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Prokaryotic communities as proxies for eukaryotic soil beta diversity in forest ecosystems

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ABSTRACT

Soils support diverse life, with microbes and soil animals playing a vital role in maintaining below and above ground ecosystem functions. The complex below-ground communities are increasingly affected by human-induced pressures like climate change and pollution, prompting increased monitoring efforts. This study aims to determine whether soil bacterial biodiversity can serve as an indicator of broader forest soil diversity by examining its multi-kingdom correlations in alpha- and beta-diversity and co-occurrence network interactions with soil fungal, protozoan, and metazoan communities, using environmental DNA metabarcoding data. The results show positive correlations in beta-diversity between bacteria and eukaryotic communities and emphasize the pivotal role of bacteria in forest soil networks in the Bavarian Forest National Park, Germany. Correlations in alpha diversity varied between eukaryotic groups and among forest types. This study also highlights the strong interconnectivity among microbial, fungal, protozoan, and metazoan communities in temperate forest soils. Here, we show that bacterial biodiversity can be a proxy for the complex world of soil eukaryotic diversity (including fungi, protists, and animal fractions) regardless of the forest type, though naturally disturbed spruce dieback stands where an interesting exception as bacterial biodiversity was less strongly connected to eukaryotes. While the strength of diversity correlations differs among groups and metabarcoding of eukaryotes will remain necessary for more detailed and functional insights, a focus on bacteria as biodiversity indicators may offer a cost-efficient first screening providing soil biodiversity information for forest management monitoring and intervention, as well as broader conservation strategies.

1. Introduction

European soils are experiencing significant degradation —defined as the physical, chemical, and biological decline in soil quality—resulting in lower below-ground diversity and reduced ecosystem services (Panagos et al., 2022). In response to these concerns, soil condition and diversity monitoring are increasingly being integrated in European policy and management, including the European Green Deal (European Commission, 2019) and the EU Soil Strategy (European Commission, 2021a). Global initiatives also emphasize the need of soil biodiversity monitoring and protection (Hågvar, 1998; Guerra et al., 2021). Among different soil types, forest soils stand out as distinctive ecosystems that warrant close consideration. Their long-term stability, which stems from the enduring presence of tree vegetation and the absence of regular human-induced disturbances, such as tillage practices and fertilisation (Wellbrock et al., 2024), potentially fosters unique and complex below-ground communities, which play essential roles in ecosystem processes and services such as nutrient cycling, carbon sequestration, and plant diversity (Wagg et al., 2014; Creamer et al., 2016; de Araujo et al., 2018). Despite their relative stability, European forest soils are subjected to increasing anthropogenic pressures such as climate change, wildfire, windthrow, insect outbreaks, nitrogen deposition, and acidification (Forzieri et al., 2021; Rousseau et al., 2024b; Skidmore et al., 2024). Given these growing human impacts, monitoring of below-ground

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processes in forests is becoming an important aspect of forest management and conservation (European Commission, 2021b; Wellbrock et al., 2024).

Below-ground diversity assessments are crucial in evaluating and monitoring soil health (Delgado-Baquerizo et al., 2020; Hitzfeld et al., 2024). However, such assessments are particularly challenging due to the exceptionally high density and diversity of soil organisms which are largely invisible to the naked eye/human observer (Wardle, 2006; Bardgett and van der Putten, 2014). Molecular tools, such as (e)DNA metabarcoding, can provide detailed and comprehensive insights into these complex and diverse communities at reduced cost and effort compared to traditional methods (Taberlet et al., 2012; Taberlet et al., 2018) and are applied in a wide variety of soil studies, including forest soil diversity assessments (Tedersoo et al., 2016; Rousseau et al., 2024b; Siegenthaler et al., 2024). These tools also enable multi-kingdom studies that examine diverse groups of soil organisms with varied functions. Such studies reveal important biotic interactions often missed when focusing on a single group (George et al., 2019; Loos et al., 2024). In addition to broad taxonomic coverage, incorporating spatial scale is essential to understanding soil biodiversity patterns, as the influence of environmental drivers varies across scales. At continental scales ($>$10,000 km^2), factors like soil pH and climate are dominant determinants of soil communities (Fierer and Jackson, 2006; Tedersoo et al., 2014). At the landscape level ($\sim$100–1,000 km^2), plant traits, land use, and edaphic variables exert a strong influence (de Vries et al., 2012; Terrat et al., 2017). At microscale levels (millimetres to centimetres), soil biophysical and chemical heterogeneity predominantly shapes soil community processes by contributing to fine-scale variation in water and resource availability, and biotic interactions (Vos et al., 2013). Most multi-kingdom soil studies focus on coarse spatial scales (i.e., continental to global level), encompassing various land-cover types, and reveal distinct responses of soil organisms to land use, environmental conditions, climate, and soil properties; among these, forests stand out for their unique below-ground communities and cross-kingdom interactions (e.g. Creamer et al., 2016; Bahram et al., 2018; de Araujo et al., 2018; George et al., 2019; Labouyrie et al., 2023). Specifically, while Bahram et al. (2018) demonstrated contrasting global diversity patterns between bacteria and fungi, attributed to variation in competition and environmental filtering, Labouyrie et al. (2023) found similar responses of bacterial and fungal diversity to land use intensification at a European-wide study, with lowest diversity in woodlands. In a study conducted across the United Kingdom, George et al. (2019) observed that soil microbial, but not animal, alpha diversity was lower in forests compared to croplands and grasslands, while beta diversity patterns remained consistent across soil organism groups. In contrast to the lower alpha diversity observed in forest soils compared to more disturbed land-use types, studies across Europe and the Brazilian Cerrado report increased multi-kingdom network density and complexity in forested ecosystems pointing to potentially more resilient and functionally robust communities (Creamer et al., 2016; de Araujo et al., 2018). The variation in multi-kingdom soil dynamics within forest ecosystems (typically at spatial levels across landscape scales of approximately 100 to 1,000 km^2) remains, however, largely understudied. Studies within ecosystems generally focus on disturbed or semi-natural landscapes, such as agricultural fields, managed grasslands or urban green spaces, revealing kingdom- and ecosystem-specific effects of land use, disturbance, management regimes, and soil nutrition on soil diversity and multi-kingdom network complexity and connecitivity (e.g., Gossner et al., 2016; Giraldo-Perez et al., 2021; Kim et al., 2021; Zhang et al., 2021; Bonanomi et al., 2022; Grierson et al., 2023). A few studies have begun to explore this complexity in natural forests: for instance, Mafa-Attoye et al. (2022) linked differences in bacterial, archaeal, and fungal diversity patterns to the presence of plant roots using root exclusion experiments at forest edges adjacent to agricultural fields. Further, Mundra et al. (2021) connected variations in multi-kingdom co-occurrence patterns to differences in soil depth and chemistry within Norwegian birch forests, and Kitagami and Matsuda (2024) compared bacterial–fungal–nematode co-occurrence networks between Japanese cedar plantations and broadleaf forests. While these studies show extensive associations between soil kingdoms and variation in those links according to (local) soil conditions, they do not provide insight into how these connections translate into landscape-scale spatial diversity patterns. A particularly intriguing but underexplored question is whether the microbial and soil animal fractions of soil communities exhibit similar biodiversity patterns across a forested landscape. Understanding how the species composition of organisms at one trophic level influences the community structure of organisms at a connected trophic level allows for deeper insights into the biological processes that shape interacting communities and the stability of their interaction networks (Tedersoo et al., 2016). Furthermore, correlations in diversity between groups enable the use of biodiversity surrogates—groups of organisms serving as proxies for assessing overall biodiversity in a given ecosystem—providing a faster and more cost-effective alternative to comprehensive inventories (Moreno et al., 2007). The use of such proxies may be particularly valuable in soil biodiversity monitoring, which remains challenging due to the vast diversity of organisms, even with the application of molecular techniques (Zinger et al., 2016; Semenov, 2021). Bacteria are strong candidates as proxies for general soil diversity, as they form the foundation of the forest soil food web, play a crucial role in nutrient cycling (Lladó et al., 2017), exhibit sensitivity to environmental changes (Fontaine et al., 2023), and have short generation times (Gibson et al., 2018). However, studies have reported inconsistent correlations between prokaryote and eukaryote diversity, with strong variations across land cover, land-use changes, and geographic scales (Ramirez et al., 2014; Prober et al., 2015; Creamer et al., 2016; Gossner et al., 2016; George et al., 2019; Oliverio et al., 2020; Wang et al., 2021; Xiong et al., 2021). This ongoing debate underscores the need for a more integrative approach to understanding microbial and eukaryotic interactions, emphasizing ecosystem-specific studies rather than broad continental or global analyses. To address this, our study aims to evaluate whether bacterial communities are interconnected with the fungal, protozoan, and metazoan components of forest soil communities and exhibit interrelated alpha- and beta-diversity patterns within a temperate forest ecosystem. By incorporating correlation analyses with network-based assessments, we aim to uncover broader diversity patterns and potential biological proxies that could enhance predictions of forest soil biodiversity.

Specifically, this study aims to determine whether bacterial soil communities serve as indicators of broader forest soil diversity patterns and whether variation in bacterial communities indicates changes in eukaryotic soil diversity. We hypothesize: (i) Forest soil prokaryote and eukaryote communities show significant correlation in patterns of beta- and alpha diversity. (ii) Multi-kingdom forest soil networks demonstrate evident connectivity among prokaryote and eukaryote taxonomic groups. (iii) Patterns of diversity and soil connectivity among prokaryote and eukaryote taxonomic groups show variation among different forest types within Bavarian Forest National Park. Combined, these results will reveal the extent to which prokaryotic and eukaryotic soil communities are interconnected and whether bacterial and eukaryotic diversity align in forest soil systems. This understanding will help clarify the role of bacterial diversity as a key component in assessing broader soil diversity processes.

2. Methods

2.1. Selection of focal groups

In this study, we focused on eight key taxonomic groups essential to forest soil ecosystems: bacteria, non-ectomycorrhizal fungi, ectomycorrhizal fungi, protozoans, nematodes, mites, springtails, and annelids. These groups are some of the most abundant and diverse eukaryote taxa in soil and play distinct roles in the food web (Tedersoo et al., 2016).

Namely, bacteria are omnipresent and play a crucial role in nutrient cycling (Torsvik et al., 2002; Starke et al., 2021). Fungi are essential for organic matter decomposition and contribute significantly to plant health (Frac et al., 2018), especially considering that many soil fungal species are obligatory or opportunistic pathogens (Termorshuizen, 2016) as well as some being symbiotic with plants and assisting with nutrient uptake (Bruyant et al., 2024). Ectomycorrhizal fungi were treated as a distinct group, though, because they dominate temperate forest fungal communities, acting as symbionts for most tree species and therefore playing a unique role in forest soils (Tedersoo et al., 2012; Labouyrie et al., 2023). Protists are highly diverse bacterivores and fungivores, serving as key prey for soil animals (Oliverio et al., 2020; Potapov et al., 2022). Nematodes encompass a wide range of feeding guilds, functioning as grazers of bacterial and fungal communities while also serving as indicators of soil health (Neher, 2001; Harkes et al., 2019). Mites, which contribute to organic matter decomposition and prey on micro- and mesofauna, and springtails, which primarily function as microbivores and detritivores, are the dominant microarthropods in forest soils and serve as indicators of soil health (van Straalen, 1998; Potapov et al., 2022). Lastly, annelids, predominantly earthworms in forest soils, act as ecosystem engineers by feeding on soil organic matter or plant residues while ingesting entire patches of soil, including a variety of organisms (Potapov et al., 2022).

2.2. Site description and sampling design

Sampling was conducted in Bavarian Forest National Park during July-August 2020 (Fig. 1). The park is situated in southeastern Germany within the Bohemian Forest, one of Central Europe's largest continuous natural forest ecosystems (Křenová and Kiener, 2013). The mountainous forests in the study area, ranging in altitude from 300 to 1400 m, are predominantly composed of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) (Cailleret et al., 2014). A stratified random sampling approach based on forest type was employed, with adjustments made for purposive sampling in areas with challenging terrain or limited accessibility. Sampling was mainly conducted along four transect lines established by the BIOKLIM Project (Bässler et al., 2015). Our sampling design was developed to capture the full range of variation in soil communities across the Bavarian Forest National Park (which encompasses an area of 24,369 ha) while also ensuring sufficient representation of community variation within its main forest types. Plots (30 × 30 m, N = 60) were classified as coniferous, deciduous or mixed (15 plots per forest type) based on a cut-off of 75 % canopy dominance (Siegenthaler et al., 2024). Fifteen unique, heterogeneous natural disturbance areas were included as "dieback" forest type. These areas emerged following severe European spruce bark beetle (*Ips typographus*) infestations since the 1980s, which caused dieback of considerable areas of spruce forest, resulting in a highly heterogenic patchwork of open areas, different stages of forest regeneration and high availability of standing and lying dead wood (König et al., 2023; Rousseau et al., 2024a). Soils were predominant acidic (pH = 3–4.5) (Rousseau et al., 2024b) spodo-dystric cambisol and dystric histosol (ESDAC, 2004). Elevation data for each plot was obtained from a digital elevation model based on LiDAR data (Zhu et al., 2020) following Duan et al. (2025).

Bulk soil samples were collected in three, randomly distributed, 9 m^2 subplots per plot from the 0–10 cm topsoil layer, which is the most diverse and biologically complex layer (Mundra et al., 2021). In each subplot, nine soil cores were collected in a 3 × 3 grid using a 5 cm diameter corer after removal of litter horizon. The cores were pooled into a sterile bag, with roots and stones removed, manually homogenized, and a subsample was transferred into a sterile 50 ml tube. To prevent cross-contamination, the soil corer was sterilized between samples using 10 % bleach, followed by a rinse with deionized water. As a field control, an aliquot of the deionized water rinse was collected every fifth plot. A further subsample was collected for soil biochemical analysis, to determine soil pH (H_2O), C:N ratio, and soil organic matter following Rousseau et al. (2024b). Samples were transported on ice and stored at −20 °C.

2.3. DNA extraction and amplification

Soil DNA was extracted using the phosphate extraction protocol from Taberlet et al. (2012). Extracellular DNA was extracted by mixing 15 g of well-homogenized soil with 15 ml of saturated phosphate buffer (Na2HPO4; 0.12 M; pH ≈ 8) followed by purification using the NucleoSpin® soil extraction kit, following the manufacturer's instructions, but excluding the lysis step. The use of phosphate buffer allowed for processing larger soil volumes, reducing the impact of local heterogeneity and increasing the sampling replicability of larger taxa, and is considered reliable for soil DNA multi-taxa surveys (Zinger et al., 2016; Pansu et al., 2021). Negative extraction controls were included for each batch of 25 soil samples. DNA concentrations were measured with a

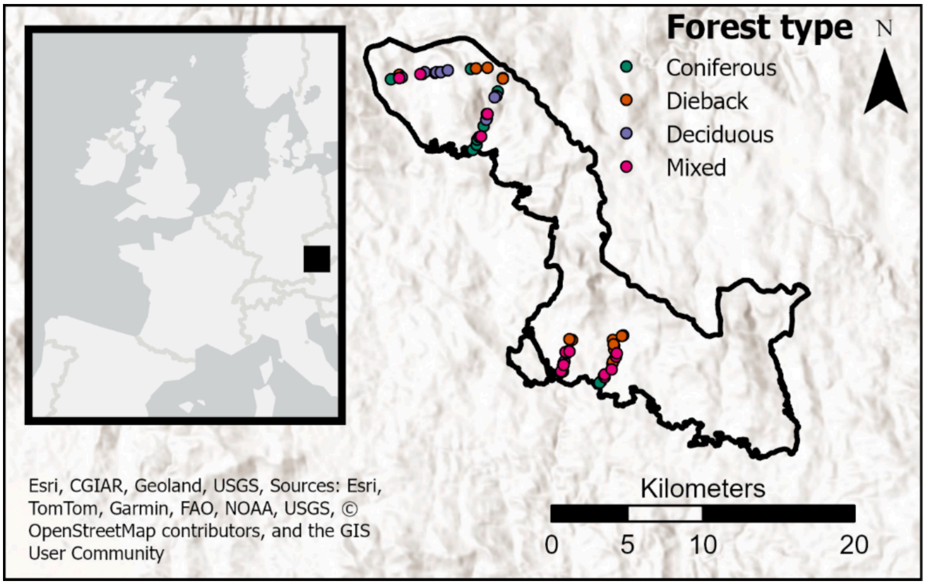

Fig. 1. Map of Bavarian Forest National Park showing the sample locations and park boundary. Samples were stratified per forest type. Dieback plots are natural disturbance areas caused by bark-beetle induces spruce forest dieback.

Biotek Synergy HTX Multi Mode Reader, using the Quant-iT PicoGreen dsDNA Assay Kit), and standardized to 5 ng/ml (samples < 5 ng/ml were not standardized). Soil samples were further diluted 100x to minimize PCR inhibition (except for COI due to low template DNA concentrations). Prior to PCR, the field and extraction controls were combined per control type.

Multiple molecular makers were used to amplify the DNA of the different target groups. Bacterial (V4 region of the 16S rRNA gene) and fungal (ITS2 rRNA region) DNA were amplified using the 515F/806R (Apprill et al., 2015; Parada et al., 2016) and ITS86f/ITS4-ngs (Turenne et al., 1999; Tedersoo et al., 2014) primer sets, respectively. Protist and metazoan (18S rRNA region) DNA was amplified using the universal All18SF/All18SR primer set (Hardy et al., 2010). Mites and springtail DNA was further amplified using a COI primer set specifically developed for mites and springtails (MiteMinBarF7/MiteMinBarR4) (de Groot and Laros, 2016). Amplification protocols and polymerase chain reaction (PCR) recipes can be found in Supplementary Table 1. Primers included a CS1 or CS2 adapter sequence at the 5′ end to enable multiplexing with the Fluidigm Access Array System (Fluidigm, South San Francisco, CA). Next Generation paired-end sequencing was performed by Genome Quebec (Montreal, Canada) on one lane of the Illumina NovaSeq 6000 SP platform using the PE250 kit. An indexing PCR was performed to add indexes and i5/i7 Illumina adapter sequences to the amplicons by Genome Quebec prior to Next Generation sequencing, and libraries were pooled equimolar.

2.4. *Bioinformatic and data analyses*

Bioinformatic analyses were conducted using the QIIME 2™ software suite v2021.8 (Bolyen et al., 2019), and statistical analyses were performed in R version 4.4.1 (https://www.R-project.org/). Primers were trimmed using Cutadapt (Martin, 2011), and DADA2 was used for pair-end read merging, denoising, chimera removal and ASV assignment (Callahan et al., 2016). Operational taxonomic unit (OTU) clustering was exclusively performed for COI, using Vsearch at 98 % identity (Rognes et al., 2016), following Rousseau et al. (2025). Post-clustering curation was carried out with LULU (Frøslev et al., 2017), and taxonomic assignments were made using the SILVA (Quast et al., 2012), UNITE (Nilsson et al., 2018) databases, using the qiime feature-classifiers for 16S, ITS and 18S. BOLDigger (Buchner and Leese, 2020) was used for COI taxonomic classification using the BOLD database (Ratnasingham and Hebert, 2007). Blank correction was applied, by removing reads where the maximum in blanks was greater than or equal to the maximum in samples, and data were filtered to retain only bacterial (16S), fungal (ITS), or microarthropod (COI) reads. Correction for tag-switching was performed following Taberlet et al. (2018) and Siegenthaler et al. (2024), and taxa with fewer than 10 total reads were removed to minimize low-frequency noise (Alsos et al., 2016; Polling et al., 2022). Fungal taxa were filtered from the 18S dataset to avoid overlap with the ITS data. Al datasets were rarefied (average of 100 iterations) (Cordier et al., 2019) to rounded lowest read depth (16S: 147000, ITS: 129000, 18S: 5000, COI: 1000 reads), using the 'rrarefy' function of the Vegan v. 2.6–8 R package (Oksanen et al., 2022), and split over the taxonomic groups of interest: bacteria (16S), non-ectomycorrhizal fungi (ITS), ectomycorrhizal fungi (ITS), protists (18S), nematodes (18S), mites (COI), springtails (COI), and annelids (18S). The rarefaction depth was chosen based on careful examination of the rarefaction curves (Supplementary Fig. 1), aiming to balance sequencing depth with sample retention. Funguild (Nguyen et al., 2016) was used to annotate fungi as non-ectomycorrhizal or ectomycorrhizal. Full details of the bioinformatic pipeline are provided in Supplementary Table 2 and information on the number of ASVs and reads per group can be found in Supplementary Table 3.

The relationships between alpha and beta diversity patterns among groups were evaluated using pairwise Spearman and Pearson correlation analyses. For beta diversity, Mantel tests (implemented in the vegan package v. 2.6–8) were conducted using Bray–Curtis dissimilarities based on Hellinger-transformed read counts and Jaccard similarities derived from presence-absence data. Alpha diversity indices, including richness and Shannon diversity, were calculated with the same vegan package. Data were averaged per plot prior to the pairwise correlation analyses and p-values were Benjamini-Hochberg adjusted for false discovery rate. Correlation matrixes were visualised using the corrplot v 0.95 R-package (Wei and Simko, 2024). Differences in alpha and beta diversity between forest types were determined using Kruskal-Wallis and PERMANOVA (999 permutations) analyses in Vegan v. 2.6–8. Differential abundance analyses were performed using the MaAsLin2 v1.20.0 R-package (Mallick et al., 2021) to identify taxonomic orders discriminating among forest types. Analyses were conducted with default settings, including total sum scaling normalization, log transformation, and a 10 % prevalence filter. To assess the influence of edaphic variables and elevation on diversity, we used generalized linear models (GLM) with a Poisson error distribution for ASV/OTU richness (count data), a Gamma error distribution for Shannon diversity (Lwin et al., 2021), and PERMANOVA (999 permutations) analyses for beta diversity using Bray–Curtis dissimilarities based on Hellinger-transformed read counts and Jaccard similarities derived from presence-absence data. Predictors were averaged per plot and scaled prior to analyses.

Interconnectivity of the taxonomic groups was assessed using multi-kingdom co-occurrence networks using the SPIEC-EASI (Sparse InversE Covariance Estimation for Ecological Association and Statistical Inference) method for multi domain data, which infers conditional dependencies rather than simple correlations (Kurtz et al., 2015; Tipton et al., 2018). To ensure consistent filtering while accounting for marker-specific sequencing depth, each marker-specific dataset was filtered individually before network construction, removing ASVs/OTUs with <20 % prevalence and <0.1 % relative abundance (Supplementary Table 3) (Röttjers and Faust, 2018). The filtered datasets were then combined in a multi-domain multi.spiec.easi object for network inference. Read counts were transformed using centered log-ratio (clr) transformation as part of the SPIEC-EASI algorithm. Taxa were not aggregated to higher taxonomic levels since this may reduce the reliability of the network properties (Röttjers and Faust, 2018). Multi-kingdom networks were generated for the full dataset, including samples across forest types, and individually per forest type (deciduous, coniferous, mixed, dieback). Networks were generated and analysed using the 'NetCoMi' v1.1.0 R-package (Peschel et al., 2020), and hub taxa ("key species") were identified based on their eigenvector centralities (above the 95th quantile), indicating nodes with a central role in the network (Ruhnau, 2000). The adjacency matrix was used to classify edges based on the groups they connect and their sign, with positive edges representing positive conditional associations (e.g., co-occurrences) and negative edges representing negative conditional associations (e.g., co-exclusions).

3. Results

3.1. *Correlations in community composition between taxonomic groups*

Prokaryote and eukaryote groups had significant ($p < 0.05$) positive Pearson correlations in community composition across all group combinations, for both Bray-Curtis dissimilarities and Jaccard similarities, according to pairwise mantel tests (Fig. 2; Supplementary Table 4). Bacterial – eukaryote correlations were generally moderate in strength (Median [range] Pearson's r: Bray-Curtis = 0.50 [0.29–0.62]; Jaccard = 0.50 [0.26–0.58]). All groups showed considerable variation in taxonomic composition between forest types, based on PERMANOVA analyses ($p < 0.01$) on Bray-Curtis dissimilarities and Jaccard similarities (Supplementary Table 5). Bacterial and eukaryotic communities showed consistent significant ($p < 0.05$) positive Pearson correlations in community composition across all forest types, except for bacteria-annelid

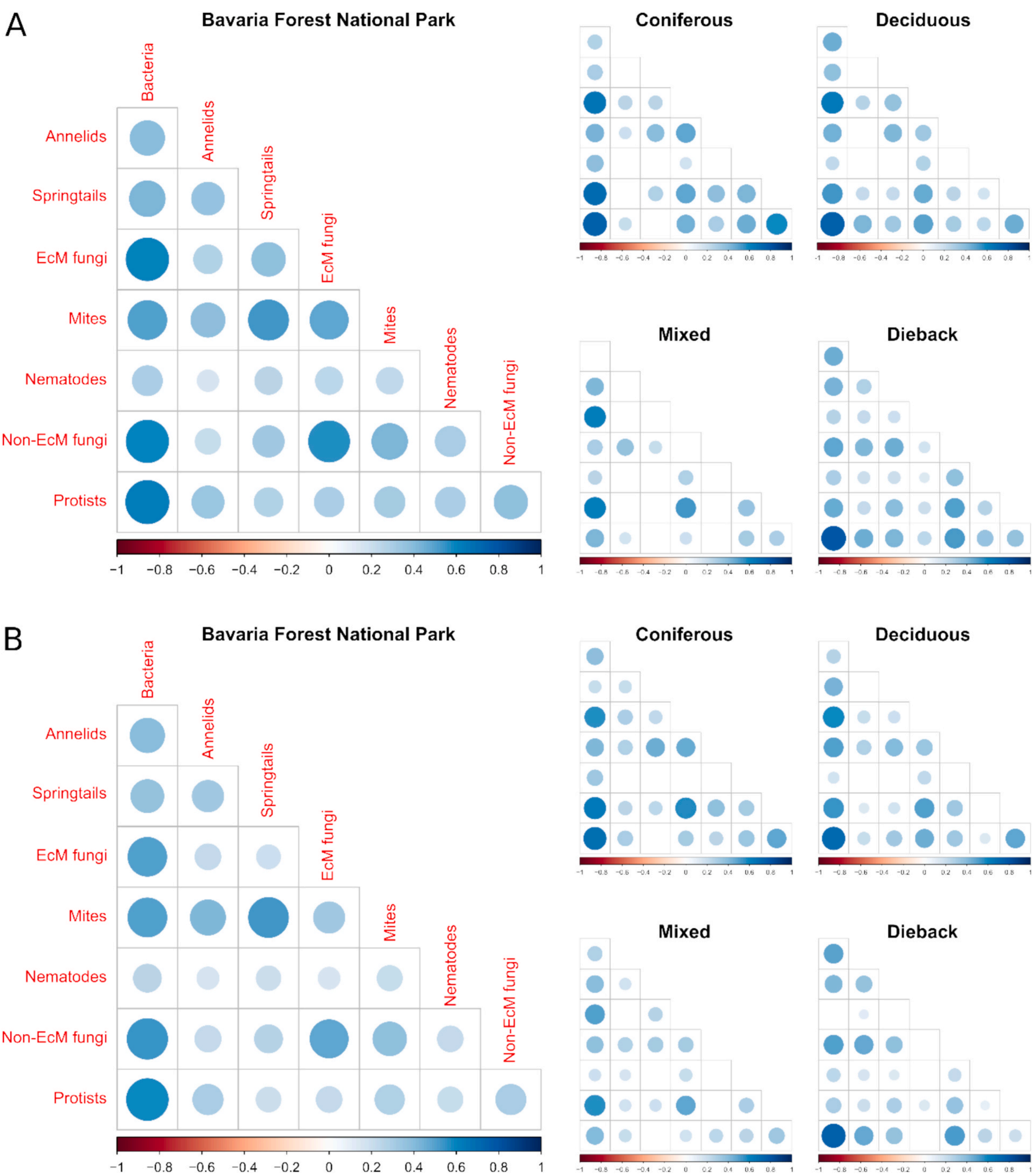

Fig. 2. Correlation matrix of pairwise Pearson Mantel correlations on (a) Bray-Curtis dissimilarities based on Hellinger-transformed reads and (b) Jaccard similarities, between multiple taxonomic focus groups for Bavaria Forest National Park. Insets show forest-type specific correlation matrixes for Bray-Curtis and Jaccard distances. Blue circles indicate significant (Benjamini-Hochberg corrected $p < 0.05$) positive pairwise correlations while empty cells show that the pairwise correlation was not significant ($p > 0.05$). Significant negative correlations were not identified. Circle colour contrast and size depict the strength of the correlation. Details of the pairwise tests are in Supplementary Table 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

correlations in the dieback plots (Fig. 2 insets; Supplementary Table 4). In contrast, pairwise correlations among eukaryotic groups varied depending on forest type and taxonomic group. No significant negative correlations were identified.

An overview of the order-level community composition of all groups is shown in Supplementary Fig. 2. To summarise the main prokaryotic and eukaryotic communities; Acidobacteriales and Acidobacteria subgroup 2 were the bacterial orders with the highest relative abundance, and are both typical acidophilic soil bacteria (Campbell, 2014; de Carvalho et al., 2016). Fungi were dominated by the non-ectomycorrhizal orders Helotiales and Atheliales and the ectomycorrhizal orders Russulales and Agaricales. Cercozoa and Ciliophora were the most abundant phyla of protists. More detailed taxonomic assignment was not possible for most protist ASVs. Regarding the metazoan taxa, mites were dominated by Sarcoptiformes and Trombidiformes, springtails by Entomobryomorpha and Poduromorpha, nematodes by Rhabditida, and annelids were almost exclusively Haplotaxida. MaAsLin2 discriminant analysis identified 134 taxonomic orders associated with at least one forest type, including 90 bacterial and 27 non-ectomycorrhizal fungal orders (Supplementary Table 6). The dieback forest type exhibited the highest number of discriminant orders (105), most of which were positively associated with this forest type.

3.2. Correlations in alpha diversity between taxonomic groups

Bacteria were the most diverse group, with a total of 49,607 ASVs remaining after bioinformatics filtering, followed by non-ectomycorrhizal (2,892 ASVs) and ectomycorrhizal Fungi (1,018 ASVs). Annelids showed the lowest diversity with 57 ASVs (Supplementary Table 3). Nematodes were not detected in 3 samples. Limited correlation in alpha diversity between bacterial and eukaryote groups was observed, as well as among the eukaryote groups, based on pairwise Spearman correlations (Fig. 3, Supplementary Table 7). No significant negative pairwise corelations were detected. Bacterial diversity consistently showed significant ($P < 0.05$) positive correlations with protists and annelids for both richness and Shannon diversity.

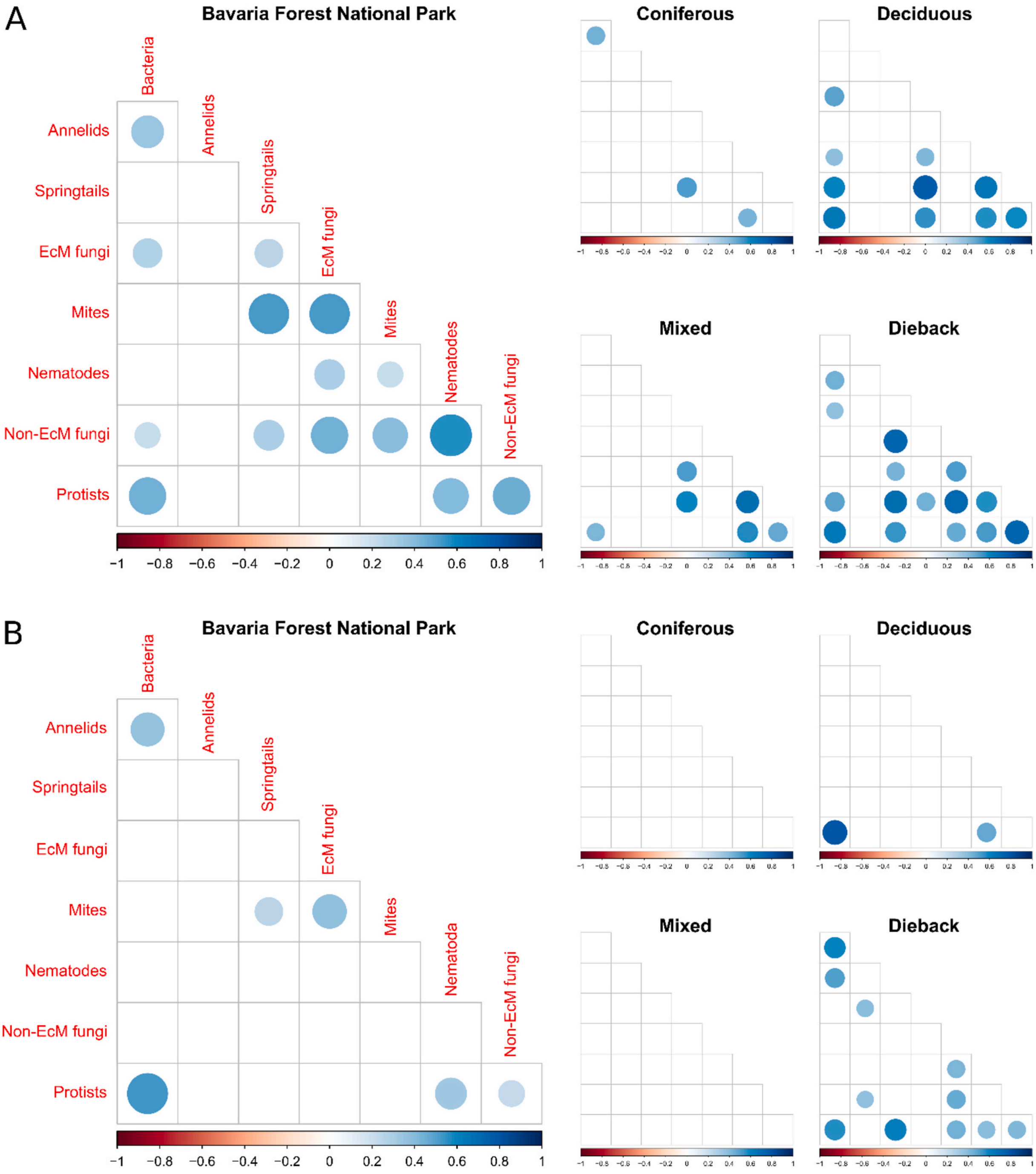

Fig. 3. Correlation matrix of pairwise Spearman correlations on (a) richness and (b) Shannon diversity, between multiple taxonomic focus groups. Insets show forest-type specific correlation matrixes for richness and Shannon diversity, respectively. Blue circles indicate significant (Benjamini-Hochberg corrected p < 0.05) positive pairwise correlations while empty cells show that the pairwise correlation was not significant (p > 0.05). Significant negative correlations were not identified. Circle colour contrast and size depict the strength of the correlation. Details of the pairwise tests are in Supplementary Table 7. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, bacterial and fungal diversity correlated only in terms of richness, while no correlations were observed between bacterial diversity and other groups.

Comparing the pairwise alpha diversity correlations within forest types (Fig. 3 insets, Supplementary Table 7), none of the eukaryotic groups showed consistent patterns in correlations with bacterial diversity across forest types. Additionally, pairwise alpha diversity correlations within the eukaryotic groups showed very little consistency across forest types. The dieback plots exhibited the highest incidence of significant pairwise correlations, both between bacteria and eukaryote groups and among eukaryotic groups. Bacteria, springtails and nematodes did not show significant ($p < 0.05$) variation in alpha diversity among forest types (Supplementary Table 8), while fungi (both ectomycorrhizal and non-ectomycorrhizal), protists, and mites did. The effect of forest type on annelids varied between alpha diversity indexes.

3.3. Network analyses

Bacterial ASVs dominated forest soil networks; in terms of number of taxa, number of edges, and hub-taxa ($N = 13$), as shown by multi-kingdom SPIEC-EASI co-occurrence network analyses (Fig. 4 and Supplementary Table 9). Nematodes represented only a very minor number of nodes ($N = 5$), and edges ($N = 12$) in the network. The earthworm Haplotaxida spp. and the protozoan ciliate Haptoria spp. were the only non-bacterial hubs (based on eigenvector centrality) in the forest soil network (Fig. 4a). Most bacterial edges linked to other bacterial taxa and were predominantly positive co-occurrences (62 %), suggesting either some form of facilitation, mutualistic relationship, or shared environmental preferences. Negative co-occurrences (38 %) were detected less frequently, potentially suggesting a lower incidence of either competition, inhibition, or antagonistic interactions, or contrasting environmental preferences. While less occurrent than bacterial within-kingdom edges, bacteria also showed a high connectivity (determined by the number of edges; Fig. 4b) with the eukaryotic groups, generally representing a major proportion of the interactions of those groups (Fig. 4c). These edges were less frequently positive (44 %; Fig. 4b) than the bacterial within-kingdom edges. Regarding intergroup connectivity, bacteria showed the highest connectivity with protists (11 % of the bacterial edges). The relative number of bacterial edges with the other eukaryotic groups was substantially lower (range: 0.4 – 3.8 %). Eukaryotic groups varied in their connectivity with other groups (Fig. 4c). For example, while both fungal groups exhibited consistent connectivity patterns with bacterial taxa (~50 % of their edges), ectomycorrhizal fungi primarily co-occurred with one another rather than with other eukaryotic groups, whereas non-ectomycorrhizal fungi showed more associations with protists. Protists had mostly positive interactions with other eukaryotic groups, except with annelids and nematodes. Annelids showed the highest relative connectivity with bacteria (63 % of annelid edges) of all groups but showed very low connectivity with fungi (6 %). Within the microarthropods, springtails and mites showed strong negative interconnectivity, with mites further frequently interacting negatively among themselves, while springtails had no within-group connections. Springtails also showed higher relative connectivity to bacteria (49 %) than mites (39 %). Both groups of microarthropods mainly had positive co-occurrences with ectomycorrhizal fungi.

When considering the different forest types within the Bavaria Forest National Park, co-occurrence networks showed high similarity, especially regarding the connectivity between bacteria and eukaryotic groups (Fig. 5; Supplementary Fig. 3, and Supplementary Table 10), and were all dominated by bacterial taxa. The dieback plots, however, showed a substantially lower number of bacterial edges compared to the other forest types (624 versus 763 to 819). Other notable observations from Fig. 5 are the similar patterns of connectivity across forest types for both bacteria and protozoa, and the high contribution of positive ectomycorrhizal-to-ectomycorrhizal edges in the spruce dieback plots, which also had a substantially lower proportion of bacteria-to-bacteria edges.

3.4. Environmental drivers of soil biodiversity

Bacterial diversity showed the strongest and most consistent responses to the selected edaphic variables and elevation (Supplementary Table 11) across all diversity metrics compared to other taxa (Table 1 and Supplementary Table 12). For both richness and Shannon diversity, bacteria showed the highest model explanatory power ($R^2 = 0.66$ and 0.68, respectively), with Alpha diversity positively influenced predominately by pH, followed by C:N ratio, and elevation. Soil organic matter elicited a negative response. In contrast, eukaryote groups showed weaker ($R^2 = 0.02$ and 0.54) and often less consistent responses. No significant relationships were found for nematode and springtail richness or Shannon diversity, annelid richness, and non-ectomycorrhizal fungal Shannon diversity. When significant, edaphic variables generally showed consistent directional effects across taxa, with soil organic matter being the only variable negatively associated with alpha diversity. Elevation was negatively associated with ectomycorrhizal fungal diversity but positively associated with protist richness and Shannon diversity, as well as annelid Shannon diversity. Beta diversity patterns were only low-to-moderate explained by the PERMANOVA models ($R^2 = 0.10$–0.36), with limited variation in variable importance of the predictors between groups. pH was the strongest predictor of community composition across most groups, except annelids which were mainly influenced by soil organic matter. The C:N ratio had limited influence, showing no significant effect on annelid, ectomycorrhizal fungal (Jaccard only), and nematode beta diversity. Elevation significantly explained beta diversity variation in all groups except annelids.

4. Discussion

4.1. Correlation patterns of beta- and alpha diversity among forest soil prokaryote and eukaryote communities

The composition of prokaryotic and eukaryotic communities in forest soil exhibited strong positive correlations, reinforcing their interconnectedness, as revealed by network analysis. These findings support our hypotheses that prokaryotic and eukaryotic communities in forest soil are closely linked in beta-diversity patterns and that multi-kingdom soil networks demonstrate clear connectivity between these taxa. These positive correlations likely result from the fact that both prokaryotic and eukaryotic community composition is primarily shaped by edaphic factors, particularly soil pH (Tedersoo et al., 2016; George et al., 2019; Labouyrie et al., 2023; Shao et al., 2023; Xue et al., 2023; Junggebauer et al., 2024). Alongside pH, soil organic matter and elevation, the latter representing a gradient in environmental and above-ground biotic changes (Bässler et al., 2009), also showed consistent effects on beta diversity across groups. The relatively low explanatory power of our eukaryotic PERMANOVA models may reflect the influence of biotic interactions, such as predation, competition, habitat modification, and symbiosis, in shaping soil animal communities, which were not included in our current models (Wardle, 2006; Potapov et al. 2022). Biotic variables likely also contribute to bacterial diversity, in addition to the dominant abiotic drivers, particularly at fine spatial scales ranging from micrometres to millimetres (Bardgett and van der Putten, 2014). The combination of shared environmental drivers and strong multi-kingdom interconnectedness may help explain the absence of negative correlations in community composition, even among distantly related groups. In such cases, ecosystem conditions may act as overarching filters of biodiversity rather than promoting niche differentiation. This underscores the role of environmental filtering in driving overall variation in soil beta diversity (Tedersoo et al., 2016). Additionally, shared evolutionary histories, functional associations, and biotic interactions may have also contributed to these interdependent shifts in community composition (Ramirez et al., 2014; Prober et al., 2015). Given these

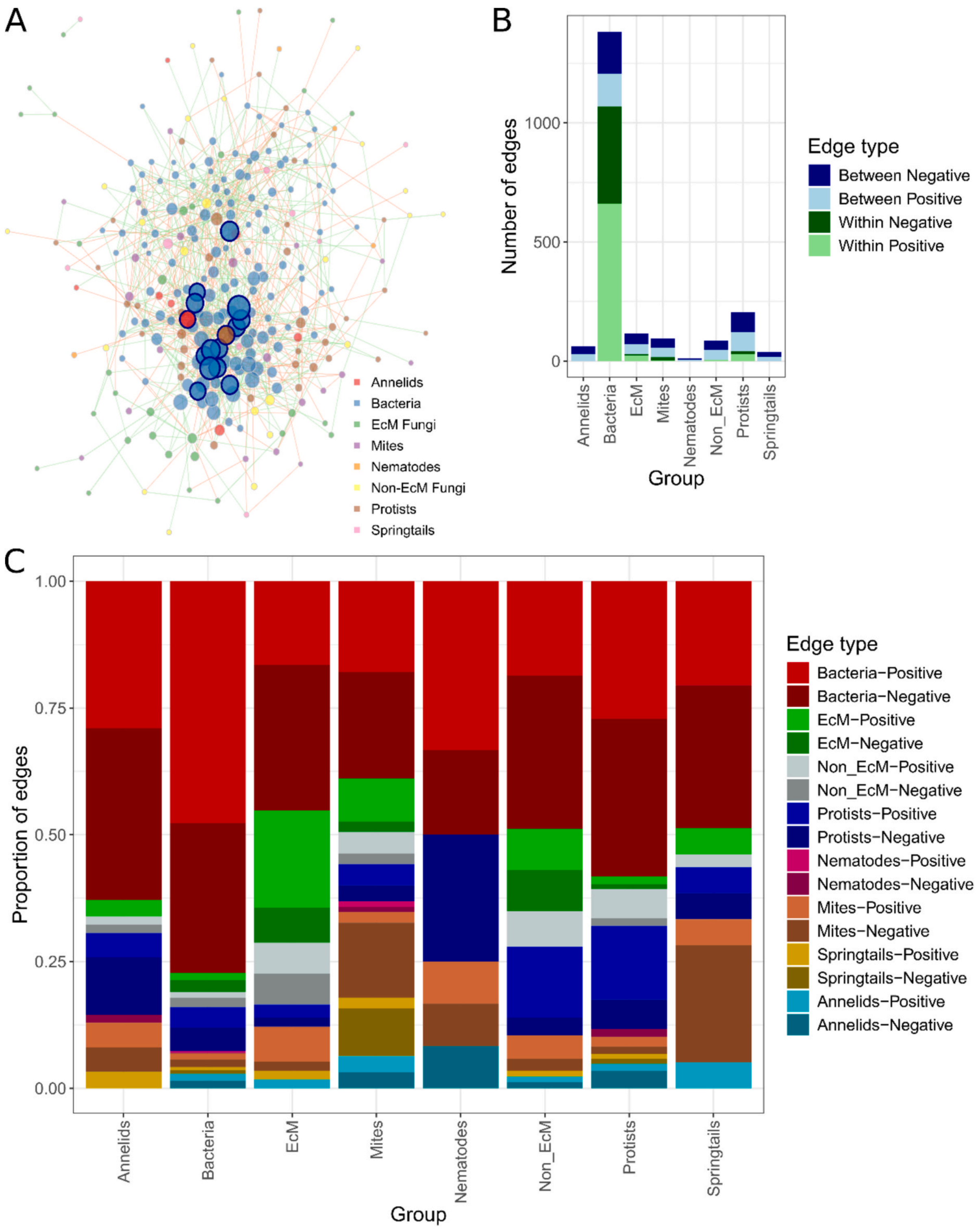

Fig. 4. Multi-kingdom SPIEC-EASI co-occurrence network analysis, based on abundant (>0.1 % relative abundance) and occurrent (>20 % prevalence) ASVs/OTUs. (a) Overall cross-kingdom structure for Bavaria Forest National Park. Taxa are represented by nodes and significant co-occurrences by edges. Nodes are coloured per taxonomic group and node size refers to node importance based on eigenvector centrality. Hub taxa (based on eigenvector centrality) are indicated with a blue outline. Positive edges (positive co-occurrences) are green while negative edges (co-exclusions) are red. Network statistics are in Supplementary Table 9. (b) Connectivity within and between taxonomic groups. The total number of positive and negative co-occurrences (edges) is shown to connect taxa within a taxonomic group or taxa between taxonomic groups. (c) Relative connectivity between taxonomic groups. The relative distribution of edges across the taxonomic groups is shown for each group, distinguishing positive and negative edges. EcM = ectomycorrhizal fungi. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

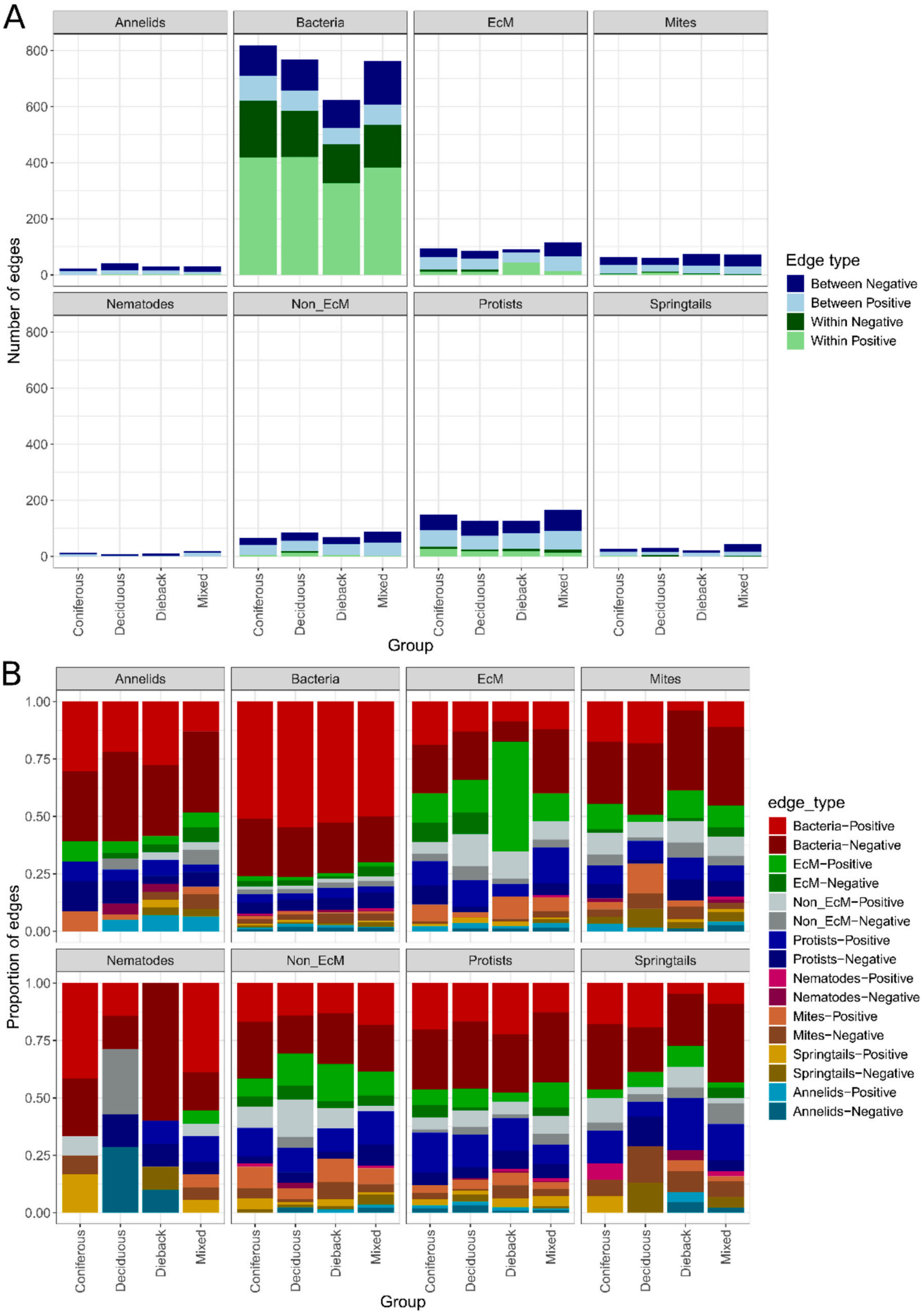

Fig. 5. Connectivity within and between taxonomic groups in forest-type specific multi-kingdom SPIEC-EASI co-occurrence network analysis, based on abundant (>0.1 % relative abundance) and occurrent (>20 % prevalence) ASVs/OTUs. (a) The total number of positive and negative co-occurrences (edges) connecting taxa within a taxonomic group or taxa between taxonomic groups. (b) Relative connectivity between taxonomic groups. The relative distribution of edges across the groups is shown for each taxonomic group, distinguishing positive and negative edges. EcM = ectomycorrhizal fungi. Network statistics are in Supplementary Table 10.

Table 1

Relationships between soil alpha and beta diversity across forest sites and environmental predictors, including edaphic variables (pH, Soil Organic Matter (SOM), C:N ratio) and elevation. (a) Scaled regression coefficients from generalized linear models (GLMs) for ASV/OTU richness and Shannon diversity, with McFadden's R2 indicating model fit. (b) Partial sums of squares from PERMANOVA models based on Jaccard (presence–absence) and Bray–Curtis (Hellinger-transformed abundance) dissimilarities. Only statistically significant predictors ($p < 0.05$) are shown; non-significant (NS) variables are omitted. See Supplementary Table 12 for full statistical details.

A	Richness					Shannon				
	Scaled Regression Coefficients				Model R^2	Scaled Regression Coefficients				Model R^2
Group	pH	SOM	C:N	Elevation		pH	SOM	C:N	Elevation	
Annelids	NS	NS	NS	NS	0.34	NS	−0.13	NS	0.07	0.31
Bacteria	0.16	−0.08	0.07	0.07	0.66	0.04	−0.02	0.02	0.02	0.68
EcM-fungi	NS	−0.22	NS	−0.12	0.54	NS	−0.14	NS	−0.08	0.29
Mites	NS	−0.17	NS	NS	0.12	NS	−0.12	NS	NS	0.13
Nematodes	NS	NS	NS	NS	0.03	NS	NS	NS	NS	0.02
Non-EcM-fungi	NS	−0.10	0.11	NS	0.13	NS	NS	NS	NS	0.07
Protists	0.18	NS	0.24	0.12	0.24	0.07	NS	0.07	0.03	0.27
Springtails	NS	NS	NS	NS	0.02	NS	NS	NS	NS	0.03

B	Jaccard					Bray–Curtis				
	Partial R^2				Model R^2	Partial R^2				Model R^2
Group	pH	SOM	C:N	Elevation		pH	SOM	C:N	Elevation	
Annelids	0.04	0.07	NS	NS	0.22	0.06	0.15	NS	NS	0.36
Bacteria	0.06	0.03	0.02	0.03	0.16	0.10	0.05	0.02	0.04	0.28
EcM-fungi	0.03	0.03	NS	0.03	0.13	0.05	0.04	0.03	0.04	0.19
Mites	0.03	0.04	NS	0.04	0.16	0.04	0.05	NS	0.05	0.21
Nematodes	0.02	0.03	NS	0.02	0.10	0.04	0.05	NS	0.03	0.13
Non-EcM-fungi	0.03	0.02	0.02	0.03	0.11	0.04	0.03	0.02	0.03	0.15
Protists	0.04	0.03	0.02	0.02	0.12	0.06	0.03	0.02	0.03	0.17
Springtails	0.04	0.03	0.03	0.03	0.15	0.04	0.05	0.03	0.04	0.22

intercorrelated shifts in beta diversity, bacterial communities may serve as potential indicators of broader soil community composition in forest ecosystems. From a monitoring perspective, single-kingdom eDNA assessments offer a cost-effective and logistically simpler alternative to multi-kingdom metabarcoding, which requires separate laboratory and bioinformatics pipelines for each marker (e.g., 16S, ITS, 18S, COI) due to the absence of truly universal primers across domains. Some general primers can be used for eukaryotic multi-kingdom analyses, such as the 18S region targeted in our study, but at the cost of taxonomic resolution, co-amplification of non-target groups, and introduction of amplification biases (Casey et al., 2021; Ficetola et al., 2024). The use of specific primers may thus still be required for further biodiversity estimates for specific taxonomic groups. Furthermore, eukaryotic metabarcoding often necessitates the use of dedicated reference databases for specific groups (e.g., for protists or nematodes), as widely used universal databases like SILVA and BOLD are often sparsely populated and poorly curated for many metazoan phyla (Vaulot et al., 2022; Baker et al., 2023). In the current study, we opted for universal databases over group-specific ones as a pragmatic and consistent approach, given the broad taxonomic scope of eukaryotic groups analysed. Overall, bacterial community screening via 16S rRNA metabarcoding may be preferred for soil biodiversity assessments due to its well-established protocols, broad adoption, and lower bias compared to multi-marker eukaryotic approaches using COI and 18S rRNA (Brauer and Bengtsson, 2022; Lara et al., 2022). While primer-free metagenomic methods are being developed as alternatives to metabarcoding for the characterisation of complex communities, these technologies are not suitable yet for large-scale assessments (landscape to continental scales) since they are still relatively costly and do not provide sufficient taxonomic resolution (Rieder et al., 2023). Furthermore, while small taxa such as microbes and protists can easily be co-analysed from the same soil sample (generally 0.25 g of soil), larger animals require additional soil volumes and sample effort for reliable detection (Taberlet et al., 2012; Zinger et al., 2016). Even with the use of larger sample volumes (15 g) and optimized extraction protocols, the detection of larger soil animals remains challenging and probably underestimates their full diversity. Accurate recovery of the eukaryotic groups may require further refinement of sampling strategies, extraction methods, and amplification protocols (Lara et al., 2022), as well as an increase in PCR replicates (Dopheide et al., 2018) and a more conservative rarefaction depth. Prioritizing bacteria for soil biodiversity monitoring could thus provide a cost-effective initial screening approach. However, since the strength of the correlation between bacterial diversity and different eukaryotic groups varies, metabarcoding of eukaryotes remains essential in some cases for deeper functional insights.

Contrary to our hypothesis, alpha diversity showed only weak correlations between bacterial and eukaryotic groups. Notably, while limited, all significant associations were positive; no negative correlations were detected. Bacterial diversity was more strongly and consistently structured by edaphic conditions, especially pH, compared to most eukaryotic soil groups, indicating differing ecological sensitivities and potentially divergent drivers of diversity. Eukaryotic alpha diversity is typically shaped by land use, vegetation cover, resource availability, and climatic conditions (Tedersoo et al., 2014; Bahram et al., 2018; George et al., 2019; Labouyrie et al., 2023). The continuous forest vegetation of the Bavarian Forest National Park (~24,369 ha), managed under nature conservation priorities for several decades, contrasts with the human-impacted agricultural and forestry landscapes examined in previous studies (Tedersoo et al., 2014; Bahram et al., 2018; George et al., 2019; Labouyrie et al., 2023), and may help explain the absence of contrasting diversity patterns between bacterial and eukaryotic groups in this study. Land use intensity warrants particular attention at broader spatial scales (i.e. landscape to continental levels): it tends to increase microbial alpha diversity while reducing diversity in soil animal communities, and also leads to a reduction in network connections between bacterial and eukaryotic taxa (Creamer et al., 2016; George et al., 2019). Correlations between taxonomic groups and their association with environmental variables, therefore, greatly depends on land use (Gossner et al., 2016; Oliverio et al., 2020; Wang et al., 2021; Xiong et al., 2021). For instance, the negative correlation observed between bacterial diversity and soil organic matter in our study contrasts with the commonly reported positive relationship between microbial diversity and organic matter content (Maestre et al., 2015; Zhang et al., 2023). This discrepancy may be specific to temperate European forests characterized by high SOM and low pH, such as the Bavarian Forest National Park, where the quality and chemical composition of organic matter, together with acidic conditions, act as environmental filters that favour copiotrophic bacterial communities with reduced diversity (Shao et al., 2019; Liu et al., 2020; Rousseau et al., 2024b). Landscape-specific studies, such as the current one, may thus assist in untangling these complex patterns by revealing belowground biodiversity correlations within a single land-use type. In Bavarian Forest National Park, only annelids and protists exhibited significant positive correlations in alpha diversity with bacterial diversity. Given their known roles in structuring soil bacterial communities (Dupont et al., 2016; Medina-Sauza et al., 2019; Bock et al., 2020), these findings suggest that biotic interactions are more dominant role in shaping their diversity patterns. This is further supported by their relatively high network connectivity to bacterial taxa compared to other eukaryotic groups. Combining alpha- and beta-diversity insights, our results show parallel community composition patterns between prokaryotes and eukaryotes in temperate forests, potentially driven by shared environmental, biotic, and evolutionary pressures, while local alpha diversity is influenced by taxon-specific factors. While bacterial communities may serve as effective proxies for monitoring broader soil community patterns, targeted eukaryotic assessments remain essential for capturing local variation in taxonomic diversity across trophic levels, particularly in forested ecosystems, where such variation can occur over spatial scales ranging from hundreds of meters to several tens of kilometres, depending on environmental gradients and forest structure.

4.2. Connectivity among prokaryote and eukaryote taxonomic groups in multi-kingdom forest soil networks

Bacterial taxa showed extensive interconnectivity with eukaryote taxa in the multi-kingdom soil network of Bavarian Forest National Park. These substantial interkingdom interactions underscore the ecological importance of soil bacteria being essential for organic matter decomposition, nitrogen fixation, and providing critical nutrients to eukaryotic soil taxa (Pollierer et al., 2012; Lladó et al., 2017). Bacteria are, for example, a key prey resource for various protist taxa (Potapov et al., 2022), which was illustrated by the strong connectivity observed between bacteria and protists in the co-occurrence networks. The key role of bacterial taxa in forest soil communities was further exemplified by the observation that the hub species in our network mainly consisted of bacterial taxa (e.g *Occallatibacter* and *Bryobacter*, Supplementary Table 9). Several of these bacterial hub species are involved in essential functions within forest soil ecosystems. For example, *Occallatibacter* can hydrolyze chitin and may play a key decomposing fungal and (micro) arthropod material (Dobrovolskaya et al., 2020). *Bryobacter*, an acid-tolerant Acidobacteriota genus, is associated with ectomycorrhizal fungi and contributes positively to plant health (Wang et al., 2022; Probst et al., 2024). The two non-bacterial hub species identified, earthworms (Haplotaxida) and the ciliate genus *Haptoria*, are also known key components of soil communities (Lara and Acosta-Mercado, 2012; Potapov et al., 2022), highlighting the importance of both prokaryote and eukaryote taxa in forest soil networks.

Forest ecosystems, with their high root density, provide abundant nutrients for bacteria, leading to bacteria-dominated networks (Mafa-Attoye et al., 2022). This nutrient availability, combined with the structural complexity and long-term stability of forest soils, contributes to highly intricate co-occurrence networks, which are associated with greater ecosystem resilience (Creamer et al., 2016; de Araujo et al., 2018; Mundra et al., 2021). High network complexity and long-term forest stability, on the other hand, may not directly translate in successional soil climax communities (Gömöryová et al., 2009; Dini-Andreote et al., 2014). Additionally to the observed high network complexity, the high proportion of positive links within these networks is typical of soil co-correlation patterns (de Araujo et al., 2018), likely reflecting the frequent occurrence of mutualistic interactions in soil habitats such as the rhizosphere (Shi et al., 2016). The structure of these networks also reveals distinct cross-kingdom dynamics. Specifically, the greater proportion of negative links between bacterial and eukaryotic taxa, compared to interactions within the bacterial kingdom, suggests ecological niche separation or predator–prey dynamics (Oliverio et al., 2020; Lee et al., 2022). However, interpreting these network interactions requires caution, as their ecological significance remains uncertain and context-dependent (Röttjers and Faust, 2018). For example, the same species interactions—such as predation—may drive both positive and negative links depending on environmental conditions (Lee et al., 2022). Taken together, these findings highlight the dense and highly interconnected nature of forest soil microbial communities. The strong cross-kingdom connectivity, particularly between bacterial and eukaryotic taxa, underscores the ecological complexity of these systems and emphasizes the central role of bacteria in shaping forest soil diversity.

4.3. Forest-type-specific variation in soil taxa connectivity and diversity patterns

Bacterial taxa showed little forest-type-specific variation in their connectivity to eukaryotic taxa in the Bavarian Forest National Park, reflected in consistent patterns of both co-occurrences and pairwise correlations in community composition. Eukaryotic taxa, on the other hand, exhibited more distinct forest-type-specific variation among taxonomic groups. Pairwise correlations in alpha diversity showed more variation between forest types, both between prokaryotic and eukaryotic taxa, and among eukaryotic groups. Forest type affects many soil processes such soil pH, litter quality and availability, microhabitat structure, and microclimatic conditions, which are known to have distinct influences on various soil groups (Urbanová et al., 2015; Siles and Margesin, 2016; Ganault et al., 2021). These factors have a greater impact on soil alpha diversity than beta diversity (Tedersoo et al., 2016; Pollierer et al., 2021), with the latter being primarily driven by variations in soil pH, particularly in bacterial communities (George et al., 2019; Rousseau et al., 2024b). Since variation in soil pH varies more within than between forest types in Bavarian Forest National Park (Abdullah et al., 2024; Rousseau et al., 2024b), tree species composition likely had a lesser role influencing the connectivity and correlations of prokaryotic with eukaryotic communities.

The disturbance areas caused by bark beetle infestation with regeneration plots were an exception to the high similarity in soil communities across forest types described above, exhibiting unique network structures and biodiversity patterns. The extensive areas of forest dieback in the Bavarian Forest National Park, caused by widespread bark beetle infestation of spruce stands over recent decades (Abdullah et al., 2019), are characterized by a mosaic of open spaces at various stages of forest regeneration. They feature abundant ground vegetation and significant standing and fallen deadwood volumes, creating high spatial heterogeneity. The natural disturbance/dieback soil communities exhibited substantially fewer bacterial edges in the co-occurrence network than those of other forest types. At the same time, the dieback network showed a marked increase in positive associations within the ectomycorrhizal fungal group. This shift was consistent with the reduced correlations in community composition between bacterial and ectomycorrhizal fungal taxa. These observations might be indicative of reduced fungal-bacterial interkingdom cooperation due to the high availability of organic matter in the form of decomposing deadwood resulting in a lower reliability of bacteria on nutrients and labile carbon provided by ectomycorrhizal fungi (de Vries and Caruso, 2016; Mafa-Attoye et al., 2022). Further, these patterns may be indicative of a switch from a symbiotic to a more saprotrophic lifestyle of ectomycorrhizal fungi after forest dieback, since shifts in the ectomycorrhizal fungal community in the dieback areas could mainly contribute to a substantial increase in the relative abundance of fungi in the order Helotiales, encompassing both symbiotic and saprotrophic fungi (Bruyant et al., 2024). Also, the significant increase in springtail diversity in the spruce dieback plots may be indicative of the high availability of saprotrophic fungi feeding on the decaying deadwood since springtails favour saprotrophic fungi as food source (Sanders et al., 2024).

Connectivity and diversity patterns of prokaryotes and eukaryotes remain stable across forest types in Bavarian Forest National Park but show local variations in disturbed areas, reflecting taxon-specific responses to land use intensity and disturbances observed in broader landscapes (Gossner et al., 2013; Creamer et al., 2016; de Araujo et al., 2018; George et al., 2019; Mafa-Attoye et al., 2022). This underscores the value of connectivity variation within a forest as potential indicators of ecosystem resilience and disturbance impacts, providing critical insights for targeted forest management and conservation strategies.

5. Conclusions

This study demonstrates the strong interconnectivity among microbial, fungal, protozoan, and metazoan components of temperate forest soil communities, revealing interrelated diversity patterns within the soil ecosystem. Specifically, the findings show that prokaryotic forest soil beta diversity could be used as a proxy, or biodiversity surrogate (Moreno et al., 2007), for eukaryotic soil community composition and underscore the potential ecological indicator role of bacteria. Despite their distinct ecological roles within the forest soil ecosystem, prokaryotic and eukaryotic organisms exhibit positive correlation patterns in their community composition across a forest landscape. Investigating these correlated biodiversity patterns is crucial for deepening our understanding of soil biodiversity trends and their implications for forest health and resilience since these correlations can provide insight in shared ecological drivers and stressors across trophic levels. Since these microbial and metazoan communities are an essential part of the plant-soil ecosystem, often contributing to the plant's holobiont (Siegenthaler et al., 2024), future research could integrate aboveground plant diversity in these belowground multi-kingdom biodiversity assessments to provide an even more holistic understanding of forested soil ecosystems. Soil quality and biodiversity are under pressure across large parts of Europe, emphasizing the need for cost-efficient monitoring of soil health indicators, including biodiversity loss (Gardi et al., 2013; Hitzfeld et al., 2024). Forest soils, often understudied, are unique ecosystems due to their long-term stability compared to highly disturbed agricultural soils. However, they are increasingly threatened by natural and anthropogenic pressures such as land-use changes, climate change, insect outbreaks, and acidification (Patacca et al., 2023; Skidmore et al., 2024). Recent advancements in predicting microbial soil communities through remote sensing techniques demonstrate significant potential for landscape-to-continental scale modelling of bacterial diversity (Skidmore et al., 2022; Skidmore, 2025). These insights underscore the importance of comprehending bacterial diversity within the broader context of overall soil diversity. By establishing a critical link between soil bacterial diversity and overall soil biodiversity, this study offers valuable guidance for developing more comprehensive strategies in soil condition assessment, forest management, and conservation efforts.

Declaration of Generative AI and AI-assisted technologies in the writing process

Statement: During the preparation of this work the author(s) used ChatGPT in order to improve the readability and language of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

CRediT authorship contribution statement

Andjin Siegenthaler: Writing – original draft, Software, Methodology, Data curation, Conceptualization. **Andrew K. Skidmore:** Writing – review & editing, Funding acquisition, Conceptualization. **Mélody Rousseau:** Methodology, Investigation. **Ivo Laros:** Methodology, Investigation. **Marco Heurich:** Writing – review & editing. **G. Arjen de Groot:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113930.

Data availability

The raw/processed data required to reproduce the above findings forms part of an ongoing study and is available from the authors on reasonable request.

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