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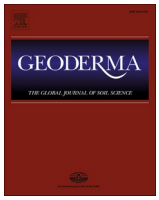

Fungal diversity as a key driver of soil multifunctionality along a European latitudinal gradient

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ABSTRACT

Soils harbor a vast diversity of microorganisms and play a crucial role in global carbon and nutrients cycles. Yet, the extent and drivers of variations in soil microbial diversity and functioning across environmental gradients at continental scales remain poorly understood. Here, we investigated the diversity and network complexity of prokaryotic and fungal communities and their relationships with soil multifunctionality (SMF) – an integrative index for C-, N- and P-cycling functions – along a 3,000-km latitudinal transect across Europe (37° to 62°N), spanning biomes from Mediterranean drylands, temperate to boreal forests. We found that SMF followed a hump-shaped latitudinal pattern, peaking at mid-latitude temperate forests and declining toward the southern Mediterranean drylands and northern boreal forests. Fungal alpha-diversity, together with mean annual precipitation (MAP), mean annual temperature (MAT), and soil pH and C/N ratio, were key contributors to SMF across latitudes, while prokaryotic alpha-diversity had little effect. Both prokaryotic and fungal communities were predominantly structured by dispersal limitation, land cover, climate and soil properties, with fungal communities more strongly limited by spatial dispersion. Our study highlights the significant role of fungal diversity in sustaining SMF along the European latitudinal gradient and demonstrates the importance of both large-scale climatic and biogeographical factors and local edaphic and land cover variables in shaping microbial diversity. Our findings offer valuable insights for the conservation of ecosystem functions.

1. Introduction

Soils harbor the largest diversity and abundance of microorganisms on Earth (Anthony et al., 2023). One gram of soil is calculated to contain 10^{10} to 10^{11} bacterial cells, 6000–50,000 bacterial species, and ~200 m of fungal hyphae (Torsvik et al., 2002; van der Heijden et al., 2008). Soils are also estimated to contain roughly 25 % of global genetic diversity (Tedersoo et al., 2014; Whitman et al., 1998). Due to their diverse metabolic capabilities, soil microorganisms are critical to key ecosystem functions, including organic carbon (OC) decomposition, nutrient cycling, greenhouse gas emissions, and primary production (Crowther et al., 2019; Schimel and Schaeffer, 2012; van der Heijden et al., 2008). However, how microbial diversity and interactions among taxa (e.g., network complexity) regulate soil multifunctionality (SMF, i.e. an integrative measure of functions including C-, nitrogen (N)-, and phosphorus (P)-cycling associated functions) across large-scale environmental gradients remains incompletely understood.

Soil microbial biodiversity (e.g., prokaryotic and fungal diversity) and their co-occurrence network associations (complexity) have been extensively studied in forests and drylands (Labouyrie et al., 2023; Liu

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et al., 2024; Lladó et al., 2018; Makhalanyane et al., 2015). It has been well documented that soil microbial diversity is shaped by a range of factors, including climate (temperature and precipitation), land cover, space (latitude and longitude), and edaphic variables (pH, texture, nutrients, organic matter, etc.) (Bahram et al., 2018; Labouyrie et al., 2023; Liu et al., 2020). In addition to their diversity, soil microbial communities often maintain highly complex networks of co-occurrence associations between taxa (Barberán et al., 2012; Ma et al., 2016), which are closely related to microbial diversity and community structure (Barberán et al., 2012; Tu et al., 2020). Yet, links between soil biodiversity, network complexity, and SMF, as well as the mechanisms driving these relationships across continental-scale environmental gradients, remain largely unexplored.

Over recent decades, research on the association between soil biodiversity and ecosystem functions (BEF) have expanded from local to global scales (Bardgett and van der Putten, 2014; Delgado-Baquerizo et al., 2017a; Fitter et al., 2005; Gonzalez et al., 2020; Graham et al., 2016; Guerra et al., 2020; Nannipieri et al., 2003; Philippot et al., 2013). Field observations (Delgado-Baquerizo et al., 2016; van der Plas et al., 2016; Zheng et al., 2019), controlled experiments (Osburn et al., 2023; Wagg et al., 2014; Wagg et al., 2019), or combinations of both (Delgado-Baquerizo et al., 2020; Delgado-Baquerizo et al., 2017b) have shown that microbial biodiversity is strongly linked to ecosystem functioning, with higher alpha diversity promoting ecosystem multifunctionality in diverse ecosystems, including drylands, grasslands, shrublands, croplands and forests. Meanwhile, several studies focusing on microbial complexity and ecosystem functions in soils undergoing disturbances, such as caused by erosion (Qiu et al., 2021), land-use change (Yang et al., 2023), and agricultural systems (Jiao et al., 2022), found that multifunctionality is positively correlated to soil microbial network complexity. Higher levels of microbial diversity and network complexity was proposed to promote functional complementarity by increasing resources use efficiency and niche differentiation (Delgado-Baquerizo et al., 2016; Wagg et al., 2014), and stability and resilience through network interactions and functional redundancy (Coyte et al., 2015; Loreau and de Mazancourt, 2013), and could also support beneficial plant–microbe relationships, such as mycorrhizal symbioses, thus promoting productivity (van der Heijden et al., 2008). However, knowledge is still lacking on how the diversity and network complexity of both prokaryotes and fungi jointly regulate SMF along large latitudinal and continental gradients.

In addition, climatic and edaphic variables also influence multifunctionality (Delgado-Baquerizo et al., 2016; Maestre et al., 2012). Climate (temperature and precipitation), land cover, and soil properties (pH, texture, nutrients, organic matter, etc.) have been shown to significantly affect soil microbial growth, respiration, carbon use efficiency, N mineralization, nitrification and denitrification through influencing microbial processes (Booth et al., 2005; Cookson et al., 2007; Han et al., 2024; Zheng et al., 2019). Yet, the direct and indirect (via the influencing on the microbial diversity) effects of climatic and edaphic variables on SMF remain little explored across large scale, such as along the natural latitudinal gradient through different European ecosystems.

Here, we investigate soil microbial diversity, network complexity, and SMF across soils from different European ecosystems, spanning a 3000 km latitudinal transect from southern Spain (37°N) to central Sweden (62°N). Specifically, we test how prokaryotic and fungal diversity and network complexity, together with climatic and edaphic drivers, shape SMF at a continental scale. We hypothesize that (1) soil microbial diversity is an important driver of SMF along the transect, but microbial network complexity provides additional explanatory power by microbial interactions; (2) The relationship between microbial diversity, network complexity and SMF vary across latitudes in response the changes in landcover, climates and soil properties. We further expect that, in extreme environments, such as the dry soils of southern Europe, aridity may exert an environmental filtration of soil resources and microbial functions, reducing the strength of the link between diversity and SMF.

2. Materials and methods

2.1. Sites description and soil collection

Fieldwork was conducted in August 2021 at 15 selected sites along a latitudinal gradient across Europe (>3000 km) from southern Spain to central Sweden (Table 1, Supplementary Fig. S1). Along the gradient, the mean annual temperature (MAT) ranged from 3.8 to 17.0 °C and the mean annual precipitation (MAP) from 265 to 1263 mm. Sampling sites spanned five different natural ecosystems with different vegetation types: Mediterranean desert (1 site, barren soils), Mediterranean shrubland (1 site), Mediterranean forests (2 sites), temperate forests (7 sites), and boreal forests (4 sites). MAT and MAP were extracted from WorldClim version 2 (https://worldclim.org/data/worldclim21.html). Land cover, classified by International Geosphere-Biosphere Programme classification, was extracted for the year 2020 with the MODIS product MCD12Q1_LC1 (Friedl et al., 2010).

At each site, five replicated soil samples from the surface top 10 cm were randomly collected within an area of 25 m^2. This resulted in the collection of a total number of 75 soil samples, which were treated independently. Soil samples were kept at 4 °C during transport to the lab. Back to the lab, the soil was immediately sieved at 4 mm mesh size, removing plants and roots material as thoroughly as possible. Upon sieving, a subsample was stored at 4 °C for enzymatic activities and microbial biomass, a second subsample was stored at −20 °C for nutrients and DNA analyses, and a third subsample was dried at 60 °C for physicochemical properties. Plant litter was collected at each site from five replicated plots with an area of 30 × 30 cm^2 and was dried at 60 °C for 48 h for biomass before being grinded for C and N analyses.

2.2. Soil physicochemical properties

Soil pH was measured by $CaCl_2$ (0.01 M) soil solution using a pH meter (2:1 volume/weight, v/w). Soil texture was analyzed by the hydrometer method. Soil water content (%) was determined by drying fresh soils at 105 °C for 24 h. Soil organic matter (SOM) was determined by loss-on-ignition, combusted at 450 °C for 4 h (Davies, 1974). Soil and litter total carbon (TC) and nitrogen (TN) were detected by an elemental analyzer (NC-2500; CE Instruments, Wigan, United Kingdom). Soil total organic carbon (TOC) was measured after HCl fumigation with an elemental analyzer (Walthert et al., 2010). Soil ammonium (NH_4^+) was extracted by KCl solution (1 M KCl:soil 4:1 v/w), measured photometrically by a FIAS 300 flow injection system (Perkin-Elmer, Waltham, MA, USA). Available phosphorus (phosphate, PO_4^{3-}) was extracted with $NaHCO_3$ solution (0.5 M $NaHCO_3$:soil 60:1 v/w) and analyzed photometrically with Malachite Green in a Tecan plate reader (Life Sciences, USA) (Kuo, 1996).

2.3. Greenhouse gas fluxes, extracellular enzyme activities and microbial biomass

In situ CO_2 and CH_4 fluxes were measured at each site under dark conditions to avoid CO_2 uptake by photosynthesis, by an ABB microportable gas analyzer (GLA131-GGA, Quebec, Canada) as described in Han et al. (2024). Gas samples for N_2O content were additionally collected after 1, 10, 20 and 30 min and stored in pre-vacuumed 3-mL glass vials (Labco, Ceredigion, UK), and measured by gas chromatography.

The activity of eight microbial extracellular enzymes involved in the C, N, and phosphorus (P) cycling were assessed: cellulose degrading (1) β-glucosidase (BG) and (2) cellobiohydrolase (CEL); (3) starch degrading α-glucosidase (AG); (4) hemicellulose degrading β-xylosidase (BX); (5) N-acetyl-glucosaminidase (NAG, N-acquiring enzyme), involved in the

Table 1
Characteristics of the sampling sites. MAT: mean annual temperature, MAP: mean annual precipitation, Tsoil = *in situ* soil temperature.

Site	Latitude (°N)	Longitude (°W (−); ° E)	Ecosystem	Land cover	MAT (°C)	MAP (mm)	*In situ* T_{soil} (°C)	Sand (%)	Silt (%)	Clay (%)
Tabernas, Spain	37.01	−2.44	Mediterranean desert	Barren	17.0	265.2	29.1	23.8	57.4	18.8
Coy, Spain	37.94	−1.78	Mediterranean shrubland	Open shrubland	13.5	401.7	23.1	57.7	27.6	14.8
Gavarres, Spain	41.90	2.91	Mediterranean forest	Evergreen needleleaf forests	13.9	719.5	25.9	72.8	21.4	5.9
Montpellier, France	43.73	3.60	Mediterranean forest	Evergreen broadleaf forests	13.6	671.4	20.7	62.2	3.9	34.0
Grenoble, France	45.27	5.55	Temperate forest	Deciduous broadleaf forests	10.2	1072.8	13.7	59.7	21.3	19.1
Lausanne, Switzerland	46.58	6.66	Temperate forest	Deciduous broadleaf forests	8.2	1263.0	13.2	65.1	19.0	16.0
Muhlbach, Germany	47.60	8.09	Temperate forest	Deciduous broadleaf forests	8.9	1190.7	14.3	47.9	39.0	13.2
Kohlerholz, Germany	51.88	10.66	Temperate forest	Deciduous broadleaf forests	7.8	804.6	13.5	38.8	38.9	22.4
Linderöd, Sweden	55.93	13.78	Temperate forest	Deciduous broadleaf forests	6.7	814.4	12.6	81.9	12.9	5.2
Gribskov, Denmark	56.01	12.36	Temperate forest	Deciduous broadleaf forests	7.7	604.3	17.4	81.3	14.4	4.4
Långasjönäs, Sweden	56.25	14.85	Temperate forest	Deciduous broadleaf forests	7.1	662.2	13.3	84.0	11.9	4.2
Dångamålaö, Sweden	56.52	15.15	Boreal forest	Evergreen needleleaf forests	6.6	668.2	14.8	84.0	8.7	7.4
Boxholm, Sweden	58.17	15.08	Boreal forest	Evergreen needleleaf forests	6.0	558.9	14.5	59.7	32.7	7.7
Gävle, Sweden	60.51	17.30	Boreal forest	Evergreen needleleaf forests	5.4	627.7	11.9	68.4	11.3	20.4
Sundsvall, Sweden	62.30	17.20	Boreal forest	Evergreen needleleaf forests	3.8	717.6	11.0	88.2	8.9	2.9

degradation of chitin and other β-1,4-linked glucosamine polymers; (6) peptides degrading Leucine aminopeptidase (LAP, N-acquiring enzyme); (7) Phosphatase (PHOS, including both alkaline phosphatase (ALP) and acid phosphatase (ACP)), breaking down phosphomonoesters and phosphodiesters; and (8) Phenol oxidase (POX), involved in polyphenol oxidation and lignin degradation. Hydrolytic enzyme activities were assessed by fluorescence with a microplate reader (TECAN 200 Infinite), by adding standards (0–100 μM for MUF: methylumbelliferyl, and AMC: 7-amino-4-methylcoumarin) to samples and controls, which were expressed as the rate of MUF or AMC released per hour related to dry weight (DW) soil (nmol MUF or AMC g^{-1} DW h^{-1}). Phenol oxidase activity was analyzed spectrophotometrically using L-DOPA (L-3,4-dihydroxyphenylamine) as a model substrate, expressed in the unit of μmol 2,3-dihydroindole-5,6-quinone-2-carboxylate (DIQC) per g DW soil per hour (μmol DIQC g^{-1} DW h^{-1}).

2.4. DNA extraction, quantification of microbial genes, and amplicon sequencing

DNA was extracted from 250 mg soil with the DNeasy Powersoil Pro Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. DNA was quantified by PicoGreen (ThermoFisher Scientific, USA), following the manufacturer's protocol.

Copies of prokaryotic 16S rRNA gene, fungal ITS2 region, *mcr*A (CH_4 production: Methyl Coenzyme M Reductase A), *pmo*A (CH_4 oxidation: particulate methane monooxygenase), *nif*H (nitrogen fixation: nitrogenase reductase), bacterial and archaeal *amo*A (ammonia oxidation: ammonia monooxygenase), *nor*B (N_2O production: nitric oxide reductase), *nos*Z (N_2O consumption: nitrous oxide reductase), and *pho*D (organic P hydrolysis: alkaline phosphatase D (ALP)) were measured by quantitative polymerase chain reaction (qPCR) as described in Han et al. (2023).

Prokaryotic and fungal community structure and composition were assessed by amplicon sequencing with the same primer pairs used for qPCR, as described in Donhauser et al. (2024). Prokaryotic 16S rRNA gene (341F/806R: CCTAYGGGDBGCWSCAG/GGACTACNVGGGTHTCTAAT, targeting V3-V4 region) and fungal ITS2 region (ITS3/ITS4: CAHCGATGAAGAACGYRG/TCCTSCGCTTATTGATATGC) were amplified according to Frey et al. (2016). PCR amplification started with a denaturation at 95 °C for 10 min, followed by 36 (prokaryotic 16S rRNA gene) or 38 (fungal ITS2 region) cycles of denaturation at 95 °C for 40 s, annealing at 58 °C for 40 s and elongation at 72 °C for 1 min, and ended with a final elongation at 72 °C for 10 min. Barcoded amplicons using the Fluidigm Access Array technology (Fluidigm) and paired end (2 × 300 bp) sequencing using the Illumina MiSeq v3 platform (Illumina Inc., San Diego, CA, USA) were done at the Genome Quebec Innovation Center (Montreal, Canada).

2.5. Sequencing data processing

Sequences were processed with DADA2 pipeline according to Donhauser et al. (2024) and Doménech-Pascual et al. (2025). We conducted stringent quality filtering to avoid spurious ASVs. Primer sequences were removed with cutadapt with default settings and were subsequently quality filtered and denoised with DADA2 (−-p-trunc-len-f 270, −-p-trunc-len-r 220, −-p-max-ee 5 for 16S rRNA gene fragment amplicons and −-p-trunc-len-f 270, −-p-trunc-len-r 230, −-p-max-ee 4 for ITS2 amplicons). Prokaryotic and fungal amplicon sequence variants (ASVs) were assigned against the SILVA v138 database (Quast et al., 2013) and UNITE ITS database (Abarenkov et al., 2023; Köljalg et al., 2013), respectively, using the scikit-learn multinomial naive Bayes classifier in QIIME2 (feature-classifier classify-sklearn) with default parameters. Contaminant sequences were removed by the isContaminant() function (method = "prevalence") in the R package decontam.

Samples were sequenced with enough depth. A total of 1′015′605 high quality sequenced reads for 16S rRNA gene (13541 ± 2904 sequences per sample on average) and 1′052′362 for ITS2 region (14031 ± 2373 on average) were recovered from the 75 samples. Reads were clustered into 5827 prokaryotic ASVs (mostly bacterial with only 45 archaeal ASVs), and 4090 fungal ASVs, respectively. An overview of the

number of reads in each soil sample is available in Supplementary Table S1. Rarefying (>6000 reads of each sample) was done for ASVs of both genes by iterative random subsampling by the function rarefy_even_depth() in the R package phyloseq. Rarefaction curves are shown in Supplementary Fig. S2.

2.6. Soil multifunctionality

Integrating C-, N, and P-cycling associated microbial functions, multifunctionality indices have been widely applied as an indicator for multiple and simultaneous ecosystem functions (Delgado-Baquerizo et al., 2016; Lefcheck et al., 2015; Wagg et al., 2014). A soil multifunctionality (SMF) index, quantifying the contribution of multiple soil microbial functions to ecosystem functioning simultaneously, was calculated using a cluster analysis and a threshold method as described in Manning et al. (2018). Briefly, an agglomerative cluster analysis was performed on the Z-transformed microbial functions, and an optimal number of clusters was chosen, ideally as the lowest number of clusters with a reasonably low total sum of squares (additional number of clusters reduces further the sum of squares). Functions were subsequently standardized (variable maxima standardization) and the SMF index was quantified according to the threshold method (Byrnes et al., 2014; Gamfeldt et al., 2008), where each cluster was assigned an equal weight. The SMF index was calculated with functions related to C-, N- and P-cycling, including soil respiration (CO_2 fluxes), CH_4 fluxes, C-acquiring enzyme activities of AG, BG, BX, CEL and POX, N_2O fluxes, N-acquiring enzyme activities of NAG and LAP, and P-cycling enzyme activity of PHOS. Here, CH_4 fluxes were included as indicators of microbial activity associated with methanogenesis and methanotrophy. In addition, C-cycling gene abundances of *mcr*A and *pmo*A, N-cycling gene abundances of *nif*H, bacterial and archaeal *amo*A, *nor*B and *nos*Z, and P-cycling *pho*D gene abundance, were also included in the calculation of SMF index as microbial functional potentials. The index represents the cycling rate of carbon and nutrients. As such, a higher value of multifunctionality index indicates higher microbial activities linked to soil carbon and nutrients cycling.

2.7. Data analyses

All analyses and plots were conducted in R v3.4.0 (http://R-project.org) using R Studio v1.1.442 (http://rstudio.com). Amplicon sequences were processed into amplicon sequence variants (ASVs) rather than operational taxonomic units (OTUs). ASVs provide single-nucleotide resolution and improve reproducibility by avoiding arbitrary clustering thresholds, in contrast to OTUs, in which closely related sequences are clustered together according to a threshold (e.g., at 97 % similarity). Studies have shown that richness differed substantially between OTUs and ASVs, but diversity patterns are usually reserved proportionally (Chiarello et al., 2022; Fasolo et al., 2024; Kerrigan and D'Hondt, 2022). In this study, ASVs were favored over OTUs because studies have shown that ASVs provide higher resolution, reproducibility, and biological accuracy than OTUs (Callahan et al., 2017; Fasolo et al., 2024). ASVs count files, ASVs taxonomy files, and mapfiles with climate and biogeochemical data, were merged into a 'phyloseq' class object with the functions phyloseq() and merge_phyloseq(), both from the R package phyloseq (McMurdie and Holmes, 2013). Microbial alpha-diversity indices (Richness and Shannon indices) were estimated by the function estimate_richness() from the dataset normalized by the function rarefy_even_depth() from the R package phyloseq. Significance of alpha-diversity indices, network complexity, and multifunctionality indices, were assessed across the biomes by the function stat_compare_means() from the R package ggpubr (Global test method: Kruskal-Wallis; Pairwise Wilcoxon Rank Sum Tests between biomes: Wilcoxon test). Distance decay curves of prokaryotic and fungal diversity were calculated along geographical distance at the ASV level based on Bray–Curtis dissimilarities. To investigate the influence of geographical distance on microbial community structures, we calculated principal coordinates of geographical distances based on a neighborhood matrix (function pcnm() in vegan), which we used as independent variables in a constrained ordination of microbial community structures. Subsequently, we applied variation partitioning to assess the contribution of environmental variables and geographical distance in structuring prokaryotic and fungal community structures (function varpart() in the R package vegan). Constrained Analysis of Principal Coordinates (CAP) was carried out at the ASV level by the function ordinate() with the method "CAP" and was tested for significance by the function capscale() from the R package vegan using Bray–Curtis dissimilarities (Han et al., 2020). The contributions of individual climatic and environmental variables, ecosystems, and land cover to both community structures were calculated by the function adonis2() from the R package vegan (PERMANOVA: permutational multivariate ANOVA; permutations: 1000). Fungal taxonomic classification was parsed into trophic guilds by the function funguild_assign() against the FUNGuild database from the R package FUNGuildR (Nguyen et al., 2016).

Microbial network for each soil sample was created by creating a matrix of relative abundances for both prokaryotic and fungal ASV tables with only the taxa present in each individual sample. Prokaryotic and fungal network for each soil sample was generated with the function make_network() from the R packages phyloseq and igraph, with the "bray" method calculating the distance between ASVs, type set as "taxa" and max.dist as 0.4. When the distance between two ASVs was less than 0.4, it produced a sample-specific network representing ASV co-occurrence patterns in that individual sample. The number of associations among ASVs was counted for each sample, and complexity was calculated as average associations per ASV (linkage density) (Wagg et al., 2019). This approach is conceptually similar to that was used by Wagg et al. (2019), who first inferred a global microbial association network from all samples combined using the SPIEC-EASI algorithm, and then derived sample-specific subnetworks by extracting only the taxa present in each individual sample. Network complexity was subsequently calculated for each sample-specific subnetwork.

Spearman correlations between alpha-diversity metrics, the SMF index, plant litter characteristics, climatic and edaphic variables were calculated by the function rcorr() and presented in a correlation plot visualized by the function corrplot() with the R package corrplot. Random forest (RF) regression (Breiman, 2001) was used to evaluate the importance of different variables, including microbial diversity and network complexity, space (latitude and longitude), climate (MAT and MAP), plant litter characteristics, and soil properties, in influencing SMF index by the rfPermute() function from the R package rfPermute, with 5000 trees and 1000 permutations. To assess model robustness, we used 10-fold cross-validation with by the function train() from the R package caret. RF models were tuned across a range of mtry values, with 5000 trees grown for each model. Model performance was evaluated using root mean square error (RMSE), R^2, and mean absolute error (MAE). The optimal model (mtry = 9) explained ~66–68 % of the variance in SMF with an RMSE of ~ 0.59, which confirms our RF model is reasonably predictive and robust (Supplementary Fig. S3). Multicollinearity of variables was tested by computing the variance inflation factor (VIF) with the function vif() from the R package caret; only variables with a VIF value below 10 were kept for RF regression. Furthermore, we applied piecewise structural equation model (piecewiseSEM) using the function psem() from the R package piecewiseSEM (Lefcheck, 2016), to evaluate the direct and indirect effects of latitude, climatic (MAT and MAP), plant litter characteristics, soil properties (pH, SOM, PO_4^{3-}, NH_4^+, C/N ratio), and microbial diversity and complexity on SMF based on expectations of a priori model (Supplementary Fig. S4). Based on Spearman correlation and RF regressions, prokaryotic alpha-diversity and network complexity, and fungal network complexity had little impact on SMF, thereby only fungal alpha-diversity was used for SEM. Moreover, a stronger linear relationship between fungal richness and SMF (R^2 = 0.18) than between fungal Shannon index and SMF (R^2 =

0.06) was observed. Therefore, to reduce collinearity, we chose fungal richness as microbial diversity index together with spatial, climatic, litter and edaphic variables to best fit SEM. piecewiseSEM breaks the global model into a set of linear models, with each path estimated separately, which then combines through tests of directed separation and allows for moderate sample size. We established each equation with less than 5 predictors with no collinearity (VIF < 3), which provided more than 15 observations per predictor with 75 samples, meeting common SEM requirements. In total, 10 variables were included in SEM analysis based on the 75 individual samples. The best fitting model was the one agreeing with the null hypothesis (P > 0.05), with the highest P value.

3. Results

3.1. Climatic, edaphic and plant litter variables

Climatic, edaphic and plant litter variables showed clear patterns with latitude, regardless of the significant variance explained by site effect (Fig. 1). MAT, *in situ* soil temperature, pH, and litter biomass decreased significantly (P < 0.001) with latitude. In contrast, *in situ* soil water content, TC, TOC, SOM, TN, NH_4^+, PO_4^{3-}, and litter N content increased significantly (P < 0.05) with latitude, with the highest values observed around 60 °N in boreal forests. MAP and litter C content showed a hump-shaped pattern, peaking at 45–50°N in mid-latitude

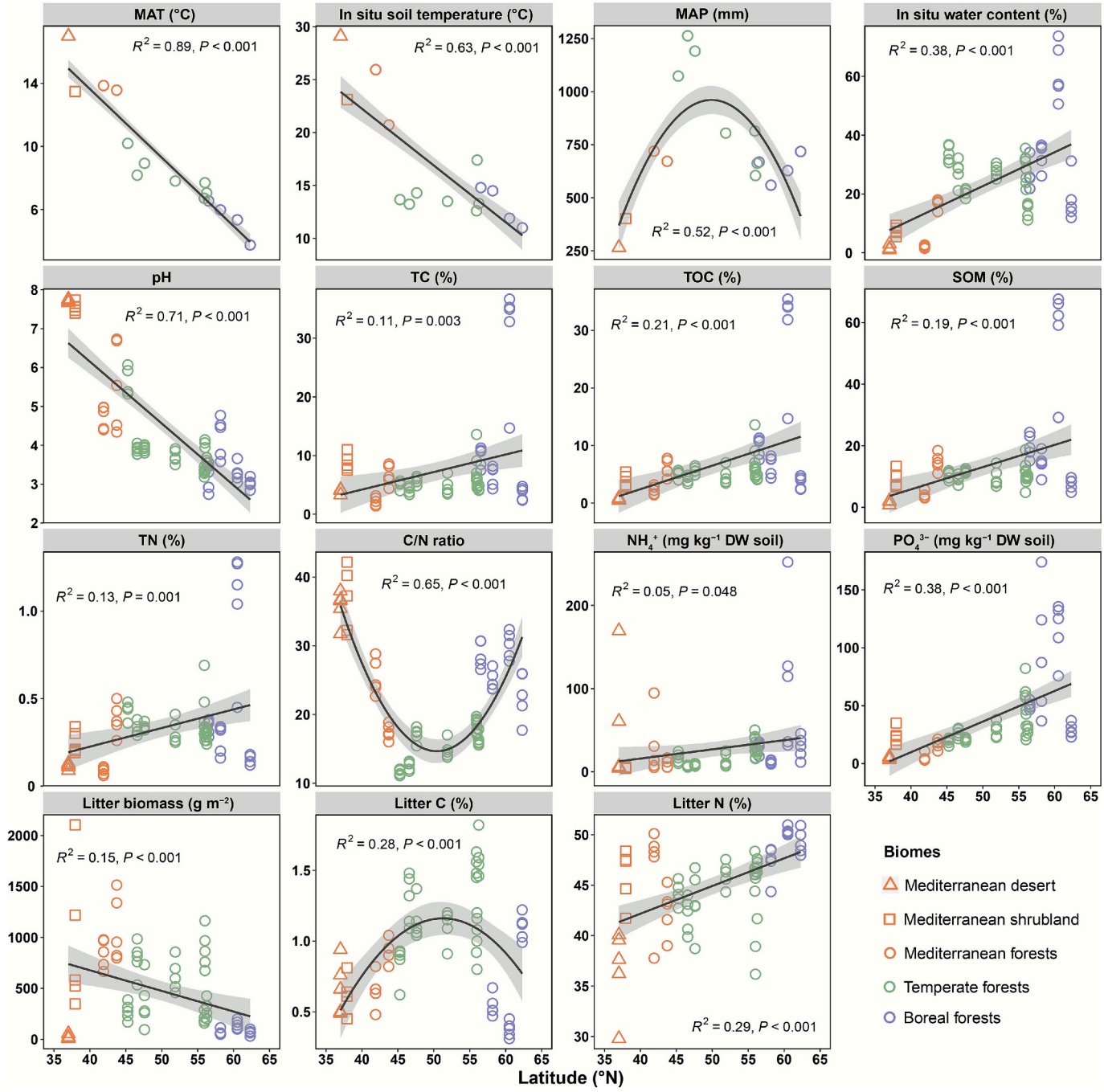

Fig. 1. Variations of climatic, edaphic and plant litter variables along latitude. MAP, Soil C/N ratio and plant litter C content best fit with polynomial regressions with a degree of 2, and the rest of the variables best fit with linear mixed models with site as a random factor (black lines). The shaded areas represent 95 % confidence level. DW: dry weight. Litter was not available at the Dångamålaö, Sweden site at 56.5° latitude.

temperate broadleaf forests. The C/N ratio displayed a U-shaped pattern along the latitudinal gradient, with the lowest values observed in temperate forests.

3.2. Microbial alpha-diversity and co-occurrence network complexity

The alpha-diversity (Richness and Shannon) indices and co-occurrence network complexity were highly correlated for both prokaryotes and fungi (all $P < 0.001$, Spearman rho ≥ 0.7). Microbial alpha-diversity indices and network complexity showed distinct patterns for prokaryotes and fungi along latitude (Fig. 2). Prokaryotic richness and network complexity globally increased with latitude ($P < 0.001$), but the highest values were observed in northern temperate forest soils around 55 °N and decreased along latitude across boreal forests. Prokaryotic richness and network complexity were significantly higher in temperate and boreal forest soils compared to Mediterranean forest and shrubland soils ($P < 0.01$; Supplementary Fig. S5). The prokaryotic Shannon index varied little with latitude ($P > 0.05$).

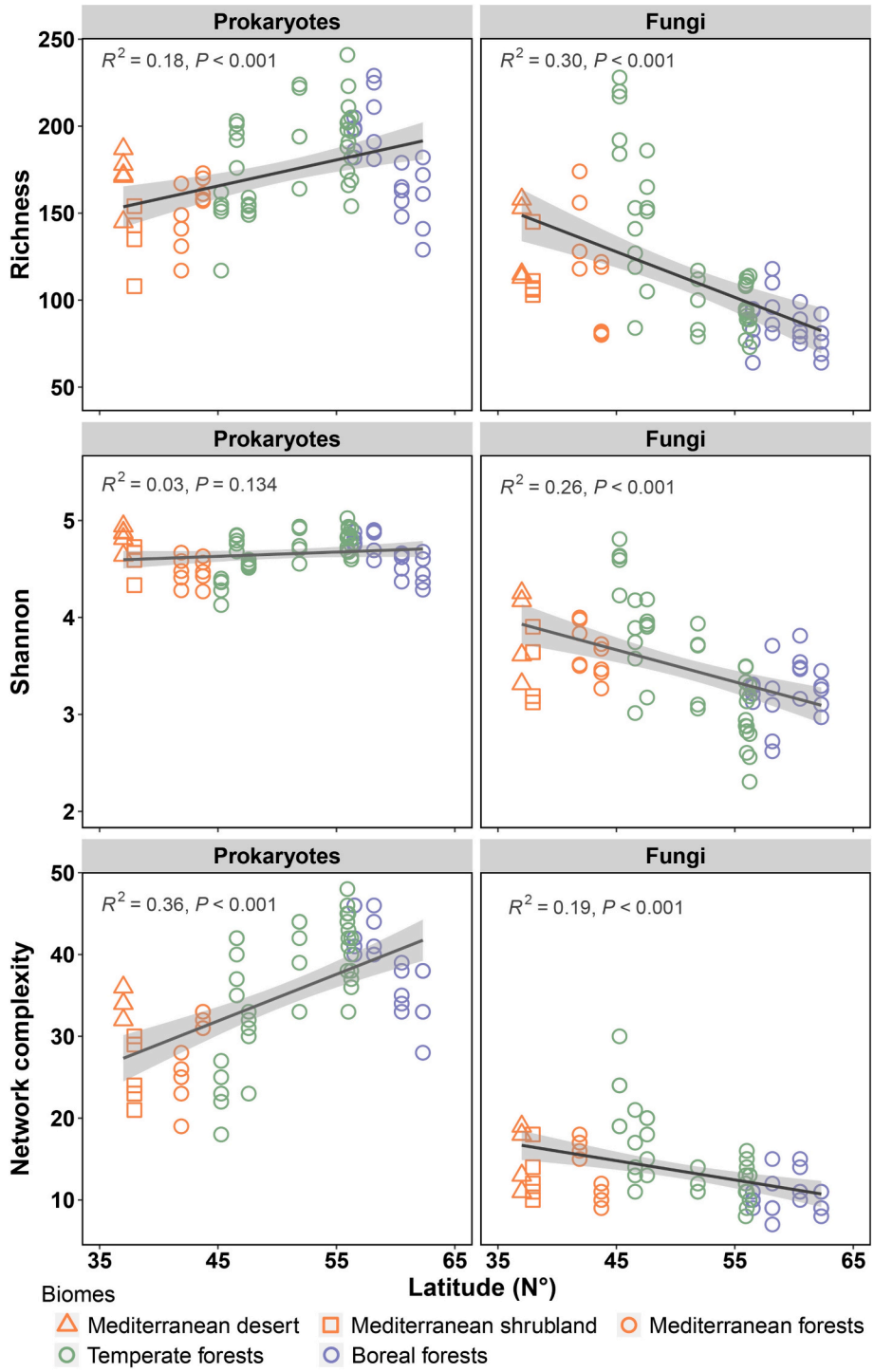

Fig. 2. Microbial alpha-diversity (Richness and Shannon) indices and co-occurrence network complexity (i.e. average network links per ASV) of prokaryotic and fungal communities along latitude. Patterns were modelled by mixed linear models linear mixed models to consider the site effect (black lines). The shaded areas represent 95 % confidence level.

Contrastingly, fungal richness, Shannon index and network complexity decreased with latitude ($P < 0.001$) (Fig. 2), with higher values observed in Mediterranean drylands and temperate forests compared to boreal forests (Supplementary Fig. S5).

3.3. Microbial community structure and composition

Both prokaryotic and fungal community structures gradually shifted along the latitudinal gradient ($R^2 = 0.12$ and 0.06 respectively, both $P < 0.001$, Fig. 3). In Mediterranean drylands, distinct differences were observed between communities in drylands, shrublands, and forests. Prokaryotic and fungal communities in temperate forests were more similar to those in boreal forests than to those in any of the three Mediterranean drylands, as indicated by a greater number of shared taxa between temperate and boreal forests (Fig. 3, Supplementary Fig. S6).

Both prokaryotic and fungal communities showed high homogeneity across the five replicates within each site (Supplementary Fig. S7). Community structure similarity for both communities decreased exponentially (linearly on a log scale) with increasing geographical distance beyond 3000 km (Supplementary Fig. S8). Variation partitioning analyses showed that geographical distance significantly influenced both communities, with prokaryotes being less structured by distance than fungi (Prokaryotes: $R^2 = 11.7$ %; Fungi: $R^2 = 19.3$ %; both $P < 0.001$). Furthermore, fugal communities were more different than prokaryotes at relatively short distance (for instance less than 1000 km; Supplementary Fig. S8). Environmental variables (Prokaryotes: $R^2 = 28.2$ %; Fungi: $R^2 = 27.0$ %; both $P < 0.001$) explained a larger portion of the variation in community structure than geographical distance. Among the environmental variables, land cover (vegetation) explained the most variation, followed by latitude, climate (MAT and MAP), soil temperature, soil texture, plant litter, and soil resources (pH, water content, phosphate, and SOM) (all $P < 0.001$, Fig. 3, Supplementary Table S2).

The dominant bacterial classes across all 75 samples were *Alphaproteobacteria* (24.2 % relative abundance), *Planctomycetes* (15.8 %), *Verrucomicrobiae* (13.6 %), *Acidobacteriae* (8.3 %), *Actinobacteria* (7.2 %) and *Gammaproteobacteria* (4.8 %) (Supplementary Fig. S9A). Among those groups, the relative abundances of *Alphaproteobacteria*, *Gammaproteobacteria*, *Planctomycetes* and *Acidobacteriae* increased significantly ($P < 0.05$) with latitude, while that of *Verrucomicrobiae* decreased ($P < 0.05$) (Supplementary Fig. S10A).

The fungal communities were dominated by the classes *Agaricomycetes* (31.9 %), *Leotiomycetes* (12.8 %), *Eurotiomycetes* (12.7 %), *Sordariomycetes* (10.4 %), *Dothideomycetes* (7.4 %) and *Mortierellomycetes* (4.7 %) (Supplementary Fig. S9B). The relative abundances of *Agaricomycetes* and *Leotiomycetes* increased significantly ($P < 0.05$) with latitude, while those of *Eurotiomycetes* and *Dothideomycetes* decreased ($P < 0.05$) (Supplementary Fig. S10B). Additionally, *Mortierellomycetes* showed a hump-shaped relationship with latitude (polynomial relationship; $P < 0.05$), with the highest relative abundance observed in southern temperate forests (45°–50° latitudes). Fungi were functionally composed of symbiotrophs (31.1 %), saprotrophs (23.9 %), saprotrophs-symbiotrophs (18.6 %), and pathotrophs-saprotrophs (6.8 %), with symbiotrophs increasing linearly and significantly ($R^2 = 0.33$, $P < 0.01$) with latitude (Supplementary Fig. S11).

3.4. Soil multifunctionality

Soil multifunctionality (SMF) – encompassing microbial functions related to C-, N- and P-cycling showed a hump-shaped pattern across latitude (Fig. 4). SMF was significantly ($P < 0.05$) higher in temperate forest soils compared to that in boreal forest soils, with similar values across the three Mediterranean drylands. SMF was also higher in Mediterranean forest soils than in boreal forest soils ($P < 0.05$). Among all functions, SMF was most influenced by the activity of the Leucine aminopeptidase (hydrolysis of peptides and proteins), followed by CH_4 fluxes and N cycling functional genes (Supplementary Fig. S12).

3.5. Relationships between microbial diversity, network complexity, and soil multifunctionality along the European latitudinal gradient

The relationships between SMF and microbial alpha-diversity (richness and Shannon index) and network complexity varied for prokaryotes

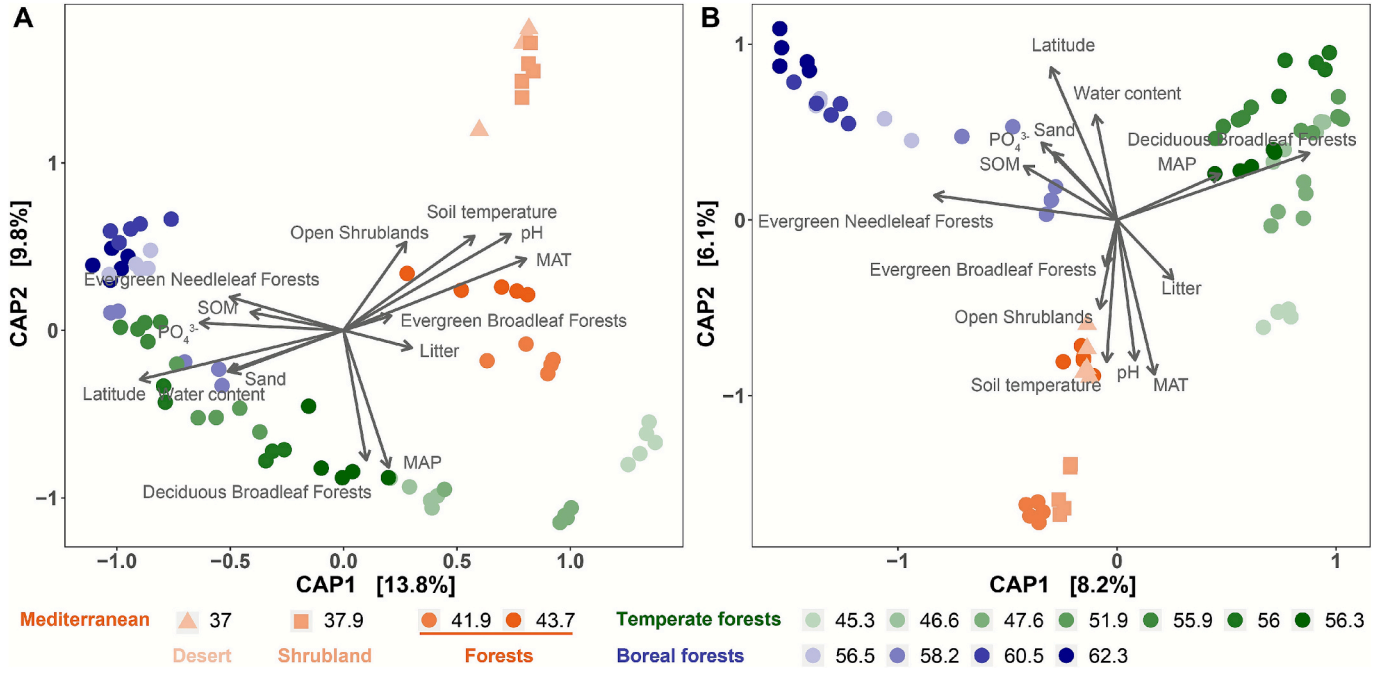

Fig. 3. Constrained analyses of principle coordinates (CAP) on the influence of geographical distance (latitude and longitude), climate, landcover, and soil properties on prokaryotic (A) and fungal (B) community structures. Parameters were chosen by stepwise model selection with the function ordistep() (direction = "both") from the R package vegan. Numbers in legend indicate latitudes at different sites. Total explanation of environmental variables was 60.0 % for prokaryotes and 49.0 % for fungi, respectively.

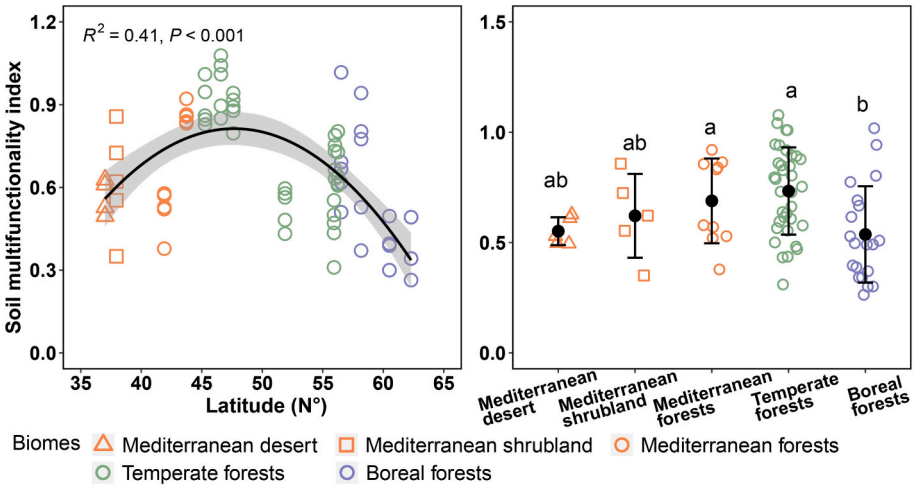

Fig. 4. Soil multifunctionality (SMF) index across latitudes (A) and ecosystems (B). Patterns of SMF along latitude were modelled by polynomial regressions with a degree of 2 (black lines). The shaded areas represent 95 % confidence level. Significance indicated by different letters were done between each two of the five ecosystems by using a pairwise Wilcoxon Rank Sum Test. Standard errors are shown in black.

and fungi along the latitudinal gradient (Fig. 5, Supplementary Fig. S13). While prokaryotic alpha-diversity and network complexity showed no significant correlation with SMF along the whole gradient (Fig. 5A), they were significantly associated with SMF in boreal forests, where they were decreasing towards higher latitudes (Supplementary Table S3, all $P < 0.001$). Fungal alpha-diversity and network complexity were also positively associated with SMF across latitudes (Fig. 5B, all $P < 0.05$). When looking at individual biomes, significant associations were only observed in temperate forests (all $P < 0.01$, Supplementary Table S3).

Random Forest regression analysis (Fig. 6A) identified similar contributing variables as Spearman's rank correlation coefficients (Supplementary Fig. S13), with SMF predicted mostly by MAP, along with MAT, edaphic variables (C/N ratio, pH, NH_4^+, PO_4^{3-}, SOM), litter N content and biomass, fungal richness, and soil texture. Structural equation model explained 44.0 % of the variance in SMF when fungal richness was applied to the model (Fig. 6B). Across latitudes, SMF was directly driven by fungal richness, soil C/N ratio and NH_4^+, and litter N content (all $P < 0.05$). Fungal richness was controlled by MAP and soil pH, which were both influenced by latitude and MAT. Interestingly, SMF was not directly determined by latitude, MAT and SOM.

4. Discussion

This study shows that microbial functional potentials across European latitudes, reflected in the soil multifunctionality index (SMF), follow a hump-shape with latitude, forming a peak in the southern temperate forests (45–47 °N) and declining towards southern Mediterranean drylands and northern boreal forests. Similar hump-shape patterns have been reported for European forest multifunctionality (taking

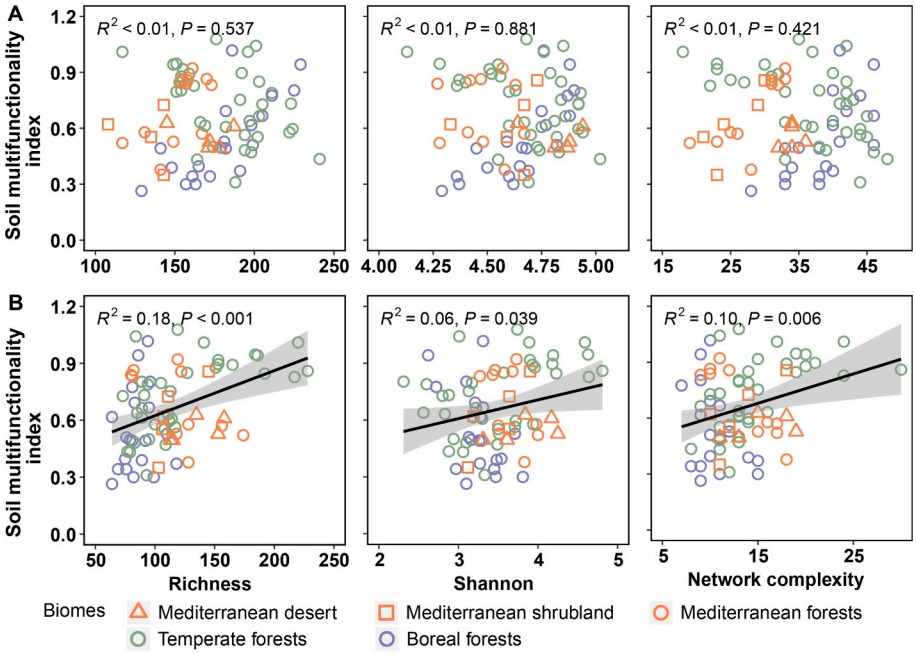

Fig. 5. Linear relationships between SMF, and prokaryotic (A) and fungal (B) alpha-diversity (richness and Shannon) indices and network complexity. Relationships between SMF and microbial alpha-diversity and network complexity were modeled by linear regressions (black lines). The shaded areas represent 95% confidence level.

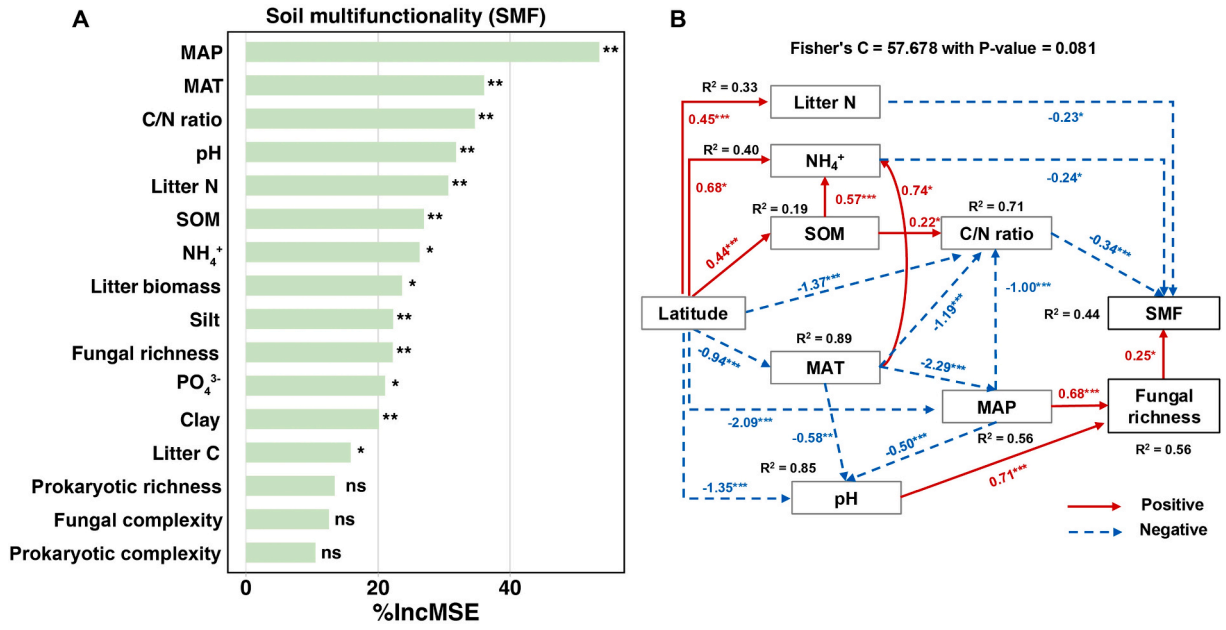

Fig. 6. Random forest regressions (A) and structural equation model (B) showing the effects of different predictors on soil multifunctionality. %IncMSE: % of increase in the mean square error. In B: Numbers adjacent to arrows indicate the effect size of the relationship. R^2 denotes the proportion of variance explained. MAT: mean annual temperature, MAP: mean annual precipitation, SOM: soil organic matter. Significance levels: ns: non-significant; *P < 0.05; **P < 0.01; ***P < 0.001.

into account mostly above ground functional parameters), where the highest multifunctionality was also found in temperate forests of central Europe (van der Plas et al., 2018), and suggesting that plant functioning diversity is reflected into soil microbial functions. The latitudinal changes in microbial functions indicate the variations of microbial communities along the latitudinal gradient. While this study includes a relatively limited number of sites per biome, with some biomes (e.g., Mediterranean desert, shrubland, and forest) represented by only one or two sites, the dataset included 75 independent soil samples across 15 sites, which provided sufficient power for the statistical models. However, the limited biome-level replication constrains the generalization of the output of this study to all European biomes. Therefore, the findings of this study should be understood as reflecting patterns and drivers observed along the European latitudinal transect, rather than as definitive representations of European biomes. Our findings further revealed that prokaryotic and fungal community structures followed similar patterns along the European latitudinal gradient. Both communities were shaped by geographical distance, land cover, climatic, and soil factors, as were found previously (He et al., 2017; Labouyrie et al., 2024; Powell et al., 2015; Ranjard et al., 2013). The significant influence of geographical distance on the prokaryotic and fungal community structures along the 3000 km environmental gradient suggests a strong dispersal limitation, especially on the fungal communities. Over relatively short distances (i.e. less than 1000 km), fungal community structure was more dissimilar than prokaryotes. This limitation can be explained by the larger size of fungal cells, limiting fungal transport at short distances. Another explanation could be due to vegetation cover. About one third (31 %) of the fungal taxa were strict symbiotrophs, therefore potentially strongly associated with specific host plants, which varied greatly with distance and across latitudes (Tedersoo et al., 2012). Symbiotrophic fungi were more predominant in the northern European latitudes, with higher relative abundances in boreal (needleleaf) and temperate (broadleaf) forests in comparison to the three Mediterranean drylands. Furthermore, among the top 100 symbiotrophic taxa, we observed that the most predominant ones were ectomycorrhizal fungi, aligning with the known augmentation of symbiotic association of ectomycorrhizal fungi with plant roots in northern latitudes (Bahram et al., 2018; Tedersoo et al., 2012). In the southern part of the European gradient, we observed that the fungal community structure of the Mediterranean desert was more similar to the Mediterranean forests, than to the Mediterranean shrubland. One possible explanation is the high clay content in Mediterranean desert and Mediterranean forest soils, which might affect fungal communities more strongly. Clay- and silt-rich soils can form large aggregates, enhancing water retention and nutrient availability (Bach et al., 2010). Xia et al. (2020) found significant positive associations between *Basidiomycota* and *Ascomycota* and soil silt/clay content, suggesting preferences of the dominating fungal phyla for fine-textured soils. Yet, more controlled experiments would be needed to explore the impact of soil silt/clay content in shaping fungal community composition and structure in dry environments with different land cover.

By integrating microbial diversity, network complexity, and multiple functional dimensions along a 3000 km latitudinal transect, our study provides continental-scale evidence that fungal diversity is a key driver of soil multifunctionality across European latitudes. Fungal alpha-diversity (richness), along with climatic (MAP and MAT), edaphic (pH, C/N ratio, NH_4^+, TN, and SOM), and plant litter biomass variables were significantly correlated to SMF across European latitudes, unlike prokaryotic diversity and network complexity. These findings align with previous studies showing that fungal diversity is a key predictor of ecosystem multifunctionality at local scales in Chinese boreal forests (Li et al., 2019a), agricultural soils (Li et al., 2019b; Xue et al., 2023), and grasslands (Li et al., 2022; Ma et al., 2022). Large-scale studies on drylands also found that soil fungal diversity was more strongly correlated to ecosystem multifunctionality than bacterial diversity (Delgado-Baquerizo et al., 2016; Hu et al., 2021). Additionally, soil biodiversity was found to support ecosystem functions in urban soils (Fan et al., 2023) and to promote primary production in croplands (Romero et al., 2024). However, in contrast to these studies, our work spanned over several natural ecosytems, including drylands, temperate and boreal forests, suggesting a high importance of fungal communities independently of the geo-climatic zone.

The intensity of the observed link between fungal diversity and SMF varied between Mediterranean drylands, temperate forests, and boreal forests, with the stronger positive association found in temperate forests and no significant correlation observed in Mediterranean drylands and

boreal forests. Although the uneven sampling across biomes (i.e. the greater number of sites in temperate forests compared to Mediterranean drylands and boreal forests) may have influenced the observed link between fungal diversity and SMF, several mechanisms could still explain the strong role of fungal alpha-diversity and environmental variables in shaping SMF.

Firstly, moderate increases in MAP and MAT have been shown to enhance soil respiration and microbial activity (Curiel Yuste et al., 2007; Zhang et al., 2023), and are also known to promote soil fungal alpha-diversity (Bahram et al., 2018; Tedersoo et al., 2014). This supports the observed rise in soil fungal alpha-diversity and SMF with increasing MAP and MAT from boreal to temperate forest. The higher aridity and temperature in Mediterranean drylands limited fungal alpha-diversity and activity, leading to a reduction of SMF, an effect further corroborated by the negative impact of MAT on fungal richness revealed by SEM analysis. Secondly, increasing soil pH generally enhances soil fungal diversity, biomass, and respiration, stabilizing between pH 5 and 6 (Pietri and Brookes, 2008; Rousk et al., 2009; Tedersoo et al., 2020). This aligns with our observed peak of fungal diversity and SMF in southern temperate forests (45–47 °N), where pH varied between 4.0 and 5.7, and is supported by the positive effect of pH on fungal alpha-diversity shown in the SEM analysis. Thirdly, fungi are known to play a key role in N cycling during the decomposition of organic matter (Liu et al., 2023). The SMF index was predominantly influenced by leucine aminopeptidase, an enzyme central to the hydrolysis of organic N compounds, emphasizing the pivotal role of N cycling processes in sustaining soil multifunctionality. The positive associations between the SMF index and the relative abundances of fungal classes such as *Sordariomycetes* and *Mortierellomycetes*, which are established producers of leucine aminopeptidase (Nampoothiri et al., 2005; Yew et al., 2016; Zheng et al., 2020), suggest a fungal-driven proteolysis that may enhance nitrogen mineralization, thereby increasing inorganic nitrogen availability for both microbial and plant uptake. Furthermore, this process may facilitate other ecosystem functions such as plant productivity, microbial biomass production, and enzymatic pathways involved in C and P cycling (Pellitier and Zak, 2018). Our results therefore support the idea that several specific microbial groups, particularly fungi with specialized enzymatic capacities, may exert disproportionate influence on ecosystem multifunctionality through their biochemical traits and activities. Another key driver of SMF is the soil C/N ratio, which showed a negative correlation with SMF, NH_4^+ and litter N content along the whole gradient, based on Spearman correlation and SEM analysis. In temperate forests, low soil C/N ratio indicated nutrient-limited soils, that could potentially promote fungal alpha-diversity, as fungi are able to live under more oligotrophic conditions than prokaryotes (Liu et al., 2020). However, higher C/N ratio at both ends of the gradient, i.e. in the boreal forests and in the Mediterranean drylands, indicated N limitation, likely restricting the activity of the microbial communities. This effect was especially pronounced in the drier southern soils, where N limitation might have severely weakened the fungal contribution to SMF. In contrast, prokaryotic alpha-diversity was unrelated to soil C/N ratio but depended considerably on soil PO_4^{3-} content, which was limited in Mediterranean drylands, and probably insufficient to support SMF.

Fungal network complexity was also linked to SMF. Microbial co-occurrence networks help reveal interactions among taxa, demonstrating their role in supporting soil biodiversity (Barberán et al., 2012; Liu et al., 2024) and functions (Fuhrman, 2009; Wagg et al., 2019). However, the link between fungal network complexity and SMF was weaker than between fungal alpha-diversity and SMF. This is likely due to functional redundancy, where multiple species perform similar roles, reducing reliance on complex network associations (Banerjee et al., 2016; Louca et al., 2018).

We included a large range of functions in the SMF, including both actual activities measurements (such as enzymes) and potential functions (such as gene abundances) to provide a more comprehensive perspective of SMF. This is the case for *pho*D gene abundance and the PHOS enzyme assays, which, although both assess a similar function, do not correlate. This can be partly attributed to the fact that the qPCR assay for the *pho*D gene quantified ALP genes, whereas the PHOS enzyme assay targeted both ALP and ACP enzyme activities. Moreover, functional genes are not always translated or expressed as active enzymes, as their expression is influenced by environmental factors, such as resource availability and nutrient demand (Chen and Sinsabaugh, 2021; Ouyang et al., 2018). Nevertheless, we considered it important to include gene abundance in the SMF index calculation, when gene abundance is not corelated to actual enzyme activity, as it represents a critical aspect of potential microbial contributions to P cycling that might not be fully captured by enzyme activity assays.

Furthermore, it is worth noting that the SMF index as calculated in this study is reflecting the soil multifunctionality from the point of view of microbial activities. As an example, CH_4 fluxes, reflecting emission of CH_4 from the soil to the atmosphere, were included as indicators of microbial activity related to C cycling, a product of methanogenesis and methanotrophy. From the climate mitigation perspective, however, since CH_4 is a potent greenhouse gas, higher CH_4 emissions would represent a reduced ecosystem multifunctionality.

The European continent will increasingly be affected by global changes (Schröter et al., 2005), especially in the Mediterranean regions, where precipitation will decrease and drought frequency and intensity will increase (Giorgi and Lionello, 2008). Mediterranean drylands are therefore expected to extend towards North (Seneviratne et al., 2006), replacing areas currently covered by forests. The replacement of forests by more arid-adapted ecosystems is expected to weaken the relationship between soil microbial communities and soil functions, driven by reduced availability of organic matter and nutrients. Accordingly, the association between fungal diversity and soil multifunctionality is likely to decline. In Mediterranean drylands, increasing aridity and desertification are already threatening plant productivity and diversity (Thuiller et al., 2005), leading the lower inputs of soil organic matter and nutrients (Albaladejo et al., 2013). Since fungal diversity, biomass and activities are strongly associated to plant diversity (Peay et al., 2013), they are also expected to decrease (Büntgen et al., 2015; Maestre et al., 2015), eventually leading to a reduction of the overall contribution of fungi to soil ecosystem functions in these regions. In central and northern Europe, while plant diversity is expected to decline in temperate and boreal forests due to global changes, losses are foreseen to be less severe than in Mediterranean drylands (Thuiller et al., 2005). Meanwhile, plant biomass and growth are likely to increase under warmer climate (Xu et al., 2024), strengthening the link between fungal diversity and soil functions in those areas, through greater plant biomass input. Enhanced fungal diversity and activities will thus contribute to the expected acceleration of organic matter decomposition in temperate and boreal forests under global warming (Baldrian et al., 2023; Treseder et al., 2016), accelerating soil carbon and nutrients cycling.

CRediT authorship contribution statement

Xingguo Han: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Anna Doménech-Pascual:** Writing – review & editing, Methodology. **Jonathan Donhauser:** Writing – review & editing, Methodology. **Constantin M. Zohner:** Writing – review & editing. **Lidong Mo:** Writing – review & editing. **Thomas W. Crowther:** Writing – review & editing. **Joan Pere Casas-Ruiz:** Writing – review & editing, Methodology. **Karen Jordaan:** Methodology. **Jean-Baptiste Ramond:** Writing – review & editing, Funding acquisition. **Anna M. Romaní:** Writing – review & editing, Funding acquisition. **Anders Priemé:** Writing – review & editing, Funding acquisition. **Aline Frossard:** Writing – review & editing, Supervision, Funding acquisition, 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.geoderma.2025.117600.

Data availability

Raw reads for prokaryotic 16S rRNA gene and fungal ITS2 region are deposited in the NCBI Sequence Read Archive (SRA) under the accession numbers PRJNA1073882 and PRJNA1161578, respectively. Environmental data and microbial functions data are available in Envidat database (https://doi.org/10.16904/envidat.644).

References

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., May, T.W., Froslev, T.G., Pawlowska, J., Lindahl, B., Poldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T.E., Ishigami, Y., Jansson, A.T., Jeppesen, T.S., Kristiansson, E., Mikryukov, V., Miller, J.T., Oono, R., Ossandon, F.J., Pauperio, J., Saar, I., Schigel, D., Suija, A., Tedersoo, L., Koljalg, U., 2023. The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. Nucleic Acids Res.

Albaladejo, J., Ortiz, R., Garcia-Franco, N., Navarro, A.R., Almagro, M., Pintado, J.G., Martínez-Mena, M., 2013. Land use and climate change impacts on soil organic carbon stocks in semi-arid Spain. J. Soil. Sediment. 13 (2), 265–277.

Anthony, M.A., Bender, S.F., van der Heijden, M.G.A., 2023. Enumerating soil biodiversity. Proc. Natl. Acad. Sci. USA 120 (33).

Bach, E.M., Baer, S.G., Meyer, C.K., Six, J., 2010. Soil texture affects soil microbial and structural recovery during grassland restoration. Soil Biol. Biochem. 42 (12), 2182–2191.

Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundra, S., Olsson, P.A., Pent, M., Polme, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. Nature 560 (7717), 233–237.

Baldrian, P., López-Mondéjar, R., Kohout, P., 2023. Forest microbiome and global change. Nat. Rev. Microbiol. 21 (8), 487–501.

Banerjee, S., Kirkby, C.A., Schmutter, D., Bissett, A., Kirkegaard, J.A., Richardson, A.E., 2016. Network analysis reveals functional redundancy and keystone taxa amongst bacterial and fungal communities during organic matter decomposition in an arable soil. Soil Biol. Biochem. 97, 188–198.

Barberán, A., Bates, S.T., Casamayor, E.O., Fierer, N., 2012. Using network analysis to explore co-occurrence patterns in soil microbial communities. ISME J. 6 (2), 343–351.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515 (7528), 505–511.

Booth, M.S., Stark, J.M., Rastetter, E., 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. Ecol. Monogr. 75 (2), 139–157.

Breiman, L., 2001. Random forests. Mach. Learn. 45 (1), 5–32.

Büntgen, U., Egli, S., Galván, J.D., Diez, J.M., Aldea, J., Latorre, J., Martínez-Peña, F., 2015. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. Fungal Ecol. 16, 6–18.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B.J., Hooper, D.U., Dee, L.E., Duffy, J.E., 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods Ecol. Evol. 5 (2), 111–124.

Callahan, B.J., McMurdie, P.J., Holmes, S.P., 2017. Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. ISME J. 11 (12), 2639–2643.

Chen, J., Sinsabaugh, R.L., 2021. Linking microbial functional gene abundance and soil extracellular enzyme activity: implications for soil carbon dynamics. Glob. Chang. Biol. 27 (7), 1322–1325.

Chiarello, M., McCauley, M., Villéger, S., Jackson, C.R., 2022. Ranking the biases: the choice of OTUs vs. ASVs in 16S rRNA amplicon data analysis has stronger effects on diversity measures than rarefaction and OTU identity threshold. PLoS One 17 (2), e0264443.

Cookson, W.R., Osman, M., Marschner, P., Abaye, D.A., Clark, I., Murphy, D.V., Stockdale, E.A., Watson, C.A., 2007. Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. Soil Biol. Biochem. 39 (3), 744–756.

Coyte, K.Z., Schluter, J., Foster, K.R., 2015. The ecology of the microbiome: networks, competition, and stability. Science 350 (6261), 663–666.

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science 365 (6455), eaav0550.

Curiel Yuste, J., Baldocchi, D.D., Gershenson, A., Goldstein, A., Misson, L., Wong, S., 2007. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Glob. Chang. Biol. 13 (9), 2018–2035.

Davies, B.E., 1974. Loss-on-ignition as an estimate of soil organic-matter. Soil Sci. Soc. Am. J. 38 (1), 150–151.

Delgado-Baquerizo, M., Eldridge, D.J., Ochoa, V., Gozalo, B., Singh, B.K., Maestre, F.T., 2017a. Soil microbial communities drive the resistance of ecosystem multifunctionality to global change in drylands across the globe. Ecol. Lett. 20 (10), 1295–1305.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat. Commun. 7.

Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., He, J.Z., Hseu, Z.Y., Hu, H.W., Kirchmair, M., Neuhauser, S., Pérez, C.A., Reed, S.C., Santos, F., Sullivan, B.W., Trivedi, P., Wang, J.T., Weber-Grullon, L., Williams, M.A., Singh, B.K., 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nat. Ecol. Evol. 4 (2), 210–220.

Delgado-Baquerizo, M., Trivedi, P., Trivedi, C., Eldridge, D.J., Reich, P.B., Jeffries, T.C., Singh, B.K., 2017b. Microbial richness and composition independently drive soil multifunctionality. Funct. Ecol. 31 (12), 2330–2343.

Doménech-Pascual, A., Rodriguez, L.C., Han, X., Casas-Ruiz, J.P., Ferriol-Ciurana, J., Donhauser, J., Jordaan, K., Allison, S.D., Frossard, A., Priemé, A., Ramond, J.B., Romaní, A.M., 2025. Soil functions are shaped by aridity through soil properties and the microbial community structure. Appl. Soil Ecol. 213, 106313.

Donhauser, J., Doménech-Pascual, A., Han, X.G., Jordaan, K., Ramond, J.B., Frossard, A., Romani, A.M., Priemé, A., 2024. Modelling soil prokaryotic traits across environments with the trait sequence database and the R package MicEnvMod. Ecol. Inform. 83.

Fan, K., Chu, H., Eldridge, D.J., Gaitan, J.J., Liu, Y.R., Sokoya, B., Wang, J.T., Hu, H.W., He, J.Z., Sun, W., Cui, H., Alfaro, F.D., Abades, S., Bastida, F., Diaz-Lopez, M., Bamigboye, A.R., Berdugo, M., Blanco-Pastor, J.L., Grebenc, T., Duran, J., Illan, J.G., Makhalanyane, T.P., Mukherjee, A., Nahberger, T.U., Penaloza-Bojaca, G.F., Plaza, C., Verma, J.P., Rey, A., Rodriguez, A., Siebe, C., Teixido, A.L., Trivedi, P., Wang, L., Wang, J., Yang, T., Zhou, X.Q., Zhou, X., Zaady, E., Tedersoo, L., Delgado-Baquerizo, M., 2023. Soil biodiversity supports the delivery of multiple ecosystem functions in urban greenspaces. Nat. Ecol. Evol. 7 (1), 113–126.

Fasolo, A., Deb, S., Stevanato, P., Concheri, G., Squartini, A., 2024. ASV vs OTUs clustering: effects on alpha, beta, and gamma diversities in microbiome metabarcoding studies. PLoS One 19 (10), e0309065.

Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M., Pitchford, J.W., Programme, N.S.B., 2005. Biodiversity and ecosystem function in soil. Funct. Ecol. 19 (3), 369–377.

Frey, B., Rime, T., Phillips, M., Stierli, B., Hajdas, I., Widmer, F., Hartmann, M., 2016. Microbial diversity in European alpine permafrost and active layers. FEMS Microbiol. Ecol. 92 (3).

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., Huang, X.M., 2010. MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets. Remote Sens. Environ. 114 (1), 168–182.

Fuhrman, J.A., 2009. Microbial community structure and its functional implications. Nature 459 (7244), 193–199.

Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89 (5), 1223–1231.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Global Planet. Change 63 (2–3), 90–104.
Gonzalez, A., Germain, R.M., Srivastava, D.S., Filotas, E., Dee, L.E., Gravel, D., Thompson, P.L., Isbell, F., Wang, S., Kefi, S., Montoya, J., Zelnik, Y.R., Loreau, M., 2020. Scaling-up biodiversity-ecosystem functioning research. Ecol. Lett. 23 (4), 757–776.
Graham, E.B., Knelman, J.E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A., Bemans, J.M., Abell, G., Philippot, L., Prosser, J., Foulquier, A., Yuste, J.C., Glanville, H.C., Jones, D.L., Angel, F., Salminen, J., Newton, R.J., Bürgmann, H., Ingram, L.J., Hamer, U., Siljanen, H.M.P., Peltoniemi, K., Potthast, K., Bañeras, L., Hartmann, M., Banerjee, S., Yu, R.Q., Nogaro, G., Richter, A., Koranda, M., Castle, S.C., Goberna, M., Song, B., Chatterjee, A., Nunes, O.C., Lopes, A.R., Cao, Y.P., Kaisermann, A., Hallin, S., Strickland, M.S., Garcia-Pausas, J., Barba, J., Kang, H., Isobe, K., Papaspyrou, S., Pastorelli, R., Lagomarsino, A., Lindström, E.S., Basiliko, N., Nemergut, D.R., 2016. Microbes as engines of ecosystem function: when does community structure enhance predictions of ecosystem processes? Front. Microbiol. 7.
Guerra, C.A., Heintz-Buschart, A., Sikorski, J., Chatzinotas, A., Guerrero-Ramírez, N., Cesarz, S., Beaumelle, L., Rillig, M.C., Maestre, F.T., Delgado-Baquerizo, M., Buscot, F., Overmann, J., Patoine, G., Phillips, H.R.P., Winter, M., Wubet, T., Küsel, K., Bardgett, R.D., Cameron, E.K., Cowan, D., Grebenc, T., Marín, C., Orgiazzi, A., Singh, B.K., Wall, D.H., Eisenhauer, N., 2020. Blind spots in global soil biodiversity and ecosystem function research. Nat. Commun. 11 (1).
Han, X.G., Beck, K., Bürgmann, H., Frey, B., Stierli, B., Frossard, A., 2023. Synthetic oligonucleotides as quantitative PCR standards for quantifying microbial genes. Front. Microbiol. 14.
Han, X.G., Doménech-Pascual, A., Casas-Ruiz, J.P., Donhauser, J., Jordaan, K., Ramond, J.B., Priemé, A., Romaní, A.M., Frossard, A., 2024. Soil organic matter properties drive microbial activity and greenhouse gas fluxes along an altitudinal gradient. Geoderma 449, 116993.
Han, X.G., Schubert, C.J., Fiskal, A., Dubois, N., Lever, M.A., 2020. Eutrophication as a driver of microbial community structure in lake sediments. Environ. Microbiol. 22 (8), 3446–3462.
He, J.H., Tedersoo, L.H., Hu, A., Han, C.H., He, D., Wei, H., Jiao, M., Anslan, S., Nie, Y.X., Jia, Y.X., Zhang, G.X., Yu, G.R., Liu, S.R., Shen, W.J., 2017. Greater diversity of soil fungal communities and distinguishable seasonal variation in temperate deciduous forests compared with subtropical evergreen forests of eastern China. FEMS Microbiol. Ecol. 93 (7).
Hu, W.G., Ran, J.Z., Dong, L.W., Du, Q.J., Ji, M.F., Yao, S.R., Sun, Y., Gong, C.M., Hou, Q. Q., Gong, H.Y., Chen, R.F., Lu, J.L., Xie, S.B., Wang, Z.Q., Huang, H., Li, X.W., Xiong, J.L., Xia, R., Wei, M.H., Zhao, D.M., Zhang, Y.H., Li, J.H., Yang, H.X., Wang, X.T., Deng, Y., Sun, Y., Li, H.L., Zhang, L., Chu, Q.P., Li, X.W., Aqeel, M., Manan, A., Akram, M.A., Liu, X.H., Li, R., Li, F., Hou, C., Liu, J.Q., He, J.S., An, L.Z., Bardgett, R.D., Schmid, B., Deng, J.M., 2021. Aridity-driven shift in biodiversity-soil multifunctionality relationships. Nat. Commun. 12 (1).
Jiao, S., Lu, Y.H., Wei, G.H., 2022. Soil multitrophic network complexity enhances the link between biodiversity and multifunctionality in agricultural systems. Glob. Chang. Biol. 28 (1), 140–153.
Kerrigan, Z., D'Hondt, S., 2022. Patterns of relative bacterial richness and community composition in seawater and marine sediment are robust for both operational taxonomic units and amplicon sequence variants. Front. Microbiol. 13.
Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., Bates, S.T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G.W., Hartmann, M., Kirk, P.M., Kohout, P., Larsson, E., Lindahl, B.D., Luecking, R., Martin, M.P., Matheny, P.B., Nguyen, N.H., Niskanen, T., Oja, J., Peay, K.G., Peintner, U., Peterson, M., Poldmaa, K., Saag, L., Saar, I., Schüessler, A., Scott, J.A., Senes, C., Smith, M.E., Suija, A., Taylor, D.L., Telleria, M.T., Weiss, M., Larsson, K.H., 2013. Towards a unified paradigm for sequence-based identification of fungi. Mol. Ecol. 22 (21), 5271–5277.
Kuo, S., 1996. Phosphorus. In: Sparks, D.L. et al (Eds.), Methods of Soil Analysis, Part 3: Chemical Methods, SSSA Book Series 5, 869-919.
Labouyrie, M., Ballabio, C., Romero, F., Panagos, P., Jones, A., Schmid, M.W., Mikryukov, V., Dulya, O., Tedersoo, L., Bahram, M., Lugato, E., van der Heijden, M. G.A., Orgiazzi, A., 2023. Patterns in soil microbial diversity across Europe. Nat. Commun. 14 (1).
Labouyrie, M., Ballabio, C., Romero, F., Panagos, P., Jones, A., Tedersoo, L., van der Heijden, M.G., Orgiazzi, A., 2024. Interaction effects of pH and land cover on soil microbial diversity are climate-dependent. Environ. Microbiol. 26 (2), e16572.
Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7 (5), 573–579.
Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S., Hector, A., Cardinale, B.J., Duffy, J.E., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat. Commun. 6.
Li, J., Delgado-Baquerizo, M., Wang, J.T., Hu, H.W., Cai, Z.J., Zhu, Y.N., Singh, B.K., 2019a. Fungal richness contributes to multifunctionality in boreal forest soil. Soil Biol. Biochem. 136.
Li, X.B., He, H.B., Zhang, X.D., Yan, X.Y., Six, J., Cai, Z.C., Barthel, M., Zhang, J.B., Necpalova, M., Ma, Q.Q., Li, Z.A., 2019b. Distinct responses of soil fungal and bacterial nitrate immobilization to land conversion from forest to agriculture. Soil Biol. Biochem. 134, 81–89.
Li, Z., Liu, X.W., Zhang, M.H., Xing, F., 2022. Plant diversity and fungal richness regulate the changes in soil multifunctionality in a semi-arid grassland. Biology-Basel 11 (6).
Liu, Y.Y., Dong, L.Z., Zhang, H.J., Deng, Y.Y., Hu, B., Wang, W., 2023. Distinct roles of bacteria and fungi in mediating soil extracellular enzymes under long-term nitrogen deposition in temperate plantations. Forest Ecol. Manage. 529.
Liu, S.E., Wang, H., Tian, P., Yao, X., Sun, H., Wang, Q.K., Delgado-Baquerizo, M., 2020. Decoupled diversity patterns in bacteria and fungi across continental forest ecosystems. Soil Biol. Biochem. 144.
Liu, X., Chu, H., Godoy, O., Fan, K., Gao, G.F., Yang, T., Ma, Y., Delgado-Baquerizo, M., 2024. Positive associations fuel soil biodiversity and ecological networks worldwide. Proc. Natl. Acad. Sci. USA 121 (6), e2308769121.
Lladó, S., López-Mondéjar, R., Baldrian, P., 2018. Drivers of microbial community structure in forest soils. Appl. Microbiol. Biot. 102 (10), 4331–4338.
Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16 (Suppl 1), 106–115.
Louca, S., Polz, M.F., Mazel, F., Albright, M.B.N., Huber, J.A., O'Connor, M.I., Ackermann, M., Hahn, A.S., Srivastava, D.S., Crowe, S.A., Doebeli, M., Parfrey, L.W., 2018. Function and functional redundancy in microbial systems. Nat. Ecol. Evol. 2 (6), 936–943.
Ma, B., Wang, H.Z., Dsouza, M., Lou, J., He, Y., Dai, Z.M., Brookes, P.C., Xu, J.M., Gilbert, J.A., 2016. Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. ISME J. 10 (8), 1891–1901.
Ma, L.N., Zhang, C.X., Xu, X.F., Wang, C.W., Liu, G.F., Liang, C.Z., Zuo, X.A., Wang, C.J., Lv, Y., Wang, R.Z., 2022. Different facets of bacterial and fungal communities drive soil multifunctionality in grasslands spanning a 3500 km transect. Funct. Ecol. 36 (12), 3120–3133.
Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J. R., Huber-Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D.L., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. Proc. Natl. Acad. Sci. USA 112 (51), 15684–15689.
Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitan, J., Gatica, M.G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J.R., Hernandez, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D.A., Romao, R., Tighe, M., Torres-Diaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335 (6065), 214–218.
Makhalanyane, T.P., Valverde, A., Gunnigle, E., Frossard, A., Ramond, J.B., Cowan, D.A., 2015. Microbial ecology of hot desert edaphic systems. FEMS Microbiol. Rev. 39 (2), 203–221.
Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., Fischer, M., 2018. Redefining ecosystem multifunctionality. Nat. Ecol. Evol. 2 (3), 427–436.
McMurdie, P.J., Holmes, S., 2013. phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PLoS One 8 (4).
Nampoothiri, K.M., Nagy, V., Kovacs, K., Szakacs, G., Pandey, A., 2005. L-leucine aminopeptidase production by filamentous fungi. Lett. Appl. Microbiol. 41 (6), 498–504.
Nannipieri, P., Ascher, J., Ceccherini, M.T., Landi, L., Pietramellara, G., Renella, G., 2003. Microbial diversity and soil functions. Eur. J. Soil Sci. 54 (4), 655–670.
Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol. 20, 241–248.
Osburn, E.D., Yang, G.O., Rillig, M.C., Strickland, M.S., 2023. Evaluating the role of bacterial diversity in supporting soil ecosystem functions under anthropogenic stress. ISME Commun. 3 (1).
Ouyang, Y., Reeve, J.R., Norton, J.M., 2018. Soil enzyme activities and abundance of microbial functional genes involved in nitrogen transformations in an organic farming system. Biol. Fert. Soils 54 (4), 437–450.
Peay, K.G., Baraloto, C., Fine, P.V.A., 2013. Strong coupling of plant and fungal community structure across western Amazonian rainforests. ISME J. 7 (9), 1852–1861.
Pellitier, P.T., Zak, D.R., 2018. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. New Phytol. 217 (1), 68–73.
Philippot, L., Spor, A., Hénault, C., Bru, D., Bizouard, F., Jones, C.M., Sarr, A., Maron, P. A., 2013. Loss in microbial diversity affects nitrogen cycling in soil. ISME J. 7 (8), 1609–1619.
Pietri, J.A., Brookes, P.C., 2008. Relationships between soil pH and microbial properties in a UK arable soil. Soil Biol. Biochem. 40 (7), 1856–1861.
Powell, J.R., Karunaratne, S., Campbell, C.D., Yao, H.Y., Robinson, L., Singh, B.K., 2015. Deterministic processes vary during community assembly for ecologically dissimilar taxa. Nat. Commun. 6.
Qiu, L.P., Zhang, Q., Zhu, H.S., Reich, P.B., Banerjee, S., van der Heijden, M.G.A., Sadowsky, M.J., Ishii, S., Jia, X.X., Shao, M.G., Liu, B.Y., Jiao, H., Li, H.Q., Wei, X.R., 2021. Erosion reduces soil microbial diversity, network complexity and multifunctionality. ISME J. 15 (8), 2474–2489.
Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41 (D1), D590–D596.
Ranjard, L., Dequiedt, S., Prévost-Bouré, N.C., Thioulouse, J., Saby, N.P.A., Lelievre, M., Maron, P.A., Morin, F.E.R., Bispo, A., Jolivet, C., Arrouays, D., Lemanceau, P., 2013.

Turnover of soil bacterial diversity driven by wide-scale environmental heterogeneity. Nat. Commun. 4.
Romero, F., Labouyrie, M., Orgiazzi, A., Ballabio, C., Panagos, P., Jones, A., Tedersoo, L., Bahram, M., Guerra, C.A., Eisenhauer, N., Tao, D., Delgado-Baquerizo, M., García-Palacios, P., van der Heijden, M.G.A., 2024. Soil health is associated with higher primary productivity across Europe. Nat. Ecol. Evol. 8 (10), 1847–1855.
Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Appl. Environ. Microb. 75 (6), 1589–1596.
Schimel, J.P., Schaeffer, S.M., 2012. Microbial control over carbon cycling in soil. Front. Microbiol. 3.
Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T.R., Gracia, C.A., de la Vega-Leinert, A.C., Erhard, M., Ewert, F., Glendining, M., House, J.I., Kankaanpää, S., Klein, R.J.T., Lavorel, S., Lindner, M., Metzger, M.J., Meyer, J., Mitchell, T.D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S., Zierl, B., 2005. Ecosystem service supply and vulnerability to global change in Europe. Science 310 (5752), 1333–1337.
Seneviratne, S.I., Lüthi, D., Litschi, M., Schär, C., 2006. Land-atmosphere coupling and climate change in Europe. Nature 443 (7108), 205–209.
Tedersoo, L., Anslan, S., Bahram, M., Drenkhan, R., Pritsch, K., Buegger, F., Padari, A., Hagh-Doust, N., Mikryukov, V., Gohar, D., Amiri, R., Hiiesalu, I., Lutter, R., Rosenvald, R., Rähn, E., Adamson, K., Drenkhan, T., Tullus, H., Jurimaa, K., Sibul, I., Otsing, E., Polme, S., Metslaid, M., Loit, K., Agan, A., Puusepp, R., Varik, I., Koljalg, U., Abarenkov, K., 2020. Regional-scale in-depth analysis of soil fungal diversity reveals strong pH and plant species effects in northern Europe. Front. Microbiol. 11.
Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Poldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T. W., Harend, H., Guo, L.D., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346 (6213), 1256688.
Tedersoo, L., Bahram, M., Toots, M., Diédhiou, A.G., Henkel, T.W., Kjoller, R., Morris, M. H., Nara, K., Nouhra, E., Peay, K.G., Polme, S., Ryberg, M., Smith, M.E., Koljalg, U., 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. Mol. Ecol. 21 (17), 4160–4170.
Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. USA 102 (23), 8245–8250.
Torsvik, V., Ovreås, L., Thingstad, T.F., 2002. Prokaryotic diversity -: magnitude, dynamics, and controlling factors. Science 296 (5570), 1064–1066.
Treseder, K.K., Marusenko, Y., Romero-Olivares, A.L., Maltz, M.R., 2016. Experimental warming alters potential function of the fungal community in boreal forest. Glob. Chang. Biol. 22 (10), 3395–3404.
Tu, Q.C., Yan, Q.Y., Deng, Y., Michaletz, S.T., Buzzard, V., Weiser, M.D., Waide, R., Ning, D.L., Wu, L.Y., He, Z.L., Zhou, J.Z., 2020. Biogeographic patterns of microbial co-occurrence ecological networks in six American forests. Soil Biol. Biochem. 148.
van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11 (3), 296–310.
van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C.C., Dawud, S.M., De Wandeler, H., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.X., Jucker, T., Koricheva, J., Milligan, H., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielinski, D., Fischer, M., 2016. Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nat. Commun. 7.
van der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Cornelissen, J.H.C., Dahlgren, J., Checko, E., Coppi, A., Dawud, S.M., Deconchat, M., De Smedt, P., De Wandeler, H., Domisch, T., Finér, L., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.X., Jucker, T., Kambach, S., Kaendler, G., Kattge, J., Koricheva, J., Kunstler, G., Lehtonen, A., Liebergesell, M., Manning, P., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Ohse, B., Paquette, A., Peñuelas, J., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Seidl, R., Selvi, F., Stenlid, J., Valladares, F., van Keer, J., Vesterdal, L., Fischer, M., Gamfeldt, L., Allan, E., 2018. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. Ecol. Lett. 21 (1), 31–42.
Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proc. Natl. Acad. Sci. USA 111 (14), 5266–5270.
Wagg, C., Schlaeppi, K., Banerjee, S., Kuramae, E.E., van der Heijden, M.G.A., 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. Nat. Commun. 10.
Walthert, L., Graf, U., Kammer, A., Luster, J., Pezzotta, D., Zimmermann, S., Hagedorn, F., 2010. Determination of organic and inorganic carbon, delta C-13, and nitrogen in soils containing carbonates after acid fumigation with HCl. J. Plant Nutr. Soil Sci. 173 (2), 207–216.
Whitman, W.B., Coleman, D.C., Wiebe, W.J., 1998. Prokaryotes: the unseen majority. Proc. Natl. Acad. Sci. USA 95 (12), 6578–6583.
Xia, Q., Rufty, T., Shi, W., 2020. Soil microbial diversity and composition: links to soil texture and associated properties. Soil Biol. Biochem. 149.
Xu, S., Ou, J., Qiao, X.X., Zeng, Z.Z., Wang, J.J., 2024. Experimental warming affects soil carbon dynamics in boreal and temperate forests: a meta-analysis. Environ. Res. Lett. 19 (10).
Xue, R., Wang, C., Zhao, L., Cao, J., Liu, M.L., Zhang, D., 2023. Agricultural intensification weakens soil multifunctionality by reducing fungal diversity. Appl. Soil Ecol. 189.
Yang, Y., Chai, Y.B., Xie, H.J., Zhang, L., Zhang, Z.M., Yang, X., Hao, S.L., Gai, J.P., Chen, Y.L., 2023. Responses of soil microbial diversity, network complexity and multifunctionality to three land-use changes. Sci. Total Environ. 859.
Yew, S.M., Chan, C.L., Kuan, C.S., Toh, Y.F., Ngeow, Y.F., Na, S.L., Lee, K.W., Hoh, C.C., Yee, W.Y., Ng, K.P., 2016. The genome of newly classified: Insights into fungal adaptation to different living conditions. BMC Genomics 17.
Zhang, Z., Li, Y., Williams, R.A., Chen, Y., Peng, R., Liu, X., Qi, Y., Wang, Z., 2023. Responses of soil respiration and its sensitivities to temperature and precipitation: a meta-analysis. Ecol. Inform. 75, 102057.
Zheng, Q., Hu, Y.T., Zhang, S.S., Noll, L., Böckle, T., Dietrich, M., Herbold, C.W., Eichorst, S.A., Woebken, D., Richter, A., Wanek, W., 2019. Soil multifunctionality is affected by the soil environment and by microbial community composition and diversity. Soil Biol. Biochem. 136.
Zheng, W.S., Lehmann, A., Ryo, M., Vályi, K.K., Rillig, M.C., 2020. Growth rate trades off with enzymatic investment in soil filamentous fungi. Sci. Rep.-UK 10 (1).