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Unravelling the facilitation-competition continuum among ectomycorrhizal and saprotrophic fungi

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ABSTRACT

Soil fungal inter-guild interactions may impact ecosystem processes significantly. In particular, competition between ectomycorrhizal and saprotrophic fungi could reduce organic matter decomposition through the "Gadgil effect". Whether fungal facilitative and competitive interactions predictably shift under moderate environmental stress, as hypothesised by the stress-gradient hypothesis (SGH), is still uncertain, particularly across multiple environmental resource gradients. Here, we quantified reciprocal interactions among fungal guilds in root tips and soil mycelia in 84 temperate forests of various tree compositions comprising a natural gradient of soil fertility and root carbon resources. The two resource gradients were negatively related. In keeping with SGH, we found that the typical interactions between fungal guilds were symmetrically positive at the lowest end of both gradients. These findings corroborate enhanced decomposition, indicating a facilitative effect generated by the ectomycorrhizal and saprotrophic fungal positive interactions. Inter-guild interactions varied with the spatial habitat and resource type gradient, with root carbon resources more strongly influencing root tip than soil mycelium communities. When both gradients were integrated, SGH held for the dominant gradient in the system. The premises of the "Gadgil effect" became apparent in the more fertile soils, but under higher C/N ratios, certain ectomycorrhizal groups, including taxa capable of mobilising nitrogen from complex organic substrates, exerted negative effects on saprotrophic fungi. Under lower soil pH and in drier, warmer climates resembling global change scenarios, soil fungal guilds positively influence each other. These interactions potentially aid in the preservation of soil biodiversity and the support of forest ecosystem function.

1. Introduction

Soil fungal biodiversity contributes significantly to terrestrial ecosystem function by influencing processes we depend on for food, health and climate regulation (Bardgett and van der Putten, 2014; van der Putten et al., 2023). A critical factor in the relationships between biodiversity and ecosystem function, and in maintaining their stability under (stress) perturbations is the species' ability to coexist through positive interspecific interactions (e.g., complementary use of resources, facilitative interactions, or reduction in the frequency and strength of competition) (Lehman and Tilman, 2000; Cardinale et al., 2006; Callaway, 2007; Loreau and de Mazancourt, 2013; García et al., 2018).

The link between species interactions and environmental stress has been theoretically synthesised in the 'stress-gradient hypothesis' (SGH, Bertness and Callaway, 1994). It posits that as competition declines, facilitation increases with increasing stress intensity (Bertness and

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Callaway, 1994; Callaway, 2007). Holmgren and Scheffer (2010) revisited the SGH, emphasizing its prevalence in moderately stressful environments rather than in conditions of extreme stress. While SGH has been widely supported (He et al., 2013; Qi et al., 2018), its universal validity is controversial because, in natural communities, species are living under multiple environmental factors operating simultaneously, having separate or combined effects on species interactions (Kawai and Tokeshi, 2007; Maestre et al., 2009; Mod et al., 2014). Species interactions can vary across a continuum from entirely symmetric (interacting partners receive the same amount of benefit/damage) to entirely asymmetric (one partner receives all, but there are no effects on another one) (Bronstein, 2009; Lin et al., 2012). The SGH-predicted advantages depend on the symmetry level in species interactions (Lin et al., 2012). Under stressful conditions when species are highly vulnerable, asymmetric facilitation only benefits one of the interacting taxa (i.e., beneficiary taxon). Another taxon (i.e., benefactor taxon) may incur vulnerability to stress and external competition (Lin et al., 2012; Hart and Marshall, 2013; Mod et al., 2014).

The relationship between environmental stress and fungal interspecific interactions is well-documented under sterile conditions. Advances in molecular identification have extended these investigations to field studies, often using species co-occurrence networks based on relative abundance correlations (Abrego et al., 2020; Hernandez et al., 2021). However, interpreting spatial co-occurrence as a proxy for biotic interactions is imprecise and offers limited ecological interpretation (Blanchet et al., 2020). Moreover, co-occurrence analyses only capture the symmetric interactions, overlooking the asymmetry in how species influence one another (Kennedy, 2010).

In temperate forests, the free-living soil saprotrophic fungi (STF) and root-associated symbiotrophs (i.e., ectomycorrhizal fungi and root endophytes) are the dominant components of the belowground mycobiome (Leake et al., 2002). Saprotrophic fungi are the primary decomposers of organic matter (Boddy et al., 2007; Baldrian and Valásková, 2008), representing a source of soil C-loss (Frey, 2019; Keller et al., 2021). Ectomycorrhizal fungi (EMF) form mutualistic relationships with plants, receiving C in exchange for enhanced nutrient acquisition (Clemmensen et al., 2013; Phillips et al., 2013; Baldrian, 2017; Frąc et al., 2018). Many root endophytes possess mycorrhizal-like functional abilities and are considered to be components in a larger context of mycorrhizal fungi (Kariman et al., 2024). The members of the two fungal guilds share some similar functional features (Martin et al., 2016; Miyauchi et al., 2020) and the same fundamental niche (Bödeker et al., 2016) that may cause competition for the non-C soil resources (Shaw et al., 1995; Leake et al., 2002). Their competitive interaction eventually leads to decreasing STF activity and a deceleration in decomposition through the "Gadgil effect" that is paramount in soil C sequestration (Gadgil and Gadgil, 1971; Fernandez and Kennedy, 2016). In contrast, a facilitative interaction may lead to a priming effect by enhancing decomposition (Choreño-Parra and Treseder, 2024; Fontaine et al., 2011). Although the competitive interactions between STF and EMF, the "Gadgil effect" premise, have been well documented (Lindahl et al., 2007; Bödeker et al., 2016; Zavišić et al., 2016; Peršoh et al., 2018), their responses to variation across natural resource gradients appear highly context-dependent (Sterkenburg et al., 2018; Fernandez et al., 2020; Mayer et al., 2023). A recent meta-analysis (Fernandez and See, 2025) suggests that the nature of EMF-STF interactions is largely shaped by EMF N acquisition strategies, which in turn are influenced by key soil properties such as pH and C/N ratios.

From a resource supply perspective, soil fungi reside in two spatially separated habitats: root tips and surrounding soil. Root-associated fungi produce extraradical mycelium that spreads into the soil (Agerer, 2001, 2006). On the other side, many free-living STFs may reside in the tree roots, likely developing a facultative endophytic lifestyle (Vasiliauskas et al., 2007; Dučić et al., 2009; Smith et al., 2017). Although they do not form a symbiosis, STF may benefit from association with roots to obtain easily available C (Baldrian and Kohout, 2017) or other nutrients (Nguyen et al., 2020). Therefore, soil and root resources are accessed by both root- and soil-resident fungal guilds, with their communities shaped by the availability of these resources (Kernaghan, 2013; Nguyen et al., 2020; Pena et al., 2023).

Across temperate forests, stands of different tree species composition may vary in soil properties (e.g., pH, moisture, bulk density, C:N ratio, or ammonium and nitrate concentrations) and root C resources (e.g., C:N ratio, glucose, fructose, or starch contents) generating gradients of soil and root resources available to soil fungi, ranging from high to low, where low resource availability is considered a competitive stress. The intensity of the stress increases as the availability of resources and overall soil fertility decrease. Here, we aim to test SGH for fungal interactions in root tips and soil mycelium, addressing the challenges in determining the interaction symmetry (direction and strength of reciprocal fungal guild influence) and decoupling of soil and root resource gradients operating simultaneously. Interaction coefficients were calculated using generalized Lotka-Volterra equations (Shang et al., 2017), quantifying the influence of one soil fungal guild on another as a function of gradients in soil fertility and root C resources. We tested the hypotheses that, with decreasing soil fertility and root resources, regardless of the stress factor type, per SGH (Bertness and Callaway, 1994), fungal guild interactions shift from negative to positive (H1) and increase the frequency of their symmetry (H2). Consequently, the premises of the "Gadgil effect" become apparent with increasing soil fertility, leading to reduced decomposition (H3). If there exists a contrast between the two resource gradients, meaning they are inversely related, then in a combined measure of fungal interactions, SGH holds true for the gradient that is most important for a particular fungal guild and its habitat (H4). Specifically, we propose that when combining the two gradients, the soil fertility gradient has a stronger impact on fungal interactions (per SGH) in soil than root fungal communities. In contrast, the root resource gradient has a greater influence on root fungal communities, particularly root-associated fungi (e.g., EMF, root endophytes).

To investigate these propositions, we analysed the fungal communities and calculated the coefficients of one guild's influence on another guild in both root tips and soil mycelium across 84 temperate forest plots. These plots, differing in proportion of tree species that do not belong to the natural vegetation, were selected to encompass a natural gradient of soil fertility and root C resources. To reduce confounding effects from the diversity of tree species, soil types, and climates on decomposition, we also focused on a subset of particular taxon interactions within a constrained local gradient. The premises for "Gadgil effects" were evaluated through correlations with fine root litter decomposition.

2. Materials and methods

2.1. Study site

The study was conducted in the Biodiversity Exploratories (Fischer et al., 2010, http://www.biodiversity-exploratories.de/startseite/) in 84 forest plots (100 × 100 m) distributed in three regions: Schwäbische Alb (A) in southwest, Hainich (H) in central, and Schorfheide-Chorin (S) in northeast Germany. The mean annual temperature and precipitation range from A to S, with intermediate values in H from 6.5 to 8.4 °C and 1000 to 500 mm, respectively.

The plots in each region consisted of mature forests, which span a gradient of the proportion of tree species that are not part of the natural forest community measured as a component (*Inonat*) of the forest management intensity index (ForMi, Kahl and Bauhus, 2014). The values of *Inonat* range from 0 (stands with only natural vegetation, European beech) to 1.0 (stands with only non-natural tree species, conifers) (Kahl and Bauhus, 2014). We selected plots ranging from 0 to 0.97 in the southwest region, from 0 to 0.93 in the central region, and 0 to 0.99 in the northeast region: pure European beech (38), mixed

European beech with other broadleaf tree species like lime, oak, ash, maple, or hornbeam (18), mixed European beech with conifer species such as Scots pine or Norway spruce (15), and pure conifers (13). Ash, maple, and hornbeam are species associated with arbuscular mycorrhizal fungi. Additionally, a subset of seven plots, exclusively composed of European beech and located in Hainich, was selected to conduct the analyses within a more homogeneous local environment.

2.2. Root and soil mycelium sample collection and processing

Root tips and soil mycelia were isolated from a composite soil sample per plot. From each plot, in total, five soil cores were collected from the top 10 cm soil using a soil corer (5 cm diameter x 10 cm depth) along two transects (North-South and East-West). Three soil cores were collected at an equal distance of 10 m along the North-South, and the other two soil cores were also collected at an equal distance of 10 m along the East-West transect. When present, the forest floor was removed before sampling. The five soil cores of each plot were pooled to obtain one composite soil sample. Subsequently, each composite soil sample was thoroughly homogenised and sieved on 2 mm mesh. Collected roots were carefully washed with tap water. Aliquots of about 1 g root tips were randomly collected and stored at −80 °C for DNA extraction.

Soil mycelium was collected from the soil using successive wet filtrations and sucrose gradient density centrifugation following the method described by (Awad and Pena, 2023). In short, an aliquot of 5.0 g sieved soil was dispersed in 100 ml deionised water using a bar stir on a magnetic stirrer (IKA Kombimag® RCT, IKA Labortechnik, Staufen, Germany) at a speed of 500 rpm for 5 min. The resulting solution was filtered using a few consecutive filtration steps. The obtained material was then vigorously shaken by hand and dispersed into 50.0 ml of a 45.5 % sucrose solution and subsequently centrifuged at 500 rpm for 1 min (Eppendorf centrifuge 5810R, Eppendorf GmbH, Hamburg, Germany). The supernatant was filtered through a 50-μm pore size nylon mesh (Franz Eckert GmbH, Waldkirch, Germany), and the precipitate was collected for DNA isolation.

2.3. DNA extraction, amplicon library construction, and Mi-Seq Illumina sequencing

The stored fine root and soil mycelium samples were freeze-dried and milled to a fine powder using the Retsch ball mill (Type MM2, Retsch, Hann, Germany) at 30 frequencies/sec for 3 min. Subsequently, the genomic DNA was isolated from ca. 30 mg root and 10 mg mycelium samples using the InnuPREP Plant DNA kit (Analytik Jena, Jena, Germany) following the manufacturer's instructions. DNA concentration was measured using the Nanodrop (Thermo Fisher Scientific, Waltham/Massachusetts, United States) and diluted to 10 ng/μl for each sample. Fungal amplicon libraries were prepared by amplifying the ribosomal internal transcribed spacer (ITS) region using the ITS1F (Gardes and Bruns, 1993) and ITS4 (White et al., 1990) primers, followed by a second amplification of ITS2 regions with the primer pair fITS7 (Ihrmark et al., 2012) and ITS4 containing the Illumina adapter sequences. The indexed PCR products were cleaned up using the AMPure XP SPRI magnetic beads (Beckman Coulter, Brea, California, USA) as described in the Illumina manual (Amplicon Library Preparation Manual). Illumina Nextera XT indices were added to the amplicon libraries using the indexing PCR, followed by another round of purification with AMPure XP beads. Purified PCR products were quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Eugen, OR, USA) in a Qubit 3.0 Fluorometer (Thermo Fischer Scientific, Dreieich, Germany) and pooled at equimolar concentrations for sequencing. Paired-end sequencing (2 × 300 bp) was carried out on an Illumina MiSeq sequencer (Illumina, Inc., San Diego, CA, USA) at the Helmholtz Centre for Environmental Research - UFZ, Halle, Germany.

2.4. Bioinformatics analysis

Bioinformatic analysis was performed to extract the high-quality reads from the paired-end sequences obtained through the Illumina MiSeq sequencing platform using MOTHUR (Schloss et al., 2009) and OBI Tools (Boyer et al., 2016) software suits as explained in Nawaz et al. (2018). In summary, read pairs were extracted from raw libraries by checking if both reads contained the expected primer at their 5′ ends. The forward primer was expected for the forward library, while the reverse primer was expected for the reverse library. The forward and reverse raw reads from the same sample were assembled using the simple-Bayesian algorithm with a threshold of 0.6 and a minimum overlap of 20 nucleotides, implemented in PANDAseq (Masella et al., 2012). To extract the high-quality reads, the assembled reads were trimmed using the following parameters: minimum length of 50; minimum average Phred score of 25 on the trimmed length; no ambiguities in the sequence length; and a maximum length of 10 homopolymers in the sequence. The trimmed reads were pre-clustered using CD-HIT-EST (Niu et al., 2010) to merge reads that likely arose from sequencing errors. A maximum dissimilarity of 1 % and only one base per indel during the pre-clustering process were allowed, following the approach suggested by Huse et al. (2010). The UCHIME algorithm (Edgar et al., 2011) was employed to identify chimeric sequences as implemented in MOTHUR. After removing the chimaeras, the reads from each sample were combined, and dereplication was performed to obtain a collection of unique sequences, which were then sorted based on their abundance. Next, the CD-HIT-EST algorithm (Fu et al., 2012) was utilized to cluster the resulting reads into operational taxonomic units (OTUs) at a sequence similarity threshold of 97 %. The most abundant sequence within each OTU was selected as the representative sequence and taxonomically assigned. For the taxonomic assignment, it was employed the naive Bayesian classifier (Wang et al., 2007) implemented in MOTHUR, utilizing the reference sequences from the UNITE database (unite.v7 version, Kõljalg et al., 2013) with default parameters.

2.5. OTU functional assignment

Bioinformatic analysis, followed by the taxonomic assignment, generated a dataset of 38985 operational taxonomic units (OTUs) assigned to fungi, representing 4260662 sequences. After filtering of singletons, doubletons, and tripletons, the number decreased to 6610 OTUs, representing 4223392 sequences. The rarefaction to a minimum common sequencing depth of 12089 reads per sample resulted in a final number of 6282 OTUs. For details, see Methods S1. Data are open access from the Biodiversity Exploratory Information System (BExIS, https://www.bexis.uni-jena.de/ddm/publicsearch/index) under the accession numbers 22006 and 21986 (Awad et al., 2022a,b).

Taxa were assigned to functional groups using FUNGuild (Nguyen et al., 2016), followed by manual checks and annotations, considering the spatial habitat (hyphal or root tip communities). The assignment coverage was about 80 %. Fungal communities were divided into guilds according to their trophic mode (saprotrophic, ectomycorrhizal, endophytic) and Grime's C–S-R strategies (competitors, stress-tolerators, and colonisers = ruderals; Grime, 1977; Crowther et al., 2014). We followed the classification from Sterkenburg et al. (2015): STF and EMF basidiomycetes as C-strategists; STF, EMF, and root-endophytic ascomycetes as S-strategists; yeasts and moulds as R-strategists. To account for variation in EMF competitive ability, we further classified EMF taxa based on the abundance of their extraradical mycelium (Hobbie and Agerer, 2009; Pena, 2016). Taxa producing extensive mycelium were considered more likely to align with the competitive strategy than low-biomass taxa.

The concept of functional guilds (Root, 1967), based on the principle of functional redundancy, has been widely applied in soil fungal systems (Talbot et al., 2014; Auer et al., 2024). However, classifying soil fungi into functional guilds inevitably simplifies the complexity of these

communities. This is due to the limited availability of specific guild classifications for many taxa and the likelihood that these guilds exist along a continuum of lifestyles (Riley et al., 2014; Pena and Tibbett, 2024).

We calculated the direction and strength of interaction coefficients in one-way interactions in the following fungal functional groups: (1) EMF basidiomycetes, divided into high-biomass (1a, long-distance and fringe exploration types) and low-biomass (1b, contact, short and smooth exploration types); (2) EMF ascomycetes; (3) STF basidiomycetes; (4) STF ascomycetes; (5) root endophytes (root-associated ascomycetes of order Leotiomycetes); and (6) yeasts and moulds (species in the orders Eurotiales, Hypocreales, Morteriellales, Mucorales, Saccharomycetales, Tremellales and Sporidiales). Additionally, we examined the interactions among dominant fungal taxa within specific functional guilds of potential relevance to the "Gadgil effect". These include the saprotrophic white-rot taxon Mycena sp. (Agaricales) and EMF taxa from Russulales and Boletales. Russulales are characterised by a limited genetic capacity for degrading plant cell walls (Miyauchi et al., 2020), whereas Boletales employ a brown-rot-specific oxidative decomposition mechanism (Rineau et al., 2012; Nicolás et al., 2019). Other groups were identified but not used in the interaction assessments: arbuscular mycorrhizal, pathogen ascomycetes, unknown ascomycetes, unknown basidiomycetes, and unknown fungi.

2.6. Calculation of soil fertility and root carbon resource indices

Soil Fertility Index (SFI) represents the ordination score on the first principal component axis (PCA1) based on a combined value of soil variables: soil pH, moisture content, bulk density, C:N ratio, ammonium and nitrate concentrations (Fig. S1a), following the method of Sterkenburg et al. (2015). Higher SFI values indicate more fertile soils (higher pH, moisture, clay content, and N availability), while lower (more negative) SFI values represent less fertile soils. Similarly, the Root C Resource Index (RRI) was calculated as the ordination score on the first PCA axis of root C variables: C:N ratio, glucose, fructose, and starch contents (Fig. S1b). Higher RRI values indicate greater C resource availability in roots. This index reflects the potential C supply available to root-associated fungi, which is known to influence fungal activity, diversity, and community composition (Heinonsalo et al., 2004; Pena et al., 2010; Kaiser et al., 2015).

Data used for SFI and RRI calculations are open access from the Biodiversity Exploratory Information System (BExIS, https://www.bexis.uni-jena.de/ddm/publicsearch/index) under the following accession numbers: 19067 (soil pH, Schöning et al., 2021a), 18386 (soil moisture, Schöning et al., 2021b), 20266 (bulk density, C/N, Schöning et al., 2021c), 19966 (soil ammonium and nitrate, Pena, 2021), 22967 (root-related parameters, Polle and Nguyen, 2022).

Soil and root parameters were measured in one composite soil sample per plot (Nguyen et al., 2020). Soil pH was measured in a weak (0.01 M) calcium chloride solution using a pH meter (Schöning et al., 2021a). Soil moisture was measured by drying the soil samples at 105 °C (Schöning et al., 2021b). Total C and N concentrations were determined by soil dry combustion (Schöning et al., 2021c). Ammonium (NH_4^+) and nitrate (NO_3^-) of soil samples were extracted from fresh soil in 1 mM $CaCl_2$ solution and spectrophotometrically analysed using ammonium and nitrate test kits (Merck, Darmstadt, Germany) following the manufacturer's instructions (Pena, 2021). Root and C and N contents were determined in the dry powder fine root samples using an Elemental Analyzer (Model SHNC–O EA1108, Carlo Erba Instruments, Milan, Italy). Glucose, fructose, and starch in fine roots were determined enzymatically by measuring NADPH production at the wavelength of 340 nm in a spectrophotometer (Type UV-DU640, Beckmann, California, USA) (Schopfer, 1989). The starch was previously enzymatically converted to glucose (Polle and Nguyen, 2022; Nguyen et al., 2020).

Soil properties varied with the regions but not with forest tree composition (Table 1). Soils in the northeast region (S) were more acidic

Table 1
Characterization of soil and root chemistry, soil pH and soil moisture in different regions, A = Schwäbische Alb, H = Hainich-Düin, S = Schorfheide-Chorin, and forest types, B = beech, BB = beech mixed with other broadleaf species, BC = beech mixed with conifer species, C = conifer. In brackets, *Inonat* mean values, representing the volume proportion of non-natural tree species in the forest stands (0 = natural vegetation; 1 = only non-natural tree species) as a component of the Forest Management Intensity index after Kahl and Bauhus (2014). Soil Fertility Index (SFI) and Root Resource Index (RRI) with the forest types and regions. Number of plot replicates: n = 2 in H_BC; 4 in A_BC; 6 in S_C; 7 in A_C and H_BB; 8 in A_B; 9 in S_BC; 11 in A_BB; 14 in S_B; 16 in H_B.

	A_B (0.06)	A_BB (0.30)	A_BC (0.33)	A_C (0.96)	H_B (0.00)	H_BB (0.00)	H_BC (0.92)	S_B (0.02)	S_BC (0.34)	S_C (0.99)
Soil variables										
C (g kg^{-1})	64.7 ± 6.85 d	60.3 ± 4.13 cd	57.7 ± 2.89 cd	70.1 ± 6.75 cd	32.6 ± 2.01 b	42.6 ± 3.7 bc	50.3 ± 5.29	21.4 ± 1.08 a	19.4 ± 2.06 a	18.1 ± 1.58 a
N (g kg^{-1})	5.00 ± 0.51 c	4.57 ± 0.29 c	4.23 ± 0.28 c	4.41 ± 0.47 c	2.48 ± 0.17 b	3.27 ± 0.28 bc	3.33 ± 0.41	1.28 ± 0.07 a	1.06 ± 0.14 a	0.87 ± 0.08 a
NO3 (µg kg^{-1})	2.58 ± 0.27 d	2.81 ± 0.51 d	1.16 ± 0.31 bd	1.31 ± 0.21 cd	1.47 ± 0.15 cd	1.29 ± 0.24 cb	2.08 ± 0.01	0.79 ± 0.13 b	0.80 ± 0.13 bc	0.27 ± 0.08 a
NH4 (µg kg^{-1})	0.27 ± 0.07 ab	0.32 ± 0.08 ab	0.22 ± 0.09 ab	1.04 ± 0.12 ac	0.5 ± 0.14 ac	0.19 ± 0.07 a	1.48 ± 1.03	0.84 ± 0.1 c	0.56 ± 0.13 ac	0.82 ± 0.17 bc
C:N	12.8 ± 0.13 a	13.1 ± 0.17 a	13.7 ± 0.32 ab	15.9 ± 0.39 a	13.2 ± 0.18 bd	13.0 ± 0.26 bd	15.1 ± 0.27	16.8 ± 0.45cd	19.4 ± 1.29 c	20.9 ± 0.95cd
Bulk density (g cm^{-3})	0.62 ± 0.06 a	0.63 ± 0.04 a	0.78 ± 0.2 ab	0.69 ± 0.04 a	0.95 ± 0.03 bc	0.9 ± 0.04 bc	0.77 ± 0.06	1.17 ± 0.02 d	1.23 ± 0.03 d	1.16 ± 0.03 cd
pH	5.43 ± 0.26 b	5.12 ± 0.16 b	4.98 ± 0.42 b	3.39 ± 0.43 ab	4.56 ± 0.2 b	5.17 ± 0.3 b	5.87 ± 0.65	3.58 ± 0.03 a	3.48 ± 0.03 a	3.53 ± 0.06 a
Water content (%)	64.5 ± 2.73 e	58.7 ± 2.81 cde	54.7 ± 4.53 de	52.6 ± 2.34 de	42.0 ± 1.28 d	48.4 ± 2.44 de	38.2 ± 11.71	17.4 ± 0.65 c	13.9 ± 1.49 b	9.02 ± 0.91 a
SFI	2.37 ± 0.28 c	2.01 ± 0.26 cd	1.1 ± 0.29 bc	−0.19 ± 0.38bc	0.27 ± 0.17 b	0.98 ± 0.25 bd	0.53 ± 0.16	−1.99 ± 0.14a	−2.42 ± 0.27 a	−2.92 ± 0.23 a
Root variables										
C (g kg^{-1})	456 ± 6.99 bd	447 ± 8.09 ac	418 ± 20.7 ac	458 ± 9.87 ac	412 ± 8.71 a	416 ± 13.6 ab	435 ± 7.61	495 ± 8.51 d	493 ± 3.76 d	471 ± 4.82 cd
Glucose (g kg^{-1})	2.72 ± 0.20 bc	2.14 ± 0.23 a	2.28 ± 0.07 ab	3.28 ± 0.32 ab	1.81 ± 0.12 a	2.3 ± 0.28 ac	2.13 ± 0.46	4.03 ± 0.51 b	3.62 ± 0.25 bc	6.77 ± 0.61 d
Fructose (g kg^{-1})	1.42 ± 0.12 ab	0.83 ± 0.17 a	1.73 ± 0.48 ab	1.35 ± 0.17 b	1.01 ± 0.09 a	1.11 ± 0.13 a	1.12 ± 0.01	2.03 ± 0.22 b	1.97 ± 0.20 b	2.41 ± 1.05 ab
Starch (g kg^{-1})	2.21 ± 0.9 a	1.96 ± 0.66 a	3.09 ± 1.38 a	16.6 ± 2.49 b	1.32 ± 0.42 a	1.54 ± 0.31 a	6.1 ± 3.6	0.84 ± 0.19 a	2.79 ± 0.88 a	15.6 ± 4.95 b
N (g kg^{-1})	13.8 ± 1.6 b	15.5 ± 1.06 b	13.3 ± 0.86 b	14.4 ± 0.67 b	12.3 ± 0.44 b	12.2 ± 0.65 b	12.2 ± 1.5	12.4 ± 0.45 a	12.6 ± 0.88 b	7.67 ± 0.82 a
C:N	35.2 ± 2.82 ab	30.1 ± 2.3 a	31.6 ± 1.63 ab	31.7 ± 2.09 ab	34.0 ± 1.23 ab	34.5 ± 2.28 ab	36.3 ± 5.1	40.5 ± 1.52 b	40.5 ± 2.99 b	64.8 ± 6.47 c
RRI	−0.36 ± 0.13 ac	−1.13 ± 0.26 a	−0.5 ± 0.24 ac	0.56 ± 0.33 c	−1.01 ± 0.13 a	−0.8 ± 0.27 ab	−0.42 ± 0.16	0.58 ± 0.27 c	0.5 ± 0.3 bc	3.58 ± 0.73 d

and drier than those in the central (H) and southwest (A) regions. The bulk density increased from A to S regions, with intermediary values in H regions. Soil N, C and NO_3^- contents were lower in S than in H and A regions, whereas C:N ratio and NH_4^+ were higher in S than A region (Table 1). Soil fertility index (SFI) decreased in the order A > H > S (Table 1). Root variables showed more evident differences among the forest types and less among the regions. In the S region, root glucose and starch contents were higher in pure conifer stands than in other forests (Table 1). Root N contents were lower, and the root C:N ratio was higher in S than in other regions (Table 1). Root resource index increased with the proportion of non-natural tree species in the forest stands (*Inonat*), showing higher values in conifer than in broadleaf forests. In contrast with SFI, RRI decreased in the order A < H < S (Table 1). The two indices were negatively correlated (R-value = −0.551, P-value <0.001). For the local gradient, we selected plots in H with 0.16 ≤ SFI ≤1.19 and −0.33 ≤ RRI ≤ −1.88.

2.7. Root decomposition

Data on root decomposition (percentage of root litter mass loss) are publicly available from BexIS, accession number 16666 (Solly et al., 2023). Root decomposition was assessed using litter bags incubated for six and twelve months in the top 10 cm of mineral soil. The litter bags, made of polyester with a mesh size of 100 μm, were filled with fine roots (<2 mm) collected from two-year-old European beech grown under controlled conditions. The reported measurements represent the mean of three replicates per plot (Solly et al., 2014).

2.8. Statistical analysis

Statistical analyses were performed using R software version 4.0.0 (R Core Team, 2024). In the first step, the rarefied OTU abundance data were z-scored scaled and environmental variables were checked for multicollinearity using a correlation score of −0.60 < r < 0.75 (Dormann et al., 2013). Spearman's rank correlations (Hmisc package, Harrell and Dupont 2019) were used to quantify associations between fungal guild abundances or interaction coefficients and SFI, RRI or root decomposition.

As the samples differ in the replicates number, the multi-rank Kruskal-Wallis test was used to determine the statistically significant differences (P < 0.05) among root or soil parameters in different regions or forest types and abundances of various fungal guilds in different compartments (roots vs soil), regions, and forest types. When the assumption of homogeneity of variance (Levene's test) was not met, Welch's ANOVA test followed by Games–Howell post hoc tests were used to reveal the significant differences between the groups (userfriendlyscience package, Peters, 2017). The distinctiveness of fungal communities in different regions, forest types, and residence compartments was tested with an analysis of similarities (ANOSIM) using the Bray-Curtis distance (vegan package, Oksanen et al., 2017).

For the comparison between the frequency of symmetrical interactions and SFI or RRI in the root tip and soil mycelium communities, pairwise comparisons of the slopes were conducted using multcomp package (Hothorn et al., 2008) with adjustment for multiple comparisons using the Tukey method.

We calculated the bidirectional interactions among distinct fungal functional groups using the generalized Lotka-Volterra model for microbial interactions in cross-sectional samples across an environmental gradient, developed by (Shang et al., 2017).

The model accounts for the effect that the presence of one guild will have on the abundance of other guilds relative to the variation of the environmental parameters. The interaction-influence (β_{ij}) represents the interaction value characterising the influence of guild *j* on guild *i* accompanying the change in SFI or/and RRI in each sample.

The model algorithms are both conceptually and mathematically fundamentally different from the correlation analysis. For example, whereas correlation aims to maximise the recovery of covariance abundance of guild *j* (A_j) and guild *i* (A_i), our interaction approach aims to derive the correct partial derivative of abundance A_i with respect to the environmental parameters and A_j. The interaction-influence β_{ij} can be beneficial ($\beta_{ij} > 0$), competitive ($\beta_{ij} < 0$), or the two species may not interact ($\beta_{ij} = 0$).

The global interaction matrix among fungal guilds was calculated by a two-step algorithm (function: interMatrix02): (1) integration of β_{ij} for all environmental parameters at the sample level, and (2) integration of the obtained sample β_{ij} at the global level across all samples. The algorithm developed and validated by Shang et al. (2017) calculates the positive or negative interaction-influence coefficients, but not the zero coefficients, when the two guilds possibly do not interact. That is because the direction of interaction-influence, either at the sample or global level, is determined based on the number of positive or negative coefficients or the median value of all positive or negative interaction coefficients. Specifically, only when the number of positive or negative coefficients form a majority of 80 % of all interactions or when the median value of either positive or negative coefficients is at least two times higher than the opposite one the global coefficient will be ascribed the respective direction (positive or negative). If the majority of positive or negative interactions was not met or median values did not differ at least by a factor of two, it is concluded that it is not possible to determine a global β_{ij} across all parameters and samples for the specific guild pair of *i* and *j*.

Relative abundance data and environmental parameters were rescaled by positional normalization in range <-1,1> ((x-median)/max (abs(x-median))) using package clusterSim. To meet the assumption of non-collinearity, data were subjected to a singularity test before analysis (function: testsingula. R code, Shang et al., 2017).

All the functions used to calculate β_{ij} are listed in the R code, Shang et al. (2017, https://github.com/amssshangyu/interaction_analysis). In short, we calculated the rate of change of guild *i* relative abundance based on the first derivative of the guild *i* abundance concerning all environmental parameters in all samples (function: rate_change02). Subsequently, the obtained data were used as input data in calculating the β of guild *j* on guild *i* abundance for each environmental parameter in each sample (function: interinf02). To account for variation in both guild *j* abundance and environmental parameters, we used the Taylor expansion function (Hazewinkel, 1990) as described in (Shang et al., 2017).

Table 2
Influence of spatial habitat root tips *vs* soil mycelia, region, forest tree species composition, and forest type (region * forest tree composition) on fungal guild community structure shown by one-way analysis of similarity (ANOSIM). Forest types: B = beech, BB = beech mixed with other broadleaf species, BC = beech mixed with conifer species, C = conifer. In three geographical regions, A = Schwäbische Alb, H = Hainich-Dün, S = Schorfheide-Chorin. Significant differences at P < 0.05 in bolded letters. Number of plot replicates: N = 2 in H_BC; 4 in A_BC; 6 in S_C; 7 in A_C and H_BB; 8 in A_B; 9 in S_BC; 11 in A_BB; 14 in S_B; 16 in H_B.

	Factors	R-value	P-value
Roots	Habitat	0.117	**0.001**
	Region	0.077	**0.002**
	Forest tree composition	0.089	**0.032**
	Forest type	0.121	**0.003**
Soil mycelia	Region	0.190	**0.001**
	Forest tree composition	0.066	0.052
	Forest type	0.185	**0.001**

3. Results

3.1. Functional group composition of the root tip and soil mycelium fungal communities

Fungal guild communities differed between root tips and soil mycelium (Table 2) and were slightly more diverse in the soil mycelium (Shannon's index = 1.81) than in root tip communities (Shannon's index = 1.63, Table S1). The lowest diversity was for EMF ascomycetes in root tips (0.32 ± 0.06, Table S1) and the highest for saprotrophic yeasts and moulds in soil mycelia (3.11 ± 0.07, Table S1).

The abundance of all guilds but EMF ascomycetes and STF basidiomycetes differed between root tip and soil mycelium communities (Fig. 1, Table S2). Root endophytes were about two times more abundant in the root tips than soil mycelia (Fig. 1). In contrast, STF ascomycetes and STF yeasts were by 1.5 and 5.0 times, respectively, more abundant in soil mycelia than roots (Fig. 1). The low-biomass EMF basidiomycetes were more abundant in the roots than soil mycelia, whereas the high-biomass mycelium EMF showed the opposite (Fig. 1). The abundance (number of reads) of the top ten fungal species within different fungal guilds in root tips and soil mycelia is detailed in Supplementary Table S3.

Both root tip and soil mycelium communities differed among the regions. However, only root tip communities varied with the composition of forest tree species (Table 2). The forest type, representing forests of different tree compositions in different regions, influenced both root tip and soil mycelium communities (Table 2). The influence was apparent on all guilds, but low-biomass EMF basidiomycetes, EMF ascomycetes and STF yeasts and moulds in root tip communities, and low-biomass EMF basidiomycetes and root ascomycetes in the soil mycelium communities (Fig. 1, Table S1). No relationships were found between the relative abundance of any fungal guilds and *Inonat* (data not shown).

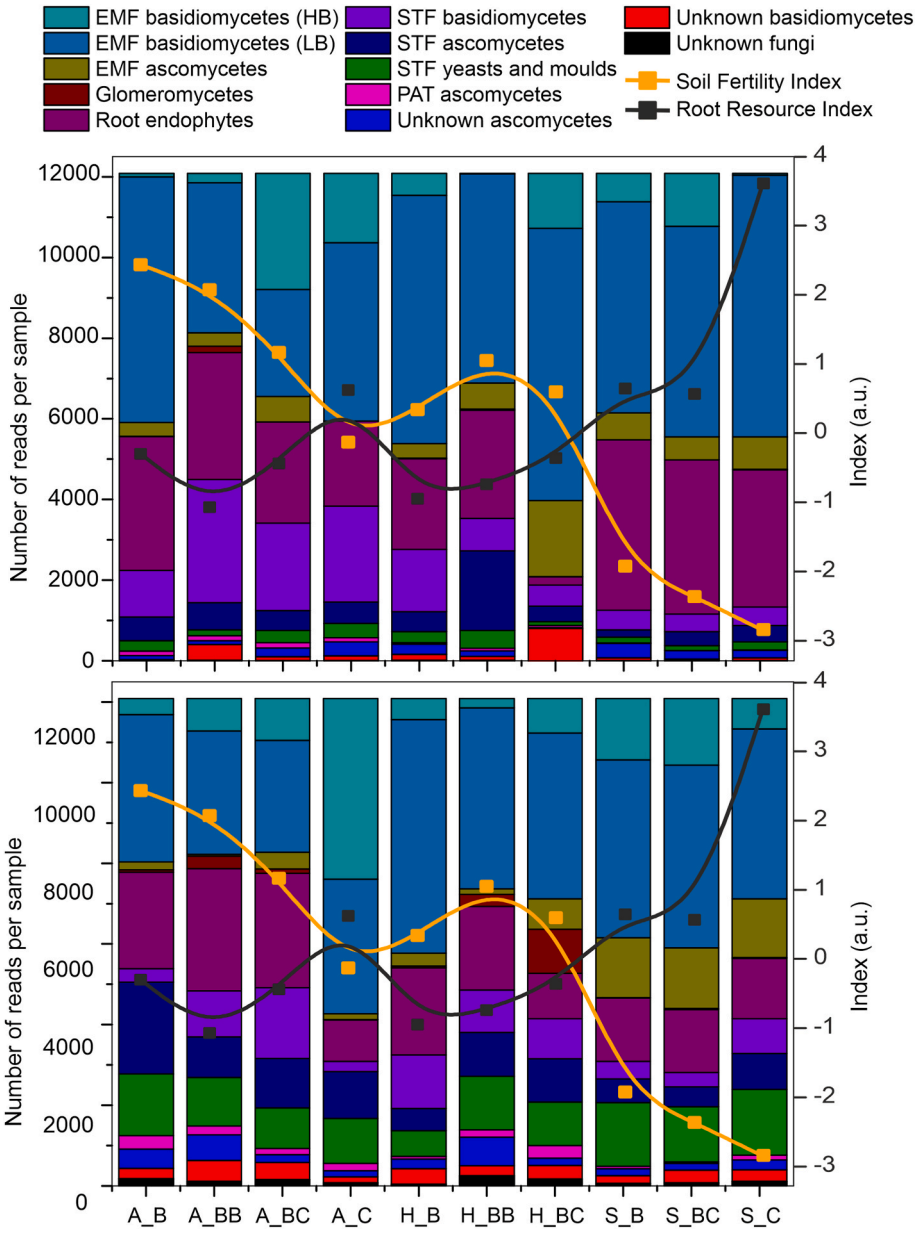

Fig. 1. Abundance of functional groups in the root (A) and soil mycelium (B) fungal communities in different regions, A = Schwäbische Alb, H = Hainich-Dün, S = Schorheide-Chorin, and forest types, B = beech, BB = beech mixed with other broadleaf species, BC = beech mixed with conifer species, C = conifer. The line graph represents the variation of the Soil Fertility Index (SFI) and Root Resource Index (RRI) with the forest types and regions. Number of plot replicates: n = 2 in H_BC; 4 in A_BC; 6 in S_C; 7 in A_C, 7 in H_BB; 8 in A_B; 9 in S_BC; 11 in A_BB; 14 in S_B; 16 in H_B.

Soil fertility index was positively associated with STF relative abundances both in the root tip and soil mycelium communities, decreasing from A to S regions (Fig. 1, Table 3). In contrast, relative abundances of EMF and root endophytes were negatively associated with SFI, increasing from A to S regions (Fig. 1, Table 3). The relationships of EMF with SFI were less evident in the root tip than in soil mycelium communities, with only the high-biomass EMF basidiomycetous relative abundance related to SFI (Fig. 1, Table 3).

Root resource index was not related to fungal guild abundances in the root communities, except STF basidiomycetous abundance, which decreased with increasing root C resources (Fig. 1, Table 3). In the soil mycelium communities, EMF and STF yeasts and moulds relative abundances increased with RRI (Fig. 1, Table 3). It is possible that increased yeast abundance reflects not only utilisation of root-derived C resources but also early colonisation and decomposition of EMF necromass.

3.2. Fungal guild interactions along the soil fertility gradient

Along the soil fertility gradient, the guild interaction coefficients (β_{ij}) changed from positive at the lowest fertility end to negative at the highest fertility end in 65 % of interactions in the root tip and 53 % of interactions in the soil mycelium communities (Table 4, Fig. S2). About 34 % of SFI-related interactions were the same in root tips and soil mycelia (Table 4). The least involved guild in the significant relationships was STF yeasts and moulds, which in the hyphal communities, revealed only one coefficient correlated with SFI (Table 4).

In the root tip communities, the strongest correlation between SFI and β_{ij}, representing the influence of guild j on guild i, was observed when i = high-biomass EMF basidiomycetes and j = root endophytes ($\rho = -0.50$, Table 4, Fig. S2). Among interactions where j = STF basidiomycetes, the correlation with SFI was stronger for low-biomass EMF basidiomycetes (i) ($\rho = -0.43$) than for high-biomass EMF (i) ($\rho = -0.20$). The reciprocal influence, where i = STF basidiomycetes and j = high/low-biomass EMF basidiomycetes also showed moderate correlations with SFI ($\rho = -0.29$/-0.22, Table 4, Fig. S2).

In the soil mycelium, the strongest correlation between SFI and β_{ij} occurred by i = STF ascomycetes and j = high-biomass EMF basidiomycetes ($\rho = -0.55$, Table 4, Fig. S2). While, in the root tip communities, the strongest relationship was i = high-biomass EMF basidiomycetes and j = root endophytes ($\rho = -0.34$, Table 4, Fig. S2).

In contrast with root tips, in the soil mycelia, the strength of the relationships between SFI and β_{ij} where i = high/low-biomass EMF basidiomycetes and j = STF basidiomycetes was greater for the high ($\rho = -0.34$) than low ($\rho = -0.22$) biomass EMF (Table 4, Fig. S2). The reciprocal influence where i = STF basidiomycetes and j = high/low-biomass EMF basidiomycetes was relatively highly related to SFI ($\rho = -0.38$/-0.33, Table 4, Fig. S2).

The analysis of dominant taxa potentially involved in the "Gadgil effect" showed that interaction coefficients of *Mycena* on EMF Russulales and Boletales taxa were negatively correlated with SFI both in root tip and soil mycelium communities (Table 4). In contrast, the influence coefficients of EMF fungi on *Mycena* showed no correlation with SFI (Table 4). Within a local gradient of moderate to high SFI values in beech forests, interaction coefficients in the mycelium communities were consistently negative across plots (Table S4). *Mycena* had a stronger influence on EMF Russulales and Boletales than the reciprocal influence of EMF fungi on *Mycena* (Table S4).

In the absence of conifers, the relationships between guild interactions and SFI retained the trend of shifting from positive interactions at the lowest fertility levels to negative interactions at the highest fertility levels (Table S5). In contrast to when conifers were present, in the soil mycelium, the bidirectional interaction between STF basidiomycetes and low-biomass EMF basidiomycetes showed no variation with SFI, whereas other interactions involving low-biomass EMF basidiomycetes and saprotrophic yeasts and moulds exhibited strong variation with SFI (Table S5).

Soil Fertility Index is a composite measure, integrating multiple soil properties, including pH and C/N ratio, which inversely vary across the three regions. When interactions were analysed separately for soil pH and C/N ratio, each individual factor was associated with fewer interactions compared to the SFI (Table S6). In the soil mycelium, the relationships between β_{ij} where i = STF basidiomycetes and j = low-biomass EMF basidiomycetes and pH were negative. Similarly, β_{ij} where i = STF basidiomycetes and j = EMF basidiomycetes and pH showed negative associations with pH. Conversely, these interactions were positively associated with the C/N ratio. This indicates that under higher weakly acidic pH conditions, the STF guild was negatively influenced by both low-biomass and all EMF basidiomycetes, whereas higher C/N ratios corresponded to positive influences. High-biomass EMF basidiomycetes showed a negative influence on STF basidiomycetes under both elevated pH and C/N ratio conditions (Table S6).

3.3. Fungal guild interactions along the root resources gradient

The interaction coefficients were less associated with RRI than SFI (Table 4, Fig. S3). Only 40 % of interactions in the root tip communities and 25 % of interactions in the soil mycelium communities showed a decrease in β_{ij} with increasing root resources. About 6 % of RRI-related interactions were the same in roots and soil mycelia (Table 4).

In the root tip communities, the strongest relationship between RRI and β_{ij} occurred by i = EMF ascomycetes and j = STF ascomycetes ($\rho = -0.37$, Table 4, Fig. S3). No relationships were found between RRI and β_{ij} or β_{ji} where i = high/low-biomass EMF basidiomycetes and j = STF basidiomycetes (Table 4, Fig. S3). The most found associations between RRI and β_{ij} were j = STF ascomycetes (Table 4, Fig. S3).

In the soil mycelium communities, the strongest relationship between RRI and β_{ij} occurred by i = root endophytes and j = STF yeasts and moulds ($\rho = -0.48$, Table 4, Fig. S3). No relationships occurred between RRI and β_{ij} where i or j = high/low-biomass EMF basidiomycetes or STF basidiomycetes (Table 4, Fig. S3). In the soil mycelium, the majority of RRI relationships with β_{ij} were by j = root endophytes (Table 4, Fig. S3). The influence coefficients of *Mycena* on EMF Boletales were correlated with RRI in both root tip and soil mycelium communities (Table 4). In contrast, the association with RRI for *Mycena* interaction with Russulales was evident only in the soil mycelium (Table 4).

In the absence of conifers, the number of significant relationships between guild interactions and RRI decreased by 75 % in root and 28 % in soil mycelium communities (Table S5). This reduction is attributed to

Table 3
Correlation between the abundance of fungal guilds and Soil Fertility Index (SMI) and Root Resource Index (RRI). EMF = ectomycorrhizal fungi, STF = saprotrophic fungi, HB = high-biomass mycelium fungi, LB = low-biomass mycelium fungi. Significant differences at $P < 0.05$ in bolded letters. N = 84.

	Roots		Soil mycelia	
	Spearman's ρ	P-value	Spearman's ρ	P-value
SFI				
EMF basidiomycetes (HB)	−0.218	**0.045**	−0.230	**0.034**
EMF basidiomycetes (LB)	−0.040	0.713	−0.295	**0.006**
EMF ascomycetes	−0.197	0.071	−0.644	**0.000**
Root endophytes	−0.274	**0.011**	0.202	0.063
STF basidiomycetes	0.344	**0.001**	0.227	**0.037**
STF ascomycetes	0.421	**0.000**	0.507	**0.000**
STF yeasts	−0.070	0.525	−0.008	0.940
RRI				
EMF basidiomycetes (HB)	0.156	0.155	0.303	**0.005**
EMF basidiomycetes (LB)	0.035	0.753	0.070	0.521
EMF ascomycetes	0.208	0.056	0.475	**0.000**
Root endophytes	0.159	0.146	−0.158	0.149
STF basidiomycetes	−0.353	**0.001**	−0.189	0.083
STF ascomycetes	−0.078	0.476	−0.148	0.178
STF yeasts	0.056	0.611	0.237	**0.029**

Table 4
Correlation (Spearman's ρ) between the fungal guild interaction influence β_{ij} and Soil Fertility Index (SMI) and Root Resource Index (RRI). B_{ij} represents the influence of guild *j* on guild *i*, where the first guild in the row name represents guild *j*, and the second one the guild *i*. EMF = ectomycorrhizal fungi, STF = saprotrophic fungi, HB = high-biomass mycelium fungi, LB = low-biomass mycelium fungi. Significant differences at P < 0.05 in bolded letters. N = 84.

B_{ij}	SFI				RRI			
	Root tips		Soil mycelia		Root tips		Soil mycelia	
	ρ	P-value	ρ	P-value	ρ	P-value	ρ	P-value
EMF ascomycetes - STF ascomycetes	−0.18	0.11	−0.20	**0.07**	−0.37	**0.00**	−0.18	0.11
STF ascomycetes - EMF ascomycetes	−0.24	**0.03**	0.12	0.27	−0.09	0.43	−0.11	0.31
STF_basidiomycetes - EMF basidiomycetes (LB)	−0.43	**0.00**	−0.22	**0.04**	−0.09	0.40	0.11	0.34
EMF basidiomycetes (LB) - STF_basidiomycetes	−0.11	0.34	−0.33	**0.00**	0.21	0.06	0.10	0.36
STF_basidiomycetes - EMF basidiomycetes (HB)	−0.20	**0.06**	−0.34	**0.00**	0.01	0.90	−0.07	0.55
EMF basidiomycetes (HB) - STF_basidiomycetes[a]	−0.38	**0.00**	−0.38	**0.00**	−0.19	0.08	0.07	0.50
Root endophytes- EMF ascomycetes	−0.31	**0.00**	0.08	0.48	−0.34	**0.00**	0.18	0.10
EMF ascomycetes - Root endophytes	−0.07	0.54	0.01	0.91	−0.07	0.50	0.03	0.82
Root endophytes- EMF basidiomycetes (LB)	−0.03	0.75	−0.27	**0.01**	0.00	0.98	0.16	0.16
EMF basidiomycetes (LB) - Root endophytes[a]	−0.24	**0.03**	−0.25	**0.02**	0.06	0.60	−0.18	0.11
Root endophytes- EMF basidiomycetes (HB)[a,b]	−0.50	**0.00**	−0.34	**0.00**	−0.27	**0.02**	−0.27	**0.01**
EMF basidiomycetes (HB) - Root endophytes	0.10	0.36	−0.16	0.14	−0.10	0.36	−0.16	0.16
EMF ascomycetes – STF yeasts and moulds	−0.35	**0.00**	−0.06	0.61	−0.13	0.23	0.10	0.38
STF yeasts and moulds - EMF ascomycetes[b]	−0.16	0.14	0.20	0.07	−0.26	**0.02**	−0.22	**0.05**
EMF basidiomycetes (LB) - STF yeasts and moulds	−0.41	**0.00**	−0.05	0.67	−0.34	**0.00**	−0.05	0.63
STF yeasts and moulds - EMF basidiomycetes (LB)[b]	−0.34	**0.00**	−0.12	0.29	−0.22	**0.05**	−0.01	0.94
EMF basidiomycetes (HB) - STF yeasts and moulds	−0.37	**0.00**	−0.10	0.38	−0.23	**0.03**	−0.07	0.52
STF yeasts and moulds - EMF basidiomycetes (HB)	−0.24	**0.03**	−0.05	0.67	−0.16	0.16	0.00	0.98
Root endophytes- STF ascomycetes[a]	−0.33	**0.00**	−0.33	**0.00**	−0.07	0.52	−0.30	**0.01**
STF ascomycetes - Root endophytes[a,b]	−0.27	**0.01**	−0.27	**0.01**	−0.30	**0.01**	−0.48	**0.00**
STF basidiomycetes - Root endophytes[a]	−0.43	**0.00**	−0.33	**0.00**	−0.09	0.43	0.09	0.42
Root endophytes- STF basidiomycetes[b]	−0.04	0.71	−0.25	**0.02**	−0.24	**0.03**	0.07	0.54
Root endophytes - STF yeasts and moulds	−0.40	**0.00**	−0.05	0.66	−0.14	0.20	−0.02	0.84
STF yeasts and moulds - Root endophytes	−0.33	**0.00**	0.06	0.56	−0.15	0.17	0.03	0.80
EMF ascomycetes - STF basidiomycetes[a,b]	−0.24	**0.03**	−0.25	**0.02**	−0.29	**0.01**	−0.23	**0.03**
STF basidiomycetes - EMF ascomycetes	0.01	0.91	−0.22	**0.05**	0.03	0.82	0.11	0.32
EMF basidiomycetes (LB) - STF ascomycetes	−0.22	**0.04**	−0.27	**0.01**	−0.33	**0.00**	−0.15	0.17
STF ascomycetes - EMF basidiomycetes (LB)	0.03	0.79	−0.26	**0.02**	−0.03	0.76	−0.24	**0.03**
EMF basidiomycetes (HB) - STF ascomycetes[a]	−0.29	**0.01**	−0.55	**0.00**	−0.30	**0.01**	0.01	0.95
STF ascomycetes - EMF basidiomycetes (HB)	−0.06	0.60	−0.18	0.11	−0.06	0.62	−0.36	**0.00**
STF basidiomycetes - EMF basidiomycetes	−0.28	**0.01**	−0.15	0.18	−0.15	0.16	0.00	0.97
EMF basidiomycetes - STF basidiomycetes	0.08	0.48	−0.13	0.24	0.18	0.10	0.17	0.12
Russulales - Mycena	0.05	0.69	0.08	0.49	−0.15	0.16	−0.31	0.00
Mycena - Russulales	−0.25	**0.02**	−0.43	**0.00**	−0.21	0.06	−0.23	**0.04**
Boletales - Mycena	−0.21	0.06	−0.17	0.13	0.00	0.98	−0.09	0.41
Mycena - Boletales	−0.45	**0.00**	−0.28	**0.01**	−0.35	**0.00**	−0.22	**0.04**

Bolded interactions in the first column: significant correlations with both SFI and RRI.
[a] Significant correlation with SFI in both roots and soil mycelia.
[b] Significant correlation with RRI in both roots and soil mycelia.

the low variation in RRI, which largely depends on root species composition. Similarly, in the beech forests analysed within the local gradient, taxon interactions in soil mycelium communities showed no variation across plots, with *Mycena* exerting a stronger influence on EMF taxa than the reciprocal influence of EMF on Mycena (Table S4).

3.4. The symmetry of fungal guild interactions along the soil fertility and root resource gradients

The guild interactions under variation in soil fertility or root C resources consisted of 33–40 % of symmetrical interactions (Fig. 2, Table S7).

The frequency of symmetrical interactions decreased with increasing soil fertility (Fig. 2A) or the root resources (Fig. 2B). The frequency of symmetrical interactions tended to decrease more with SFI in the soil mycelium than root tip communities (regression slope differed, $P = 0.047$, Fig. 2A) and decreased more with RRI in the root than soil mycelium communities ($P = 0.020$, Fig. 2B). The median number of symmetrical interactions did not differ among forest types in either root or soil mycelium communities (Table S7).

3.5. The relationship between fungal guild interactions and root litter decomposition

Root litter mass loss during six and twelve months of incubation was negatively correlated with SFI (ρ = −0.37 and ρ = −0.40, respectively) and positively correlated with RRI (ρ = 0.44 and ρ = 0.50, respectively) (Fig. S4).

In the soil mycelium communities, the reciprocal interaction coefficients between STF basidiomycetes and high-biomass EMF basidiomycetes (ρ = 0.46/0.22) and STF basidiomycetes and EMF ascomycetes (ρ = 0.44/0.22) were positively correlated with fine root decomposition (Table 5, Table S8). Additionally, among the taxa analysed, the influence coefficients of *Mycena* on EMF Boletales showed a positive correlation with root litter decomposition (ρ = 0.28, Table 5).

3.6. The global measure of inter-guild influences integrating both gradients in different forest types and regions

The calculation of global interaction-influences, accounting for variations in soil fertility and root resources, was conducted across various forests (Fig. 3) and regions (Fig. 4). However, it was observed that the requisite minimum gradient range for calculating these interaction-influences was not achieved in the forests where beech is mixed with other broadleaf species.

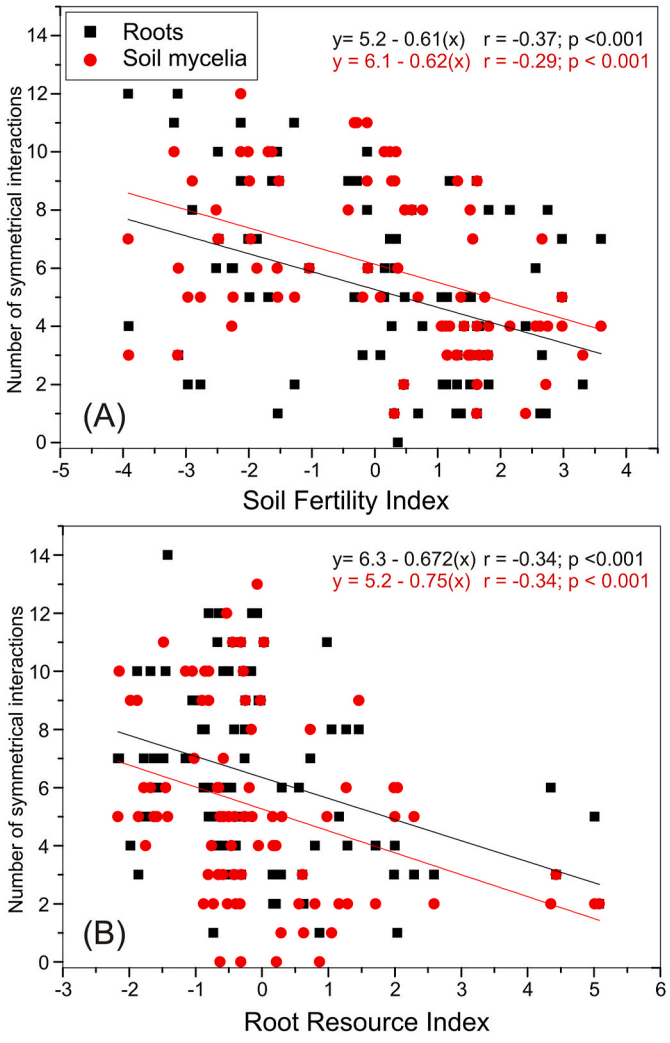

Fig. 2. Frequency of symmetrical interactions across the soil fertility (A) and root resource (B) gradients in root and soil mycelium communities. Each dot represents the observed number of symmetrical interactions from 16 interactions in each sample. The solid lines represent the regression model in the root (black) and soil mycelium (red) communities. Higher values of the Soil Fertility Index (SFI) correspond to more fertile soils (positive values), while lower values indicate poorer soils (negative values). Similarly, higher Root Resource Index (RRI) values correspond to greater root carbon resource availability. N = 84. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In conifer forests, fungal communities were dominated by negative interaction coefficients. In root tip communities, 67 % of total interaction-influences were negative (Fig. 3A), while in mycelium communities, they reached 55 % (Fig. 3B). Root tip communities included some of the strongest negative influences when i = EMF ascomycetes and j = low/high-biomass EMF basidiomycetes, root endophytes, and EMF ascomycetes in root communities (Fig. 3A). The influence of root endophytes was dominant negative in all interactions in the root communities (Fig. 3A).

In beech mixed with conifer species, in the root tip communities, the percentage of negative and positive interactions were similar, close to 45 % (Fig. 3C). In the mycelium communities, the negative coefficients were 29 %, while the positive coefficients were 57 % of total interactions. In both spatial habitats, a similar percentage (14 %) of total interactions were uncertain. This was the highest value of uncertain coefficients among all forest types (Fig. 3C and D). In the mixed forests, in the mycelium communities, EMF ascomycetes positively influenced

Table 5
Correlation (Spearman's ρ) between the fungal guild interaction influence βij and root litter decomposition,- the percentage of mass loss after six months. βij was calculated in the soil mycelium communities across the Soil Fertility Index (SMI) and Root Resource Index (RRI). Bij represents the influence of guild j on guild i, where the first guild in the row name represents guild j, and the second one the guild i. EMF = ectomycorrhizal fungi, STF = saprotrophic fungi, HB = high-biomass mycelium fungi, LB = low-biomass mycelium fungi. Significant differences at P ≤ 0.05 in bolded letters. N = 84.

B_{ij}	SFI		RRI	
	ρ	P-value	ρ	P-value
EMF ascomycetes - STF ascomycetes	0.09	0.43	0.10	0.39
STF ascomycetes - EMF ascomycetes	−0.18	0.10	−0.05	0.64
STF_basidiomycetes - EMF basidiomycetes (LB)	0.02	0.83	0.10	0.38
EMF basidiomycetes (LB) - STF_basidiomycetes	0.14	0.20	0.33	**0.00**
STF_basidiomycetes - EMF basidiomycetes (HB)	0.46	**0.00**	0.37	**0.00**
EMF basidiomycetes (HB) - STF_basidiomycetes	0.22	**0.05**	0.18	0.12
EMF ascomycetes - STF basidiomycetes	0.44	**0.00**	−0.18	0.10
STF basidiomycetes - EMF ascomycetes	0.22	**0.05**	0.31	**0.00**
EMF basidiomycetes (LB) - STF ascomycetes	0.11	0.32	0.00	0.98
STF ascomycetes - EMF basidiomycetes (LB)	0.06	0.60	−0.13	0.26
EMF basidiomycetes (HB) - STF ascomycetes	0.30	**0.01**	0.05	0.63
STF ascomycetes - EMF basidiomycetes (HB)	0.00	0.98	−0.12	0.29
STF basidiomycetes - EMF basidiomycetes	−0.02	0.86	0.07	0.51
EMF basidiomycetes - STF basidiomycetes	−0.21	0.06	0.23	**0.04**
Russulales - Mycena	−0.14	0.22	−0.15	0.19
Mycena - Russulales	0.04	0.72	−0.03	0.76
Boletales - Mycena	−0.14	0.22	0.08	0.49
Mycena - Boletales	0.28	**0.01**	0.23	**0.04**

all other guilds (Fig. 3D). However, in the root communities, their influence was predominantly negative (Fig. 3C).

In contrast with other forest types, in beech forests, the positive interaction-influences dominated both the root tip (63 % positive and 35 % negative, Fig. 3E) and mycelium (59 % and 37 %, Fig. 3F) communities. A small number of coefficients accounting for 2 % in root and 4 % in soil mycelium were uncertain (Fig. 3E and F).

Several guilds appeared to be either negatively or positively influenced by all other guilds. For example, EMF ascomycetes in conifer (Fig. 3A and B) and beech forests (Fig. 3E and F) or the low-biomass EMF basidiomycetes (Fig. 3B–F). The number of negative interactions increased in the order beech < mixt < conifer forests, a pattern that was paralleled by an increase in RRI.

The global interaction-influences in the three regions, where SFI and RRI were inversely related, revealed a higher number of uncertain values than in the forest types (Fig. 4). The highest uncertainty (20 %) occurred in the mycelium communities of A and S regions (Fig. 4B).

In A region characterised by the highest SFI and lowest RRI, the percentage of negative influences (53 % in roots and 57 % in mycelium communities) exceeded the positive influences (39 % and 22 %, Fig. 4A and B). In the H region, where the two indices showed similar moderate values, the percentage of negative interaction remained similar with A region in the root tip communities (57 %, Fig. 4C) but massively decreased in the mycelium communities (22 %, Fig. 4D). In the S region, characterised by the lowest SFI but the highest RRI, the negative interactions decreased to 29 % in the root tip (Fig. 4E) and 31 % in mycelium communities (Fig. 4F).

Eleven of the 32 fungal interaction coefficients were individually correlated with both soil fertility and root resource gradients, either in the root, soil mycelium, or both communities (Table 4). All these double correlated root community coefficients, but i = STF yeasts and moulds

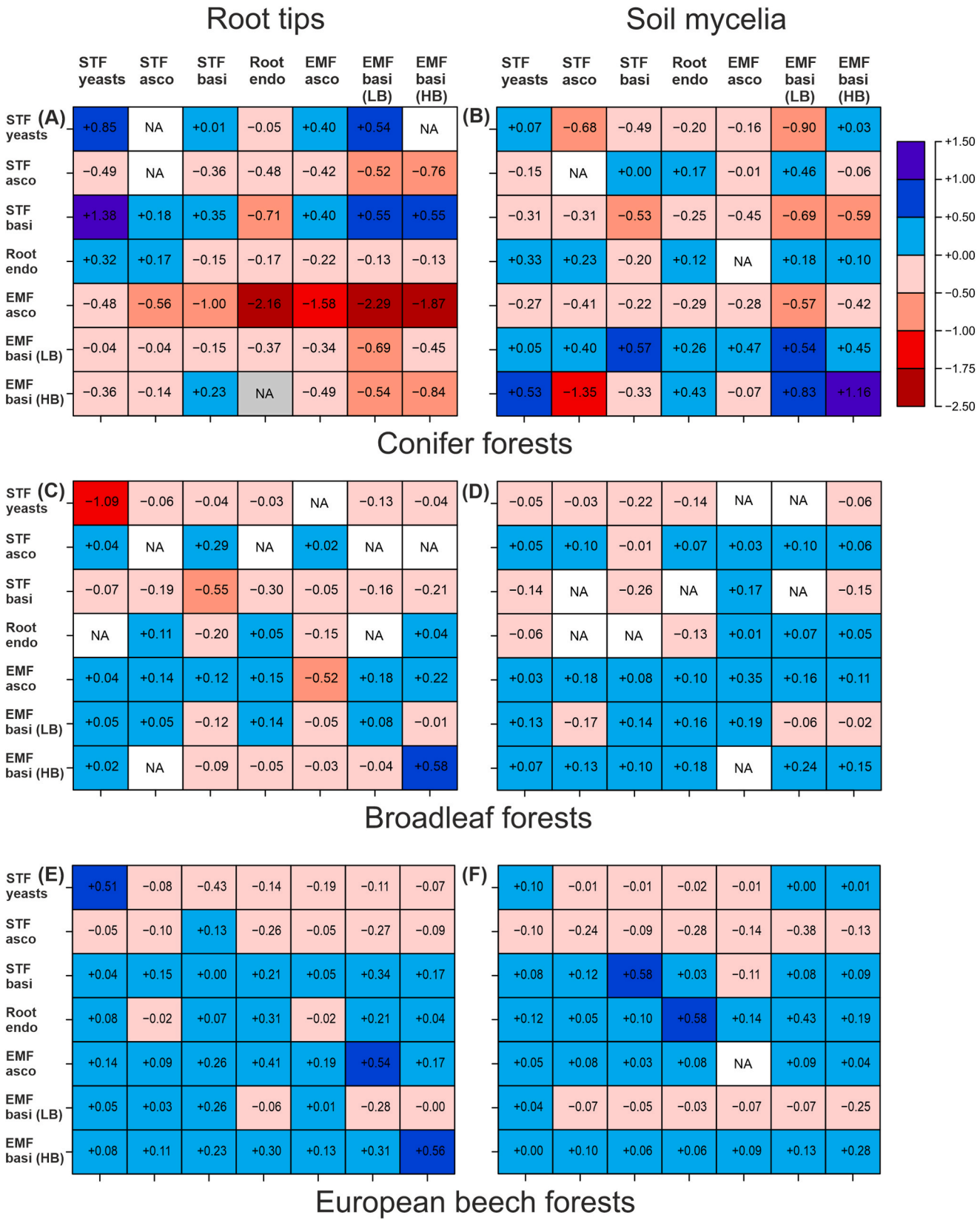

Fig. 3. Global interaction influence (β_{ij}) of guild j on guild i calculated across all samples in forests of conifer (A, B), beech mixed with conifer species (C, D), and beech (E, F) in the root (the left columns) and soil mycelium (the right columns) fungal communities. The interacting guilds *j* is represented by x-axis (columns) and *i* by y-axis (rows) names. The grey NA cells represent uncertain interactions. EMF = ectomycorrhizal fungi, STF = saprotrophic fungi, HB = high-biomass mycelium fungi, LB = low-biomass mycelium fungi. Number of plot replicates: n = 13 conifer, 15 beech mixed with conifer species, and 38 beech forests.

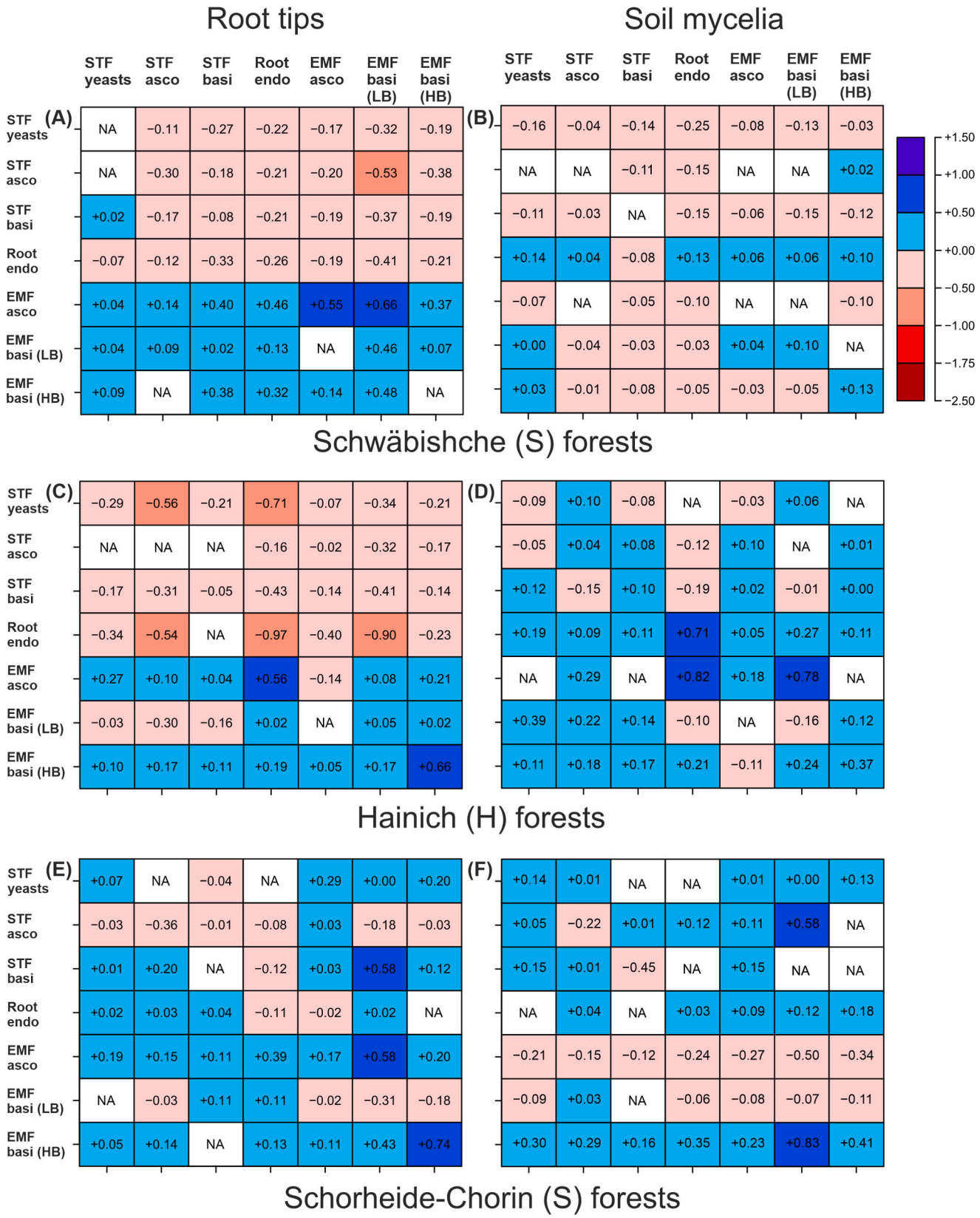

Fig. 4. Global interaction influence (β_{ij}) of guild j on guild i calculated across all samples in the three regions: S = Schwäbische Alb (A, B), H = Hainich-Dün (C, D), and S = Schorheide-Chorin (E, F). In the root (the left columns) and soil mycelium (the right columns) fungal communities. The interacting guilds *j* is represented by x-axis (columns) and *i* by y-axis (rows) names. The grey NA cells represent uncertain interactions. EMF = ectomycorrhizal fungi, STF = saprotrophic fungi, HB = high-biomass mycelium fungi, LB = low-biomass mycelium fungi. Number of plot replicates: n = 30 in A, 25 in H, and 29 in S.

and j = low-biomass EMF basidiomycetes, were negative in A and positive in S regions as per SGH considering SFI gradient (Fig. 4A–C, E). In the mycelium communities, only one of five coefficients followed the SFI gradient in confirming SGH (i = EMF ascomycetes and j = EMF basidiomycetes); the other two followed RRI gradient (i = STF ascomycetes and j = low-biomass EMF basidiomycetes, and = root endophytes); and other two were positive in all regions (Fig. 4B–D, F).

A pattern of negative influences of all EMF guilds on STF yeasts, STF ascomycetes, STF basidiomycetes, and root endophytes occurred in the root communities in the A and H regions (Fig. 4A–C).

The global interaction influences among dominant fungal taxa, including *Mycena* sp and EMF taxa from Russulales and Boletales, across all plots, revealed stronger intra-guild interactions compared to inter-guild influences (Table S9). *Mycena* exerted negative influences on other *Mycena* taxa, while Boletales positively influenced other Boletales, both in root tip and soil mycelium communities. Inter-guild interactions were generally negative but moderate in magnitude (Table S9).

4. Discussion

4.1. Soil fungal guild interactions differ with the spatial habitat and gradient type but the majority support SGH

We found a significant relationship between variation in soil fertility and direction and strength of the guild's influence in about 50–60 % of all interactions. In all cases, fungal influences become more positive with increasing stress (i.e. decreasing soil fertility). A similar result, but to a lesser magnitude (20–40 %), was also apparent for the root C resource gradient when the guild influences become more positive with the decreasing root C resources. These results confirm SGH in the soil fungal communities. Furthermore, we observed that 63 % of fungal interactions were related either to soil fertility or the root C resource gradient. When examining the individual components of SFI separately, a lower number of interactions was associated with each component compared to the composite SFI. These findings correspond to the broadly accepted view that the type and intensity of environmental stress are critical for testing SGH, as species may respond differently depending on the specific environmental factor (Kawai and Tokeshi, 2007; Maestre et al., 2009; Mod et al., 2014).

Our results revealed that the relationships of fungal guild interactions with stress gradients differed with the fungal spatial habitat and were more frequent in the root tip than in soil mycelium communities. We may explain these differences by changes in fungal functional traits associated with their residency (Garcia et al., 2016) that are further linked to their competitive abilities or tolerance to stress (Fernandez et al., 2023). Root-associated fungi, in particular, exhibit a rapid functional response to nutrient availability, demonstrating significant dynamics in their ability to acquire nutrients. This includes a potential shift in the symbiotic relationship, from invested to appropriated benefits for EMF (e.g., N; Pena and Tibbett, 2024). Such a shift resembles a saprotrophic-like or extreme parasitic lifestyle, which likely influences their interactions with other fungal guilds. However, we cannot exclude the root influence. Specifically, we speculate that the observed pattern is the effect of the plant's active role in partnering with fungi to meet nutrient acquisition needs or other physiological requirements (Goldmann et al., 2016; Khokon et al., 2023; Jörgensen et al., 2024). This also accords with the findings that the number of beneficial versus negative plant interactions with soil microorganisms increases with the stress intensity (Hernandez et al., 2021). Our results show, for example, that in the root tip communities, the root endophytes showed no variation in their influence on the low-biomass EMF or STF basidiomycetes along the soil fertility gradient, but they increased their positive influence on the high-biomass EMF with decreasing soil fertility. Kennedy et al. (2014) have suggested that the change in the EMF interspecific interactions from strong to less competition with increasing abiotic stress might result in a facilitation effect of enhancing fungal abilities to cope with the stress. Given that the high-biomass fungi have an essential role in resource acquisition by accessing a larger soil volume and more complex enzymatic abilities than the low-biomass fungi (Pena, 2016), their benefit from other fungi is likely to play a crucial role in improving plant nutrition. Moreover, in the root fungal communities, the influence of root endophytes on the high-biomass EMF showed the most robust relationship with soil fertility among all other interactions. The relationship was also maintained in the mycelium communities, where the root endophytes were less abundant than in the root communities. All these findings confirm the importance of root endophytes' influence on providing support for EMF under resource stress, as has been reported by other studies. For example, positive interactions between root endophytes and EMF are among the most common interactions observed in plant roots under the harsh conditions of Arctic climates (Abrego et al., 2020) and during oak seedling establishment (Yamamoto et al., 2014). This facilitative mechanism might be related to the exceptionally high ability of Leotiomycetes to tolerate and cope with decreasing soil fertility (Tedersoo et al., 2014; Sterkenburg et al., 2015). This is further supported by our observation of increased Leotiomycetes abundance in roots as soil fertility declines.

4.2. Saprotrophic – ectomycorrhizal fungal interactions change from positive to negative with increasing soil fertility, supporting the premises of the "Gadgil effect"

The interactions between STF and EMF fungi have long been studied because their competition potentially leads to decreased decomposition through suppression of STF (Gadgil and Gadgil, 1971) or EMF (*Cortinarius* sp., Lindahl et al., 2021) activities. We found a clear pattern that STF-EMF reciprocal negative influence prevailed under high soil fertility and gradually switched to positive influence with decreasing soil fertility. These findings corroborated with decreased root litter decomposition under higher fertility, confirming our hypothesis about the premises of the "Gadgil effect" as per SGH. Fernandez and See (2025) reported similar findings, observing higher decomposition rates under lower pH and higher C:N ratios, conditions that resemble the low-fertility end of our gradient. However, they clarified that in acidic soils (pH < 5), this may occur because EMF acquire N either through their oxidative capabilities, competing with STF for complexed organic N (Lindahl and Tunlid, 2015; Lindahl et al., 2021), or by accessing inorganic N, produced by STF. In the latter case, EMF can facilitate STF activity by enhancing their function through priming mechanisms (Phillips et al., 2012), as EMF hyphae commonly exude labile carbon compounds into the hyphosphere (Gorka et al., 2019; Wen et al., 2022). Interestingly, we observed a positive influence of both low- and high-biomass EMF basidiomycetes on STF basidiomycetes under conditions of lower pH and higher C:N ratios. However, when we analysed the effects of soil pH and C:N ratio separately, distinct patterns emerged. Low-biomass EMF positively influenced STF under both lower pH and higher C:N ratios, whereas high-biomass EMF negatively influenced STF under higher C:N ratios, with no significant effect related to pH variation. The high-biomass EMF basidiomycetes include two EMF genera, for which it has been demonstrated that they may degrade the organic matter to retrieve N: *Cortinarius*, via oxidative enzymes (Lindahl et al., 2021), and *Paxillus*, through Fenton-like chemistry (Op De Beeck et al., 2018). Thus, it appears likely that while low-biomass EMF facilitated STF activity, high-biomass EMF competed with STF. To explore this further, we analysed the genus *Mycena* (STF basidiomycetes), *Russulales* (included in the low-biomass EMF), and *Boletales* (high-biomass EMF). Consistent with the SGH, we observed more positive interactions between *Mycena* and both EMF groups under lower fertility conditions (i.e., lower pH and higher C:N ratio), supporting a higher decomposition rate. However, we found no clear evidence endorsing a consistent contrast in STF responses to low-versus high-biomass EMF. We interpret this as a consequence of the overly simplistic assumption that all species within a genus or order share the same N acquisition strategies. In

reality, there is considerable functional diversity in N uptake, and taxonomic orders include a wide range of taxa spanning distinct ecological guilds (Pena, 2016).

A positive relationship between fungal interactions and decomposition was particularly apparent for the STF basidiomycetes and high-biomass EMF basidiomycetes, which included taxa potentially involved in lignin decay (e.g., *Suillus*, *Paxillus*, *Cortinarius*, Miyauchi et al., 2020; Chen et al., 2024). This is important because fine root litter serves as a primary source of lignin-derived organic matter in forest soils. Notably, another study in temperate broadleaf forests (Argiroff et al., 2022) reported a shift in soil community composition, with a decline in EMF taxa capable of degrading lignin under higher inorganic N availability in fertile soils.

We have to note that the stress gradient, typically for temperate forests, includes an overall low inorganic N availability. In the most fertile sites, characterised by a soil pH around 5 and a C:N ratio of 12, inorganic N concentrations remain low relative to plant and microbial nutritional demands. For example, Nadelhoffer et al. (1984) reported typical HN_4^+ and NO_3^-concentrations in temperate forest soils ranging from approximately 2.7 to 20.6 μg/g and up to 37.3 μg/g, respectively, whereas values in our study were substantially lower, suggesting limited N availability. On the other side, we refer to moderate stress. Although the original SGH proposes a monotonic increase in the importance of positive interactions with stress intensity (Bertness and Callaway, 1994), numerous empirical studies revealed a hump-shaped pattern: negative interactions dominate at the extremes, and positive interactions occur at intermediate levels of stress gradient (Maestre and Cortina, 2004; Michalet et al., 2006, 2014). Particularly, when the most limiting resource levels are so low that they impair the benefactor from providing it to the beneficiary, the facilitation switches to competition (Holmgren and Scheffer, 2010). Thus, a moderate stress level can explain the overall bidirectional positive influences found in our study at the lower fertility end. Moreover, the importance of stress intensity in testing SGH was evident in our results, as we found a clear pattern of the shift from negative to positive influence at the same SFI value for all guilds.

4.3. The frequency of symmetrical interactions increases with stress intensity

The reciprocal positive influence found between STF and EMF fungi shows symmetrical mitigation of low-fertility effects by symmetric facilitation: EMF prime STF activity and STF produce nutrients to benefit EMF. Under low nutrients, the symmetry of interaction-influence is paramount in explaining SGH (Lin et al., 2012; Hart and Marshall, 2013). Otherwise, the asymmetry will limit facilitation by limiting the growth of the benefactor guild (Hart and Marshall, 2013). Being a benefactor comes at an overall cost (Bronstein, 2009; Schöb et al., 2014) that needs to be returned according to natural selection (Darwin, 1859; Bronstein, 2015). The occurrence of symmetrical positive interactions under harsh conditions enhances the importance of facilitation in maintaining fungal coexistence under environmental variations (Loreau and de Mazancourt, 2013). However, this has been primarily acknowledged for plants (Callaway, 2007; Soliveres et al., 2015; Takimoto, 2020).

In general, the increase in the frequency of symmetrical interactions with decreasing soil fertility was more substantial for soil mycelium than root communities, while the relationship with root resources was stronger for root than soil mycelium communities. These findings indicate a tight and direct link between the occurrence of symmetrical facilitation and stress conditions because the immediate resident communities were the more affected ones.

The soil fertility decreases from the southwest (A) to central (H) and northeast (S) regions. The latter one is characterised by a warmer and drier climate. Other studies have reported no differences in fungal diversity among the regions either in the soil (Wubet et al., 2012; Goldmann et al., 2015) or in roots (Schröter et al., 2018). However, a consistent analysis of ectomycorrhizas (Pena et al., 2017) revealed a lower diversity in S than A and H regions. The biodiversity loss that occurs in high-stress environments commonly has larger consequences for the ecosystem functioning than in low-stress environments, and positive species interactions are required to mediate the stress impact on the biodiversity-ecosystem functioning relationship (García et al., 2018). Our results imply that symmetrical positive interactions among soil fungal guilds are critical in maintaining ecosystem functions under stressful environmental conditions.

4.4. Under two environmental stress gradients, SGH holds true for the dominant gradient in the system

In most studies, SGH predictions are based on a single stress gradient, which is commonly identified as the main stress in the system (Adams et al., 2022). Here, we included two resource-related gradients of importance in the temperate forests, the soil fertility and root C resources. The two gradients were inversely related, excluding, thus, their simple addition in generating the net effects on fungal species interactions. About 38 % of interaction coefficients were individually correlated with both soil fertility and root resource gradients, indicating the influence of both gradients.

We calculated the global interaction coefficients, integrating both stress gradients, in three forest types, which differed in RRI but not in SFI. We reasoned that if SGH holds true for the dominant stress gradient in the system, the number of fungal negative interactions should increase with RRI. The results confirmed our predictions, with the highest number and the strongest negative interactions apparent in the conifer forests (the highest RRI) and the positive interactions in the beech forests (the lowest RRI). This finding is supported by a larger saprotrophic fungal biomass that may result in a general competitive pressure for EMF in the conifer than in beech forests (Awad et al., 2019).

The global interaction coefficients for the three regions, when SFI and RRI gradients were inversely related, showed that the number of negative interactions exceeded the positive interactions in A region (highest SFI, lowest RRI), with the opposite case in S region (lowest SFI, highest RRI), supporting SGH for the soil fertility gradient. We assume that soil fertility is the dominant gradient in the system because, under the effect of a single gradient, we found more significant correlations between stress intensity and interaction coefficients for SFI than RRI. This assumption is also supported by the interaction coefficients, which were individually correlated with both SFI and RRI, as their global value showed support for SFI effects per SGH. It is worth noting that the SFI incorporates a wider range of parameters than the RRI, and therefore, may capture a broader spectrum of environmental influences. However, many of the global coefficients along the two gradients were uncertain or showed no variation. We may speculate that this is the result of the simple addition of inversely related stress effects, but at the same time, the variance of biotic interactions may reflect the complexity of the species-specific responses to abiotic conditions (Wang et al., 2008; Maestre et al., 2009; Maalouf et al., 2012; Mod et al., 2014). The concept of the dominant stress gradient in the system includes two components: the context-dependency, which here is the fungal habitat, and the severity of stress gradients (He et al., 2013; Mod et al., 2014). In support of the context-dependency component and confirming our initial hypothesis, we found that RRI effects were more prominent in root than mycelium communities. In keeping with this, we also found that forest tree composition had a stronger influence on root than mycelium communities. In the region analysis, when both gradients were well represented, the importance of the habitat was less apparent. We found a similar number of global interactions associated with SFI or RRI, both in root and mycelium communities. Furthermore, by exclusively considering the interactions that were correlated with both SFI and RRI, when only one gradient was considered, we found stronger effects of SFI in the root than in the mycelium communities. These findings are not surprising given the large influence of soil factors on the root-associated

fungal communities (Schröter et al., 2018; Nguyen et al., 2020).

We specifically expected that RRI affects the interactions involving root-associated fungi (EMF, root endophytes) as root chemistry is a driver of fungal community structure (Nguyen et al., 2020) and fungal biomass (Awad et al., 2019). In accordance with our prediction, the global interactions in conifer, beech, and mixed forests showed that root endophytes, which had a dominant negative influence in all interactions in the root communities, were influenced by RRI. Root endophytes have a close metabolic connection with the host for receiving nutrients and protection (Khare et al., 2018). They are known for their ability to suppress fungal pathogens (Card et al., 2016). In pine (Wagg et al., 2008) and oak seedlings (Yamamoto et al., 2014), root endophytes (Yamamoto et al., 2014) and mycorrhizal fungi were spatially segregated, indicating competitive interactions.

We have analysed the interactions of EMF Russulales and Boletales with the STF *Mycena*, considering the differences in their ability to decompose recalcitrant organic matter. Russulales with a reduced capacity, Boletales, which evolved within a clade of brown-rot saprotrophs, and *Mycena*, which is a white-rot saprotroph (Miyauchi et al., 2020; Chen et al., 2024). By integrating both stress gradients, we found strong negative intra-specific influences for *Mycena* that are common for wood-decaying basidiomycetes (Boddy, 2000) but moderate, with many remaining uncertain influences between *Mycena* and EMF taxa. These results align with our findings at the guild level, supporting the validity of grouping fungi into functional guilds for analysis. However, there are limitations to this approach, as many ecological functions are specific to individual fungal species (Pena and Tibbett, 2024). The use of functional guilds in this study was not intended to provide an exhaustive or error-free depiction of fungal ecology. Rather, it serves as a pragmatic framework for exploring community-level patterns and functions across environmental gradients. By focusing on overarching patterns and processes, we aimed to identify broad ecological trends rather than definitive species-specific interactions. Further studies should aim to integrate species-specific functional traits and genetic capacities into guild-level analyses, enhancing the resolution of ecological insights and addressing the variability within functional groups.

5. Conclusions

Our study shows that in temperate forests, fungal guilds exhibit reciprocal positive rather than negative effects on each other at the lower levels of soil fertility or root C resource gradients, supporting SGH. These findings corroborate enhanced decomposition, indicating a facilitation effect generated by the STF-EMF positive interactions. However, a more detailed analysis, examining soil pH and C/N ratio separately, revealed nuanced effects of different EMF groups on STF. High-biomass EMF, including taxa known for accessing N from complex organic substrates, negatively influenced STF basidiomycetes, which are key decomposers of recalcitrant N sources. Thus, while composite measures such as the SFI and RRI capture broader fertility gradients more effectively than their individual components, a more precise understanding of the "Gadgil effect" requires examining specific environmental variables and taxon-level responses. Overall, under conditions of lower soil pH and drier, warmer climates, resembling projected climate change scenarios, STF and EMF guilds tend to positively influence each other, giving rise to facilitative interactions that may represent a solution to maintain nutrient turnover, supporting ecosystem productivity under limited resources.

CRediT authorship contribution statement

Rodica Pena: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Abdallah Awad:** Writing – review & editing, Investigation. **Ali Nawaz:** Writing – review & editing, Methodology, Investigation. **Yu Shang:** Writing – review & editing, Software. **Tesfaye Wubet:** Writing – review & editing, Funding acquisition, Data curation. **Mark Tibbett:** Writing – review & editing, Funding acquisition.

Data availability

The data that support the findings of this study are openly available in Biodiversity Exploratory Information System (BExIS, https://www.bexis.uni-jena.de/ddm/publicsearch/index) under the accession numbers 1666, 19067, 18386, 20266, 19966, 22967, 22006 and 21986.

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.soilbio.2025.109865.

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