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Functional convergence of soil fungal communities with biotic homogenization in a biodiversity hotspot

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Functional convergence of soil fungal communities with biotic homogenization in a biodiversity hotspot

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Abstract

Aims

Soil fungal communities play critical roles in ecosystem functions. However, soil fungal communities are becoming homogenization under human disturbance although the functional consequences remain poorly understood.

Methods

Here we investigated soil fungal community composition, diversity, and functional guild structure across agroecosystems, grasslands, and forests in four isolated valleys of the Mountains of Southwest China, a globally recognized biodiversity hotspot. We characterized the patterns of biotic homogenization and the relative abundance of functional guilds. Community assembly processes were inferred using the iCAMP framework.

Results

Agroecosystems harbored 30.3% higher phylotype richness than grasslands but exhibited significantly lower β-diversity (3.25% and 4.71% lower than grasslands and forests, respectively) and higher biotic homogenization degrees. Agroecosystems hosted more abundant plant pathogens than forests and grasslands (by 361.5% and 354.0%, respectively) and more saprotrophs (by 91.3% and 72.8%), but substantially fewer ectomycorrhizal fungi (93.3% lower than forests). Soil fungal communities in agroecosystems showed the highest importance of homogeneous selection, whereas heterogeneous selection was lowest, consistent with the homogenization pattern. The richness and abundance of plant pathogens and saprotrophs increased whereas those of ectomycorrhizal fungi decreased with biotic homogenization. Bin-level assembly analysis revealed that the assembly processes were associated with functional guilds. Soil total

phosphorus, nitrate, and C:P ratio were key environmental drivers of homogenization and functional guild shifts.

Conclusions

These findings demonstrate that agricultural activities drive fungal community convergence through environmental filtering, with cascading effects on functional guilds that may compromise ecosystem multifunctionality and long-term soil health.

Keywords

soil mycobiome, biotic homogenization, community assembly, functional guild, agricultural intensification, biodiversity hotspot

Introduction

Soil fungi play pivotal roles in soil nutrient cycling, plant health, and agricultural sustainability (Delgado-Baquerizo et al. 2020). Understanding how soil fungal community composition shifts, especially changes in functional guilds, is essential for predicting ecosystem functional trajectories under environmental change (Peng et al. 2024). Biotic homogenization, the increased similarity of communities across space, is a major ecological consequence of human-driven environmental change, with a consequence of species

turnover reduction and functional diversity erosion at regional scales (Banerjee et al. 2026). Homogenization has been documented across diverse taxa, including plants (Yang et al. 2021), arthropods (Gossner et al. 2016), birds (Devictor et al. 2008), and marine fishes (Stuart-Smith et al. 2021). In soil ecosystems, urban greenspaces exhibit more homogeneous microbial communities than adjacent natural ecosystems (Delgado-Baquerizo et al. 2021). Agricultural activities(Banerjee et al. 2024), grassland use (Gossner et al. 2016) and eucalypt plantation (Ribero et al. 2025) substantially transforms soil microbiome composition, leading to biotic homogenization. Some ubiquitous fungi span multiple contrasting ecosystems (Egidi et al. 2019), and may become dominant across ecosystems under homogenization. Furthermore, agricultural and ecosystem transformations can alter soil functions, leading to loss of plant-beneficial microbes and increase in plant pathogens(Epp Schmidt et al. 2017; Ohigashi et al. 2025; Banerjee et al. 2026). In particular, some plant-symbiotic fungi such as ectomycorrhizal fungi (ECM) (Epp Schmidt et al. 2017) and arbuscular mycorrhizal fungi (AMF) (Banerjee et al. 2024), tend to be lost in human-disturbed environments, thereby affecting plant productivity, community composition, and ecosystem multifunctionality in the long term. However, the functional consequences of homogenization and the mechanisms driving it remain poorly understood.

Community assembly processes, including homogeneous selection, heterogeneous selection, homogenizing dispersal, dispersal limitation, and drift, are the main forces driving community assembly and compositional change (Stegen et al. 2013; Ning et al. 2020). Homogeneous selection and heterogeneous selection are the deterministic processes (Dini-Andreote et al. 2015) that drive communities to converge (i.e., homogenize) and diverge, respectively. Although the roles of these processes in microbial community assembly have been extensively studied (Ning et al. 2020; Peng et al. 2024; Livne-Luzon et al. 2026), their

roles in connecting microbial community homogenization and biotic functional changes remain unclear.

The Mountains of Southwest China, a globally recognized biodiversity hotspot, were shaped by the uplift of the Tibetan Plateau, which created sharp geomorphological gradients with parallel isolated valleys harboring agroecosystems, grasslands, and forests in proximity (Tang et al. 2006; Huang et al. 2016). Compared with extensively disturbed agroecosystems, the grasslands in this area are subjected to moderate grazing, whereas most forests experience minimal disturbance from harvesting activities. This natural setting provides a unique platform to compare soil fungal communities across ecosystems with similar geological history but contrasting land-use intensities. We addressed three questions: (i) Do agricultural activities homogenize soil fungal communities in this biodiversity hotspot? (ii) How do functional guilds of soil fungal communities change with homogenization? (iii) What assembly processes drive soil fungal community homogenization and shifts in functional guilds?

Materials and Methods

Study area and soil sampling

The uplift of the Tibetan Plateau creates a sharp geomorphological gradient with elevation decreasing from north to south, forming multiple isolated rivers and valleys that run in parallel across Southwest China. This region is a globally recognized biodiversity hotspot (Huang et al. 2016), hosting vast numbers of plant, animal, and microbial species, many of which are endemic (Tang et al. 2006). Agroecosystems, grasslands, and forests are distributed in a mosaic pattern in this region, providing an ideal natural platform to compare the characteristics of soil microbiome across multiple ecosystems (Yan et al. 2024).

We adopted a pairwise sampling strategy by simultaneously collecting soils from different ecosystems within the same site where possible. Thirty-one sites across four river valleys (Yangtze River, Mekong River, Salween River, and Red River) were selected, yielding 83 samples: 31 from agroecosystems, 22 from grasslands, and 30 from forests (Fig. 1S). At each plot (1 m × 1 m), four soil cores (0–10 cm depth) were collected, combined into one composite sample, and thoroughly mixed. Sampling tools were rinsed with plot soil before sampling to eliminate potential contamination. Five grams of each composite sample were placed into sterile vials and transported to the laboratory in a portable refrigerator. The remaining soil was brought back to the laboratory to measure soil chemical properties.

Soil fungal amplicon sequencing and bioinformatics

Soil samples were shipped to Biomarker Technologies Co. Ltd. for DNA extraction and sequencing following standard protocols. DNA was extracted using MN NucleoSpin 96 Soil kits (MACHEREY-NAGEL GmbH & Co. KG, Germany) following manufacturer instructions. The ITS1F/ITS2 primer set was used for amplification with the following thermocycler program: 5 min at 95 °C; 35 cycles of 30 s at 95 °C, 30 s at 50 °C, 40 s at 72 °C; and a final extension of 7 min at 72 °C. The constructed libraries were sequenced on an Illumina HiSeq2500 platform (2 × 250 bp paired-end).

Raw reads were primarily filtered using the DADA2 package (Callahan et al. 2016) in R (R Core Team 2025) to truncate primers and low-quality ends and remove low-quality reads. The remaining reads were processed through the QIIME2 pipeline (Bolyen et al. 2019) for paired-end joining and denoising with DADA2 (default parameters). Taxonomic classification was performed against the UNITE fungal database v8 (Kõljalg et al. 2005). A phylogenetic tree was constructed by FastTree2 (Price et al. 2010). Non-fungal amplicon sequence variants (ASVs) were removed in subsequent analyses. Sequences were rarefied

to the minimum sequencing depth across all samples, retaining 12,976 reads per sample for downstream analyses. Functional guilds (e.g., plant pathogens, saprotrophs, ECM, and AMF) were assigned using FUNGuild (Nguyen et al. 2016). ASVs with unassigned guilds were grouped as "other".

Soil chemical properties

Sub-samples of soil were sieved to 1 mm to remove plant debris and stones. Soil ammonium (NH_4^+) content was quantified by a modified Berthelot-salicylate method (Weatherburn 1967), and nitrate (NO_3^-) was determined by a single-reagent method (Doane and Horwáth 2003) using 2 $mol \cdot L^{-1}$ KCl extraction. Soil pH was measured with a glass electrode in a 1:2.5 (soil:water) suspension. Soil total carbon (TC) and total nitrogen (TN) were measured by elemental analyzer (vario MICRO cube, Elementar Corporation, Germany) after drying and grinding. Soil total phosphorus (TP) was measured by molybdate colorimetry (Nottingham et al. 2015). The C:N, C:P, and N:P ratios were calculated from TC, TN, and TP.

Statistical analysis

Phylotype taxonomy and abundance tables from QIIME2 were imported into R (R Core Team 2025) via the qiime2R package (Bisanz 2018) and combined with sample metadata to form a phyloseq object (McMurdie and Holmes 2013). Phylotype richness was estimated using the phyloseq::estimate_richness. β-diversity was calculated using the vegdist function of the vegan package (Oksanen et al. 2020) based on Bray–Curtis distances. The effects of ecosystem type on fungal composition were tested by permutational multivariate analysis of variance (PERMANOVA) via the vegan::adonis2 function. Principal coordinate analysis (PCoA) was performed using the ape::pcoa function (Paradis and Schliep 2019) on log(x+1)-transformed Bray–Curtis distances.

We investigated the correlations of the dissimilarity of fungal communities with environmental and geographic distance using the vegan::mantel.partial function. The dissimilarity of fungal communities (Bray–Curtis distances) were calculated by the vegan, and geographic distance was calculated by the distm function of the geosphere package (Hijmans 2026). The best subset of environmental variables having the maximum correlation with community dissimilarity was determined by the vegan::bioenv function. Finally, soil pH, C:P ratio, N:P ratio, and ammonium content were selected to calculate environmental distance. Homogenization degrees (1/distance to centroid) were calculated using the usedist package (Bittinger 2020). Correlations of homogenization degrees with environmental factors and functional guild composition were analyzed with the hmisc packages and visualized with the ggcor in R. Generalists (Levins' niche breadth > 0.90) and specialists (Levin's niche breadth < 0.55 with p.adj < 0.05 via null model simulation) were identified by the MicroNiche package (Finn et al. 2020) with ecosystem types as the environmental categories being compared. Multiple comparisons were performed by the pairwise_wilcox_test function using the rstatix package (Kassambara 2025) with the Bonferroni method to adjust p values where appropriate. The results of analyses were visualized with ggplot2 (Wickham 2016).

Community assembly processes were inferred using the iCAMP framework (Ning et al. 2020) to quantify the relative importance of homogeneous selection, heterogeneous selection, homogenizing dispersal, dispersal limitation, and drift. The iCAMP analysis was conducted with default parameters (1000 randomizations). To assess the contribution of functional guilds to assembly processes, we performed a bin-level analysis following the iCAMP framework. Bins were defined by the iCAMP pipeline based on phylogenetic clustering (Ning et al. 2020). The proportions of functional guilds within each bin were calculated as the percentages of ASV members of each functional guild.

Results

Changes in fungal community composition, diversity, and homogenization

Soil fungi exhibited significant differentiation in community composition among different ecosystem types (PERMANOVA: $F_{2,80} = 2.00$, $p = 0.001$; Fig. 1a,c). At the phylum level, Mortierellomycota and Ascomycota in agroecosystems were more abundant (186.7% and 55.0% higher, respectively) than in forests (Fig. 1a). Mortierellomycota was also more abundant (197.1%) in agroecosystems than in grasslands. The relative abundance of functional guilds also differed among ecosystem types (Fig. 1b), with plant pathogens being more abundant in agroecosystems than in forests and grasslands (361.5% and 354.0% higher, respectively; $P < 0.001$ for both pairwise tests). Agroecosystems also harbored more abundant saprotrophs than forests (91.3% higher, $p = 0.008$) and grasslands (72.8% higher, $p = 0.053$). By contrast, ECM fungi were less abundant in agroecosystems and grasslands than in forests (93.3% and 96.4% lower, respectively; $p < 0.001$ for both). AMF was 96.3% more abundant in grasslands than in forests ($p = 0.013$) but not differ between agroecosystems and forests ($p = 0.061$).

Agroecosystems had 30.3% greater phylotype richness than grasslands ($p = 0.007$) but did not differ from forests ($p = 0.402$; Fig. 1d). In contrast, agroecosystems had the lowest β-diversity (3.25% and 4.71% lower than those of grasslands and forests, respectively; $p < 0.001$ for both pairwise tests) (Fig. 1e). In line with this, the homogenization degree (1/distance to centroid) was significantly higher in agroecosystems than in forests (3.77% higher, $p < 0.001$) and grasslands (2.84% higher, $p = 0.004$) (Fig. 1f), confirming that soil fungi in agroecosystems are more homogeneous.

The dissimilarity of community composition was positively related to both environmental distance (partial Mantel test, $r = 0.177$, $p < 0.001$; Fig. 2a) and geographic distance (partial

Mantel test, r = 0.131, p = 0.003; Fig. 2b), indicating that both environmental filtering and spatial dispersal limitation could affect the soil fungal community composition.

The relative abundance of generalists and specialists did not differ significantly among ecosystems (p > 0.05 for both; Fig. 3a,b). However, the homogenization degree was positively correlated with the relative abundance of generalists in each ecosystem (p < 0.001) (Fig. 3c) and negatively correlated with the relative abundance of specialists in grasslands (p = 0.026) and forests (p < 0.001) (Fig. 3d). Interestingly, at the equivalent abundances of generalists and specialists, agroecosystems showed higher homogenization degrees than other ecosystems (Fig. 3c,d). These results collectively suggest that the homogenization differences between agroecosystems and natural ecosystems were driven by similar composition resulting from shared taxa across sites, rather than by changing in the abundances of generalists and specialists.

Assembly processes and functional changes

Using iCAMP to quantify the assembly processes affecting community homogenization, we found that the importance of homogeneous selection in agroecosystems was 18.3% higher than in forests (p = 0.002) but did not differ from that in grasslands (p = 0.244) (Fig. 4). In contrast, heterogeneous selection was the highest in forests and lowest in agroecosystems (40.6% and 58.7% lower than in grasslands and forests, respectively; p < 0.001 for all pairwise tests). Dispersal limitation showed highest in grasslands and lowest in agroecosystems (p < 0.05 for all pairwise tests). Drift was higher in agroecosystems than in other ecosystems (p < 0.001 for both pairwise tests). Homogenizing dispersal was consistently low across all ecosystem types (relative importance < 1%).

Both the abundance and richness of plant pathogens were positively related to the biotic homogenization degrees (abundance: r = 0.27, p= 0.013; richness: r = 0.32, p = 0.003) (Fig.

233 5). Saprotrophs showed a similar pattern (abundance: r = 0.28, p = 0.010; richness: r = 0.56,
234 p <0.001). By contrast, the abundance and richness of ECM fungi were negatively correlated
235 with homogenization degrees (abundance: r = -0.34, p = 0.029; richness: r = -0.32, p =
236 0.003). AMF showed no significant correlation with homogenization degrees (p > 0.05).
237 Biotic homogenization degrees were positively related to soil NO_3^- (r = 0.45, p < 0.001) and
238 TP (r = 0.27, p = 0.013), and negatively related to soil C:P ratio (r= -0.22, p = 0.047). These
239 results indicate that environmental changes induced by agricultural activities, particularly
240 elevated soil nitrate and reducing C:P ratio, may drive soil fungal homogenization and alter
241 the composition of functional guilds.

242 The richness and abundance of functional guilds were correlated with several
243 environmental factors (Fig. 5). Plant pathogen abundance was positively correlated with TP
244 (r = 0.26, p = 0.017) and NO_3^- (r = 0.30, p = 0.007) and negatively correlated with C:P ratio
245 (r = -0.24, P = 0.030). Saprotroph richness showed similar correlations with TP and NO_3^-
246 but was negatively correlated with C:N ratio (TP: r = 0.26, p = 0.018; NO_3^-: r = 0.25, p =
247 0.020; C:N ratio: r = -0.28, p = 0.010). ECM fungi abundance was negatively correlated with
248 TP (r = -0.22, p = 0.042), while ECM richness positively correlated with C:P ratio (r=0.36, p <
249 0.001), N:P ratio (r = 0.27, p = 0.013) and NH_4^+ (r = 0.33, p = 0.003).

250 Bin-level analysis of the association between assembly processes and functional
251 composition revealed that bins containing high proportions of plant pathogens reduced
252 heterogeneous selection (r = -0.07, p = 0.002) and dispersal limitation (r = -0.11, p <0.001),
253 but promoted homogenizing dispersal (r = 0.09, p < 0.001) (Fig. 6a,p,u), supporting the
254 positive effects of plant pathogens on biotic homogenization. On the other hand, bins
255 containing high proportions of saprotrophs promoted homogeneous selection (r = 0.07, p =
256 0.001) and reduced dispersal limitation (r = -0.06, p = 0.011) (Fig. 6i,s), indicating that

saprotrophs can also contribute to biotic homogenization via different pathways. By contrast, bins containing high proportions of ECM fungi contributed positively to heterogeneous selection (r= 0.10, $p < 0.001$) and negatively to dispersal limitation (r = -0.06, $p = 0.012$) (Fig. 6b,q). Bins containing high proportions of AMF contributed positively to dispersal limitation (r = 0.19, $p < 0.001$) (Fig. 6r).

Discussion

Composition shifts in agroecosystem homogenization

Our results showed that agroecosystems in this biodiversity hotspot harbor more homogeneous soil fungal communities than adjacent grasslands and forests, despite higher local phylotype richness (Fig. 1). This pattern aligns with global evidence that land-use intensification reduces β-diversity across taxa (Gossner et al. 2016; Delgado-Baquerizo et al. 2021; Peng et al. 2024). The 30.3% higher richness in agroecosystems likely reflects the influx of perturbation-adapted species, consistent with the "α-β diversity" paradox under biotic homogenization (Rodrigues et al. 2013; Delgado-Baquerizo et al. 2021; Sun et al. 2025), indicating that local diversity gains come at the cost of regional diversity.

A number of studies have proposed that homogeneous communities tend to be dominated by generalists, along with the loss of specialists (Gossner et al. 2016; Banerjee et al. 2024), although concrete evidence is still scarce (Vahter et al. 2025). Here, the generalists and specialists were defined by the niche breadth across multiple ecosystems, which is useful to reveal the effects of land transformation on microbial communities under environmental changes. It should also be noted that occupying wide spatial ranges in homogeneous agroecosystems does not necessarily imply large niche breadth (Finn et al. 2020). We found no evidence of the association between agroecosystem homogenization and generalist/specialist shifts by the comparison of multiple ecosystems. There were no

significant differences in the relative abundance of generalists or specialists among different ecosystems. However, agroecosystems showed higher homogenization degrees at equivalent generalist and specialist abundances (Fig. 3). Combined with the pattern of β-diversity, these results indicate that homogenization was driven by the similar composition of shared taxa across sites, rather than by a simple increase in generalist dominance. This finding contrasts with the widely held view that agriculture-induced homogenization is driven by the dominance of generalists (Banerjee et al. 2026). This discrepancy may lie behind the fundamental mechanisms of homogenization. Agricultural activities create homogeneous environments (Wang et al. 2022), favoring perturbation-tolerant specialists with broad spatial ranges, which are frequently misclassified as generalists. Interestingly, we found a clear increase in homogenization degrees with generalist dominance within each ecosystem and was accompanied by a decrease with specialist abundances in grasslands and forests. Collectively, our results indicate that agriculture-induced homogenization (relative to other ecosystems) did not stem from generalist dominance and specialist loss, even though homogenization within each ecosystem was accompanied by shifts in generalists and specialists.

Environmental drivers in agroecosystem homogenization

Using iCAMP, we found that homogeneous selection in agroecosystems exceeded those in grasslands and forests. Conversely, heterogeneous selection was the highest in forests. This shift from heterogeneous to homogeneous selection along the land-use intensity gradient mirrors homogenization patterns observed across different ecosystems (West et al. 2023; Aslani et al. 2024; Ohigashi et al. 2025). Agricultural practices such as tillage(Hu et al. 2024), fertilization(Zhang et al. 2026) and monoculture cropping, can create similar environments across geographically separated sites, thereby selecting for similar soil fungi.

This is consistent with our finds that community dissimilarity was correlated with environmental distance after accounting the effects of geographic distance, confirming the role of environmental filtering in shaping fungal communities.

Changes in functional guilds with biotic homogenization

Our results showed that agroecosystems enriched plant pathogens and depleted ECM fungi, consistent with previous studies (Labouyrie et al. 2023; Banerjee et al. 2024; Peng et al. 2024; Ohigashi et al. 2025). These functional shifts were linked to soil environmental drivers such as soil total phosphorus, nitrate, and C:P ratio. Agricultural activities, particularly monoculture cropping, fertilization, and crop residue removal, elevate soil nitrate and phosphorus while depleting organic carbon, creating conditions that favor fast-growing pathogens (Lekberg et al. 2021) and saprotrophs over symbiotic fungi.

Biotic homogenization was associated with functional guild composition. Biotic homogenization was positively correlated with the richness and abundance of plant pathogens and saprotrophs but negatively correlated with those of ECM fungi. Our bin-level assembly analysis provides a mechanistic understanding of how assembly processes connect homogenization with functional guild shifts. Bins enriched in plant pathogens promoted homogenizing dispersal and reduced heterogeneous selection and dispersal limitation, suggesting that host-dependent pathogens spread more readily in homogeneous agroecosystems dominated by a few crop species (Labouyrie et al. 2023; Yan et al. 2024; Ohigashi et al. 2025). Saprotroph-enriched bins enhanced homogeneous selection and reduced dispersal limitation, consistent with the widely available crop residues that create uniform resource environments (Zhang et al. 2026). Conversely, ECM fungi-enriched bins promoted heterogeneous selection, reflecting their dependence on specific host trees and environments (van der Linde et al. 2018) and exhibit vulnerable responses to land

329 transformations (Epp Schmidt et al. 2017). These results suggested that agroecosystems
330 enriching plant pathogens and saprotrophs would reduce heterogeneous selection and
331 dispersal limitation while enhancing homogeneous selection, thereby promoting biotic
332 homogenization through both pathways. On the other hand, the depletion of ECM fungi in
333 agroecosystems may further reduce heterogeneous selection, contributing to
334 homogenization.

335 Implications for ecosystem multifunctionality

336 The convergence of soil fungal communities toward pathogen- and saprotroph-dominated
337 states in agroecosystems has cascading implications for ecosystem multifunctionality (van
338 der Plas et al. 2016). First, pathogen enrichment increases disease loads for crops and
339 spillover risk to native plants (Faust et al. 2018), potentially reducing agricultural yields and
340 inhibiting native plant re-establishment (Liang et al. 2016; Savary et al. 2019). Second,
341 saprotroph dominance may accelerate organic matter decomposition, reducing soil carbon
342 storage, a critical concern given the role of soils as carbon sinks under global change (Frank
343 et al. 2024). Third, ECM fungi loss disrupts the mycorrhizal networks that facilitate nutrient
344 exchange and plant-plant communication (Liang et al. 2020), hampering the potential for
345 host-plant recolonization when agricultural lands are abandoned, creating a legacy effect
346 that impedes forest restoration potential and soil carbon sequestration (Barber et al. 2026)
347 in this biodiversity hotspot. Fourth, the homogenization reduces the portfolio effect of
348 biodiversity that buffers ecosystem functions against variable environmental changes at
349 regional scales (Wagg et al. 2019).

350 Conclusions

351 Agricultural activities drive homogenization of soil fungal communities in this biodiversity
352 hotspot through promoting homogeneous selection and reducing heterogeneous selection.

This homogenization restructures functional guilds by enriching pathogens and saprotrophs while depleting ectomycorrhizal fungi. Environmental variables were the drivers of soil fungal community homogenization and shifts in functional guilds. Our findings highlight that ecological assembly processes connected homogenization and shifts in fungal functional guilds, and bin-level assembly analysis can reveal guild-specific mechanistic pathways. Managing inputs of soil carbon, phosphorus and nitrogen may mitigate homogenization and preserve beneficial fungal functions in agricultural ecosystems.

In this biodiversity hotspot, agricultural activities restructured functional guilds, enriching plant pathogens and saprotrophs while depleting ectomycorrhizal fungi. Agricultural activities also homogenized soil fungal communities by strengthening homogeneous selection and weakening heterogeneous selection, and this homogenization was driven mainly by similar species composition of shared taxa across sites rather than by shifts in generalist or specialist abundances. The resulting community convergence Soil total phosphorus, nitrate, and C:P ratio were key environmental drivers of biotic homogenization and functional guild shifts. Our findings highlight that ecological assembly processes connected homogenization and shifts in fungal functional guilds, suggesting that agriculture-induced community homogenization may, through pathogen enrichment and the loss of symbiotic fungi, with cascading effects on compromised ecosystem multifunctionality and long-term soil health.

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Author Contributions

Bangguo Yan, Yi Sun and Guangxiong He: Conceptualization. Mengyin Zhang, Liangtao Shi and Guangxiong He: methodology. Bangguo Yan, Yi Sun, Guangxiong He, and Mengyin Zhang: investigation. Lin Li and Yi Sun: Formal analysis. Bangguo Yan: writing – original draft. Bangguo Yan, Yi Sun, Lin Li and Liangtao Shi: writing – review & editing. Haidong Fang and Liangtao Shi: resources. Haidong Fang and Liangtao Shi: supervision. All authors have read and agreed to the published version of the manuscript.

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.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability

The raw data of mycobiome in this study are openly available in NGDC SRA at https://ngdc.cncb.ac.cn/gsa under the GSA accession number CRA007949.

References

Aslani F, Bahram M, Geisen S, et al (2024) Land use intensification homogenizes soil protist communities and alters their diversity across Europe. Soil Biol Biochem 195:109459. https://doi.org/10.1016/j.soilbio.2024.109459

Banerjee S, Dasgupta D, Van Der Heijden MGA (2026) Agricultural intensification, microbial homogenization and loss of rare microbiota. Nat Rev Microbiol. https://doi.org/10.1038/s41579-026-01315-w

Banerjee S, Zhao C, Garland G, et al (2024) Biotic homogenization, lower soil fungal diversity and fewer rare taxa in arable soils across Europe. Nat Commun 15:327. https://doi.org/10.1038/s41467-023-44073-6

Barber RA, Underwood BC, Clarkson JJ, et al (2026) Ectomycorrhizal community composition and extramatrical hyphal proportion predict soil carbon stocks at the landscape scale. Funct Ecol 40:2490–2505. https://doi.org/https://doi.org/10.1111/1365-2435.70369

Bisanz JE (2018) Qiime2R: Importing QIIME2 artifacts and associated data into R sessions

Bittinger K (2020) Usedist: Distance matrix utilities

Bolyen E, Rideout JR, Dillon MR, et al (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat Biotechnol 37:852–857. https://doi.org/10.1038/s41587-019-0209-9

Callahan BJ, McMurdie PJ, Rosen MJ, et al (2016) DADA2: High-resolution sample inference from Illumina amplicon data. Nat Methods 13:581–583. https://doi.org/10.1038/nmeth.3869

Delgado-Baquerizo M, Eldridge DJ, Liu Y-R, et al (2021) Global homogenization of the structure and function in the soil microbiome of urban greenspaces. Sci Adv 7:eabg5809. https://doi.org/10.1126/sciadv.abg5809

Delgado-Baquerizo M, Reich PB, Trivedi C, et al (2020) Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nat Ecol Evol 4:210–220. https://doi.org/10.1038/s41559-019-1084-y

Devictor V, Julliard R, Clavel J, et al (2008) Functional biotic homogenization of bird communities in disturbed landscapes. Glob Ecol Biogeogr 17:252–261. https://doi.org/10.1111/j.1466-8238.2007.00364.x

Dini-Andreote F, Stegen JC, van Elsas JD, Salles JF (2015) Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. Proc Natl Acad Sci 112:. https://doi.org/10.1073/pnas.1414261112

Doane TA, Horwáth WR (2003) Spectrophotometric Determination of Nitrate with a Single Reagent. Anal Lett 36:2713–2722. https://doi.org/10.1081/AL-120024647

Egidi E, Delgado-Baquerizo M, Plett JM, et al (2019) A few Ascomycota taxa dominate soil fungal communities worldwide. Nat Commun 10:2369. https://doi.org/10.1038/s41467-019-10373-z

Epp Schmidt DJ, Pouyat R, Szlavecz K, et al (2017) Urbanization erodes ectomycorrhizal fungal diversity and may cause microbial communities to converge. Nat Ecol Evol 1:0123. https://doi.org/10.1038/s41559-017-0123

Faust CL, McCallum HI, Bloomfield LSP, et al (2018) Pathogen spillover during land conversion. Ecol Lett 21:471–483. https://doi.org/10.1111/ele.12904

Finn DR, Yu J, Ilhan ZE, et al (2020) MicroNiche: an R package for assessing microbial niche breadth and overlap from amplicon sequencing data. FEMS Microbiol Ecol 96:fiaa131. https://doi.org/10.1093/femsec/fiaa131

Frank S, Lessa Derci Augustynczik A, Havlík P, et al (2024) Enhanced agricultural carbon sinks provide benefits for farmers and the climate. Nat Food 5:742–753. https://doi.org/10.1038/s43016-024-01039-1

Gossner MM, Lewinsohn TM, Kahl T, et al (2016) Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540:266–269. https://doi.org/10.1038/nature20575

Hijmans RJ (2026) Geosphere: Spherical trigonometry

Hu R, Zheng B, Liu Y, et al (2024) Deep tillage enhances the spatial homogenization of bacterial communities by reducing deep soil compaction. Soil Tillage Res 239:106062. https://doi.org/https://doi.org/10.1016/j.still.2024.106062

Huang J, Huang J, Liu C, et al (2016) Diversity hotspots and conservation gaps for the Chinese endemic seed flora. Biol Conserv 198:104–112. https://doi.org/10.1016/j.biocon.2016.04.007

Kassambara A (2025) Rstatix: Pipe-friendly framework for basic statistical tests

Kõljalg U, Larsson K-H, Abarenkov K, et al (2005) UNITE: a database providing web-based methods for the molecular identification of ectomycorrhizal fungi. New Phytol 166:1063–1068. https://doi.org/10.1111/j.1469-8137.2005.01376.x

Labouyrie M, Ballabio C, Romero F, et al (2023) Patterns in soil microbial diversity across Europe. Nat Commun 14:3311. https://doi.org/10.1038/s41467-023-37937-4

Lekberg Y, Arnillas CA, Borer ET, et al (2021) Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. Nat Commun 12:3484. https://doi.org/10.1038/s41467-021-23605-y

Liang M, Johnson D, Burslem DFRP, et al (2020) Soil fungal networks maintain local dominance of ectomycorrhizal trees. Nat Commun 11:2636. https://doi.org/10.1038/s41467-020-16507-y

Liang M, Liu X, Gilbert GS, et al (2016) Adult trees cause density-dependent mortality in conspecific seedlings by regulating the frequency of pathogenic soil fungi. Ecol Lett 19:1448–1456. https://doi.org/10.1111/ele.12694

Livne-Luzon S, Hibner A, Herol L, et al (2026) Richness, community structure and distance decay of soil fungi along a sharp aridity gradient in monodominant pine forests. Plant Soil 522:949–967. https://doi.org/10.1007/s11104-026-08556-x

McMurdie PJ, Holmes S (2013) Phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. PLoS ONE 8:e61217

Nguyen NH, Song Z, Bates ST, et al (2016) FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol 20:241–248. https://doi.org/https://doi.org/10.1016/j.funeco.2015.06.006

475 Ning D, Yuan M, Wu L, et al (2020) A quantitative framework reveals ecological drivers of
476 grassland microbial community assembly in response to warming. Nat Commun
477 11:4717. https://doi.org/10.1038/s41467-020-18560-z

478 Nottingham AT, Turner BL, Stott AW, Tanner EVJ (2015) Nitrogen and phosphorus
479 constrain labile and stable carbon turnover in lowland tropical forest soils. Soil Biol
480 Biochem 80:26–33. https://doi.org/https://doi.org/10.1016/j.soilbio.2014.09.012

481 Ohigashi T, Madegwa YM, Karuku GN, et al (2025) Agricultural land use induces broader
482 homogenization of soil microbial functional composition than taxonomic
483 composition in sub-Saharan Africa. Soil Biol Biochem 209:109895.
484 https://doi.org/10.1016/j.soilbio.2025.109895

485 Oksanen J, Blanchet FG, Friendly M, et al (2020) Vegan: Community Ecology Package

486 Paradis E, Schliep K (2019) Ape 5.0: an environment for modern phylogenetics and
487 evolutionary analyses in R. Bioinformatics 35:526–528

488 Peng Z, Qian X, Liu Y, et al (2024) Land conversion to agriculture induces taxonomic
489 homogenization of soil microbial communities globally. Nat Commun 15:3624.
490 https://doi.org/10.1038/s41467-024-47348-8

491 Price MN, Dehal PS, Arkin AP (2010) FastTree 2 – Approximately Maximum-Likelihood
492 Trees for Large Alignments. PLoS ONE 5:e9490.
493 https://doi.org/10.1371/journal.pone.0009490

494 R Core Team (2025) R: a language and environment for statistical computing. R Foundation
495 for Statistical Computing, Vienna, Austria

496 Ribero MN, Schiaffino MR, Filloy J (2025) Grassland afforestation drives biotic
497 homogenisation of soil microbial communities at a regional scale. Mol Ecol
498 34:e17617. https://doi.org/https://doi.org/10.1111/mec.17617

499 Rodrigues JLM, Pellizari VH, Mueller R, et al (2013) Conversion of the Amazon rainforest to
500 agriculture results in biotic homogenization of soil bacterial communities. Proc Natl
501 Acad Sci 110:988–993. https://doi.org/10.1073/pnas.1220608110

502 Savary S, Willocquet L, Pethybridge SJ, et al (2019) The global burden of pathogens and
503 pests on major food crops. Nat Ecol Evol 3:430–439.
504 https://doi.org/10.1038/s41559-018-0793-y

505 Stegen JC, Lin X, Fredrickson JK, et al (2013) Quantifying community assembly processes
506 and identifying features that impose them. ISME J 7:2069–2079.
507 https://doi.org/10.1038/ismej.2013.93

508 Stuart-Smith RD, Mellin C, Bates AE, Edgar GJ (2021) Habitat loss and range shifts
509 contribute to ecological generalization among reef fishes. Nat Ecol Evol 5:656–662.
510 https://doi.org/10.1038/s41559-020-01342-7

Sun X, Robinson JM, Delgado-Baquerizo M, et al (2025) Unforeseen high continental-scale soil microbiome homogenization in urban greenspaces. Nat Cities 2:759–769. https://doi.org/10.1038/s44284-025-00294-y

Tang Z, Wang Z, Zheng C, Fang J (2006) Biodiversity in China's mountains. Front Ecol Environ 4:347–352. https://doi.org/10.1890/1540-9295(2006)004%5B0347:BICM%5D2.0.CO;2

Vahter T, Astover A, Davison J, et al (2025) Agricultural disturbance reduces arbuscular mycorrhizal fungal diversity and biomass by excluding specialist species. New Phytol 248:2079–2091. https://doi.org/https://doi.org/10.1111/nph.70548

van der Linde S, Suz LM, Orme CDL, et al (2018) Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558:243–248. https://doi.org/10.1038/s41586-018-0189-9

van der Plas F, Manning P, Soliveres S, et al (2016) Biotic homogenization can decrease landscape-scale forest multifunctionality. Proc Natl Acad Sci 113:3557–3562. https://doi.org/10.1073/pnas.1517903113

Wagg C, Schlaeppi K, Banerjee S, et al (2019) Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. Nat Commun 10:4841. https://doi.org/10.1038/s41467-019-12798-y

Wang H, Liu S, Li H, et al (2022) Large-scale homogenization of soil bacterial communities in response to agricultural practices in paddy fields, China. Soil Biol Biochem 164:108490. https://doi.org/https://doi.org/10.1016/j.soilbio.2021.108490

Weatherburn MW (1967) Phenol-hypochlorite reaction for determination of ammonia. Anal Chem 39:971–974. https://doi.org/10.1021/ac60252a045

West JR, Lauer JG, Whitman T (2023) Tillage homogenizes soil bacterial communities in microaggregate fractions by facilitating dispersal. Soil Biol Biochem 186:109181. https://doi.org/10.1016/j.soilbio.2023.109181

Wickham H (2016) Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York

Yan B, Sun Y, He G, et al (2024) Temperature sensitivity of soil-borne fungal phytopathogens depends on niche breadth and land use types. Fungal Ecol 68:101329. https://doi.org/10.1016/j.funeco.2023.101329

Yang Q, Weigelt P, Fristoe TS, et al (2021) The global loss of floristic uniqueness. Nat Commun 12:7290. https://doi.org/10.1038/s41467-021-27603-y

Zhang G, Zhang J, Yu R-P, et al (2026) Organic amendments induce crop-specific soil biotic homogenization associated with SOC sequestration: Evidence from a 35-year intercropping experiment. Soil Tillage Res 263:107255. https://doi.org/https://doi.org/10.1016/j.still.2026.107255

Figure captions

Fig. 1 Composition and diversity of soil fungal communities across multiple ecosystems. Fungal community composition differed among agroecosystems, grasslands, and forests at both the phylum (a) and functional guild (b) levels. Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity at the ASV level revealed clear separation of communities across ecosystem types (PERMANOVA: $p = 0.001$) (c). Phylotype richness (d),

β-diversity (e), and homogenization degree (calculated as 1/distance to centroid) (f) were compared across the three ecosystem types.

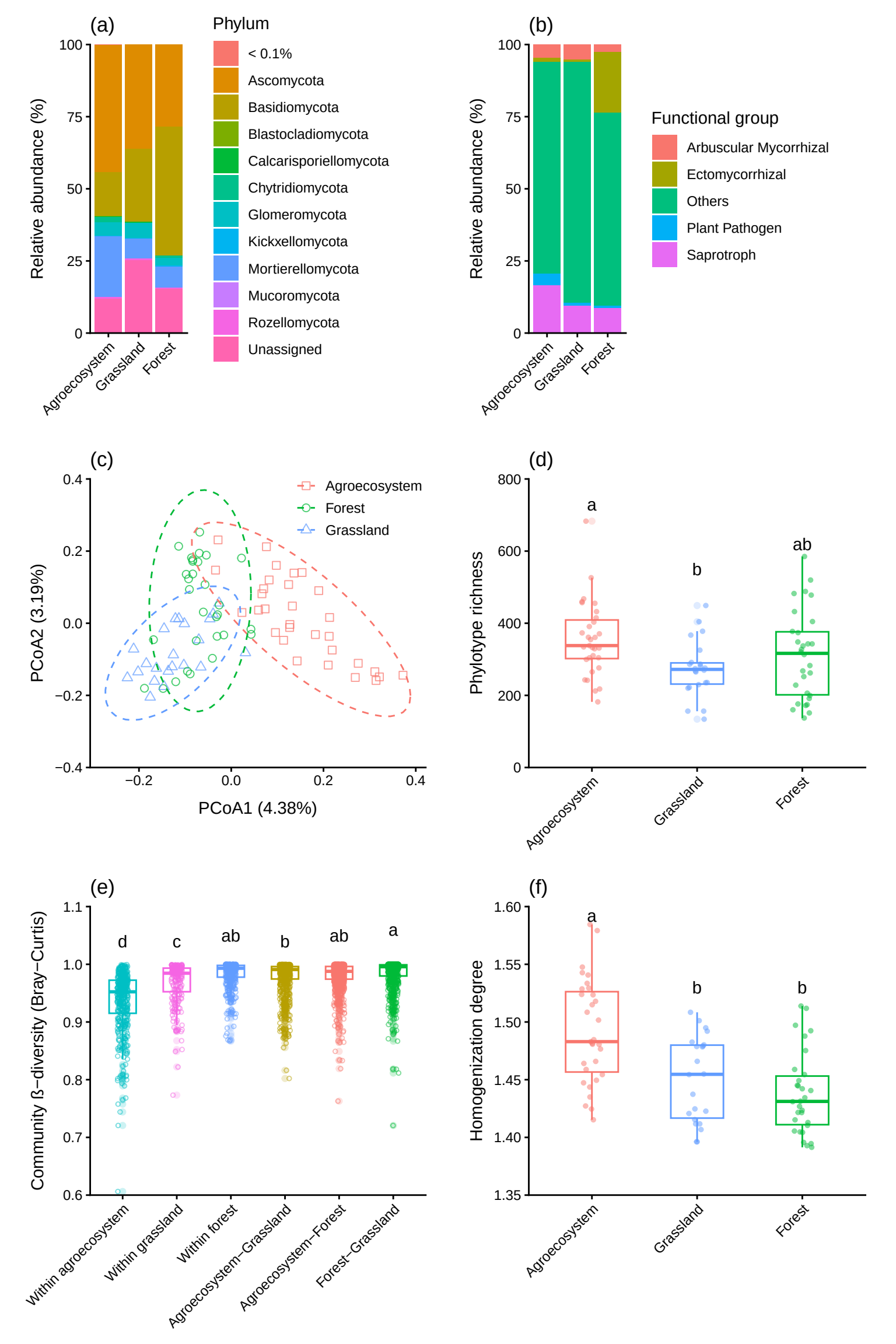
Fig. 2 Correlations between soil fungal community dissimilarity (Bray–Curtis) and environmental distance (a) and geographic distance (b).

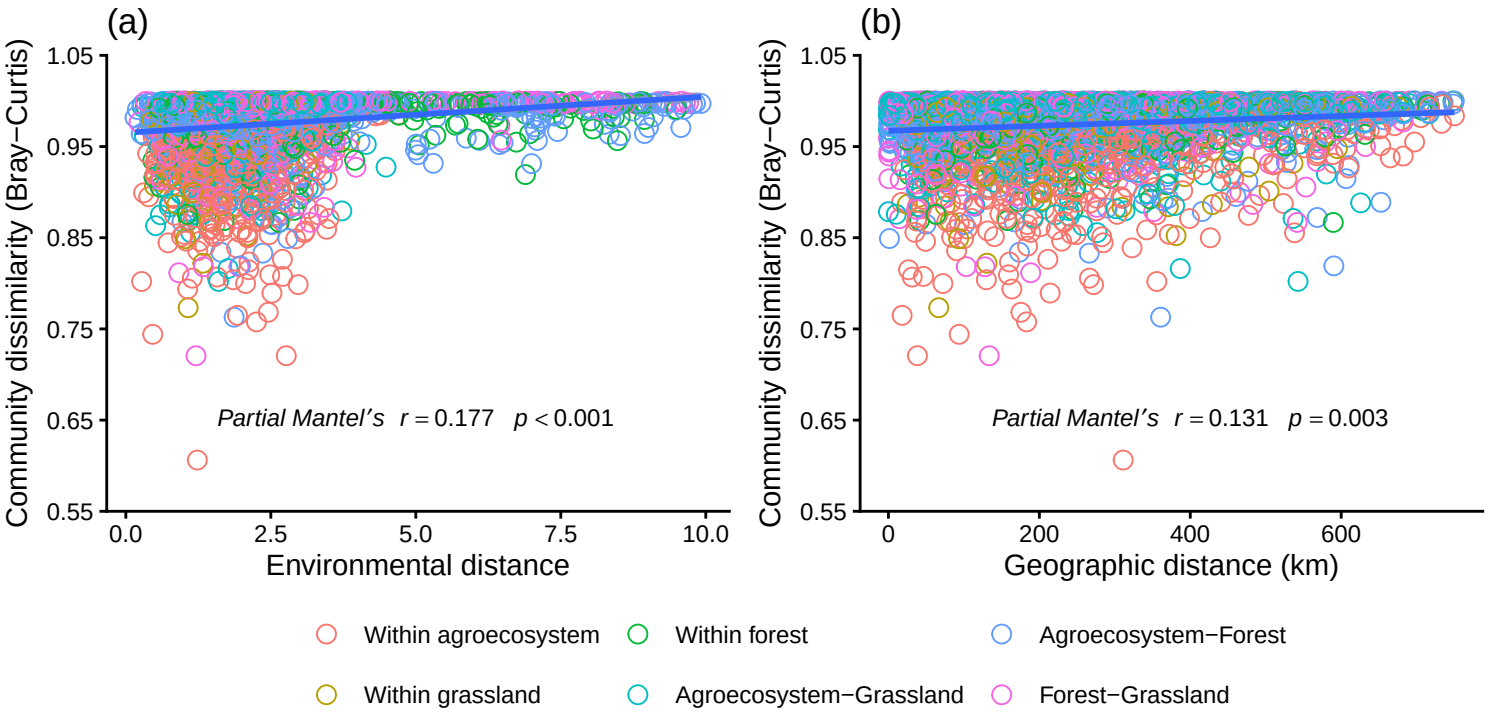
Fig. 3 Relative abundance of generalists (a) and specialists (b) in agroecosystems, grasslands, and forests. Homogenization degree was positively correlated with the relative abundance of generalists within each ecosystem type (c) and negatively correlated with the relative abundance of specialists in grasslands and forests (d).

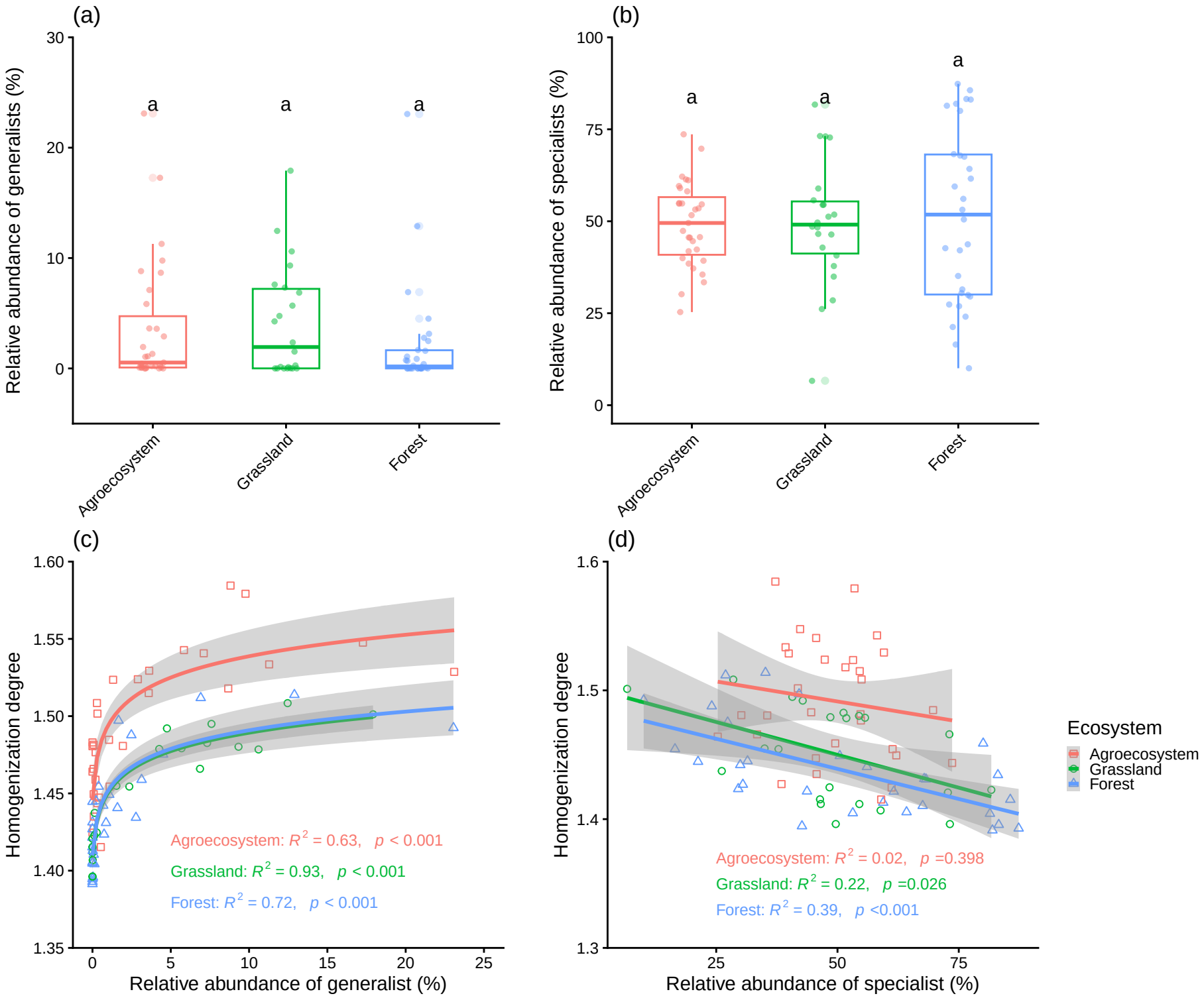
Fig. 4 Variation in soil fungal community assembly processes across agroecosystems, grasslands, and forests.

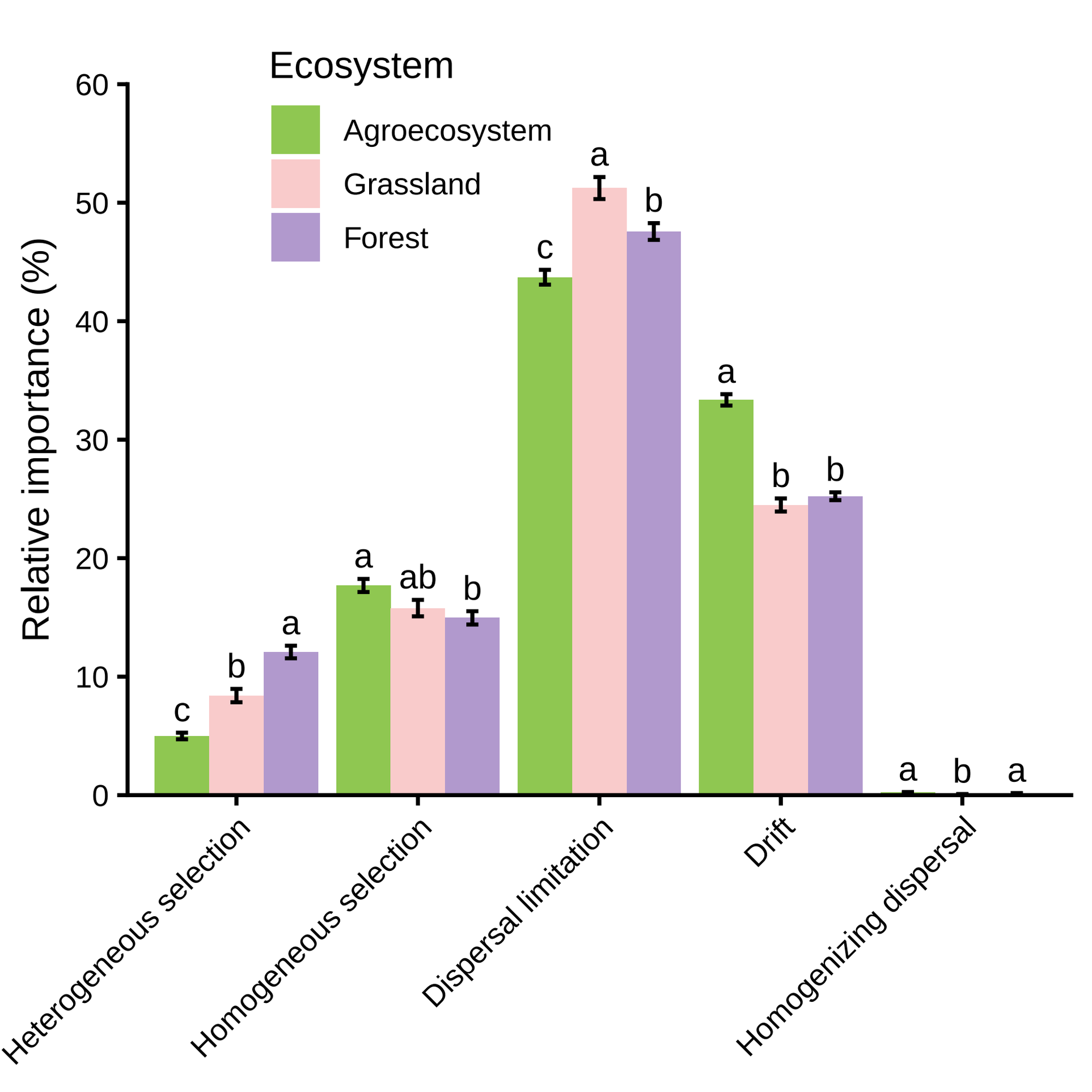
Fig. 5 Correlations among homogenization degree, the relative abundance and richness of functional guilds, and environmental variables (soil pH, TC, TN, TP, ammonium, nitrate, C:N ratio, N:P ratio, and C:P ratio).

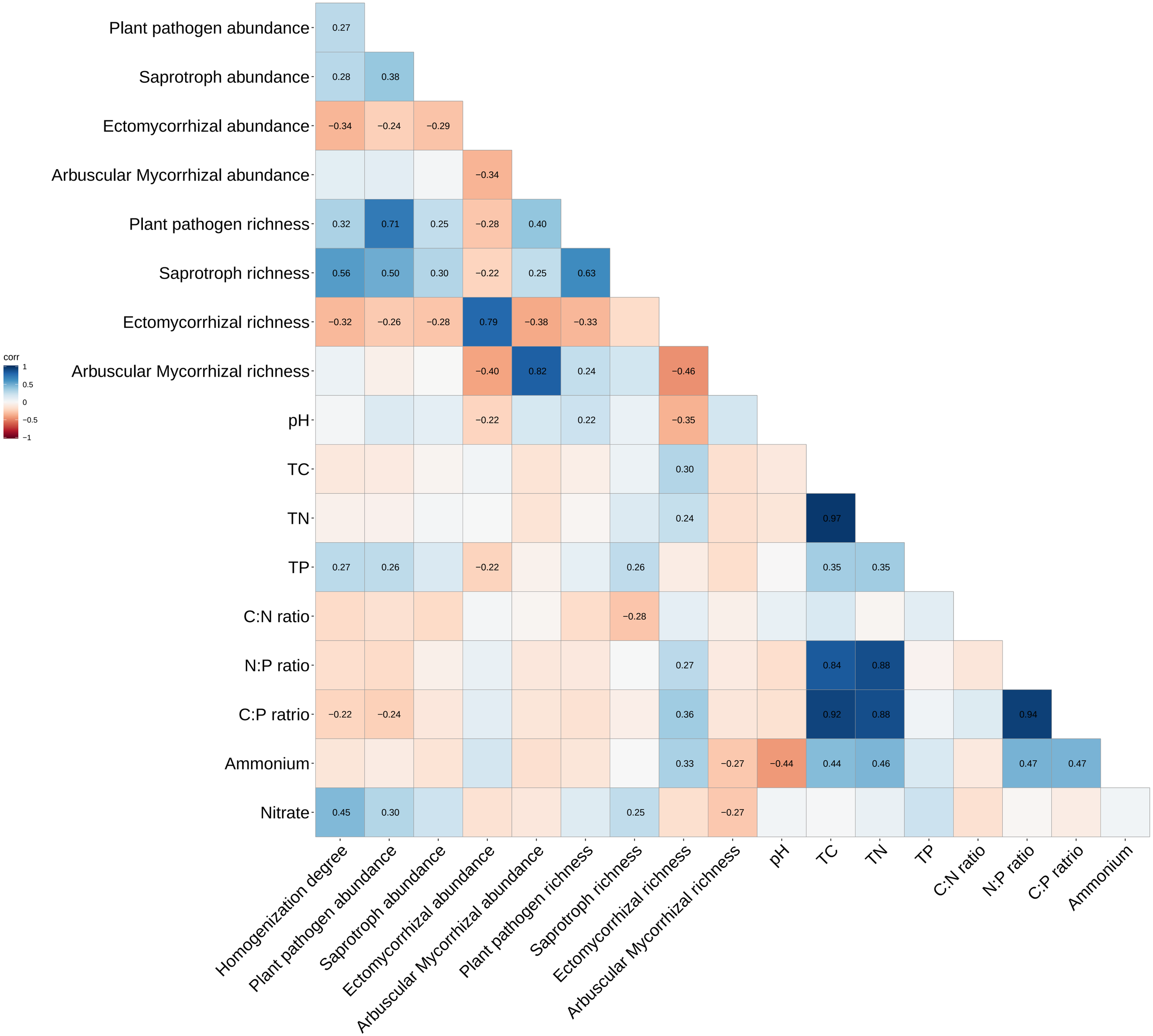
Fig. 6 Associations between the contribution of each phylogenetic bin (derived from iCAMP analysis) to community assembly processes (homogeneous selection, heterogeneous selection, homogenizing dispersal, dispersal limitation, and drift) and the proportion of functional guilds within each bin. Only statistically significant relationships are displayed with fitted regression lines.


(a)
Phylum
< 0.1%
Ascomycota
Basidiomycota
Blastocladiomycota
Calcarisporiellomycota
Chytridiomycota
Glomeromycota
Kickxellomycota
Mortierellomycota
Mucoromycota
Rozellomycota
Unassigned
Relative abundance (%)
100
75
50
25
0
Agroecosystem
Grassland
Forest
(b)
Functional group
Arbuscular Mycorrhizal
Ectomycorrhizal
Others
Plant Pathogen
Saprotroph
Relative abundance (%)
100
75
50
25
0
Agroecosystem
Grassland
Forest
(c)
Agroecosystem
Forest
Grassland
PCoA2 (3.19%)
0.4
0.2
0.0
−0.2
−0.4
−0.2
0.0
0.2
0.4
PCoA1 (4.38%)
(d)
Phylotype richness
800
600
400
200
0
a
b
ab
Agroecosystem
Grassland
Forest
(e)
Community ß−diversity (Bray−Curtis)
1.1
1.0
0.9
0.8
0.7
0.6
d
c
ab
b
ab
a
Within agroecosystem
Within grassland
Within forest
Agroecosystem−Grassland
Agroecosystem−Forest
Forest−Grassland
(f)
Homogenization degree
1.60
1.55
1.50
1.45
1.40
1.35
a
b
b
Agroecosystem
Grassland
Forest


(a)
(b)
Community dissimilarity (Bray−Curtis)
1.05
0.95
0.85
0.75
0.65
0.55
0.0
2.5
5.0
7.5
10.0
Environmental distance
Partial Mantel's r = 0.177 p < 0.001
0
200
400
600
Geographic distance (km)
Partial Mantel's r = 0.131 p = 0.003
Within agroecosystem
Within forest
Agroecosystem−Forest
Within grassland
Agroecosystem−Grassland
Forest−Grassland


(a)
Relative abundance of generalists (%)
30
20
10
0
a
a
a
Agroecosystem
Grassland
Forest
(b)
Relative abundance of specialists (%)
100
75
50
25
0
a
a
a
Agroecosystem
Grassland
Forest
(c)
Homogenization degree
1.60
1.55
1.50
1.45
1.40
1.35
0
5
10
15
20
25
Relative abundance of generalist (%)
Agroecosystem: R^2 = 0.63, p < 0.001
Grassland: R^2 = 0.93, p < 0.001
Forest: R^2 = 0.72, p < 0.001
(d)
Homogenization degree
1.6
1.5
1.4
1.3
25
50
75
Relative abundance of specialist (%)
Agroecosystem: R^2 = 0.02, p =0.398
Grassland: R^2 = 0.22, p =0.026
Forest: R^2 = 0.39, p <0.001
Ecosystem
Agroecosystem
Grassland
Forest


Ecosystem
Agroecosystem
Grassland
Forest
Relative importance (%)
60
50
40
30
20
10
0
c
b
a
a
ab
b
c
a
b
a
b
b
a
b
a
Heterogeneous selection
Homogeneous selection
Dispersal limitation
Drift
Homogenizing dispersal


corr
1
0.5
0
−0.5
−1
Plant pathogen abundance
Saprotroph abundance
Ectomycorrhizal abundance
Arbuscular Mycorrhizal abundance
Plant pathogen richness
Saprotroph richness
Ectomycorrhizal richness
Arbuscular Mycorrhizal richness
pH
TC
TN
TP
C:N ratio
N:P ratio
C:P ratrio
Ammonium
Nitrate
0.27
0.28 0.38
−0.34 −0.24 −0.29
−0.34
0.32 0.71 0.25 −0.28 0.40
0.56 0.50 0.30 −0.22 0.25 0.63
−0.32 −0.26 −0.28 0.79 −0.38 −0.33
−0.40 0.82 0.24 −0.46
−0.22 0.22 −0.35
0.30
0.24 0.97
0.27 0.26 −0.22 0.26 0.35 0.35
−0.28
0.27 0.84 0.88
−0.22 −0.24 0.36 0.92 0.88 0.94
0.33 −0.27 −0.44 0.44 0.46 0.47 0.47
0.45 0.30 0.25 −0.27
Homogenization degree
Plant pathogen abundance
Saprotroph abundance
Ectomycorrhizal abundance
Arbuscular Mycorrhizal abundance
Plant pathogen richness
Saprotroph richness
Ectomycorrhizal richness
Arbuscular Mycorrhizal richness
pH
TC
TN
TP
C:N ratio
N:P ratio
C:P ratrio
Ammonium

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
(q)
(r)
(s)
(t)
(u)
(v)
(w)
(x)
(y)

Relative importance in heterogeneous selection(%)
Relative importance in homogeneous selection (%)
Relative importance in drift (and others) (%)
Relative importance in dispersal limitation (%)
Relative importance in homogenizing dispersal (%)

Proportion of plant pathogens (%)
Proportion of ectomycorrhizal fungi (%)
Proportion of arbuscular mycorrhizal fungi (%)
Proportion of saprotrops (%)
Proportion of other fungi (%)

r=−0.07 *p*=0.002
r=0.10 *p*<0.001
r=0.07 *p*=0.001
r=0.14 *p*<0.001
r=−0.18 *p*<0.001
r=0.09 *p*<0.001
r=−0.11 *p*<0.001
r=−0.06 *p*=0.012
r=0.19 *p*<0.001
r=−0.06 *p*=0.011
r=−0.07 *p*=0.001
r=0.09 *p*<0.001

Agroecosystem
Forest
Grassland vs Agroecosystem
Agroecosystem vs Forest
Grassland
Grassland vs Forest

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