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FARZAD ASLANI

# Towards revealing the biogeography of belowground diversity

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# Towards revealing the biogeography of belowground diversity

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# LIST OF ORIGINAL PUBLICATIONS

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**II.** **Aslani, F.,** Tedersoo, L., Põlme, S., Knox, O., Bahram, M. 2020. Global patterns and determinants of bacterial communities associated with ectomycorrhizal root tips of *Alnus* species. Soil Biology and Biochemistry. 148, 107923

**III.** **Aslani, F.,** Juraimi, A.S., Ahmad-Hamdani, M.S., Hashemi, F.S.G., Alam, M.A., Bahram, M. 2019. The role of arbuscular mycorrhizal fungi in plant invasion trajectory. Plant and Soil. 441:1–14.

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I. Performed data analysis and wrote the manuscript

II. Performed molecular analysis, data analysis and wrote the manuscript

III. Generated the idea and wrote the manuscript

# 1. INTRODUCTION

Belowground biota are highly diverse and complex, ranging from microscopic components (bacteria and archaea), to fungi, protists and animals. Belowground microbial and animal organism groups can regulate aboveground biodiversity and the functioning of terrestrial ecosystems. Despite this, our knowledge on belowground biodiversity is poorly understood, compared to aboveground communities. Understanding taxonomic and functional diversity of belowground communities, their distributions and their functions in ecosystems can help us to improve predictions of future changes in soil fertility, plant production, and climate.

Belowground constitutes the largest repository of organic matter on earth, more than the atmosphere and vegetation combined (Schlesinger and Bernhardt, 2013). Belowground communities govern the rate and biochemical pathway of this organic matter which in turn influence soil fertility, plant productivity, and the climate change (Crowther et al., 2019). Differences in the belowground biodiversity can lead to significant variation in biogeochemistry, for example, land use change from forests to grasslands drive differences in the structure of soil communities (Delgado-Baquerizo et al., 2018a) and subsequently drive enormous variation in nutrient cycling (Malik et al., 2016). By assessing abundance, taxonomic and functional diversity and composition of belowground biodiversity along with environmental variables regulating their variations, we can enhance our understanding of global biogeochemical cycling in current and future climate scenarios.

Traditionally, abiotic factors, such as climate and soil properties, and biotic factors such as aboveground herbivory were recognized as drivers of plant community variations. Recent studies have demonstrated the role of plant – belowground biodiversity feedbacks in influencing plant performance and community composition (Bardgett and van der Putten, 2014; Wilschut and Geisen, 2021; Geisen et al., 2022). These studies show how plant-belowground biodiversity interplay can influence plant communities both directly (via changing herbivory, symbiosis, or pathogenesis) and indirectly (via changing soil chemical properties) (Wardle et al., 2004; Bezemer and van Dam, 2005). These biotic interactions can change the competitive ability, fitness and evolutionary adaptation of plant species. For instance, fungal diversity and mycorrhizal types directly or indirectly affect plant dispersal and competition that shape plant diversity (Tedersoo et al., 2020).

## 1.1 Biotic factors

Plant species regulate root-associated and soil biodiversity and composition (Fitzpatrick et al., 2018; Wen et al., 2020). Microbial communities colonize roots in two steps: the rhizosphere harbors a subset of the bulk soil community and, the rhizoplane selects a subset of the rhizosphere community (Bulgarelli et al., 2013; Sasse et al., 2018). Therefore, variations in root microbiome depend on

both free-living soil microbes (bulk soil species pool) and plant variables including genetic factors, root morphology and root exudation (Wilschut et al., 2021). There is mixed evidence on the relative importance of environment, plant identity and their interactions in shaping soil microbial communities depending on geographic scale. Untangling the relative importance of these factors might shed light on the strength of plant influence on soil microbial communities and provide insight into the mechanisms by which plants regulate soil communities.

Soil and root microbiome differ among plant species (Burns et al., 2015; Lareen et al., 2016; Sweet and Burns, 2017; Liu et al., 2020) and even within individuals of a single species (Wagner et al., 2016). It has been found that phylogenetic host distance correlates with root microbiome structure in various plant species such as *Salicaceae*, *Poaceae* (Bouffaud et al., 2014), *Arabidopsis* (Schlaeppi et al., 2014), Rice (Edwards et al., 2015), and Maize (Bouffaud et al., 2014). Closely related plant species usually share similar characteristics, such as root morphology and production of secondary metabolites, which may contribute to shaping their associated microbial communities (Saleem et al., 2018; Pang et al., 2021). Several studies have assessed whether the diversity of plant exudates correlates with microbial diversity and found a link between plant exudation profiles and microbiome compositions (Sasse et al., 2018). Moreover, the addition of a diverse exudates to plant monocultures increased microbial diversity (Steinauer et al., 2016). Plant functional traits and habitat specialization also explain soil microbial community diversity, and composition (Barberán et al., 2015; Boeddinghaus et al., 2019). For example, forest specialist and habitat generalist plant species associated with different arbuscular mycorrhizal fungal communities (Öpik et al. 2009). Growing evidence indicates that host plant traits have a significant impact on the structure of belowground communities across various habitats (Becklin et al. 2012), successional stages (Martínez-García et al. 2015) and elevational gradients (Li et al. 2014; Saitta et al. 2018). It has also been reported that plant functional traits -such as specific leaf area index, leaf nitrogen and nitrogen fixation – can determine the distribution of soil bacteria and fungi communities at the regional scale (Delgado-Baquerizo, 2018a). Despite shifts in soil properties, variation in arbuscular mycorrhizal fungal (AMF) community composition over different ecosystem successional stages is explained by changes in plant communities (Martínez-García et al. 2015). In addition, a global-scale meta-analysis showed that plant community composition is directly associated with AMF community composition, whereas the effect of climate and other ecosystem properties remained indirect and secondarily mediated by host plants (Yang et al. 2012). Plant mycorrhizal niche space (PMNS) – defined as a plant's ability to exploit and shape the mycorrhizal fungi pool of a habitat based on its dependency on mycorrhizal fungi and traits (Aslani et al., 2019) – can predict changes in the belowground in association with plant community variations. For example, the life cycle is a plant trait, as a component of PMNS, that could affect AMF communities. Annual and perennial plants can harbor different AMF communities in the root, rhizosphere and bulk soil (Alguacil et al. 2012). In addition, plant-life form (herbaceous versus woody) can also act as a major determinant of AMF

community structure. Varela-Cervero et al. (2015) reported that similar AMF communities were harbored by herbaceous plant species (*Thymus zygis* and *Thymus mastichina*). López-García et al. (2014) found that annual herbs, perennial herbs and perennial semi-woody plants are associated with distinct AMF communities. Another major component of PMNS stems from ecological adaptations (ecosystem type) or ecological requirements of plant species (Öpik et al. 2009). In this context, plants associate with AMF according to their habitat preferences (habitat range). Veresoglou and Rillig (2014) suggested that the ecosystem type of plants, rather than their phylogenetic relatedness, determines the structure of AMF communities. For instance, forest specialist and habitat generalist plants tend to associate with specialist and generalist AMF, respectively (Davison et al. 2011; Öpik et al. 2009).

We still know very little about tripartite associations between roots, symbiotic mycorrhizal fungi and bacteria and their responses to different environmental parameters. Since roots and fungi can provide plant-derived C directly to the soil ecosystem, they are important niches for colonization of bacteria and other microorganisms (Hassani et al., 2018; Gohar et al., 2022). Thus, plants influence soil and root associated microbial communities via mycorrhizal fungi. The fungi colonizing individual roots had a strong effect on the associated bacterial communities, closely related species within the same ectomycorrhizal genus had distinct bacterial microbiomes. Izumi and Finlay (2011) reported some selective effects of particular ectomycorrhizal symbionts on associated bacteria in *Betula pubescens* roots. Analysis of bacterial communities associated with *Pinus muricata* roots has also provided some evidence that bacterial communities in the roots were affected by fungal species identity (Nguyen and Bruns, 2015). However, other studies have failed to demonstrate any significant effect of ectomycorrhizal fungi colonizing plant roots on the associated bacterial communities (Tanaka and Nara, 2009; Uroz et al., 2012). Generally, the results from these studies showed little to no specificity of bacteria to fungal hosts. However, an emerging pattern from these studies is that bacteria in the genera *Burkholderia, Bacillus, Clostridium, Azospirillum, Pseudomonas*, and the order Rhizobiales might have a strong link with fungal associated roots (Izumi et al., 2007; Nguyen and Bruns, 2015).

## 1.2 Abiotic factors

Recent studies, using molecular techniques, revealed that the global distributions of bacterial (Bahram et al., 2018), protistan (Oliverio et al., 2020), mycorrhizal (Öpik et al., 2006; Tedersoo et al., 2014) and faunal (Wu et al., 2011) taxa in soil are restricted by variations in climatic, soil and plant conditions. These studies indicate that multiple factors jointly determine the structure of various microbial groups, but the major underlying factors differ among bacteria, fungi, protists, and soil animals. While soil pH is of particular importance in determining bacterial diversity (Bahram et al., 2018; Delgado-Baquerizo et al., 2018b), fungi respond most strongly to climate (Tedersoo et al., 2014), protists to soil moisture

(Oliverio et al., 2020), and nematodes to soil texture (van den Hoogen et al., 2019). Climate variables and habitat cover were reported as more important factors in structuring earthworm communities than soil properties on a global scale (Phillips et al., 2019). Soil springtails were primarily affected by climatic variables followed by soil properties (Potapov et al., 2022). In addition, vegetation type determines the abundance and diversity of microbial groups locally and on a regional scale (Bahram et al., 2020; Geisen et al., 2018; Nielsen et al., 2010; Wilschut et al., 2019).

Recent studies have also shown that soil biota may not follow the latitudinal gradient of diversity pattern, i.e. species diversity peaks in the tropics and gradually drop towards the poles (Gaston, 2000). For example, bacterial richness may peak in mid-latitude soils with approximately neutral pH (Bahram et al. 2018), whereas, the richest fungal communities have been reported at low and high latitudes (Tedersoo et al., 2014; Větrovský et al., 2019). Thus, fungal and bacterial diversity exhibited contrasting patterns over the latitudinal gradient (Bahram et al., 2018). For soil animals, nematode abundance was found highest in sub-Arctic regions (van den Hoogen et al., 2019) while the relative abundance of springtails showed a U-shaped pattern across the latitudinal gradient (Potapov et al., 2022). It worth noting that contrasting responses to latitudinal gradients may occur for abundance, biomass and diversity of soil animals (Bahram et al., 2018: Potapov et al., 2022). Latitudinal diversity patterns may also differ for functional groups. For example, the richness of EM fungi peaks in high-latitude forests, supporting the greatest proportion of EM trees (Tedersoo et al., 2014), whereas AM diversity peaks in tropical regions (Davison et al., 2015; Hu et al., 2019). This suggests a lack of coupling between aboveground and belowground diversity at global scales, hinting that patterns of aboveground and belowground diversity are governed by different mechanisms, which are also scale dependent. Despite our accumulated knowledge about biogeographic patterns of soil biota, the underlying mechanisms of the distribution patterns remain little explored (Xu et al., 2020).

## 1.3 Mechanisms underlying community assembly

Historically, the niche-based or the neutral theories have been used to examine and interpret community assembly. The niche theory emphasizes the importance of both biotic and abiotic factors (deterministic processes) that affect the identities and abundance of species (Chesson, 2000). The neutral theory stresses that random factors (stochastic processes) can largely mediate the assembly and dynamic changes in community structures through birth, death, colonization, extinction, and speciation (Chave, 2004; Zhou and Ning, 2017). Nowadays, it has become widely accepted that soil biota biogeographic patterns are affected by both deterministic and stochastic processes (Martiny et al. 2006). Several studies have supported the importance of deterministic factors such as edaphic and biotic factors, in determining microbial community structure (Gralka et al., 2020). In contrast, various theoretical, observational, and experimental studies clearly

demonstrate the importance of stochastic processes in shaping microbial community structure, succession, and biogeography (Zhou and Ning, 2017). The challenge lies in quantifying their relative influences and the mechanisms underlying their dynamics across space and time. Chase and Myers (2011) developed a framework that disentangles the relative importance of these processes in variations of species composition over spatial and environmental gradients. They used null-model approaches to compare observed patterns of species composition to null expectations. A larger deviation from the null expectation indicate more important role of deterministic processes.

There is a little information about the factors that influence the relative importance of the different assembly mechanisms. Trait-based approaches could clarify the mechanisms underlying community assembly, and ecosystem responses to environmental change. The functioning of a community is ultimately governed by the traits expressed by individuals and not their taxonomic identity *per se*. Functional traits can include structural, morphological, biochemical, or genetic characteristics of organisms, which determine the performance of individuals in time or space. It is believed that species functional traits could have critical impacts on mediating stochastic community assembly (Fukami et al., 2015) and environmental filtering in shaping community structures (Kraft et al., 2015; Goberna et al., 2014). For example, the relative importance of stochastic assembly processes is higher in larger organisms with higher productivity (e.g., Chase, 2010), probably because of higher priority effects (Steiner, 2014; Fukami, 2015). Further, it has been shown that the distribution of habitat generalists may be primarily determined by neutral processes due to their general indifference to the variation in habitat conditions (Liao et al., 2016).

Using phylogenetic information is another way to infer community assembly processes, as phylogenetic distance could be related to ecological niche distance (phylogenetic signal) (Losos 2008). For example, studies have detected phylogenetic overdispersion, phylogenetic clustering and neutral effect in microbial communities (de Cárcer 2019). Combining phylogeny with ecological information of species could contribute to a better understanding of community assembly processes. The idea of differentially conserved traits may generally help to predict compositional variation in any microbial system. Specifically, changes in the environment that select on shallow or deep traits should alter microbiome composition at various taxonomic levels (Lennon et al., 2012). Thus, the resolution at which microbiome composition varies among samples may provide information about the phylogenetic conservation of the traits under selection (Martiny et al., 2015). Despite the promiscuity of horizontal gene transfer in bacteria, microbial traits appear to be phylogenetically conserved. For instance, traits such as pH and salinity preference are relatively deeply conserved, such that taxa within deep clades tend to share the trait (Martiny et al., 2015). These results suggest a predictive framework whereby the taxonomic resolution of microbiome variation among samples provides information about the traits under selection, developing predictions for how microbial composition responds to changing environmental conditions.

# 2. HYPOTHESES AND OBJECTIVES

The overarching hypothesis of this thesis is that different processes underlie belowground biodiversity variations depending on compartment niche (soil vs root-associated), plant host phylogeny and functional properties and organism's functional traits. In particular, we hypothesized that plant's ability to exploit and shape the mycorrhizal fungi pool of a habitat can be determined by its dependency on mycorrhizal fungi and functional traits (III). We also conducted an observational study to test the hypothesis that in contrast to free living (Bahram et al., 2018), root-associated bacterial communities are mostly determined by host plant phylogeny (II). By assessing distribution patterns of soil fungi, protists, and animals (i.e., the eukaryome), we further expected to find a link between organism traits, such as body size and dispersal ability, and the relative importance of ecological processes in structuring soil biodiversity (I).

These hypotheses were addressed via four main objectives concerning belowground biodiversity changes in association with biotic (e.g., plant species and root associated ectomyzorrhiza fungi) and abiotic factors, and taxonomic and functional traits of organism groups.

1) To review literature on how plant functional traits and mycorrhiza status structure the soil mycorrhizal fungi mediating plant invasion.
2) To determine the relative contributions of *Alnus* species phylogeny, *Alnus* root-associated ectomycorrhizal (EcM) fungi phylogeny, and environmental and spatial factors to the structure of root-associated bacterial communities.
3) To evaluate latitudinal diversity patterns for soil fungi, protists, and animals (including Nematoda, Arthropoda, and Annelida).
4) To assess a potential link between traits of soil eukaryotes and their diversity patterns and assemblage mechanisms.

# 3. MATERIALS AND METHODS

## 3.1 Sampling

To evaluate plant and its associated ectomycorrhizae species impacts on the root bacterial communities, a survey study was performed. Root and rhizosphere soil samples of 19 *Alnus* species were collected as described by Põlme et al. (2013) from 85 sites across all continents where *Alnus* is distributed (except North Africa, which shares *Alnus glutinosa* with Eurasia) (Fig. 1). Six soil samples (15 × 15 cm–10 cm depth) comprising *Alnus* roots were randomly collected at least 10 m apart in an area of 2500 $m^2$ at each study site. Soil samples were placed into plastic bags and processed within 48 h after collection. Roots were carefully cleaned under tap water and placed into large Petri dishes filled with water. Ectomycorrhizal (EcM) morphotypes were distinguished based on color and roughness of mantle, presence of emanating hyphae and rhizomorphs under stereomicroscope. Two EcM root tips from each morphotype per soil sample were stored in CTAB buffer (1% cetyltrimethylammonium bromide, 100 mM Tris–HCl (pH 8.0), 1.4 M NaCl, 20 mM EDTA) for molecular analyses. *Alnus* roots were confirmed under a stereomicroscope based on root morphology (presence and shape of EcM and actinorhizal root nodules).

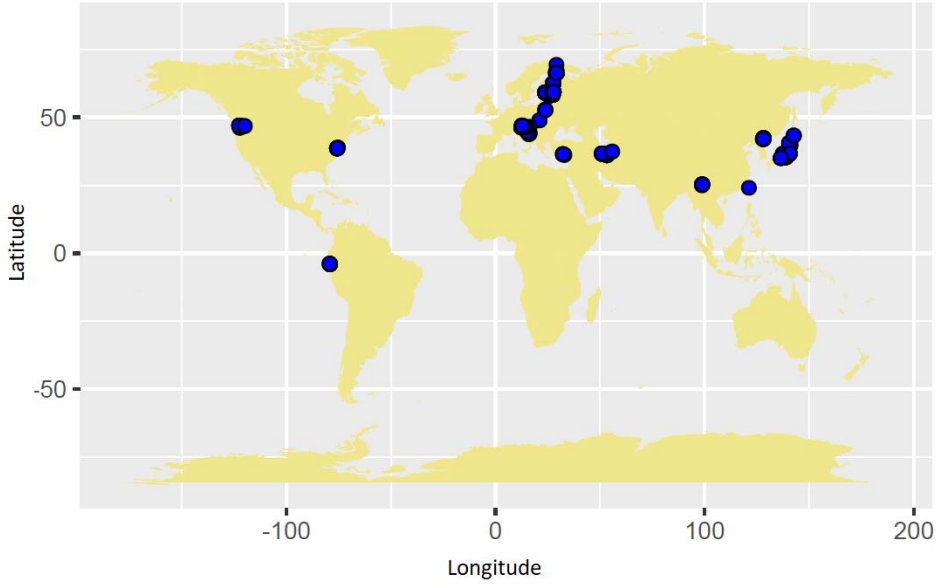


**Figure 1.** Sampling sites locations (II; Fig. S2)

To assess distribution patterns and assembly mechanisms of soil organism groups in a trait-based framework, we used a global set of samples that were collected from plots of homogeneous vegetation, minimally affected by humans, following a standardized sampling and processing scheme (Tedersoo et al., 2014). We selected the 193 plots out of 365 based on geographical evenness (to minimize spatial autocorrelation) and high-quality DNA. 40 soil subsamples (5 cm diameter to 5 cm depth) were collected from each study plot (2500 $m^2$). We randomly selected 20 trees located at least 8 m apart. In two opposite directions, 1 to 1.5 m from each tree trunk, loose debris was removed from the forest floor. Polyvinyl chloride (PVC) tubes (5 cm in diameter) were hammered into the soil down to 5 cm depth. The 40 soil cores were pooled, coarse roots and stones were removed, and a subset of the soil was air-dried at <35 °C.

## 3.2 Molecular analyses

We applied amplicon sequencing to taxonomically characterize ectomycorrhizal root-associated bacterial communities. DNA extraction and identification of EcM fungi have been described in Põlme et al. (2013). To identify bacteria, the 16S rRNA gene V4 region was amplified using a universal prokaryote primer pair, 515F (5′ GTGYCAGCMGCCGCGGTAA -3′) and 926R (5′- GGCCGYCAA TTYMTTTRAGTTT -3′) from each root tips following Bahram et al. (2018). It was reported that this primer pair has a better coverage of prokaryotic taxa in field and mock communities compared with another universal primer pair (515F-C/806R) (Parada et al. 2016). Forward and reverse primers were indexed with 12-base unique multiplex identifiers in the 5′-end. The 25 µl PCR mix comprised 17 µl sterilized H2O, 5 µl 5 × HOT FIREPol Blend MasterMix (Solis Biodyne, Tartu, Estonia), and 0.5 µl each primer (200 nM) and 2 µl DNA extract. We included negative control samples in both PCR and sequencing runs. DNA was amplified using the following thermocycling conditions: 95 °C for 15 min, 30 cycles of 95 °C for 30 s, 50 °C for 45 s and 72 °C for 1 min, with a final extension step at 72 °C for 10 min.

The quality of PCR products was evaluated under UV light by electrophoresis of 5 µl PCR product on 1% agarose gel for 30 min. PCR products with no visible band or a strong band were excluded and their PCR mix amplified using 27 or 33 cycles, respectively to provide as similar as possible bands for all samples. From each PCR product, 5 µl was pooled into seven libraries. Libraries were purified with FavourPrep Gel/PCR Purification Kit (Favorgen-Biotech Corp., Austria). Sequencing was performed using 2×300 paired-end chemistry on an Illumina MiSeq platform in the Estonian Genome Center (Tartu, Estonia).

To identify soil eukaryotes a 2.0 g amount of each of homogenized composite samples was subjected to DNA extraction using the PowerMax Soil DNA Isolation Mini kit (MoBio) following the manufacturer's instructions (Tedersoo et al., 2014). We used universal eukaryote primers 1389f and 1510r in the polymerase chain reaction (PCR) mix to amplify the V9 region of the 18S rRNA gene

(Amaral-Zettler et al., 2009). It is shown that the use of 1389F/1510R primer pair detected a higher number of OTUs compared with 1380F/1510R (Wilcox and Hollocher, 2018). These universal primer pairs are known to detect various prokaryote and eukaryote organism groups, as well as, enable us to compare our results with other studies (Mahé et al., 2017; Zhang et al., 2021; Cohen et al., 2021; Ladin et al., 2021). Forward and reverse primers were indexed with 10-base to 12-base unique multiplex identifiers. The PCR mixture was prepared with 0.3 µl DNA extract, 0.5 µl each of the primers, 5 µl 5xHOT FIREPol Blend Master Mix (Solis Biodyne), and 16 µl double-distilled water. We performed PCR using the following thermocycling conditions: 95 °C for 15 min, 30 cycles of 95 °C for 30 s, 50 °C for 45 s and 72 °C for 1 min, with a final extension step at 72 °C for 10 min. Amplicon pools were quality-checked and quantified using Bioanalyzer HS DNA Analysis Kit (Agilent) and Qubit 2.0 Fluorometer with dsDNA HS Assay Kit (Thermo Fisher Scientific), respectively, and sequenced on an Illumina HiSeq 2500 platform (2 × 250 paired-end mode) at the Estonian Genome Center (Tartu, Estonia) following Bahram et al. (2018).

## 3.3 Bioinformatics

We used the LotuS pipeline (Hildebrand et al., 2014) for 16S and 18S rRNA amplicon sequence processing as outlined in Bahram et al. (2018). Reads were demultiplexed and quality-filtered based on the following settings: trimming of reads after an accumulated error of 1, rejecting reads of average quality <28 and estimated accumulated error >2.5 (probability ≥0.01). Chimeric reads were removed using both de novo and reference-based chimera checking algorithms and the RDP reference database (http://drive5.com/uchime/rdp_gold.fa) in UCHIME (Edgar, 2011). The passed reads were clustered with UPARSE (Edgar, 2013) at 97% sequence similarity. Representative sequences for each non-singleton OTUs were chosen for taxonomic assignment by aligning full-length sequences with lambda (Hauswedell et al., 2014) to the SILVA v.123 database (Pruesse et al., 2007) and using the LotuS least common ancestor (LCA) algorithm (Hildebrand et al., 2014). Based on taxonomic assignments, we selected bacteria, fungi, protists, and animals for further analyses.

## 3.4 Statistical analysis

All statistical analyses were conducted using specific packages in R statistical computing environment (v.3.6.1).

### 3.4.1 Multivariate and correlation-based analysis

The OTU-by-sample matrix was Hellinger-transformed and standardized using the function *decostand* in *vegan* package (Oksanen et al., 2020) in R statistical computing environment (v.3.6.1). Of highly correlated variables (R > 0.90), those that explained relatively less community variation were removed to reduce collinearity. To evaluate the extent of spatial autocorrelation, geographical coordinates of plots were transformed into principal coordinates of neighbor matrices (PCNM) eigenvectors using *vegan* and *packfor* (Dray et al., 2016) packages.

Mantel tests – as implemented in *vegan* package – were conducted to determine the correlation between community structure dissimilarity (Bray-Curtis), environmental dissimilarity (Euclidean) matrices, and geographical distance. We computed the geographic distance between sampling sites using *distm* function of the *geosphere* package (Hijmans, 2019). To disentangle explained (e.g., the unique and shared effects of environmental and spatial vectors) and unexplained variation in phylogenetic dissimilarity matrix, we conducted variation partitioning separately for each organism group using *vegan* package. To test the effects of biome and continent on community structure, we used permutational multivariate analysis of variance (PERMANOVA) with Bray-Curtis dissimilarity and 999 permutations as implemented in *adonis* function in the *vegan* package.

### 3.4.2 Regression analysis

To assess latitudinal diversity patterns and the relationship between Operational Taxonomic Unit (OTU) diversity (Shannon index) and environmental gradients, linear and polynomial regressions were chosen based on the adjusted coefficient of determination ($R^2_{adj}$) and visualized using *ggplot2* package (Wickham, 2016). Shannon diversity index was calculated based on residuals of OTU diversity in relation to the square root of the number of obtained sequences to account for differences in sequencing depth according to Tedersoo et al. (2014). Relative abundances of dominant phyla were compared across biomes using the Kruskal–Wallis test followed by Benjamini–Hochberg's correction for multiple comparisons, as implemented in *dplyr* package (Wickham et al., 2020).

### 3.4.3 Network Analysis

Network inference analyses were conducted using the sparse correlations for compositional data (SparCC) program (Friedman and Alm, 2012). These analyses sought to recover linear associations between bacterial OTUs, by identifying co-occurring OTUs with similar habitat preferences. Correlations with greater than 0.2 were prepared for the network reconstruction. Because abundances of OTUs from amplicon-based datasets are compositional (zero-inflated data), traditional

correlation analysis of this type of data is not reliable. Thus, we applied SparCC method which is capable of estimating correlation values from compositional data to find linear relationships between OTUs (Kurtz et al., 2015). The network analysis was performed using *sparcc* functions in *SpiecEasi* packages (Kurtz et al., 2017) and network structure was visualized with Gephi software (https://www.sciencedirect.com/science/article/pii/S0038071717302122 Bastian et al., 2009) using undirected type (no direction for edges) and the Fruchterman–Reingold layout.

### 3.4.4 Phylogenetic tree construction

To calculate phylogenetic distance between all pairs of OTUs, we generated sequence alignments of representative sequences of OTUs using mafft (version 7; Katoh & Standley, 2013), followed by masking alignment to minimize alignment ambiguity (Lane, 1991) with default parameters (including maximum relative frequency of gap characters in a column = 1; minimum relative frequency of at least one non-gap character in a column = 0.4). Following this, we built the phylogenetic trees using RAxML (version 8) with a GTRCAT model with 100 bootstrapped replicates (Stamatakis, 2014). Using the generated tree, we computed distances between all pairs of tips of the phylogenetic tree using *distTips* function in the *adephylo* package (Jombart & Dray, 2008).

The phylogenetic distances of *Alnus* species were adopted from Põlme et al. (2013). For EcM fungal species, phylogenetic distances were calculated based on taxonomic ranks following the classification-based algorithms of Tedersoo et al. (2018). To quantify the relative effect of EcM fungal and *Alnus* phylogenies, their phylogenetic distance matrices were translated into a principal coordinate analysis of neighbor matrices (PCNM) according to Dray et al. (2006) using the *vegan* package. The PCNM vectors were forward selected using *step* function in the *vegan* package.

### 3.4.5 Null model analysis

To infer the relative importance of ecological processes on organism groups with various body sizes and niche breadths, we selected the most abundant phyla representing ≥10% of the total fungal, protist and animal reads. The average body size of each phylum was obtained from Briones (2014), Zinger et al. (2019) and Luan et al. (2020). To determine the average niche breadth for each organism group, we calculated the niche breadth for each OTU based on the Levins' index (Levins, 1968) as implemented in *niche.width* function of *spaa* package (Zhang, 2016). We used Community Assembly Mechanisms by Phylogenetic bin-based null model analysis (iCAMP) framework developed by Ning et al. (2020) from a previous framework (Stegen et al., 2013). Individual populations in a community might differently respond to ecological processes (Caruso et al., 2011; Hanson

et al., 2012; Ning et al., 2020). Therefore, the iCAMP framework quantifies the relative importance of different ecological processes for each phylogenetic group (bin) rather than only for the entire community, leading to obvious improvement in quantitative performance (Ning et al., 2020). Here we divided OTUs into different groups ('bins') based on their phylogenetic relationships (phylogenetic binning). To assess phylogenetic signal, we calculated Pearson correlation between the pairwise phylogenetic distances and niche preference differences for each individual bin with Mantel test (I; Table S2). Finally, we performed an abundance-based null model analysis based on a phylogenetic dissimilarity metric using beta Net Relatedness Index (βNRI) and taxonomic dissimilarity metric using Bray–Curtis-based Raup–Crick (RCbray) (Stegen et al., 2012, 2013) for each bin. These methods enabled us to evaluate the deviation between the observed phylogenetic/Bray–Curtis dissimilarity and the null-expected phylogenetic/Bray–Curtis dissimilarity. To generate null expectations of community dissimilarities for each sample pair, average phylogenetic and Bray–Curtis dissimilarities of 999 randomly assembled pairs of communities were calculated. The fraction of pairwise comparisons across communities (samples) with $|\beta NRI| > 1.96$ was considered a selection threshold. The RC metric was applied for pairwise comparisons with $|\beta NRI| \leq 1.96$. The fraction of pairwise comparisons with $|RC| > 0.95$ was considered an indicative of dispersal limitation or homogenizing dispersal, whereas with $|RC| \leq 0.95$ was interpreted as the contribution of drift (ecological drift and other processes such as stochastic speciation, weak selection, normal-rate stochastic dispersal). The fractions of ecological processes across all bins were weighted by the relative abundance of each bin and integrated to obtain the relative importance of ecological processes at the whole community level.

The output of null-model-based approaches depends on the sampling effort and species pool setting (Chase & Myers, 2011). Comparing two communities with different regional species pool sizes, the absolute magnitude of the deviation from the null model expectation would be higher (showing stronger deterministic effects) in the community with a larger species pool size. To overcome this weakness, we modified iCAMP framework to test different regional pool settings to count species in each continent sharing the same regional pool. We set each continent as a regional pool in the null model algorithm. We calculated the relative importance (%) of selection (e.g., heterogeneous selection and homogeneous selection), dispersal (e.g., dispersal limitation and homogenizing dispersal), and drift for each pair of communities (samples) and obtained the mean of percentage of ecological processes for each organism group. Following this, we compared the mean of each individual process among organism groups using a Kruskal-Wallis Test.

# 4. RESULTS

## 4.1 Plant mycorrhizal niche space impacts on soil mycorrhizal fungi (III)

Evidence from literature suggest that based on plant mycorrhizal niche space (PMNS), we can classify plant species into different groups according to their traits such as life form (woody vs herbaceous), life cycle (annual, biennial, perennial), ecosystem types, mycorrhizal status (mycorrhizal vs non-mycorrhizal) (III; Fig. 3). This classification could be useful for a) predicting the potential invasiveness of each plant in a particular habitat, b) predicting plant invasion impacts on the mycorrhizal communities in a new habitat, and c) enhancing our knowledge to restore invaded areas. Exploring the effects of plant traits and phylogeny on their associated mycorrhizal fungi as an important component of PMNS is an important step towards a more predictive understanding of plant-plant competition.

## 4.2 Taxonomic profile of bacterial community (II)

We characterized the bacterial communities associated with root tips of *Alnus* species and soil eukaryotic communities. We found 3694 OTUs from the root tips of *Alnus* spp. belonging to 36 bacterial phyla. The top 10 most abundant phyla were considered as dominant phyla, including Proteobacteria (*Alphaproteobacteria*, 13.2%; *Gammaproteobacteria*, 11.9%; *Deltaproteobacteria*, 9.2%), *Bacteroidetes* (11.1%), *Planctomycetes* (10.2%), *Actinobacteria* (9.0%), *Chloroflexi* (6.5%), *Firmicutes* (5.5%), *Verrucomicrobia* (4.8%), *Acidobacteria* (4.7%). Other phyla accounted for 13.9% of OTUs and 38% of total abundance (Fig. 2).

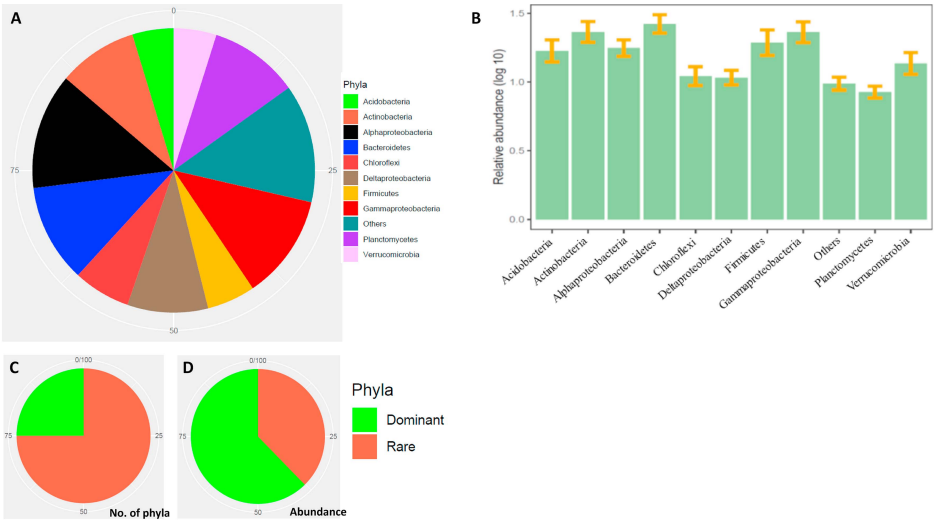


**Figure 2.** The proportion of phyla dominate the bacterial communities across the sites. A) The proportion of bacterial phyla detected over sampling sites. B) Comparison of abundance (mean ± confidence interval) of dominant phyla C) Number of dominant and rare phyla relative to the total detected phyla D) Abundance of dominant and rare phyla relative to the total abundance (II; Fig. 1).

There were several significant correlations between the abundance of phyla and environmental variables (Fig. 3). For instance, *Bacteroidetes* dominated at higher latitudes in sites with higher Mg, pH, phosphate and Ca concentration, whereas negative correlations were observed between *Bacteroidetes* abundance and altitude and precipitation. *Armatimonadetes* was positively correlated with altitude but negatively with Mg, pH, and latitude. Furthermore, soil pH had a positive effect on the relative abundance of Bacteroidetes, *Chloroflexi*, *Rokubacteria*, and *Verrucomicrobia*, but a negative effect on *Armatimonadetes*.

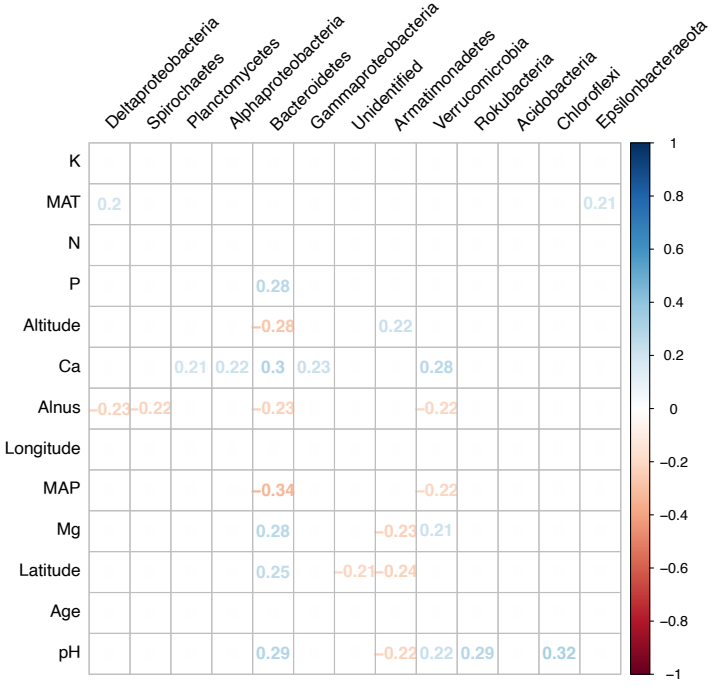


**Figure 3.** Spearman correlations between environmental variables and abundance of 16S-based bacterial phyla (class for Proteobacteria) (II; Fig. S2)

## 4.3 Taxonomic profile of soil eukaryome (I)

Altogether 56.6%, 11.3%, and 17.7% of soil eukaryotic reads were assigned to fungi, protists, and animals, respectively (Fig. 2). Fungal reads were clustered into 2105 OTUs including 1000 Ascomycota (47.5% OTUs; 36.0% fungal reads) and 730 Basidiomycota (34.6% OTUs; 60.0% fungal reads). The 2558 protist OTUs belonged to 7 kingdoms, with SAR supergroups (Stramenopila, 9.91%; Alveolata, 43.99%; Rhizaria, 36.34%) and Amoebozoa (6.24%) accounting for 96.48% of protist reads and 93.57% of OTUs. Animals comprised 1143 OTUs, with Annelida (5.7% OTUs; 17.3% reads), Arthropoda (48.3%; 54.3%), Nematoda (23.2%; 11.5%), and Rotifera (4.0%; 8.7%) collectively accounting for 81.0% of OTUs and 86.0% of reads (Fig. 4).

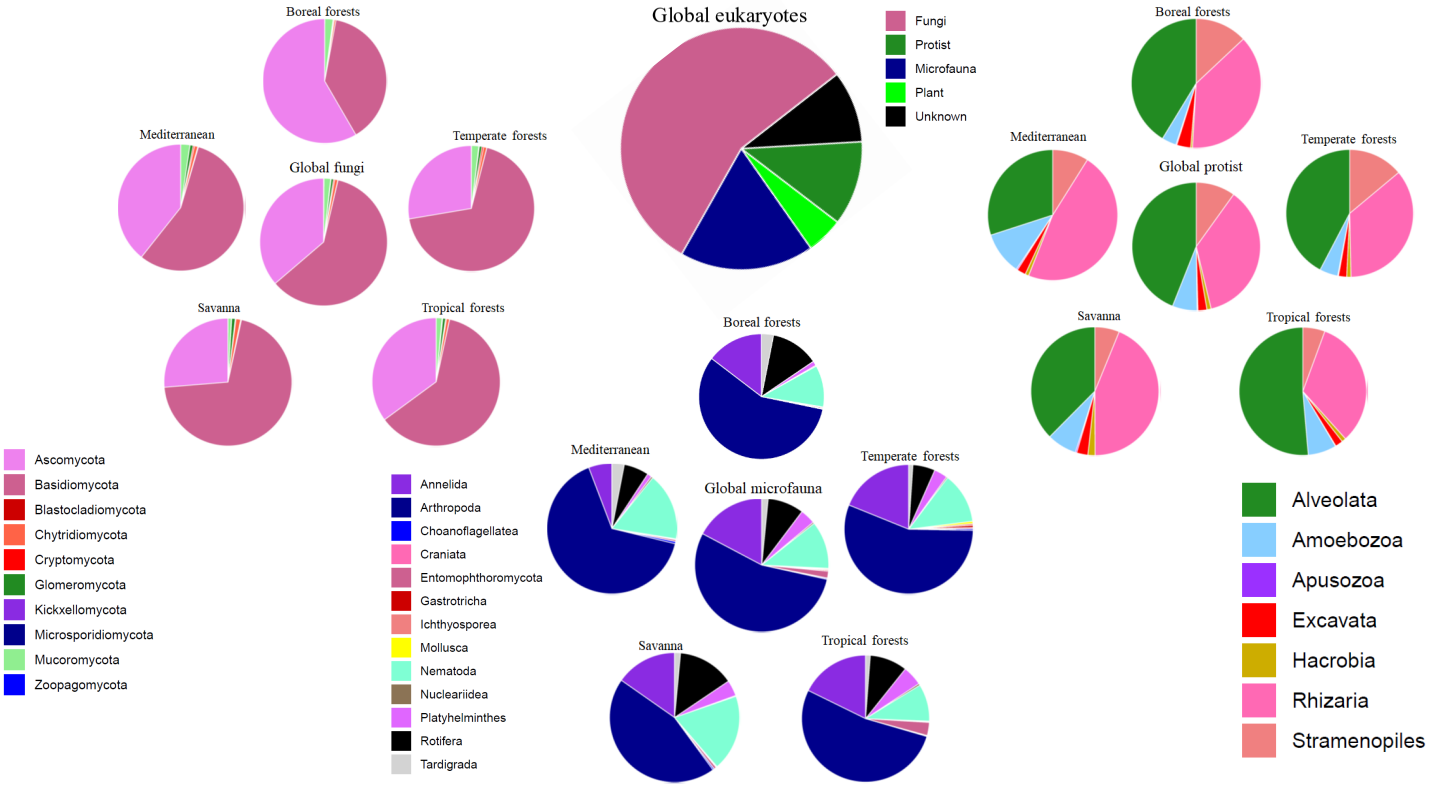


**Figure 4.** Taxonomic profile of eukaryote communities across biomes (I; Fig. S2).

The relative abundance of these groups varied among biomes (Table 1). Basidiomycota was significantly more abundant in tropical forests compared with boreal forests ($p < 0.05$). Alveolata was the dominant group in tropical forests, Rhizaria prevailed in Mediterranean biomes, and Stramenopila was relatively more abundant in temperate forests compared with tropical forests ($p < 0.05$). Of animals, Arthropoda and Annelida were relatively most abundant in tropical forests compared with temperate and savanna biomes. By contrast, Nematoda and Rotifera were most abundant in savannas (Table 1).

**Table 1.** Cross-biome comparison of relative abundance of dominant taxa in each organism group using Kruskal-Wallis test with Benjamini-Hochberg's correction for multiple comparisons (I; Table S2)

| | **Nematoda** | | | |
|---|---|---|---|---|
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | **0.02** | – | – | – |
| Savannas | **0.00** | 0.40 | – | – |
| Temperate forests | 0.07 | 0.23 | 0.05 | – |
| Tropical forests | 0.14 | 0.08 | **0.02** | 0.40 |
| | **Annelida** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.13 | – | – | – |
| Savannas | 0.24 | 0.82 | – | – |
| Temperate forests | 0.41 | 0.05 | 0.13 | – |
| Tropical forests | 0.06 | **0.02** | 0.05 | 0.05 |
| | **Arthropoda** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.65 | – | – | – |
| Savannas | 0.06 | **0.04** | – | – |
| Temperate forests | 0.49 | 0.29 | 0.10 | – |
| Tropical forests | 0.11 | 0.18 | **0.00** | **0.00** |
| | **Rotifera** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.33 | – | – | – |
| Savannas | **0.04** | **0.01** | – | – |
| Temperate forests | **0.04** | 0.98 | **0.00** | – |
| Tropical forests | **0.03** | **0.01** | 0.48 | **0.00** |

| | **Alveolata** | | | |
|---|---|---|---|---|
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.93 | – | – | – |
| Savannas | 0.93 | 0.93 | – | – |
| Temperate forests | 0.93 | 0.89 | 0.93 | – |
| Tropical forests | 0.11 | **0.02** | **0.02** | **0.01** |
| | **Rhizaria** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.12 | – | – | – |
| Savannas | 0.19 | 0.31 | – | – |
| Temperate forests | 0.12 | 0.30 | 0.91 | – |
| Tropical forests | 0.19 | **0.00** | **0.00** | **0.00** |
| | **Stramenopila** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.57 | – | – | – |
| Savannas | 0.57 | 0.18 | – | – |
| Temperate forests | 0.57 | 0.57 | 0.14 | – |
| Tropical forests | 0.19 | 0.02 | 0.57 | **0.00** |
| | **Ascomycota** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.85 | – | – | – |
| Savannas | 0.85 | 0.83 | – | – |
| Temperate forests | 0.83 | 0.83 | 0.96 | – |
| Tropical forests | 0.83 | 0.83 | 0.83 | 0.83 |
| | **Basidiomycota** | | | |
| | Boreal forests | Mediterranean | Savannas | Temperate forests |
| Mediterranean | 0.45 | – | – | – |
| Savannas | 0.21 | 0.73 | – | – |
| Temperate forests | 0.06 | 0.49 | 0.64 | – |
| Tropical forests | **0.01** | 0.06 | 0.06 | 0.06 |

The values represent the corrected p value of Kruskal-Wallis test using Benjamini-Hochberg's correction for multiple comparisons. Those are <0.05 considered significant (bolded).

## 4.4 Bacterial community variations (II)

PERMANOVA and distance-based linear model revealed that *Alnus* phylogeny was the most important explanatory variable for structure and richness of root-associated bacteria (structure: adjusted $R^2_{adj}$ = 0.172; richness: $R^2_{adj}$= 0.185) (II, Table 1), whereas edaphic variables (e.g., soil Ca, Mg, N, P, K, pH) were of secondary importance (structure: $R^2_{adj}$= 0.151; richness: $R^2_{adj}$= 0.141) (II; Fig. 2). Spatial PCNM vectors (adjusted R2 = 0.132) explained OTU structure relatively more than climatic factors (MAT and MAP; $R^2_{adj}$= 0.092), while climate ($R^2_{adj}$= 0.116) was more effective predictor of OTU richness followed by spatial vectors ($R^2_{adj}$= 0.082). To partition variation into pure and shared effects of different variable groups, we used variation partitioning analysis. This analysis confirmed that biotic fraction (phylogenetic vectors of *Alnus* and EcM) is the principal predictor of both OTU structure and richness (II; Fig. 3).

Mantel test results also revealed significant relationships between bacterial community composition dissimilarity and biotic and abiotic variables. Among all variables tested, bacterial community dissimilarity showed the strongest correlation with the phylogenetic distance of *Alnus* species (r = 0.33; p = 0.007), and to lesser extent, with phylogenetic distance of EcM fungi (r = 0.20; p = 0.042). Moreover, a significant negative correlation was found between phylogenetic distance and number of shared OTUs (II; Fig. 4 and Fig. 5C). This analysis showed that more phylogenetically distant *Alnus* species and EcM fungi harbored more dissimilar bacterial communities. In contrast, the bacterial diversity showed no correlation with phylogenetic distance of *Alnus* ($R^2_{adj}$: −0.001148; p-value: 0.3708) and EcM fungi ($R^2_{adj}$ −0.0007194; p-value: 0.3437), although the diversity differed between *Alnus* species and EcM fungi (II; Fig. 4 and Fig. 5C). The climatic (r = 0.24; p = 0.001) and edaphic (r = 0.15; p = 0.001) also showed significant correlations with the bacterial community dissimilarity.

## 4.5 Host preference of bacterial OTUs (II)

SparCC network analysis revealed co-occurrence patterns of bacterial OTUs. The obtained network consisted of three components, representing three groups of co-existing OTUs, sharing similar habitats. We then compared the relative abundance of co-existing OTUs across their associated *Alnus* and EcM hosts. The results showed each component (OTU group) has significantly higher relative abundance in certain *Alnus* species (II; Fig. 6, Table 2), while no clear trend was observed for association between OTU groups and EcM species. For instance, thirteen OTUs clustered into the first ecological group, were mostly hosted by *A. subcordata and A. incana*. In contrast, OTUs belonged to the second ecological group tended to associated with *A. fauriei, A. viridis*, and *A. rubra*. Finally, the third bacterial group was found most in the root tips of *A. serrulata, A. sieboldiana*, and *A. nepalensis* compared to other species. These OTUs were among the most abundant OTUs, such that they constitute more than 49% of the total abundance. Therefore, network analysis clustered abundant OTUs into three groups with different *Alnus* species.

**Table 2.** Co-occurrence bacterial taxa and their *Alnus* species preferences (II; Table S1)

| Class | Order | Family | Genus | OTU | Co-occurrence groups | Host species |
|---|---|---|---|---|---|---|
| Bacteroidia | Cytophagales | Microscillaceae | Ohtaekwangia | OTU_100 | Group1 | A.acuminata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Rhizobacter | OTU_103 | Group1 | A.incana |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Comamonas | OTU_108 | Group1 | A.subcordata |
| Bacteroidia | Chitinophagales | Chitinophagaceae | Terrimonas | OTU_112 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | ? | OTU_118 | Group1 | A.subcordata |
| Gammaproteobacteria | Gammaproteobacteria | Unknown_Family | Acidibacter | OTU_119 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Rhizobacter | OTU_127 | Group1 | A.subcordata |
| Bacteroidia | Cytophagales | Microscillaceae | Chryseolinea | OTU_128 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Ideonella | OTU_130 | Group1 | A.subcordata |
| Deltaproteobacteria | Myxococcales | Haliangiaceae | Haliangium | OTU_133 | Group1 | A.subcordata |
| Alphaproteobacteria | Rhizobiales | Rhizobiaceae | Mesorhizobium | OTU_134 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | ? | OTU_14 | Group1 | A.subcordata |
| Alphaproteobacteria | Rhizobiales | Beijerinckiaceae | Bosea | OTU_142 | Group1 | A.incana |
| Spirochaetia | Spirochaetales | Spirochaetaceae | Salinispira | OTU_150 | Group1 | A.subcordata |
| Bacteroidia | Cytophagales | Microscillaceae | ? | OTU_164 | Group1 | A.incana |
| Alphaproteobacteria | Sphingomonadales | Sphingomonadaceae | Sphingopyxis | OTU_165 | Group1 | A.subcordata |
| Bacteroidia | Chitinophagales | Chitinophagaceae | ? | OTU_177 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Massilia | OTU_22 | Group1 | A.glutinosa |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Polaromonas | OTU_233 | Group1 | A.incana |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | ? | OTU_236 | Group1 | A.subcordata |

| Class | Order | Family | Genus | OTU | Co-occurrence groups | Host species |
|---|---|---|---|---|---|---|
| Bacteroidia | Flavobacteriales | Flavobacteriaceae | Flavobacterium | OTU_25 | Group1 | A.incana |
| Alphaproteobacteria | Rhizobiales | Rhizobiaceae | Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium | OTU_28 | Group1 | A.subcordata |
| Alphaproteobacteria | Rhizobiales | Rhizobiaceae | Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium | OTU_42 | Group1 | A.subcordata |
| Bacteroidia | Chitinophagales | Chitinophagaceae | ? | OTU_44 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Variovorax | OTU_56 | Group1 | A.subcordata |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | ? | OTU_69 | Group1 | A.glutinosa |
| Bacilli | Lactobacillales | Enterococcaceae | Enterococcus | OTU_71 | Group1 | A.subcordata |
| Actinobacteria | Pseudonocardiales | Pseudonocardiaceae | Lechevalieria | OTU_74 | Group1 | A.acuminata |
| Actinobacteria | Corynebacteriales | Corynebacteriaceae | Lawsonella | OTU_105 | Group2 | A.fauriei |
| Alphaproteobacteria | Rhizobiales | Xanthobacteraceae | Bradyrhizobium | OTU_11 | Group2 | A.viridis |
| Actinobacteria | Propionibacteriales | Propionibacteriaceae | Cutibacterium | OTU_13 | Group2 | A.fauriei |
| Gammaproteobacteria | Oceanospirillales | Halomonadaceae | Halomonas | OTU_15 | Group2 | A.viridis |
| Gammaproteobacteria | Pseudomonadales | Moraxellaceae | Acinetobacter | OTU_21 | Group2 | A.fauriei |
| Gammaproteobacteria | Alteromonadales | Pseudoalteromonadaceae | Pseudoalteromonas | OTU_23 | Group2 | A.viridis |
| Clostridia | Clostridiales | Lachnospiraceae | ? | OTU_230 | Group2 | A.viridis |
| Gammaproteobacteria | Pseudomonadales | Moraxellaceae | Acinetobacter | OTU_26 | Group2 | A.fauriei |

| Class | Order | Family | Genus | OTU | Co-occurrence groups | Host species |
|---|---|---|---|---|---|---|
| Actinobacteria | Micrococcales | Micrococcaceae | Micrococcus | OTU_37 | Group2 | A.fauriei |
| Bacilli | Bacillales | Bacillaceae | Bacillus | OTU_49 | Group2 | A.viridis |
| Bacteroidia | Bacteroidales | Prevotellaceae | Prevotella_9 | OTU_50 | Group2 | A.rubra |
| Actinobacteria | Corynebacteriales | Corynebacteriaceae | Corynebacterium_1 | OTU_58 | Group2 | A.rubra |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Aquabacterium | OTU_8 | Group2 | A.viridis |
| Alphaproteobacteria | Rhodobacterales | Rhodobacteraceae | Paracoccus | OTU_89 | Group2 | A.fauriei |
| Gammaproteobacteria | Betaproteobacteriales | Burkholderiaceae | Burkholderia-Caballeronia-Paraburkholderia | OTU_24 | Group3 | A.serrulata |
| Bacteroidia | Chitinophagales | Chitinophagaceae | ? | OTU_29 | Group3 | A.serrulata |
| Actinobacteria | Catenulisporales | Actinospicaceae | Actinospica | OTU_33 | Group3 | A.nepalensis |
| Actinobacteria | Frankiales | Acidothermaceae | Acidothermus | OTU_39 | Group3 | A.sieboldiana |
| Alphaproteobacteria | Rhizobiales | Beijerinckiaceae | Roseiarcus | OTU_47 | Group3 | A.sieboldiana |
| Gammaproteobacteria | Gammaproteobacteria | Unknown_Family | Acidibacter | OTU_51 | Group3 | A.sieboldiana |
| Gammaproteobacteria | WD260 | uncultured_eubacterium_WD260 | ? | OTU_63 | Group3 | A.sieboldiana |
| Gammaproteobacteria | Gammaproteobacteria | Unknown_Family | Acidibacter | OTU_65 | Group3 | A.sieboldiana |
| Actinobacteria | Frankiales | Acidothermaceae | Acidothermus | OTU_66 | Group3 | A.sieboldiana |
| Actinobacteria | Micrococcales | Microbacteriaceae | ? | OTU_76 | Group3 | A.serrulata |
| Bacteroidia | Chitinophagales | Chitinophagaceae | Chitinophaga | OTU_86 | Group3 | A.nepalensis |

## 4.6 Eukaryotic community variations (I)

Mantel tests revealed that the structure of soil eukaryome is associated with both soil and climate variables. While the structure of fungal and protist communities was strongly related to soil pH, the community structure of animals was mainly related to mean annual precipitation (MAP), soil moisture and fire history (Table 3). More specifically, the community structure of Nematoda was mostly related to MAP and soil pH, whereas that of Arthropoda was mainly related to fire history, MAP, and soil moisture, and Annelida was more influenced by fire history followed by soil moisture (Table 3).

**Table 3.** Spearman Correlations between community dissimilarity (Bray-Curtis) and environmental dissimilarity (Euclidean) based on Mantel tests (I; Table 1).

| Variables | Fungi | Protist | Animal | Nematoda | Arthropoda | Annelida |
|---|---|---|---|---|---|---|
| pH | $0.412^{**}$[1] | $0.407^{**}$ | $0.254^{**}$ | $0.316^{**}$ | $0.169^{**}$ | $0.066^{*}$ |
| Moisture | $0.217^{**}$ | $0.187^{**}$ | $0.300^{**}$ | $0.220^{**}$ | $0.272^{**}$ | $0.222^{**}$ |
| Soil carbon | $0.1603^{**}$ | $0.201^{**}$ | $0.194^{**}$ | $0.150^{**}$ | $0.191^{**}$ | $0.139^{**}$ |
| MAP | $0.269^{**}$ | $0.326^{**}$ | $0.345^{**}$ | $0.319^{**}$ | $0.276^{**}$ | $0.138^{**}$ |
| MAT | $0.297^{**}$ | $0.378^{**}$ | $0.264^{**}$ | $0.242^{**}$ | $0.217^{**}$ | $0.067^{**}$ |
| Aridity index | $0.130^{**}$ | $0.167^{**}$ | $0.054^{ns}$ | $0.085^{*}$ | $0.042^{ns}$ | $0.024^{ns}$ |
| Fire | $0.158^{**}$ | $0.089^{**}$ | $0.298^{**}$ | $0.165^{**}$ | $0.287^{**}$ | $0.324^{**}$ |

[1]Mantel r; **: $p < 0.01$; *: $0.01 < p < 0.05$; Non-significant: ns

The PERMANOVA analysis revealed cross-biome differences in most soil organism groups including fungi (biome effect: $R^2_{adj} = 0.109$, $p < 0.01$), protists ($R^2_{adj} = 0.129$, $p < 0.01$), Nematoda ($R^2_{adj} = 0.127$, $p < 0.01$) and Arthropoda ($R^2_{adj} = 0.098$; $p < 0.01$) but not Annelida (I; Fig. 3). The biome effect was relatively stronger than continent effect for all organism groups (continent effect: fungi, $R^2_{adj}= 0.063$; protists, $R^2_{adj} = 0.066$; animals, $R^2_{adj} = 0.069$; $p < 0.01$).

Eukaryotic microbes and animals also showed contrasting latitudinal gradient of diversity patterns. Shannon index of fungi and protists showed a hump-shaped relationship with absolute latitude (I; Fig. 4). By contrast, Arthropoda and the total animal diversity showed a U-shaped pattern, with the highest diversity in tropical forests (I; Fig. 4), whereas the diversity of Nematoda and Annelida decreased linearly towards poles (I; Fig. 4). Our analysis also showed that larger-bodied organisms exhibited a relatively stronger latitudinal gradient of diversity, compared to microbes (I; Fig. 4).

Among all tested variables, MAP and soil pH were the strongest predictors of fungal diversity ($R^2_{adj} = 0.058$; $p < 0.001$) and protist diversity ($R^2_{adj} = 0.098$, $p < 0.001$), respectively. By comparison, MAP and mean annual temperature (MAT) were the strongest diversity determinants for Arthropoda (MAP: $R^2_{adj} = 0.056$; MAT: $R^2_{adj} = 0.098$; $p < 0.001$), Annelida (MAP: $R^2_{adj} = 0.174$; MAT $R^2_{adj} = 0.035$; $p < 0.001$), and Nematoda (MAP: $R^2_{adj} = 0.127$; MAT: $R^2_{adj} = 0.016$; $p < 0.001$) (Fig. 5).

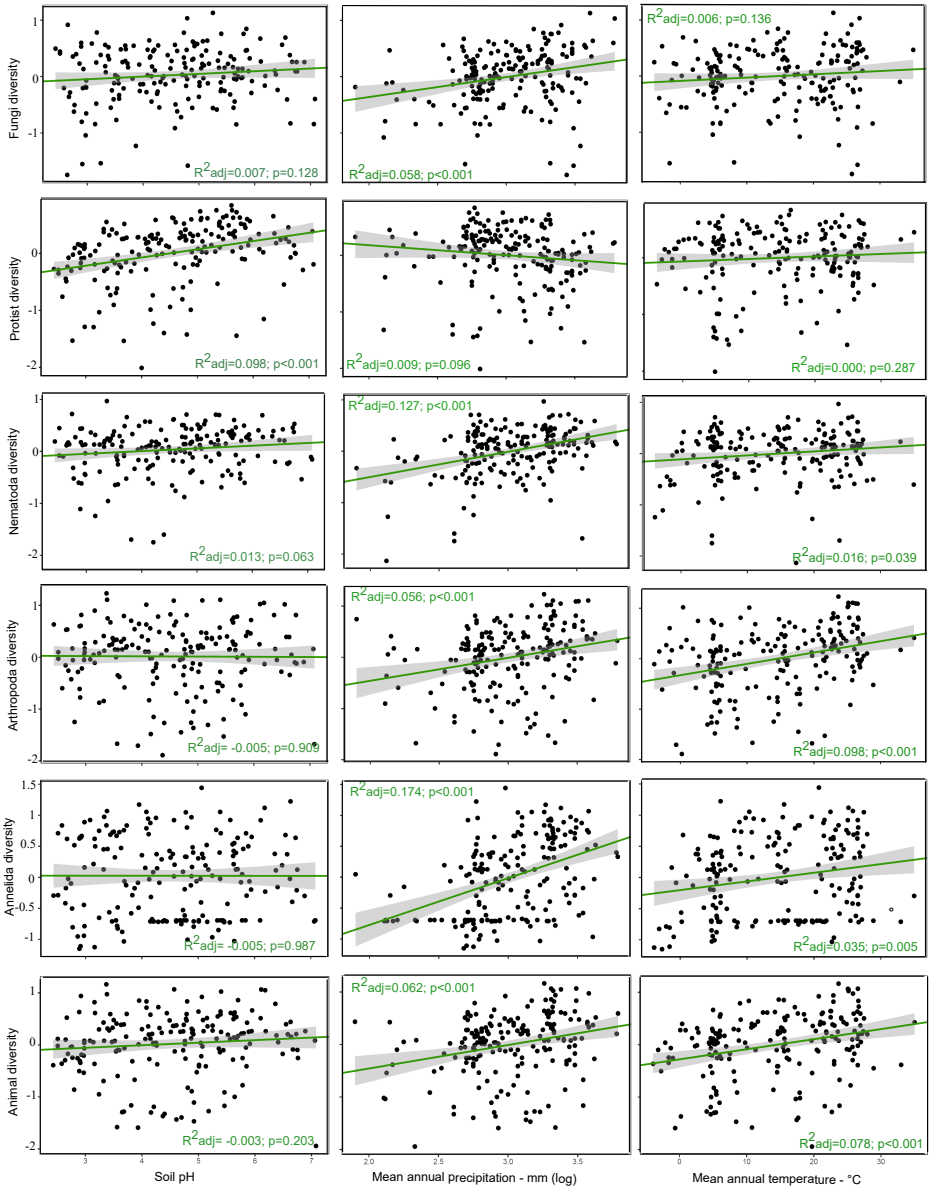


**Figure 5.** The relationships between the diversity of the eukaryotic organisms and environmental gradients (I; Fig. S4).

## 4.7 Effects of ecological processes on community assembly (I)

On average, larger organisms had a narrower niche compared with smaller groups, as reflected in the negative correlation between body size and niche breadth ($r = -0.803$, $p < 0.05$). Our analysis showed that drift was the most important ecological process driving the community assembly of all organism groups. Dispersal was the second most important ecological processes for all organism groups, except for the smallest-bodied groups, Rhizaria and Basidiomycota. Drift affected more strongly animal groups (78.0%, 66.2%, and 75.5% for Annelida, Arthropoda, and Nematoda, respectively) compared with protist groups (47.9%, 65.9%, and 59.7% for Alveolata, Stramenopiles, and Rhizaria, respectively) and fungal groups (44.1% and 38.4% for Ascomycota and Basidiomycota, respectively) (I; Fig. 1). This points to a greater role of drift in shaping animal assemblages compared to eukaryotic microbes (I; Fig. 2a). By contrast, the relative importance of selection was higher for the smaller-bodied organism groups such as fungi (25.9%, 36.6% for Ascomycota and Basidiomycota, respectively) and protists (18.1%, 14.1%, and 20.4% for Alveolata, Stramenopiles, and Rhizaria, respectively) compared with animals (8.9%, 6.7% and 3.7% for Annelida, Arthropoda, and Nematoda, respectively). We found that body size was positively related to drift ($R^2_{adj} = 0.146$, $p < 0.01$) and negatively related to selection ($R^2_{adj} = 0.195$, $p < 0.01$) in community assembly (I; Fig. 1). By contrast, niche breadth was negatively related to drift ($R^2_{adj} = 0.073$, $p < 0.01$) and positively to selection ($R^2_{adj} = 0.115$, $p < 0.01$). Variation partitioning analyses supported this finding: more than 50% of the community structure of microbes (52% and 60% for fungi and protists, respectively) was explained by environmental factors and spatial vectors and their shared effects, whereas a large proportion of the community variation of Annelida (79%), Arthropoda (61%), Nematoda (62%), and all animals (69%) remained unexplained (I; Fig. 2b). Similarly, Mantel tests indicated that fungi and protists were more strongly correlated with environmental dissimilarity matrix (Mantel $r = 0.440$ and $r = 0.512$ respectively; $p < 0.001$) compared with Nematoda ($r = 0.275$; $p < 0.001$), Arthropoda ($r = 0.239$; $p < 0.001$), Annelida ($r = 0.076$; $p < 0.001$), and the whole animal community ($r = 0.315$; $p < 0.001$) (I; Fig. 2c). Nevertheless, the community structure of microbes and animals showed comparable correlations with geographic distance (I; Fig. 2c, Fig. 4).

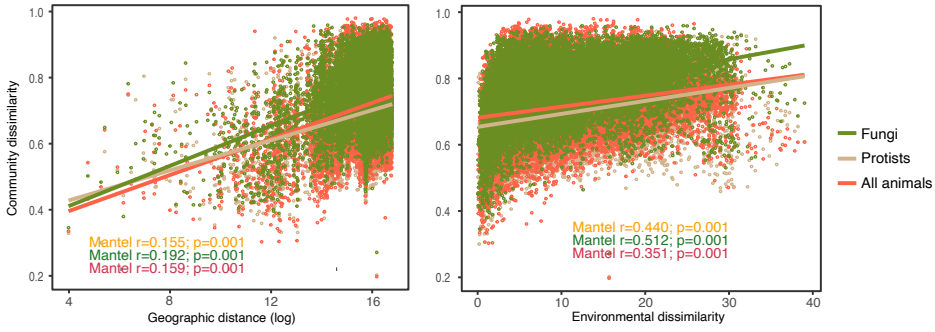


**Figure 6.** Relationships between the dissimilarity of eukaryotic communities (Bray–Curtis) and geographic distance (log) as well as environmental distance (Euclidean distance) (I; Fig. S3).

# 5. DISCUSSION

## 5.1 Plant traits impacts on soil mycorrhizal mediating plant invasion

Several studies have reported contrasting results regarding the effects of mycorrhizal fungi on plant invasion, from significant (Busby et al. 2013) to negligible (Rodríguez-Caballero et al. 2018) effects. Furthermore, there have been different observations regarding the mycorrhizal status of invasive plants and their potential invasiveness. For instance, Menzel et al. (2017) showed that mycorrhizal invasive plants can outcompete Non-Mycorrhizal (NM) invasive plants, whereas NM plant species comprise a greater proportion of invasive plants globally (Pringle et al. 2009). The relationship between mycorrhizae and plant invasion has been the subject of two review articles. Pringle et al. (2009) provided a framework based on the mycorrhizal status of invasive plants and the distribution and availability of mycorrhizae in novel habitats (biogeography and dispersal). The framework facilitates the prediction of invasiveness of an alien plant species based on whether the alien plant is NM, facultative, and flexible, i.e., able to associate with local mycorrhizal fungi in new habitats. In their review, Shah et al. (2009) highlighted the impact of the mycorrhizal status of invasive plants on the nutrient competition between native and invasive plants and the feedback between invasive plants and mycorrhizal fungi. These reviews and most of the research studies focused on the place of origin (invasive status) of plants and mycorrhizal status of invasive plants to explain the mycorrhizae-mediated plant invasion.

We argue that these factors may not be sufficient to explain the potential invasiveness of a plant species and that other drivers may also be at play. We addressed this gap by focusing on research on how plant invasion is mediated by the plant mycorrhizal niche space (PMNS) of both native and invasive species, defined as their potential to exploit and shape the mycorrhizal fungi pool of a habitat depending on their dependence on mycorrhizal fungi status and functional traits. We characterized some biotic factors that influence PMNS. We suggest the relative contribution of mycorrhizal traits, qualitative and quantitative traits of plant species provide an opportunity to develop models to classify plant species into different PMNS. The model could help to predict the plant-to-plant competition in a particular habitat by comparing distance between their PMNS. A better understanding of the factors driving the mycorrhizal niche of plants will inform ecologists about the magnitude and direction of the role of mycorrhizal fungi in plant invasion trajectories as well as the impact of plant invasion on the structure of soil fungal communities in new habitats.

## 5.2 Biotic and Abiotic factors

### 5.2.1 Host impacts on the bacterial community

We evaluated the structure of bacterial communities associated with EcM root tips of *Alnus* species on a global scale, using comparable sampling, molecular analysis and data analysis methods (II). By controlling other factors, the results suggest that *Alnus* species phylogeny not only significantly affect bacterial richness (II; Table 1) but also strongly correlates with bacterial community structure (II; Fig. 4D), indicating the *Alnus* species phylogenetic imprint on bacterial communities associated with their mycorrhizal roots. Similar trends have been observed between phylogenetic relatedness of host plants and plant-associated and free-living soil fungal communities (Tedersoo et al., 2013; Yang et al., 2019; Koyama et al., 2019). In addition, several studies have been shown that host phylogeny is an important determinant of the root-associated bacterial communities (Naylor et al., 2017; Yeoh et al., 2017).

Plant phylogeny also appears to be the main determinant of *Alnus*-associated EcM fungal and root nodulating *Frankia* actinobacterial community structure (Põlme et al., 2013, 2014). However, the observed effect on mycorrhiza-associated bacteria is relatively weaker compared with these effects on the structure of EcM fungi (43%) and Frankia (37%) (Põlme et al., 2013, 2014). Such differences in the magnitude of host effects can be explained by two phenomena: both EcM fungi and *Frankia* form intimate relationships with host plants; and EcM fungi of *Alnus* are exceptional in their high reciprocal partner specificity in EcM symbiosis in general (Tedersoo et al., 2009; Wang et al., 2019). Other studies have similarly reported a stronger plant host control over root- and soil-associated fungal communities than bacterial communities (Barberán et al., 2015; Burns et al., 2015; Bergelson et al., 2019). The association between phylogenetic relatedness of *Alnus* species and the structure of root-associated microbial communities could be attributed to the similarities in genes responsible for plant immunity and root morphology (Bergelson et al., 2019) and also in phylogenetically related functional traits (Wang et al., 2019). Taken together, phylogenetic signals from *Alnus* species explained a significant proportion of root-associated microbiome structure, although the magnitude of host phylogeny effects depended on the microorganism groups.

We also found an association between EcM fungal phylogeny and the structure of bacterial communities (II; Fig. 5C and 5D). There is inconsistency among studies that have evaluated the structure of the bacterial communities inhabiting EcM root tips. Some studies reported a significant influence of EcM fungi in determining the assembly of bacterial communities (Nguyen and Bruns, 2015; Izumi and Finlay, 2011; Uroz et al., 2007), whereas others found no variations between bacterial communities associated with different EcM fungal species (Uroz et al., 2012; Bruke et al., 2008). These studies have been conducted on only one host plant species in relatively small sampling areas in different ecosystems. Furthermore, host plant genetic, growth stage and environmental variations, such

as N content (Marupakula et al., 2016, 2017) could alter the EcM fungi effects on their associated bacterial communities. For instance, the effects of some particular EcM fungi disappeared in illuvial soil with higher N content (Marupakula et al., 2017).

Despite EcM-associated bacteria being most closely associated with fungal hyphae and directly nourished by plant exudates modified by EcM fungi, the correlation strength for bacteria and EcM fungi was much lower than for bacteria and *Alnus* species phylogeny. Phylogenetically distant EcM fungi offer distinct nutrient-rich hot spots for their associated bacterial symbiosis by creating various chemical properties and releasing different secondary metabolites (Pent et al., 2020). These contrasting phylogenetic-related chemical characteristics of fungal species enable them to harbor different bacterial communities to support their functional roles in ecosystems (Uroz et al., 2007; Pent et al., 2020). In our study, EcM fungal effects, at least partly, might be confounded with the strong effects of *Alnus* species in driving root-associated EcM fungal communities (Polme et al., 2013), meaning that it is unlikely that Alnus species independently influence EcM fungal and bacterial communities. *Alnus* species have been shown to determine EcM fungi, as microbial hubs (Agler et al., 2016), which in turn affect the bacterial communities. Therefore, ectomycorrhizosphere may also mediate the *Alnus* phylogeny effects on bacterial communities. Moreover, root-associated fungi could alter root architecture (Ditengou et al., 2015) and the chemical profile of plant root exudates, which in turn alter the bacterial communities (Huang et al., 2014). In such a complex system, it remains unknown what the pure effect of each host is, but our results demonstrate the importance of phylogenetic relatedness of hosts, whether *Alnus* or EcM fungi on the assembly of their associated bacterial communities.

*Alnus* species and EcM fungi harbor bacterial communities from the soil microbiome reservoir, which is in turn are shaped by abiotic variables especially soil pH (Philippot et al., 2013; Bahram et al., 2018; Erlandson et al., 2018). Not surprisingly, edaphic variables were the second most important factor determining bacterial structure and richness. The general trend is like associations between these variables and soil bacterial diversity, but the strength of relationships is much weaker in the root, compared to soil-associated bacteria (Zhalnina et al., 2015; Bahram et al., 2018), possibly because of the confounding effect of biotic factors. This finding corroborates previous studies indicating that the structure of root-associated bacterial communities is less affected by soil conditions because of heterogeneous microenvironment provided by root exudates, root immune system, plant hormones and ectomycorrhizosphere (Lebeis et al., 2015; Lareen et al., 2016; Hu et al., 2018; Zhalnina et al., 2018).

Network analysis revealed significant co-occurrence patterns for three groups of OTUs, which consisted of thirty, sixteen and thirteen abundant taxa. The relative abundance patterns showed that OTUs within each group associated with specific *Alnus* species (host preference clusters), but this was not the case for EcM fungi. This evidence corroborates the capability of the *Alnus* species to select bacterial communities, and also indicates host preference of most abundant

bacterial taxa. At the bacterial family level, there are only a few overlapping taxa between host preference clusters: *Beijerinckiaceae* and *Chitinophagaceae* were common families in group one and three, and *Burkholderiaceae* family were found in all three clusters (Table 2). The host preference of bacterial taxa could be related to their particular functions in the *Alnus* species as plant selection of bacterial community is based on the functional traits of bacteria rather than their taxonomic structure (Yan et al., 2017). For instance, species of *Sphingomonadaceae* family are known to be able to enhance plant growth under various abiotic stresses such as salinity and drought (Asaf et al., 2020) and *Flavobacteriaceae* spp. tend to enhance plant defense (Kolton et al., 2014). Species of *Burkholderiaceae* are known to increase disease resistance by producing antimicrobial compounds against plant pathogens (Riera et al., 2017) and express genes encoding host plant resistance (Zhang et al., 2017), and certain families (e.g., *Xanthobacteraceae*, *Halomonadaceae* and *Rhizobiacea*) are putative N-fixers. These data suggest that *Alnus* species associate with both nodulating Frankia actinobacteria and certain free-living EcM-associated proteobacteria that have a capacity to fix atmospheric N. The contribution of these free-living bacteria to their host's N budget in the mycorrhizosphere remains to be determined. Taken together, co-occurrence of root-associated bacterial phylotypes could be attributed to the selective power of host plant and host preference of bacterial taxa.

### 5.2.2 Abiotic impacts on soil eukaryotes

Our global study indicates that biome type, climate, soil factors, and fire history may all affect the eukaryome structure, but their impact differs among major groups of organisms. All studied soil organism groups (except Annelida) exhibited differences in community structure across biomes, but the effect of continents was relatively weaker, supporting the importance of climate and vegetation type in shaping the eukaryome (Bahram et al., 2020; van den Hoogen et al., 2019; Nielsen et al., 2010; Oliverio et al., 2020; Tedersoo et al., 2014; Wilschut et al., 2019).

Our results suggest that organism groups with different body sizes and niche breadths respond differently to environmental variables. The community structure of microbial groups was affected more strongly by soil pH, whereas MAP, soil moisture, and fire history were the main determinants of animal groups (Table 3). Microbial responses to environmental variables have also been shown to depend on gross morphology and microbial domain (Daws et al., 2020). Other studies have reported different environmental variables underlying the distribution of bacteria and fungi (Bahram et al., 2018), as well as between bacteria and protists (Oliverio et al., 2020; Xiong et al., 2021). Thus, it is tempting to speculate that traits such as body size and thereby niche breadth may determine how soil organisms respond to environmental change.

Different groups of small eukaryotes differed in diversity patterns in relation to latitude (I; Fig 4), which are partly related to the prevalence of different edaphic

and climatic predictors of diversity (Fig. 3). Similarly to aboveground macroorganisms (Gaston, 2000) and in line with the known effect of climate on soil animal diversity (Bastida et al., 2020), soil animal diversity increased towards the equator with increasing MAT and MAP. Conversely, the diversity of protists was mainly driven by soil pH, which is only weakly related to latitude. Similarly, a regional-scale study demonstrated that soil properties, particularly soil pH, determined soil microbial diversity but not animal diversity (George et al., 2019). Furthermore, there was a positive relationship between the strength of latitudinal diversity gradient and body size, which corroborates previous meta-analyses on a wide range of organisms (Hillebrand & Azovsky, 2001; Kinlock et al., 2018). Taken together, both the shape and strength of the latitudinal diversity gradient appear to depend on organisms' body size and their associations with environmental variables.

## 5.3 Niche and neutral processes

Our data indicate that the relative effects of ecological processes differ among organism groups within the soil eukaryome, which could be partly ascribed to the differences in body size as well as niche breadth. Despite their wider niche breadth and smaller body size, the community structure of fungi and protists was determined more strongly by deterministic processes (heterogeneous and homogeneous selections) compared with animals. This finding suggests that microbes with broader niches may be able to adapt to broader ranges of environmental conditions globally (Lennon et al., 2012). In line with this result, deterministic processes showed relatively stronger effects on the assembly of bacterial communities, with higher dispersal rate, compared to fungal communities (Powell et al., 2015). Higher dispersal rates along with more rapid population growth rates, resulting from a smaller body size, can lead to relatively stronger deterministic processes, through better abilities to arrive at new habitats and faster establishment. In addition, smaller organisms respond more rapidly to environmental change (Korhonen et al., 2010; Vellend et a., 2014). By contrast, a lower dispersal rate may hamper species to colonize various environmental conditions and thus reduce the effects of environmental selection on community assembly (Leibold et al., 2004). Compared to microbes, animals are known to be less abundant and diverse in soils (Decaëns, 2010), which may contribute to the greater stochasticity in their community structure (Jia et al., 2018) due to their narrower niches (Hanson et al., 2012). Alternatively, larger-bodied, less abundant, and less widespread organisms are probably more prone to extinction (Fodelianakis et al., 2021) and thus show more stochastic distribution patterns compared to smaller-bodied taxa (De Bie et al., 2012; Nemergut et al., 2013; Zinger et al., 2019).

Several studies have shown that larger-bodied organisms with narrower ecological niches are more strongly affected by deterministic processes (Chen et al., 2021; Farjalla et al., 2012; Luan et al., 2020; Soininen et al., 2013). Different ecosystems, geographical scales, and statistical approaches may affect the

relative importance of community assemblage processes (Evans et al., 2017; Forbes & Chase, 2002; Hanson et al., 2012; Ladau & Eloe-Fadrosh, 2019; Zhou & Ning, 2017). At the local scale, smaller organisms with higher dispersal rates are commonly ubiquitous and their community assembly is governed by stochastic processes due to small environmental gradients (Bahram et al., 2016). By contrast, broader environmental gradients and more diverse vegetation types could result in stronger environmental filtering of organisms with wider niche breadth.

## 5.4 Limitations of study

We note that accurate estimates of ecological processes remain a challenge because of the complexity of natural communities and their interactions as well as methodological limitations in inferring these processes. There are several limitations to inferring the relative importance of ecological processes using null-model-based approaches. The results may vary depending on null model algorithms, similarity metrics for randomization, selection of arbitrary thresholds between observed community dissimilarity, and the mean of the null distribution, spatial scale, and regional species pool (Ning et al., 2019). Therefore, the results should be cautiously interpreted on a relative basis (Zhou & Ning, 2017) such as our relative comparison among organism groups.

We also note that since null model-based β-deviation might be influenced by sampling effort (Bennett & Gilbert, 2016; Xing & He, 2021), we performed null model tests with and without rarefaction. Although rarefication led to the overestimation of drift processes, we observed very similar patterns (Fig. 7). It is in line with a previous study showing that rarefication, as a random sub-sampling process, added artificial stochasticity to the results of the iCAMP framework, compared to the original communities (Ning et al., 2020). Sampling effort might also have an effect on the variations and assembly mechanisms of animal communities, especially for low abundant groups (Jia et al., 2018; Lynch & Neufeld, 2015). In addition, some limitations regarding the used primers and sequencing depth in uncovering certain eukaryotic groups (Tedersoo et al., 2015), especially the low resolution of 18S region for targeting animal groups (de Groot et al. 2016) may contribute to higher stochasticity in community assembly of animal groups. 16S and 18S rRNA sequencing allow us to detect organism groups only at the coarse taxonomic levels, which is a limitation to explore distribution patterns at the genus and species levels. More sampling sites, sequencing depth and resolution together with experimental studies are needed to obtain more confident results for a global-scale assessment.

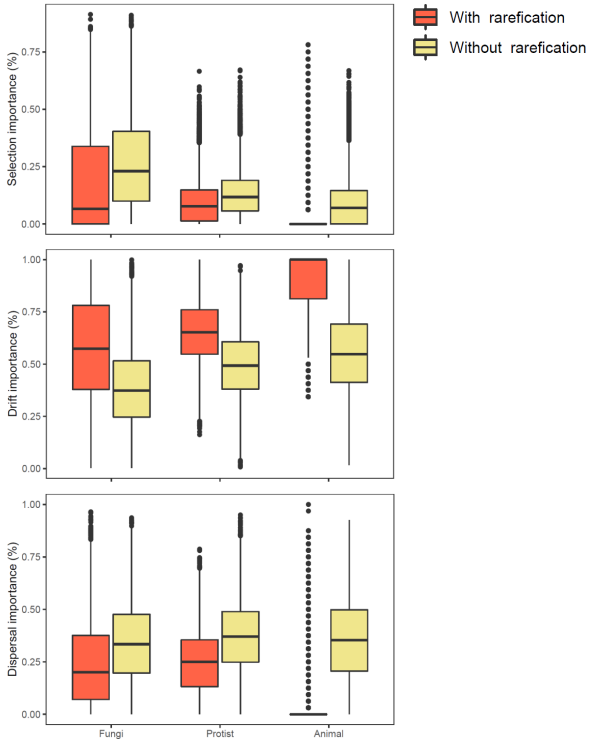


**Figure 7.** The importance of ecological processes in the community assembly of fungi, protist and animal with and without rarefication (I; Fig. S5).

Further, an adequate phylogenetic signal is necessary for the null model-based approach to infer ecological processes (Stegen et al., 2012, 2013). Within-bin phylogenetic signal test showed that the phylogenetic distance of most (but not all) of the bins of organism groups significantly correlated with the Euclidean distance matrix of at least one environmental factor (I; Table S2). In the previous study with simulated microbial communities, iCAMP showed robustness to this level of low phylogenetic signal, and the accuracy and precision were still adequate (>0.8) although indeed reduced (Ning et al., 2020).

# 6. CONCLUSION

My thesis provides evidence for plant-belowground interactions, as well as soil eukaryome variations over environmental and spatial changes at large scale studies. The main conclusions from these studies follow.

- We introduced PMNS as a plant's ability to exploit and shape the mycorrhizal fungal pool depending on its dependency on mycorrhizal fungi association status and, plant functional traits. PMNS of plant species may enable us to better predict soil mycorrhizal fungi communities in a particular habitat (III).

- Our observational study on the root tips of *Alnus* species demonstrates the associations between plant phylogenetic distance and their microbial community variation. The *Alnus* phylogeny effect on the associated bacterial community structure was weaker compared with that on EcM fungi and *Frankia* (Põlme et al., 2013, 2014), which we attribute to more intimate associations in the latter groups and the potentially blurring effect of EcM fungal species (II).

- Co-occurrence of root-associated bacterial phylotypes could be attributed to the selective power of host plant and host preference of bacterial taxa (II).

- In contrast to soil, biotic variables were relatively more important in shaping root-associated bacterial communities (II).

- Our global survey suggests that drift is a key ecological process in shaping global community assembly of soil eukaryotes, but its relative strength depends on functional traits such as organism's body size and niche breadth. These functional traits also determine the strength and direction of the association of soil organism groups to environmental effects and latitude (I).

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# SUMMARY

Distribution of belowground biodiversity in response to changes in biotic and abiotic factors is critical not only for protecting these communities but also for predicting their potential responses to environmental changes. Belowground microbial and animal organism groups significantly regulate aboveground biodiversity and the functioning of terrestrial ecosystems. Despite this, our knowledge on belowground biodiversity still is much less than aboveground than diversity and structure of aboveground communities. My thesis focused on the role of both biotic (e.g., phylogeny and traits of plant and ectomycorrhizal species) and abiotic factors in belowground biodiversity. By conducting review and research studies, we examined how spatial, environmental, and plant species changes affect the belowground composition and diversity and what ecological processes underlie the community variations in association with organism functional groups. We introduced plant mycorrhizal niche space (PMNS) as a plant's ability to exploit and shape the mycorrhizal fungal pool depending on its dependency on mycorrhizal status and plant functional traits. We provide a model to classify plant species into different PMNS, helping to predict soil mycorrhizal fungi community in a particular habitat by comparing PMNS distance between plant species. Further, we aimed to determine the relative contributions of *Alnus* species and their associated mycorrhizal fungi, spatial, edaphic and climatic factors to the structure of root-associated bacterial communities. We used high-throughput identification of bacteria based on 369 ectomycorrhizal root tips of 19 *Alnus* species from 85 sites across the globe. We found that the *Alnus* species phylogeny was the primary determinant for the composition of root-associated bacterial communities, followed by edaphic, spatial and climate variables. In addition, we found *Alnus* species-specificity for some highly abundant bacterial phylotypes. We also conducted a molecular analysis of 193 composite soil samples spanning the world's major biomes to provide a holistic understanding of the processes shaping the global distribution of soil fungi, protists, and animals (i.e., the eukaryome). Our analysis showed that the importance of selection processes was higher in the community assemblage of smaller-bodied and wider niche breadth organisms. Soil pH and mean annual precipitation were the primary determinants of the community structure of eukaryotic microbes and animals, respectively. We further found contrasting latitudinal diversity patterns and strengths for soil eukaryotic microbes and animals. Taken together, this thesis shows the role of plant functional traits in structuring soil mycorrhizal communities mediating plant-to-plant competition such that there is a negative relation between the similarity of PMNS and the role of mycorrhizal fungi in plant invasion and alteration of mycorrhizal fungi following invasion. It also highlights the importance of biotic variables in shaping root-associated bacterial communities and shows that different processes underlie root-associated and soil bacterial communities on a global scale. Finally, our results point to a potential link between body size and niche breadth in soil eukaryotes and the relative effect of ecological processes and environmental factors in driving their biogeographic patterns.

# SUMMARY IN ESTONIAN

## Mullaorganismide biogeograafia

Maa-aluse bioloogilise mitmekesisuse jaotumine vastavalt biootiliste ja abiootiliste tegurite muutustele on kriitilise tähtsusega mitte ainult nende koosluste kaitsmiseks, vaid on oluline ka prognoosimaks, kuidas need kooslused keskkonnamuutustele võivad reageerida. Maa-alused mikroobsete ja loomsete organismide rühmad reguleerivad maapealset bioloogilist mitmekesisust ja maismaaökosüsteemide toimimist. Sellest hoolimata on meie teadmised maa-alusest bioloogilisest mitmekesisusest palju väikesemad kui teadmised maapealsete koosluste mitmekesisuse ja struktuuri kohta. Minu doktoritöö keskendub nii biootiliste (nt taimede ja ektomükoriissete seeneliikide fülogenees ja tunnused) kui ka abiootiliste tegurite rollile maa-aluses elurikkuses. Vaatluslikke ja rakenduslikke uuringuid tehes tuvastasime, kuidas ruumi-, keskkonna- ja taimeliikide muutused maa-aluseid kooslusi ja elurikkust mõjutavad ning millised ökoloogilised protsessid on organismide funktsionaalrühmadega seotud koosluse varieeruvuse aluseks. Võtsime kasutusele taimede mükoriisa niširuumi (PMNS – *plant mycorrhizal niche space*) mõiste, mis tähistab taimede võimet kasutada ja kujundada mükoriissete seente kogumit, olenedes selle sõltuvusest mükoriisa staatusest ja taime funktsionaalsetest tunnustest. Lõime mudeli, mille järgi taimeliigid erinevatesse PMNS-idesse jaotada, aidates taimeliikide vahelise PMNS-i kauguse võrdluse abil ennustada mullas leiduvate mükoriissete seente kooslust konkreetses elupaigas. Lisaks seadsime eesmärgi määrata kindlaks perekond lepp (*Alnus*) liikide ja nendega seotud mükoriissete seente, ruumiliste, edaafiliste ja klimaatiliste tegurite suhtelise panuse juurtega seotud bakterikoosluste struktuuri. Kasutasime bakterite määramiseks suure läbilaskevõimega sekveneerimismeetodit. See analüüs hõlmas üle maailma 85 kohast kogutud 19 lepaliigi 369 ektomükoriisset juuretippu. Leidsime, et lepaliikide fülogenees oli juurtega seotud bakterikoosluste peamine mõjutaja, millele järgnesid edaafilised, ruumilised ja klimaatilised muutujad. Lisaks leidsime, et mõned arvukad bakterite fülotüübid on liigispetsiifilised teatud lepaliikidele. Samuti viisime läbi maailma suurematest bioomidest kogutud 193 liitmullaproovi molekulaaranalüüsi, et anda terviklik arusaam protsessidest, mis kujundavad mullaseente, protistide ja loomade (ehk kokkuvõttes eukarüoomi) globaalset levikut. Meie analüüs näitas, et valikuprotsesside olulisus oli suurem väikesemate ja laiema nišiulatusega organismide kooslustes. Mulla pH ja aasta keskmine sademete hulk olid vastavalt eukarüootsete mikroobide ja loomade koosluste struktuuri peamised määrajad. Tuvastasime, et eukarüootide rühmadel võivad esineda vastandlikud mitmekesisuse mustrid laiuskraadi grandiendil. Käesolev doktoritöö näitab taimede funktsionaalsete tunnuste rolli mulla mükoriissete koosluste struktureerimisel, mis vahendavad taimedevahelist konkurentsi nii, et eksisteerib negatiivne seos PMNS-i sarnasuse ja mükoriissete seente rolli vahel. Samuti rõhutab doktoritöö biootiliste muutujate olulisust juurtega seotud bakterikoosluste kujundamisel ja

näitab, et globaalses mastaabis on juurtega seotud ja mullabakterite koosluste aluseks erinevad protsessid. Meie tulemused osutavad ka potentsiaalsele seosele mulla eukarüootide keha (raku) suuruse ja niši laiuse vahel ning nende biogeograafilisi mustreid juhtivate ökoloogiliste protsesside ja keskkonnategurite suhtelise mõju vahel.

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# PUBLICATIONS

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2018–2022 Botany and Mycology, University of Tartu, Ph.D.
2012–2015 Weed Science, Universiti Putra Malaysia (UPM), Ph.D.

**Employment**

2016–2018 Universiti Putra Malaysia (UPM), Postdoctoral Researcher
2012–2015 Universiti Putra Malaysia (UPM), Research Assistant

**Scientific Publications**

Gohar, D., Põldmaa, K., Tedersoo, L., **Aslani, F.,** Bahram, M. 2022. Global diversity and distribution of mushroom-inhabiting bacteria. *Environmental Microbiology Reports.* https://doi.org/10.1111/1758-2229.13045.

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- 2019 Dora Plus mobility scholarship
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**Toetused ja stipendiumid**

- 2019 Dora Pluss Tegevus
- 2017 Geran Putra Berimpak (GP-IPB), Research Management Centre (RMC), UPM
- 2017 The Higher Institution Centers of Excellence (HICoE), Ministry of Higher Education (MOHE), Malaysia
- 2017 Fundament al Research Grant Scheme (FRGS), Ministry of Education (MOE), Malaysia
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- 2022 Reaalteaduste doktorantide konverents, Voore, Estonia
- 2019 HTS/Sangeri DNA järjestuste andmekogumite tuvastamine ja avaldamine, Dragør, Denmark

# DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
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4. **Andres Mäe**. Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
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