20 m) containing two or three selected structuring plant species were located at each altitude. (b) At the canopy limit of the structuring plant species, a 1 m x 1 m botanical survey was performed. (c) In the center of this quadrat, a soil monolith (0.25 m x 0.25 m x 0.15 m) was extracted.

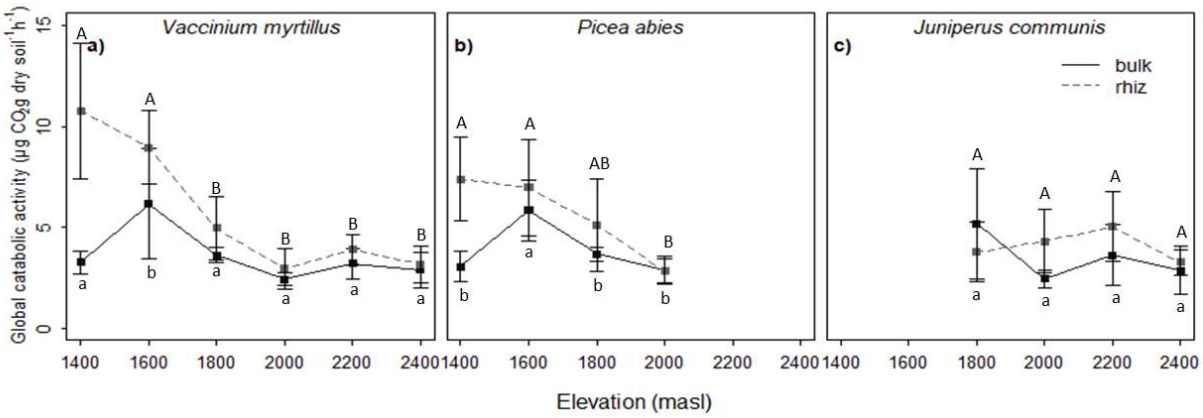


Figure 2. Global catabolic activity of bulk soil (solid line) and rhizospheric soil (dotted line) beneath a) *Vaccinium myrtillus*, b) *Picea abies* and c) *Juniperus communis*. Data are means ± standard deviation. Significant differences ($p < 0.05$) assessed by Tukey's HSD test are shown in lowercase (bulk soil) and uppercase (rhizospheric soil) letters.

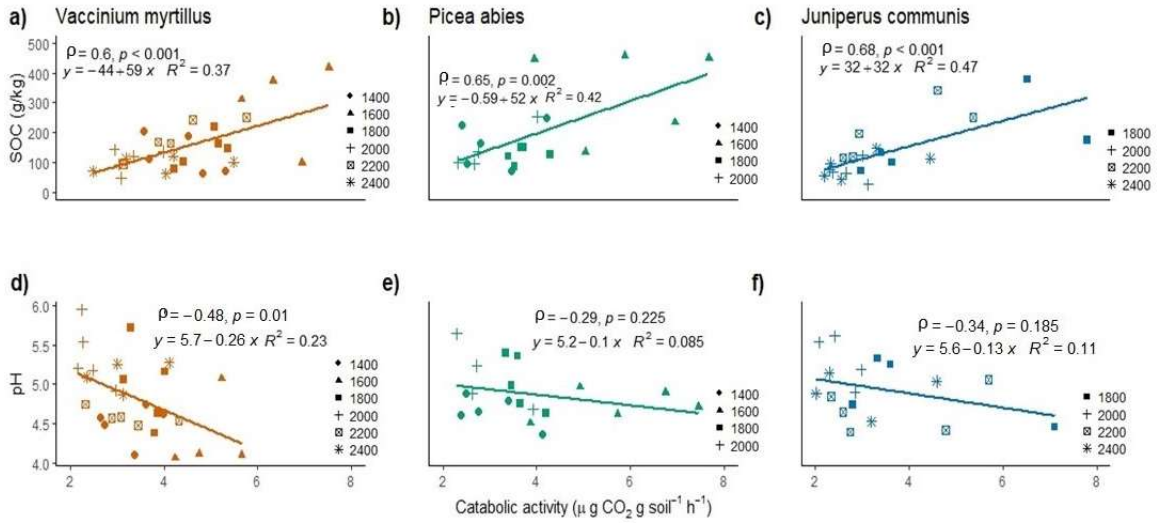


Figure 3. Scatter plots for Spearman correlations between bulk soil global catabolic activity with soil organic carbon (SOC) and pH for *V. myrtillus* (orange), *P. abies* (green) and *J.communis* (blue) along the elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are shown. Lines are linear regressions through data.

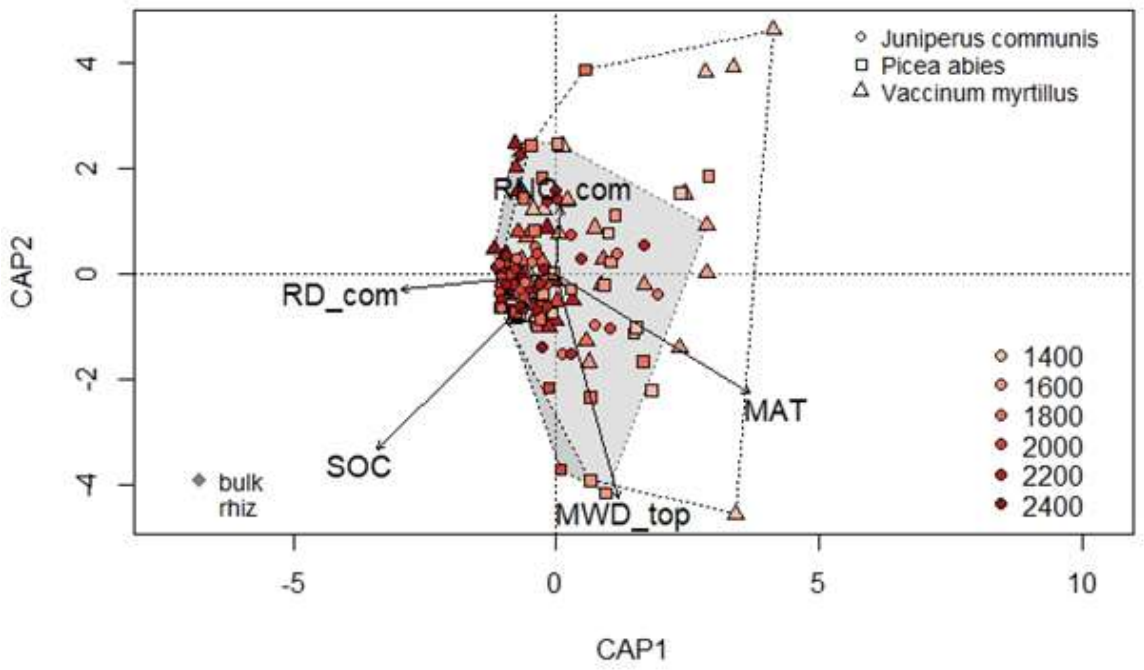


Figure 4. Distance-based redundancy analysis ordination (db-RDA) of global microbial catabolic activity for six altitudinal bands from light red (lower elevations) to dark red (higher elevations) for bulk (convex hull polygon grey) and rhizospheric (convex hull polygon white) soils for *Vaccinium myrtillus* (triangles), *Picea abies* (squares) and *Juniperus communis* (diamonds). Vectors of environmental factors (soil physical and chemical properties, species- and community- level root traits and climatic data) selected by stepwise regression are shown in the constrained ordination. MAT is mean annual temperature; MWD_{top} is mean weight diameter of topsoil aggregates; SOC is soil organic carbon; RD_{com} is root diameter and RNC is root nitrogen content.

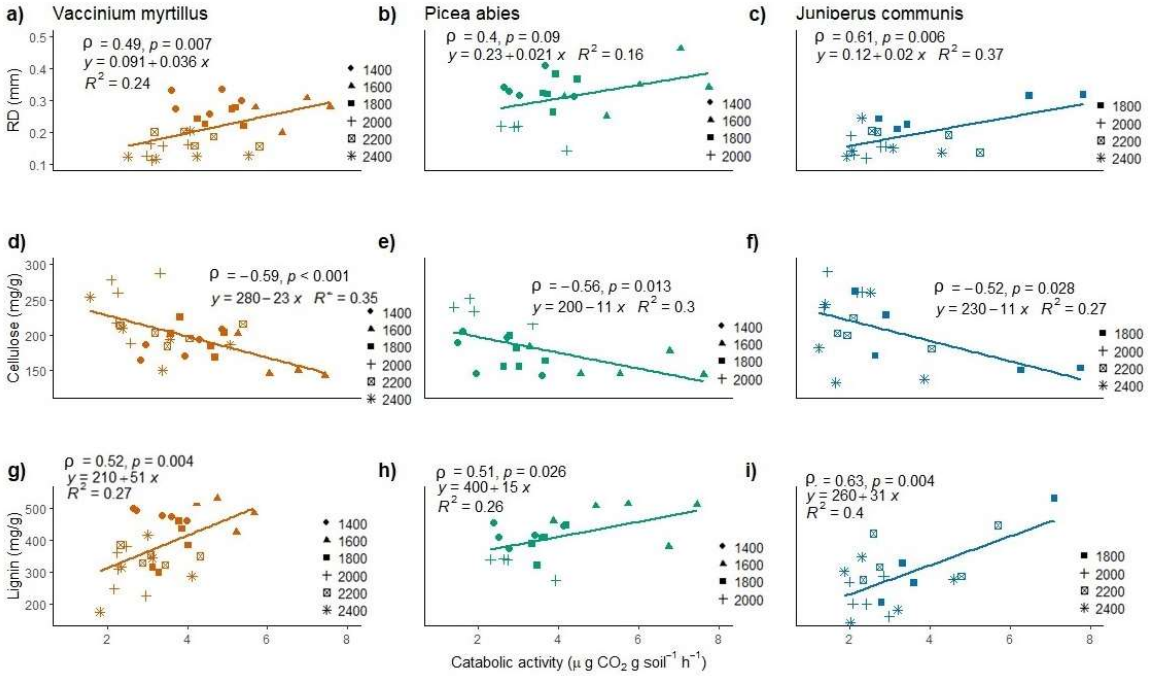


Figure 5. Scatter plots for Spearman correlations between bulk soil global catabolic activity with root diameter (*RD*), cellulose and lignin root content at the *community*-level for *V. myrtillus* (orange), *P. abies* (green) and *J. communis* (blue) along the elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are shown. Lines are linear regressions through data.

2.2 Supplementary materials (figures)

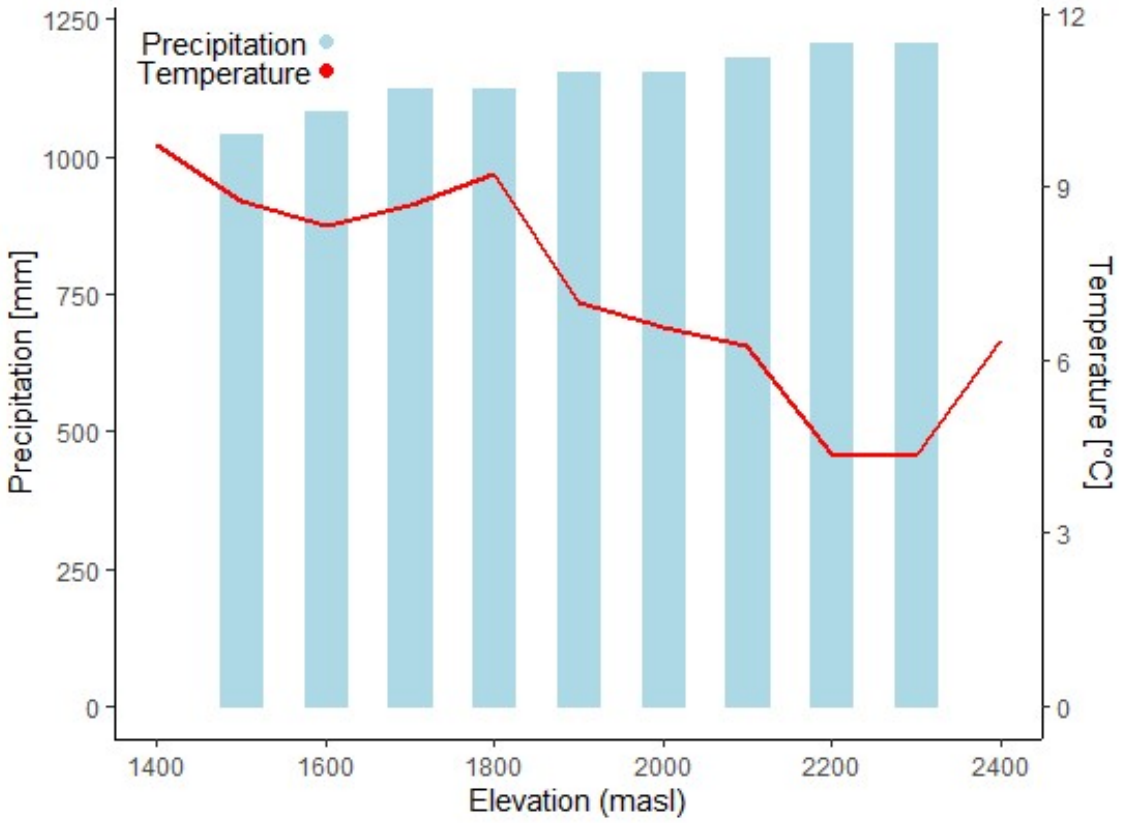


Figure S1. Mean annual temperature (MAT) and mean annual precipitation (MAP) over the 2004-2014 period along the elevational gradient. Data were calculated using the AURELHY model (Piedallu *et al*., 2013; Piedallu *et al*., 2016, Stokes et al., 2021).

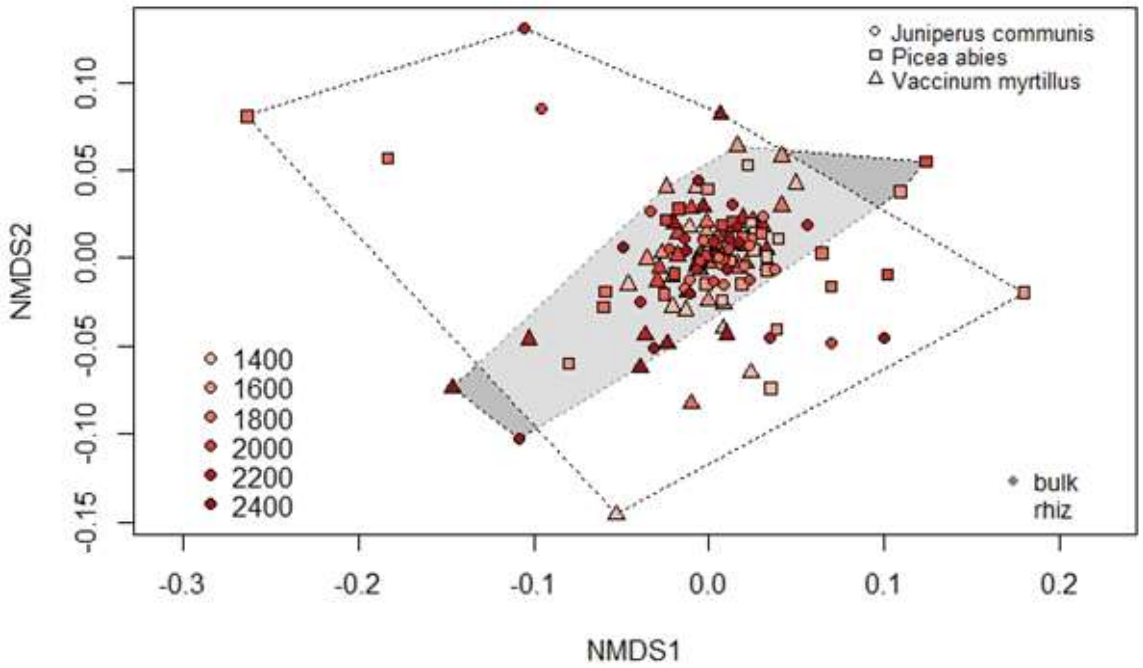


Figure S2. Non-metric multidimensional scaling (NMDS) of global microbial catabolic activity for six altitudinal bands from light red (lower elevations) to dark red (higher elevations) for bulk (convex hull polygon grey) and rhizospheric (convex hull polygon white) soils for *Vaccinium myrtillus* (triangles), *Picea abies* (squares) and *Juniperus communis* (diamonds).

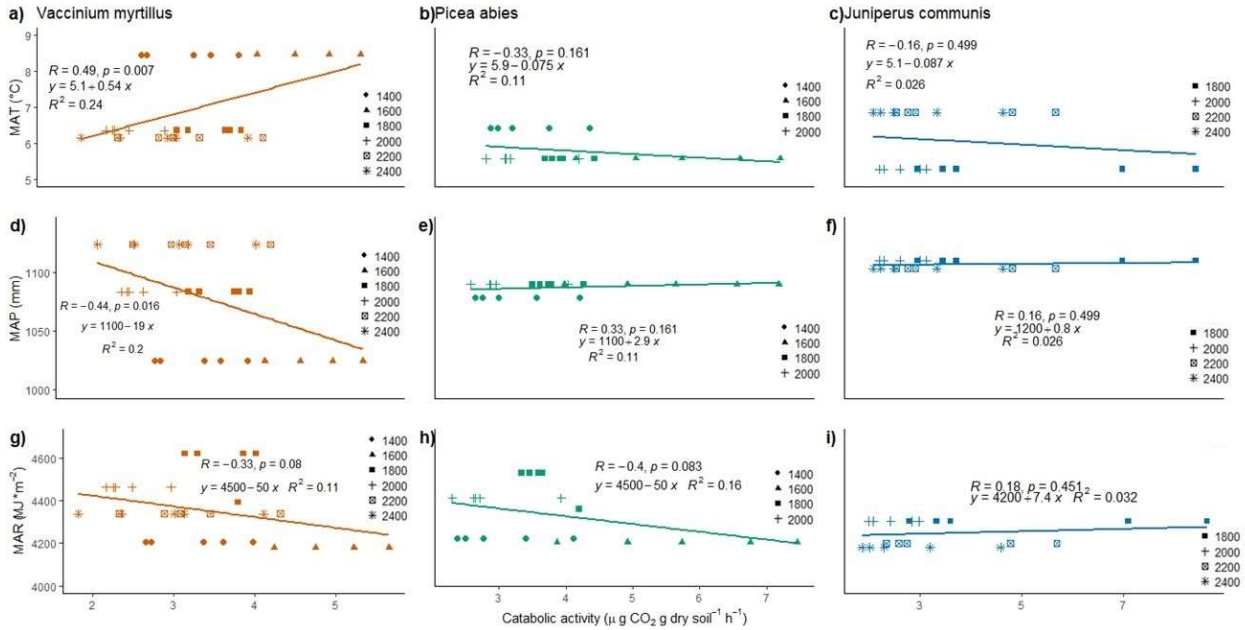


Figure S3. Scatter plots for Spearman correlations between bulk soil global catabolic activity with mean annual temperature (MAT), mean annual precipitation (MAP) and mean annual radiation (MAR) for *V. myrtillus* (orange), *P. abies* (green) and *J. communis* (blue) along the elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are shown. Lines are linear regressions through data.

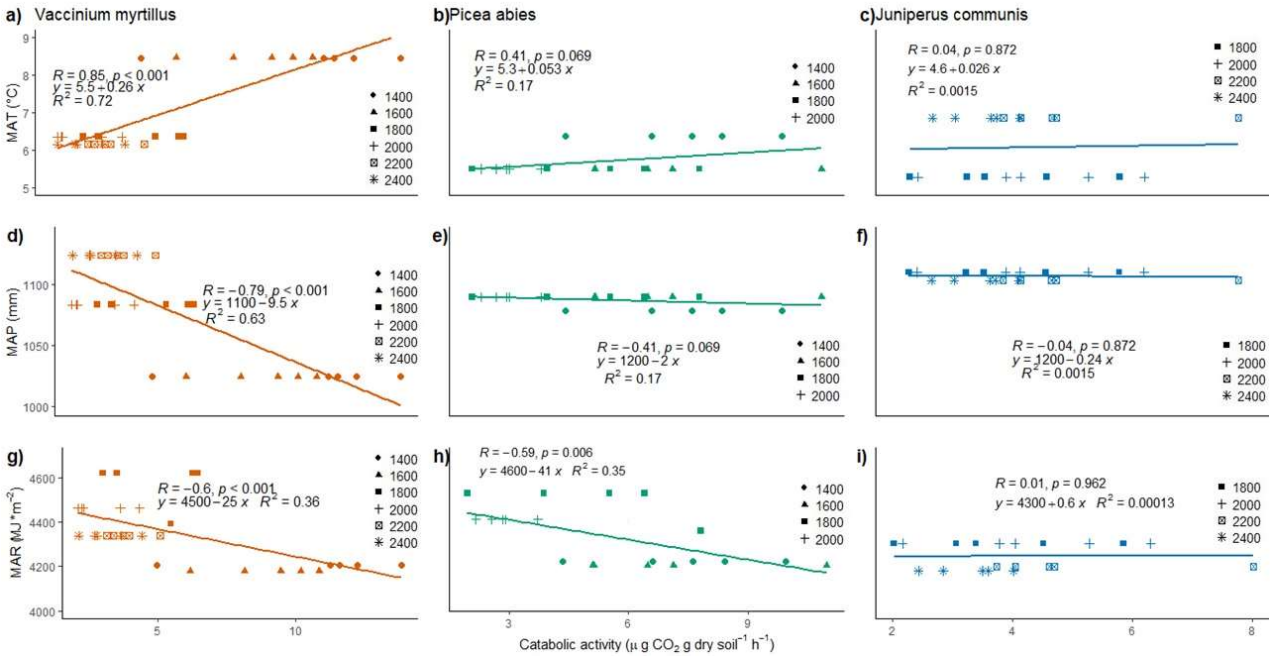
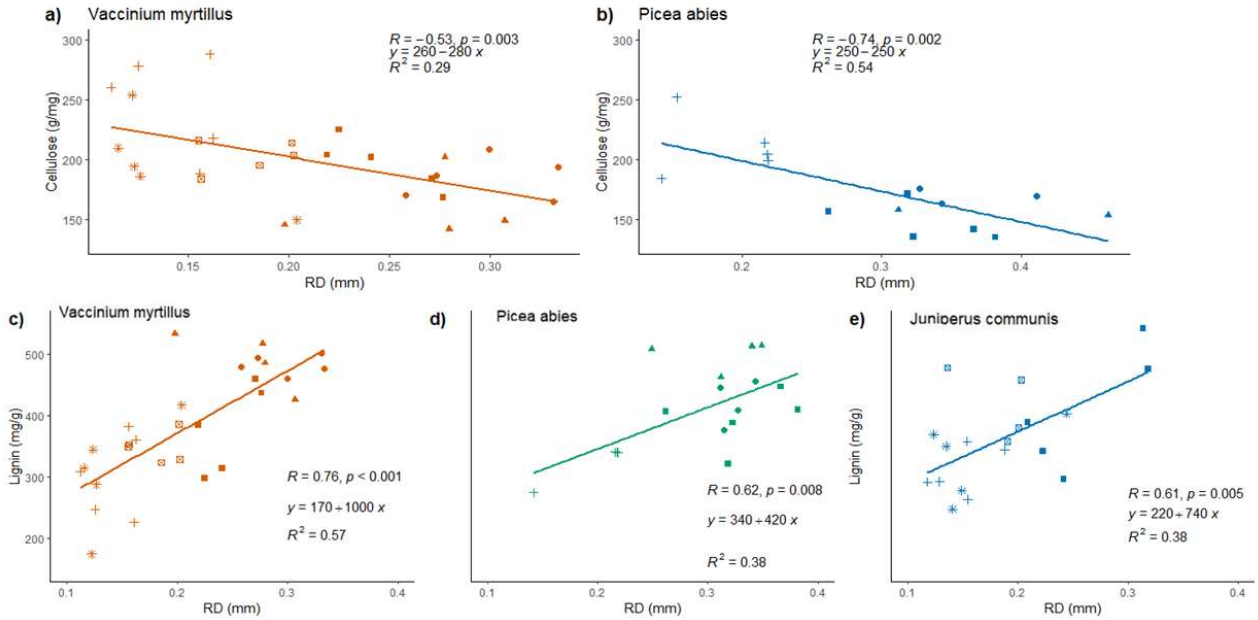


Figure S4. Scatter plots for Spearman correlations between rhizospheric soil global catabolic activity with mean annual temperature (MAT), mean annual precipitation (MAP) and mean annual radiation (MAR) for *V. myrtillus* (orange), *P. abies* (green) and *J. communis* (blue) along the elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are shown. Lines are linear regressions through data.



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69 **Figure S5**. Scatter plots for Spearman correlations between RD_{com}, $Cellullose_{com}$ and
70 $Lignin_{com}$ content for *V. myrtillus* (orange), *P. abies* (green) and *J. communis* (blue) along the
71 elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are
72 shown. Lines are linear regressions through data.

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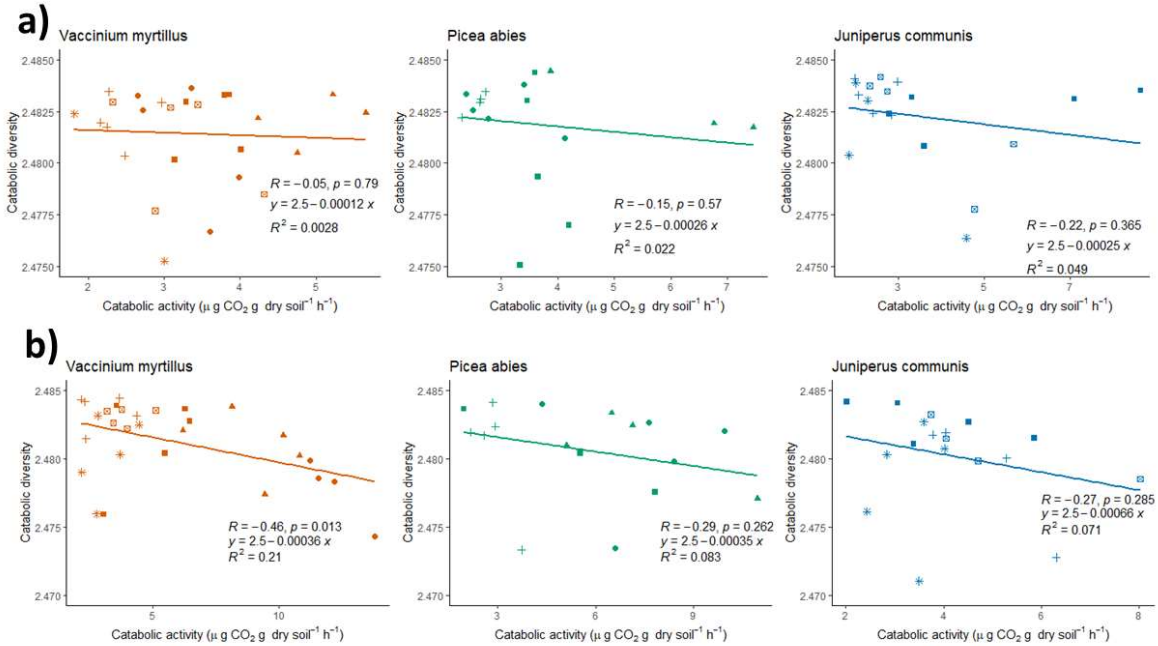

Figure S6. Scatter plots for Spearman correlations catabolic activity and diversity in bulk (a) and rhizospheric (b) soil for *V. myrtillus* (orange), *P. abies* (green) and *J. communis* (blue) along the elevational gradient. Correlation coefficients (ρ), *p-values*, regression equations and R^2 are shown. Lines are linear regressions through data.

80