Low root functional dispersion enhances functionality of plant growth by influencing bacterial activities in European forest soils

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Summary

Current studies show that multispecies forests are beneficial regarding biodiversity and ecosystem functionality. However, there are only little efforts to understand the ecological mechanisms behind these advantages of multispecies forests. Bacteria are among the key plant growth-promoting microorganisms that support tree growth and fitness. Thus, we investigated links between bacterial communities, their functionality and root trait dispersion within four major European forest types comprising multispecies and monoculture plots. Bacterial diversity revealed no major changes across the root functional dispersion gradient. In contrast, predicted gene profiles linked to plant growth activities suggest an increasing bacterial functionality from monospecific to multispecies forest. In multispecies forest plots, the bacterial functionality linked to plant growth activities declined with the increasing functional dispersion of the roots. Our findings indicate that enriched abundant bacterial operational taxonomic units are decoupled from bacterial functionality. We also found direct effects of tree species identity on bacterial community composition but no significant relations with root functional dispersion. Additionally, bacterial network analyses indicated that multispecies forests have a higher complexity in their bacterial communities, which points towards more stable forest systems with greater functionality. We identified a potential of root dispersion to facilitate bacterial interactions and consequently, plant growth activities.

Introduction

The increased demand for forest goods like timber and the subsequent human interventions have led to drastic changes of forest ecosystems. For instance, more monocultures than multispecies forest plantations have been established (Liu et al., 2018). To evaluate how this reduction of tree species richness affects forest functionality, many studies analysed biotic and abiotic interactions, biodiversity and ecosystem processes that support the provision of ecosystem services (Nelson, 2013). However, fewer attempts have been made to understand the underlying mechanisms (Morin et al., 2011; Forrester and Bauhus, 2016). There are even fewer studies investigating how forest functionality relies on microbial diversity (Brockerhoff et al., 2017; Chen et al., 2020), although soil bacterial communities and their gene pools impact forest functionality (Lladó et al., 2018; Mercado-Blanco et al., 2018). Some of the important bacterial-borne genes maintaining forest functionality are related to nutrient turnover and improved tree performance during biotic and abiotic stress (Terhonen et al., 2018; Sui et al., 2019; Puri et al., 2020). The importance of soil bacteria to support tree fitness, health and nutrition is commonly accepted, e.g. some bacterial groups act as tree growth promoters through phytohormones synthesis, nitrogen fixation, phosphate solubilization, synthesis of siderophores, or reduction of ethylene levels (Mercado-Blanco et al., 2018). Therefore, different molecular approaches,
such as analysis of functional gene markers, metagenomic shotgun sequencing, or functional predictions inferred from 16S gene sequencing have been used to characterize bacterial functionality in different ecosystems (Morales et al., 2010; Lammel et al., 2015; Dukunde et al., 2019; Escalas et al., 2019; Lajoie et al., 2019; Song et al., 2019). Such approaches increasingly focus on the taxonomical and functional diversity of tree microbiomes (Terhonen et al., 2018; Terhonen et al., 2019). But despite the high amount of studies analysing bacterial diversity and composition in forest soils, very few link bacterial functionality and tree traits to reveal mechanistic effects (Barberán et al., 2015; Hanif et al., 2019; Shigyo et al., 2019; Chen et al., 2020).

Tree species modify their environment through their trait expressions, which in turn alter bacterial communities and their impacts on forest functionality (Pei et al., 2016; Eisenhauer and Powell, 2017; Khilfa et al., 2017). For instance, tree root rhizodepositions and root necromass supply the bacterial nutrient cycling (Eisenhauer et al., 2017; Leisso et al., 2017; Lopez et al., 2020; Tian et al., 2020). Likewise, abiotic factors such as topography, soil nutrients and water availability apply selecting pressures on roots leading to belowground tree species trait differentiation (Gratani, 2014; Mori et al., 2019). Different expression of tree traits such as root diameter, root tissue density (RTD) or specific root length (SRL) can induce different associations between trees and soil bacteria (Merino-Martin et al., 2020). For example, the proportion of total photoassimilates released as root exudates vary from 20% to 80% according to root trait expression (Saleem et al., 2018). This affects bacterial colonization and biofilm formations, which has cascading effects on tree health and performance (Noirot-Gros et al., 2018). Root traits reflect a fine adaptation to environmental conditions and therefore many root traits may coexist at each location, thus divergent root trait compositions are observed among different tree communities (Schellenberger Costa et al., 2017). It is assumed that high root trait divergence reflects increased soil heterogeneity and the emergence of multiple stable niches for bacterial communities (Curd et al., 2018; Dukunde et al., 2019). Therefore, different root trait expressions in a particular space can potentially host different bacterial taxa, which may proportionally contribute to higher bacterial functionality (White, 2019; Vieira et al., 2020).

In general, functional diversity is defined as ‘the value and the range of those species and organismal traits that influence ecosystem functioning’ (Tilman, 2001; Laureto et al., 2015). Functional diversity considers organisms as dynamic entities that interact with each other and react to their environment (Calow, 1987; Laureto et al., 2015). Within the functional diversity framework, the ecological functional dispersion (FDIs) metric represents a measure of functional similarity amongst the dominant community members (Villéger et al., 2010). A high dispersion reflects a high grade of niche differentiation, which can decrease the competition (Mason et al., 2005). For example, species that differ in resource use, raise niche complementarity and will allow more complete use of the resources available within a community with less competition for similar niches, thus leading to higher productivity and invasion resistance (Petchey, 2003; Mason et al., 2005).

In the present study, we considered root-functional dispersion (R-FDIs) to be an explanatory value of the deterministic effects of tree species composition on bacterial communities. Furthermore, we considered that within these bacterial communities, the abundance of genes with effects on plant performance is a proxy for bacterial functionality. Based on this double assumption, this study aimed at analysing how tree root-functional dispersion affects soil bacterial communities and their functionality. We approached this question by characterizing tree root traits of 34 European multispecies and corresponding monospecific forest plots to define an R-FDIs index. Using Illumina sequencing from 16S, we then correlated the R-FDIs to soil bacterial communities and their functional gene profiles deduced from an in silico analysis. Moreover, we identified the most important bacterial taxa related to the maintenance of tree health and fitness.

**Results**

**Bacterial abundances and diversity across the functional dispersion**

Bacterial relative abundances across the R-FDIs gradient in forest mixtures were the highest for *Proteobacteria* and *Acidobacteria* (Fig. 1A), followed by *Actinobacteria*, *Verrucomicrobia* and *Bacteroidetes*, which showed similar relative abundances with increasing R-FDIs. However, bacterial abundance variation was dynamic around 1.2 and 2 of the R-FDIs (Fig. 1A). The observed bacteria operational taxonomic unit (OTU) richness and Shannon diversity related to the R-FDIs increased from monospecific to multispecies stands and also within the multispecies stands (Fig. S3). The individual Shannon diversities at the phylum level revealed an increasing trend of Shannon diversity of *Acidobacteria*, *Chloroflexi* and *Bacteroidetes* but were only weakly related to R-FDIs (Fig. 1B).

**Bacterial functionality across root functional dispersion**

Bacterial functionality ($M_{\text{average}}$) increased from monospecific to multispecies stands (Fig. S4). However, the highest gene abundance was reached at low R-FDIs values of the multispecies forest stands, for both the
individually considered bacterial genes (Fig. S5) and the bacterial multifunctionality indices ($M_C$, $M_N$, $M_P$, $M_S$, $M_{Abiotic}$ and $M_{Biotic}$, or $M_{overall}$; Fig. S6). In addition, for all gene groups, an increase in R-FDis values leads to a decrease of bacterial functionality (Fig. 2). We found significant Spearman correlations between the R-FDis and the $M_{overall}$ (Rho = -0.34, $p = 0.04$), as well as for $M_C$, $M_P$ and $M_{Abiotic}$ and $M_{Biotic}$.

**PGPA-related bacterial functionality affected by tree species richness, root functional dispersion (R-FDis) and tree plot composition**

Figure 3A shows the bacterial functionality or tree multispecies stands sorted by R-FDis. In general, plots with lower R-FDis had higher bacterial functionality. It appeared that when the forest plot composition stimulated the abundance of a particular plant growth-promoting activity (PGPA; $M$ indices), all the other PGPA exhibited this similar trend. An exception was the abundance of genes related to the S cycle, which displayed contrasting results for very high or low R-FDis. Our models indicated that the tree plot composition had a significant effect on the $M_{overall}$, whereby each gene group supported tree fitness, health and nutrition, by substantially decreasing Akaike information criterion (AIC) values (>10 units) compared with the effect of the tree richness or R-FDis (Table S1). Evaluating the effect of tree species richness or R-FDis as unique fixed variables on gene functionality, we found a weak response. However, when we used these two variables together in our model, the model significance improved. Moreover, our models indicated that C, P, abiotic and biotic stressor genes responded positively to tree species richness and R-FDis, but genes associated with S, and N cycles responded to a lesser extent. In addition, we found a significant effect of evergreen proportion trees in the plot on all the $M$ indices (Table S1). The results indicate that the higher proportion of evergreen trees negatively influence the bacterial functionality (Fig. S7). Since the relevance of tree composition on gene PGPA abundances was revealed, Fig. 3B shows the respective monospecific bacterial functionality arranged by $M_{overall}$. The higher values are related to C, P and S. Moreover, some of the monospecific stands had higher abundances than their respective mixture plots.

**Bacterial taxa involved in multifunctionality and their composition under forest systems**

We identified the bacterial communities with significantly different abundances under small and great $M_{overall}$. From a total of 25221 bacterial OTUs only 1.4% showed a differential abundance. Plots with small $M_{overall}$ were associated to higher number of differential OTUs, 226 compared with 129 OTUs in great $M_{overall}$ plots. The phylum Proteobacteria accounted for the highest number of OTUs and the phyla Spirochaetae, Latescibacteria, Ignavibacteria, Gall 15, Fibrobacteres, Elusimicrobia and Cyanobacteria just accounted for one OTU. In general, for each phylum the small $M_{overall}$ stands showed a higher number of differential OTUs than great $M_{overall}$ stands, but the phyla Spirochaetae, Planctomycetes, Latescibacteria, Gemmatimonadetes, Elusimicrobia, Cyano-bacteria and Chloroflexi showed higher differential OTUs with great $M_{overall}$ (Fig. 4).

Community composition of preselected bacterial OTUs was performed as network analysis (Fig. 5; Table 1).
network indicated a high connectance for multispecies compared with monospecific forest stands. This overall level of connectivity of tree multispecies plots was reflected by the higher number of edges within the network of the multispecies forest stands. The clustering coefficient was also higher in the multispecies forest, especially in stands with low R-FDis. In addition, we found more totally isolated plots amongst the monospecific forest stands. This analysis revealed a higher complexity of multispecies forest stands than of monospecific ones. However, within the multispecies forest stands, the complexity was higher in low R-FDis plots, and subsequently in plots with high and medium R-FDis values respectively. Our cluster detection analysis for multispecies showed nine groups with a modularity of 0.29 and three totally isolated plots, and monospecific stands 12 groups with a modularity of 0.42 and six totally isolate plots (Fig. S8). We found correlations between R-FDis and linkage density ($r = 0.44, p < 0.001$). In addition, we identified correlations between linkage density with the $M_{overall}$ ($r = 0.33, p < 0.001$). The analysis of similarities (ANOSIM) results showed that forest type ($R = 0.4561, p = 0.001$) and plot composition ($R = 0.2768, p = 0.001$) shaped the bacterial community compositions, and the effects of forest system and R-FDis were not significant.

**Discussion**

**Bacterial communities and R-FDis**

Our study evaluated soil bacterial communities from four different forest types under varying environmental conditions, which cover a broad range of root traits of common European trees. This gradient of R-FDis did not show significant correlations with the bacterial relative abundances or its diversity considering the eight dominant phyla. These missing relationships could be an indication of confounding effects by other factors strongly affecting bacterial diversity such as annual precipitation, soil organic matter, pH and nutrient availability (Uroz et al., 2016; Tian et al., 2018). Alternatively, the diversity of tree-associated soil bacteria can rather be influenced by tree species identity than by tree species richness (Chen et al., 2019; Dukunde et al., 2019). Our results complement this existing knowledge by adding that an increasing dissimilarity of absorptive roots traits does not per se alter bacterial diversity. Thus, a divergent root system also needs an appropriate root trait combination to improve bacterial biodiversity. However, we found a positive trend with increasing bacterial abundance and diversity from monospecific to multispecies forest plots. This finding indicates that soil bacterial diversity is sensitive to shifts in root trait expressions, since root trait expressions vary from...
homo- to heterogeneous in multispecies forests. Likewise, a homogeneous root expression reduces the bacterial recruitment in monospecific forests and can be linked to reduced utilization of soil nutrients and a general lower nutrient availability for trees (Pretzsch et al., 2017; Wu et al., 2019). Several studies reported that homogeneous root exudation patterns cause soil acidification and excessive release of substances, inhibiting the growth of plant species, which hence also affect associated bacterial diversity (Hinsinger et al., 2003; Shi et al., 2011; Steinauer et al., 2016).

**Bacterial functionality response to R-FDis**

The derived bacterial functionality of PGPA-related genes responded significantly to R-FDis. The increasing PGPA from monospecific to multispecies forest stands supports the idea of existing synergies between tree biodiversity and ecosystem services (Brockerhoff et al., 2017; Mori et al., 2017). Our results add that multispecies forests can stimulate their own tree growth and fitness by increasing the abundances of bacterial genes related to nutrient turnover and adaptation to biotic and abiotic stress (BaldrIan, 2016; Lladó et al., 2017). Furthermore, low levels of root trait dispersion have a greater effect on gene abundances compared with high root trait dispersion levels. From a root perspective, root trait dispersion is positive, because it may be indicative of complementary soil resource acquisition strategies and reduced competition (Mason et al., 2005; Barry et al., 2019). However, our study displays that high root trait dispersion and therefore niche heterogeneity acts inversely by decreasing bacterial PGPA genes.

**Fig. 3. Bacterial functionality in relation to R-FDis and tree plot tree composition:** (A) the multispecies plot tree composition in order of R-FDis values; (B) the monospecies plot tree composition in order of $M_{\text{overall}}$ abundances; Aa, Abies alba; Ap, Acer pseudoplatanus; Bp, Betula pendula; Cb, Carpinus betulus; Cs, Castanea sativa; Fs, Fagus sylvatica; Oc, Ostrya carpinifolia; Pa, Picea abies; Ps, Pinus sylvestris; Qc, Quercus cerris; Qi, Quercus ilx; Qp, Quercus petraea; Qr, Quercus robur.
abundances. An explanation could be that divergent root trait expressions generate an even root niche complementarity that involves several adequate microhabitats to soil microbes (Lamb et al., 2011). These microhabitats are enriched in suitable life conditions, decreasing the necessity for bacteria to trigger high gene abundance to compete for nutrients (Barret et al., 2011; Loeppmann et al., 2016). Alternatively but not excluding the previous explanations, high root trait dispersion levels may cause a negative complementarity effect, which is reflected by decreasing PGPA gene abundances, and commonly linked to a dominance of antagonistic bacterial interactions (Becker et al., 2012).

Considering the shown importance of tree species identity and tree type on the bacterial communities and their activities, Colin et al. (2017) likewise demonstrated that soil mineral type and tree species determine taxonomical and functional characteristics of the bacterial communities. Oppositely, Dukunde et al. (2019) did not find that predicted metabolic functional profiles follow tree species identities. Such discrepancies in soil functionality can be related to the study design and used approaches such as molecular methods, bacterial cultural assays, soil substrate tests or predicting tools (Blagodatskaya and Kuzyakov, 2013). Despite the use of predicted functional profiles that represent microbial activity only indirectly, experimental data support our findings (Asshauer et al., 2015; Koo et al., 2017; Lajoie et al., 2019). Although such tree species identity effect is context-dependent, i.e. sensitive to soil characteristics, our results show also that generally, broadleaf tree species support higher bacterial functionality than evergreen tree species (Ribbons et al., 2018). Leaf litter and root rhizodepositions from evergreen tree species lead to low soil pH, which mediates microbial processes, and subsequently affects bacterial communities, their enzyme dynamics and efficiency (Mueller et al., 2012; Cesarz et al., 2013; Purahong et al., 2016; Liado et al., 2018; Ribbons et al., 2018, Blonska et al., 2016). Blörska et al. (2016) additionally indicated that spruce and pine stimulate the enzymatic activities less than oak or hornbeam. These results harmonize with ours, displaying higher microbial gene abundances in monospecific plots of oaks and hornbeam. In multispecies forests, the bacterial functionality was affected by the plot tree composition and its relative tree abundances, i.e. tree dominance, which could enhance or diminish the PGPA gene abundances in regard to their monospecific equivalents (Laliberté and Legendre, 2010).

**Differential abundance groups and bacterial functionality**

Despite the generally high relative abundance of bacteria in our soils, only a few taxa (355 OTUs) responded with...
differential abundance between plots with small and great \( M_{\text{overall}} \). This might be linked to the fact that in soil, just a small portion of the bacteria is active, which are partly functional-redundant (Blagodatskaya and Kuzyakov, 2013; Baldrian, 2016; Romanowicz et al., 2016; Louca et al., 2018). As to be expected, many of the differential abundant bacterial taxa belong to Proteobacteria, Actinobacteria and Acidobacteria, which often represent the core microbiome, covering main soil functions (Lladó et al., 2017; Verma et al., 2019). The bacterial genera of Burkholderia, Rhizobium and Streptomycetes are also known for covering ‘basic’ functions such as respiration, nitrogen, phosphorus cycling and organic matter decomposition (Lladó et al., 2017; Verma et al., 2019; Jia and Whalen, 2020). In accordance with these reports, we also found representative bacteria covering similar functions (see supplementary Differential OTU Table). Likewise, we identified OTUs in great \( M_{\text{overall}} \) plots that could enhance the PGPA due to their enrichment. For example, Planctomycetes can contribute to high multifunctionality due to its capacity to perform as slow-acting degraders of various biopolymers (Ivanova et al., 2016; Dedysh and Ivanova, 2018). Gemmatimonadetes, a phylum with versatile metabolism adapted to low soil moisture and able to mobilize and accumulate polyphosphate (Zhang et al., 2003; DeBruyn et al., 2011), showed high abundances in multispecies forests. Chloroflexi is closely related not only to the nitrogen and

Table 1. Properties of networks displayed in Fig. 5 for bacterial communities in monospecific and multispecies forest plots.

|                  | Monospecifics | Multispecies |
|------------------|---------------|--------------|
|                  | R-FDis - null | R-FDis - low | R-FDis - medium | R-FDis - high |
| Number nodes     | 30            | 34           |                |              |
| Number edges     | 42            | 127          |                |              |
| Clustering coefficient | 0.4693878 | 0.6677116 | 5.6 ± 1.33ab | 8.4 ± 1.35a |
| Linkage density (complexity) | 2.8 ± 0.40a | 11.0 ± 1.68a | 5.6 ± 1.33ab | 8.4 ± 1.35a |
| Clustering coefficient (for R-FDis) | 0.42 ± 0.06a | 0.86 ± 0.09a | 0.55 ± 0.10a | 0.63 ± 0.07a |

Note: Different letters indicate significantly differences according to ANOVA (\( p < 0.05 \)) and Tukey-HSD post hoc test.

Fig. 5. Network of multispecies and monospecific forest plots based on bacterial community composition of OTUs with differential abundances; sizes and colours indicate overall multifunctionality \( M_{\text{overall}} \) and shape root functional dispersion (R-FDis); dashed lines show plot modules; Aa, Abies alba; Ap, Acer pseudoplatanus; Bp, Betula pendula; CB, Carpinus betulus; Cs, Castanea sativa; Fs, Fagus sylvatica; Oc, Ostrya carpinifolia; Pa, Picea abies; Ps, Pinus sylvestris; Qc, Quercus cerris; Qi, Quercus ilex; Qp, Quercus petraea; Qr, Quercus robur.
sulfur cycles (Hanada, 2014), but also to the less studied chlorine cycle (Krzmarzick et al., 2012). Thus, abundance changes for this phylum could affect the soil forest functionality associated with ‘rare’ cycles. Our examples indicated that bacterial communities in multispecies plots accomplish the same functions as bacterial communities in monospecific plots, despite their lower number of taxa with differential abundances. However, we believe that in multispecies forests, bacterial communities are more adaptable and resilient towards the disturbance, because of the increased number of bacterial taxa, executing ‘rare’, e.g. methanogenesis and mineralization of recalcitrant organic pollutants, and ‘basic’ functions (Jia and Whalen, 2020). In addition, bacterial communities in multispecies plots display an enriched bacterial trait diversity, which explains higher forest functionality, too.

Our results also showed a differential abundance of *Firmicutes* associated with small *Moverall* plots. *Firmicutes* and its associated *Bacteroidetes* are commonly reported as dominant in human microbiomes (Castaner et al., 2018; Li and Ma, 2020). However, this phylum also plays an important role in soils by facilitating bioremediation processes (Gupta et al., 2018), especially in recalcitrant soils under evergreen trees (Ramirez et al., 2012; Lladó et al., 2017; Wei et al., 2017). Accordingly, these harder soil conditions in small *Moverall* plots may favour *Firmicutes* differential abundances. Thus, members of the *Firmicutes* could be seen as indicator species for soil functionality, since they compete intensely with other taxa and react rapidly to belowground niche variations. Generally, bacterial community composition, their interactions and subsequently their activities resulting in various abundance patterns are often uncoupled from bacterial functionality (Louca et al., 2018; Liu et al., 2019). Therefore, bacterial functionality is neither necessarily related to higher bacterial differential abundances nor to belowground niche heterogeneity.

Bacterial composition, R-FDis and bacterial functionality

Multispecies forest plots recruited more similar bacterial communities, which led to a three times higher connectivity compared with their monospecific counterparts. Previous co-occurrence network analyses suggested that microbial contribution to ecosystem functioning is superior in systems with high complexity and is characterized by high resilience and resistance against environmental disturbances (Karimi et al., 2017; Wagg et al., 2019). Following this idea, the studied multispecies plots could develop greater *Moverall* than monospecific plots, because multispecies forest has a higher probability to build up cooperative interactions for resources and keep their functionality under fluctuating conditions. Furthermore, multispecies systems have higher complexity in their bacterial communities, particularly in low R-FDis levels, which could indicate a more stable system and explain the great *Moverall* (Pimm, 1984; Landi et al., 2018).

For our study, the interpretation of modularity could hint towards a particular tree plot composition, able to host the bacterial communities of its module plot members and to a less extent from plots of neighbouring modules. Correspondingly, the link density of the module suggests how robust the module is. The organic matter inputs to soil come primarily via rhizodeposition and litter (Vogt et al., 1991; Gumina and Kuzyakov, 2015), and consequently cause a selective influence on microbial communities and their physiology (Grayston et al., 1998; Ayres et al., 2009; Augusto et al., 2015; Nacke et al., 2016). Although the monospecific plots showed higher modularity than the multispecies ones, the link density in multispecies plots represents a higher probability to harbour a variety of bacteria and maintain functionality due to a better soil organic matter input. In addition, the positive correlation between the root trait dispersion and the linkage density could indicate that the root trait divergence facilitates an increased number of bacterial interactions as a mechanistic influence on soil functionality (Valiente-Banuet et al., 2015; Eisenhauer and Powell, 2017; Karimi et al., 2017). Moreover, the link density correlated with *Moverall* could impact plant traits and performance as a tree-bacterial functional feedback (Fitzpatrick et al., 2018; Complant et al., 2019).

We initially expected that R-FDis as a useful tool to explain bacterial community composition in forests, because root traits have been identified as explanatory variables of microbial communities (Merino-Martín et al., 2020). However, in our study, we did not find a direct effect of R-FDis on the bacterial community composition. Possibly, our root trait divergence did not have the capacity to represent the diverse input that influences the bacterial communities. Accordingly, the inclusion of other root traits related to rhizodepositions, root hair length and density could be beneficial to further explain the bacterial patterns. Similarly, our study does not contemplate intraspecific root trait variation that plays an important role in the root-microbial association, particularly in the resource acquisition potential of trees (Pérez-Izquierdo et al., 2019). Additionally, we consider that the impact of root dispersion on bacterial community composition could increase when analysing rhizosphere soil instead of root zone soil, because this root proximity shapes bacterial composition intensively (Schöps et al., 2018).

Overall, our study marks the first step to quantify a subset of PGPR gene activities to tree health and performance with predictive methods. Future scientific efforts should aim to gain more holistic views of these PGPR activities by using meta-databases with complete genome sequences that associate with predicted microbial phenotypes. This would allow to decipher detailed...
mechanistic above-belowground interaction in forest ecosystems.

Experimental procedures

Sampling site and design

In the frame of the project SoilForEurope (http://website.cefe.cnrs.fr/soilforeurope/), we used 64 plots of the FunDivEUROPE platform (Baeten et al., 2013). These sites are located along a latitudinal gradient in four major European forest types: boreal forests (Finland), hemiboreal forests (Poland), mountainous beech forests (Romania) and thermophilous deciduous forests (Italy). Soil cores with roots of the dominant tree species were collected from the 64 plots that comprise 13 main tree species and 33 different tree species compositions. Plots with three dominant trees species comprise Abies alba, Acer pseudoplatanus, Betula pendula, Carpinus betulus, Castanea sativa, Fagus sylvatica, Ostrya carpinifolia, Picea abies, Pinus sylvestris, Quercus cerris, Quercus ilex, Quercus petraea and Quercus robur. The plot design and sampling procedure have previously been described (Gillespie et al., 2020). In brief, in 30 × 30 m mature forest plots, we took our samples from five 10 × 10 m subplots. Soil samples were collected at an equidistance of three trees belonging to one (monospecific) or different (multispecific) species (Vivanco and Austin, 2008). After the forest floor was removed for each subplot, we sampled the upper 10 cm soil with a split-tube sampler (Eijkelkamp, inner diameter 5.3 cm), two soil cores were taken, one for molecular microbe evaluation and the other for root trait analyses. Soil samples for molecular analyses were transported at -4°C. Soil and root samples were frozen and stored at -20°C until further processing.

Wet laboratory assays

Root traits. Intact soil cores taken adjacent to the soil core samples for microbial molecular analyses were used to explore root traits. From each of these intact cores, roots were separated from mineral particles using a sieve cascade (2 and 1 mm mesh size) followed by the flotation method (Bauhus and Bartsch, 1996). The skeleton content (>2 mm in diameter) was retrieved to calculate the fine-earth volume of each soil sample. Living absorptive fine roots, defined as the three most distal root orders, of the target tree species were classified according to the functional classification approach by McCormack et al. (2015) and separated from transport (higher order roots), dead and understory plant roots. We used absorptive fine roots, because of their fast adaptive response to changes in abiotic and biotic conditions and their close interactions with bacterial communities (Pregitzer et al., 2007; Merino-Martin et al., 2020). Traits for absorptive fine roots encompassed diameter, SRL, length density, tissue density, ectomycorrhizal (ECM) colonization intensity and nitrogen concentration. For individual subsamples per tree, the degree of ECM colonization was determined using a microscope by counting the root tips colonized by ECM fungi per centimetre. Absorptive roots were subsequently scanned with a flatbed scanner (at a resolution of 800 dpi). The software WinRhizo (Regent Instruments, Québec, Canada, 2009) was used to analyse the root scans to measure root length (cm), surface area (cm²), volume (cm³) and diameter (mm) for each sample. Oven-dried samples (40°C, at least 72 h) were weighted with a precision scale (0.0001 g) to quantify SRL (m g⁻¹) and RTD (g cm⁻²). Root length density (cm cm⁻³) was calculated as root length per fine-earth volume. Finally, the samples were milled to determine total organic nitrogen concentrations by dry combustion (Elementar Vario El Cube).

Molecular sequencing of bacterial communities. From the core soil samples for microbial analysis, the roots were sorted out by hand and soil homogenized by sieving at a 2 mm mesh size. The molecular procedure was in accordance with Habiyaremye et al. (2020). Briefly, total genomic DNA was extracted from 0.5 g of each subplot sample using the Power Soil™ DNA Isolation Kit (Qiagen Laboratories, Solana Beach, USA) following the manufacturer’s instructions. After pooling DNA at the plot level, we performed amplification of bacterial 16S V4 using the primers P5_8N_515F and P5_7N_515F together with P7_2N_806R and P7_1N_806R (Caporaso et al., 2011; Caporaso et al., 2012; Moll et al., 2018). PCR amplification was performed by using KAPA 7.50 μl of HiFi HotStart ReadyMix DNA Polymerase (Kapa, ROCHE or Sigma) and 0.3 μl of each primer with 2 μl of template in 15 μl reaction. PCR conditions were 3 min at 95°C, followed by 30 cycles of 95°C for 50 s, 55°C for 50 s and 72°C for 60 s, with a final extension of 72°C for 7 min. Each amplification reaction was verified by agarose gel electrophoresis with ethidium bromide staining on 1.5% agarose gel. PCRs products were purified with AMPure XP beads (Beckman Coulter, Krefeld, Germany). Subsequently, the Illumina index and sequencing adapters were added by PCR using Nextera XT Illumina Index Kit (Illumina) according to the manufacturer’s instructions. Library quantification was done with Quant-IT PicoGreen dsDNA assay and the Agilent High Sensitivity DNA assay in Agilent 2100 Expert, following Illumina recommendations. Finally, samples were normalized and pooled with equal amounts of each sample. Illumina MiSeq sequencing was performed at the Department of Soil Ecology, UFZ – Helmholtz Centre for Environmental Research in Halle (Saale), Germany. Sequence data have been deposited in the European Nucleotide Archive with the
accession number PRJEB33611 and experiment accession ERX4203279–ERX4203342.

**Bacterial biomass.** We determined the bacterial biomass using the phospholipid fatty acid analysis method described by Pei et al. (2017). Shortly, membrane lipids were extracted from 2 g of freeze-dried soil with a mixture of citrate buffer chloroform, methanol and (0.9:1:2, by volume). The chloroform phase containing the dissolved fatty acids was collected and evaporated by N2. Afterwards, fatty acids were converted to methyl esters using acid methylation. These products were then analysed by GC–MS (Agilent, HP DB5 column) for peak quantification and identification. The peak areas were converted into nmol g soil\(^{-1}\) based on an internal standard of known concentration (13:0 tridecanoic methyl ester). Soil total microbial biomass was calculated by summing all microbial lipids related to bacterial biomarkers, such as i15:0 for (Gram-positive bacteria), 16:1ω7c (Gram-negative bacteria) and 10Me16:0 (actinomycetes).

**Approaches for R-FDis, bacterial communities and their functionality**

**Root functional dispersion.** R-FDis represents the mean distance in a multidimensional trait space of an individual species to the centroid of all species within a community (Anderson, 2006; Laliberté and Legendre, 2010). It accounts for species abundances by shifting the position of the centroid towards the more abundant species and weighting distances of individual species by their relative abundances (Laliberté and Legendre, 2010). R-FDis were analysed for each forest type using the trait values, and the relative basal area of the target trees as a proxy for abundances of the tree species (Fig. S1). We calculated R-FDis of absorptive roots using the package ‘FD’ for R (Laliberté and Legendre, 2010; Laliberté et al., 2014). The study of the R-FDis focused on multispecies stands, due to the fact that communities composed of only one species have no root dispersion, and thus lead to R-FDis values of 0 (Laliberté and Legendre, 2010). Monospecific stands, however, were used as a reference in comparison with multispecies forests.

**Bioinformatics and bacterial communities.** Raw bacterial sequences were extracted based on their unique barcodes and were truncated by cutting off the primer sequence. Bioinformatics workflow was mainly based on MOTHUR (Schloss et al., 2009) and OBITools (Boyer et al., 2016) implemented in the pipeline DeltaMP (https://github.com/lehtendu/DeltaMP; Schöps et al., 2018). Sequences with a length range from 50 to 600 bp were quality-filtered allowing only five mismatches in the primer sequence and trimmed by a minimum quality Phred score of 28. The paired-end reads were merged employing a PandaSeq algorithm (Masella et al., 2012), with a threshold of 0.6 and a minimum overlap of 20 nucleotides. The sequences were clustered into OTUs by 97% sequence identity using cd-hit-est v4.6.1 (Fu et al., 2012). The taxonomy of the representative sequence per OTU was assigned using the SILVA 123 database using the Bayesian classifier (Schloss et al., 2009; Quast et al., 2013).

Diversity and statistical analyses were performed using the software R (version R-3.6.1). Bacterial communities were analysed using the ‘phyloseq’ (McMurdie and Holmes, 2013) and ‘vegan’ (Oksanen et al., 2017) packages. To maintain sample saturation (Fig. S2), sequencing data were rarefied at the cutoff of 80 000 reads per sample, following the suggestions for big libraries with more than 1000 sequences per sample (Weiss et al., 2017). We kept all OTUs with at least two sequence reads in more than 10% of the samples. For better visualization, we only showed the relative abundances and the Shannon diversity of the eight dominant bacterial phyla.

**Bacterial gene profiles as estimations for PGPA.** We obtained gene profiles by using the Tax4Fun, a software package that predicts the functional capabilities of bacterial communities based on 16S rRNA datasets (Asshauer et al., 2015). Tax4Fun uses the taxonomic profile of each bacterial OTU and links it to a set of pre-computed metabolic reference profiles. Tax4Fun estimates the metabolic reference profiles based on the KEGG (Kyoto Encyclopaedia of Genes and Genomes) database (Kanehisa and Goto, 2000; Kanehisa et al., 2014). We considered the retrieved gene abundances and diversity as a proxy for bacterial functionality. From the overall gene diversity, we choose 20 genes known for stimulating PGPA. We have sorted these 20 genes into six PGPA-related gene groups, i.e. C, N, P, S cycles, and resistances mechanism against biotic or abiotic stressors (Table 2).

The abundance values of the 20 chosen genes were normalized with the total bacterial biomass (Aggio et al., 2011). Afterwards, we performed multifunctionality analyses by calculating Z-scores, i.e. centre and scaling of the mean with standard deviation. The mean of all of these Z-scores provides the overall multifunctionality index \(M_{\text{overal}}\), expressing the functionality of the 20 chosen genes for the 64 sampled forest plots (Maestre et al., 2012). Furthermore, we calculated individual multifunctionality indices \(M_C\), \(M_N\), \(M_P\), \(M_S\), \(M_{\text{abiotic}}\) and \(M_{\text{biotic}}\) for the six gene groups. Differences among forest systems were analysed using analysis of variance followed by the Tukey-HSD post hoc test. Spearman correlation analysis was performed to examine the relationships between \(M\) and R-FDis. Linear mixed models were performed using the R package ‘lme4’ (Bates et al., 2015). We evaluated the influence of tree species richness, R-FDis, tree plot composition and proportion of...
Table 2. Selected predicted genes based on the KEGG database.

| Gene group | KEGG; Scientific name | Common name | PGPA | References |
|------------|------------------------|-------------|------|------------|
| C cycle   | K05349; beta-glucosidase [EC:3.2.1.21] | Beta-glucosidase | Cleaving of cellobiose to free glucose molecules by hydrolysis of β-glucosidic linkages | Zang et al. (2018) |
|           | K01179; endoglucanase [EC:3.2.1.4] | Endoglucanase | Hydrolyze of cellulose, xylan and mixed β-(1→3,1→4)-glucan, by break the internal β-(1→4) or β-(1→3) bonds within glucose chains | López-Mondéjar et al. (2016) |
|           | K01198; xylan 1,4-beta-xyllosidase [EC:3.2.1.37] | Xylosidase | Degradation of polysaccharide xylan into xylose. Catalysing the hydrolysis of the glycosidic linkage (β-1,4) of xylolides | |
|           | K01181; endo-1,4-beta-xylanase [EC:3.2.1.8] | Xylanase | | |
| P cycle   | K01078; acid phosphatase [EC:3.1.3.2] | Phosphatase | Transformation of P from soil organic matter into available forms. Hydrolytic enzymes that cleave the ester bond between the phosphate group and the organic residue of the organic phosphates | Evazi and Tabatabai (1977); Margalef et al. (2017) |
|           | K01507; inorganic pyrophosphatase [EC:3.6.1.1] | Pyrophosphatase | | |
| S cycle   | K01130; arylsulfatase [EC:3.1.6.1] | Arylsulfatase | Controls the acquisition of organic sulfur in soils. Hydrolyzing the bond between the sulfate group and the aromatic ring structure in compounds with the general formula R-OSO₃H | Gahan and Schmalenberger (2014) |
| N cycle   | K00531; nitrogenase [EC:1.18.6.1] | Nitrogenase | Nitrogenase, the enzyme complex catalysing N₂ fixation. Reduced ferredoxin:dinitrogen oxidoreductase (ATP-hydrolysing) | Pajares and Bohannan (2016); Kuypers et al. (2018); Isobe et al. (2020) |
|           | K10944; ammonia monoxygenase subunit A [EC:1.14.99.39] | Ammonia monoxygenase | Conversion of N into usable forms by oxidation. The enzyme catalyses the first reaction in the pathway of ammonia oxidation to nitrate | |
|           | K01428; urease subunit alpha [EC:3.5.1.5] | Urease | Transformation of urea to ammonia and carbon dioxide. The enzyme catalyses the hydrolysis of exogenous urea and is the terminal step of purine, pyrimidine and arginine degradation | |
|           | K05601; hydroxylamine reductase [EC:1.7.99.1] | Hydroxylamine reductase | This enzyme participates in nitrogen metabolism acting on other nitrogenous compounds as donors with a cytochrome as an acceptor | |
| Abiotic stress | K13654; GntR family transcriptional regulator, colanic acid and biofilm gene transcriptional regulator | Biofilm | The physiological response signal to induce drought-response pathways. Proteins controlled colanic acid and biofilm regulation. Are necessary proteins in the linear homopolymer poly-beta-1,6-N-acetyl-β-glucosamine, for biofilm formation | Timmusk et al. (2014); Kasim et al. (2016) |
|           | K1935; biofilm PGA synthesis protein PgaA | Biofilm | | |
|           | K01609; indole-3-glycerol phosphate synthase [EC:4.1.1.48] | Growth | Indole-3-acetic acid (IAA) can act as a reciprocal signalling molecule in microbe-plant interactions. This plant hormone of the auxin class regulates various aspects of plant growth and development | Spaepen and Vanderleyden (2010) |

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Table 2. Continued

| Gene group | KEGG; Scientific name | Common name | PGPA | References |
|------------|------------------------|-------------|------|------------|
| Biotic stress | K15320; 6-methylsalicylic acid synthase [EC:2.3.1.165] | Defence | Salicylic acid (SA) levels during pathogenic plant–microbe interaction often facilitate the building up of the resistance and systemic resistance. SA induced resistance against many necrotic or systemic viral, bacterial and fungal pathogens in plants | Hayat et al. (2012) |
| | K00297; methylenetetrahydrofolate reductase (NADPH) [EC:1.5.1.20] | Defence | Ethylene (ET) production, which is induced at the initiation of leaf senescence. Methylene tetrahydrofolate reductase (MetF) catalyses the reduction of 5,10-methylenetetrahydrofolate to 5-methyltetrahydrofolate | Ravanbakhsh et al. (2018) |
| | K16090; catecholate siderophore receptor | Growth/defence | Bacteria utilize iron sources such as low-molecular-weight iron chelators termed siderophores. This enzyme is involved in the active transport across the outer membrane of iron complexed with catecholate siderophores | Clarke et al. (2001) |

These genes are characterized by stimulating plant growth promotion activities (PGPA). White and grey areas to subgroup PGPA related genes are either related to nutrients cycles or resistances mechanism against biotic and abiotic stressors.
evergreen trees in the plot on $M$, using forest type as a random factor. Model evaluation was done taking into account the AIC (Akaike, 1981), also impact of the variables and simplicity were tested according to the principle of parsimony.

**Differential abundances and bacterial network community.** To identify the functional most important bacterial taxa, we identified and classified forest plots between ‘great’ and ‘small’ bacterial functionality while considering $M_{\text{overall}}$. Using these two categorical groups of bacterial functionality, we performed DESeq2 coupled with the ‘Wald’ test (Love et al., 2014) to identify OTUs differentially abundant ($p$-adjust value <0.01) in either group. Based on the literature, we identified bacterial selection strategies at the order level of these OTUs (Fierer et al., 2007; Ho et al., 2017). These differentially abundant OTUs were also used for subsequent network construction to evaluate the bacterial community. Thereby, each node represents a plot and each edge a significant relation under the Morisita distance matrix, which is able to deal with sample size and diversity (Morisita, 1961; Wolda, 1981). Our threshold of maximal ecological distance to define ‘connected’ samples was 0.2. We used the igraph package to create sample networks (Csardi and Nepusz, 2005). These networks were then visualized with the gnet2 part of the ‘network’ package (Butts, 2008b), using the ‘fruchtermanreingold’ layout to obtain an overall distribution pattern of the nodes (Fruchterman and Reingold, 1991; Butts, 2008a). Group attributed layout, where colour and size were defined by $M_{\text{overall}}$ and shaped by R-FDis. We further categorized R-FDis as null (monospecific forest plots), low, medium and high (multispecies forest plots). We described the network property clustering coefficient for each forest system and categorical R-FDis. Besides, we compared the categorical R-FDis using the linkage density (complexity) described as the average number of edges per node. Additionally, cluster detection (modularity) was performed via random walks with the ‘walktrap.community’ and ‘membership’ functions (Pons and Latapy, 2005), from igraph package. Pearson correlations were used to evaluate relations between R-FDis and linkage density, as well as linkage density and $M_{\text{overall}}$. ANOSIM was used to define the impact of forest type, plot composition (tree species composing the plot), forest system (monospecific vs. multispecies) and R-FDis on bacterial community composition.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Appendix S1**: Supporting Information.

**Appendix S2**: Supporting Information.