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Short Communication

Fungal diversity drives soil health and agricultural sustainability in black soils

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Microeukaryotes and soil animals (i.e., eukaryotes) are abundant and diverse. They form complex biotic association networks and perform critical ecological roles across ecosystems. Soil fungal diversity is strongly and positively correlated with tree growth rates and biomass in European forests [1], while increased arbuscular mycorrhizal fungi diversity has been reported to enhance plant diversity, nutrient capture capacity, and productivity in grasslands [2]. Additionally, soil carbon (C) emissions increased by 25% following the removal of the pill bug, which feeds on soil fungi [3], indicating that the simplification of biotic network structures may impair soil C sequestration. According to the Food and Agriculture Organization of the United Nations, soil health is defined as “the ability of the soil to sustain the productivity, diversity, and environmental services of terrestrial ecosystems” [4]. However, the relative contributions of soil eukaryotic diversity and network structure to farmland soil health—including soil fertility, C sequestration, crop productivity, productivity stability, pathogen control, and soil biodiversity—remain largely unknown.

Sustainable agriculture is a core component of the global Sustainable Development Goals (SDGs) promoted by the United Nations. Its objectives extend beyond achieving high and stable crop productivity to include enhancing farmland soil biodiversity, maintaining soil fertility, and promoting C sequestration—all of which reflect the multifunctionality of healthy soils [4]. Achieving these multiple objectives in sustainable agricultural management has become increasingly critical under the pressures of global climate change. Here, we argue that soil eukaryotic diversity and its network structure represent a key link in meeting these multi-objectives in sustainable agriculture.

Northeast China is a major corn (*Zea mays*) cultivation region, accounting for more than one-third of the national cultivation area and producing 42% of China’s total corn yield [5]. However, owing to environmental changes and anthropogenic pressures, the risk of black soil degradation is increasing, thereby hindering sustainable production [6]. In this study, we conducted a comprehensive survey of soil eukaryotic diversity across 260 cornfield plots spanning the entire black soil region of Northeast China (Fig. 1, Method S1 online). Using PacBio metabarcoding combined with an updated bioinformatic pipeline (Methods S2–S4 online), we achieved a detailed classification of eukaryotic diversity in both taxonomic and functional guild dimensions (Fig. S1 online). The eukaryotic community was classified into four major groups: fungi, protists, algae, and metazoa (Table S1, Fig. S2 online). In addition, we constructed soil eukaryotic biotic association networks and calculated

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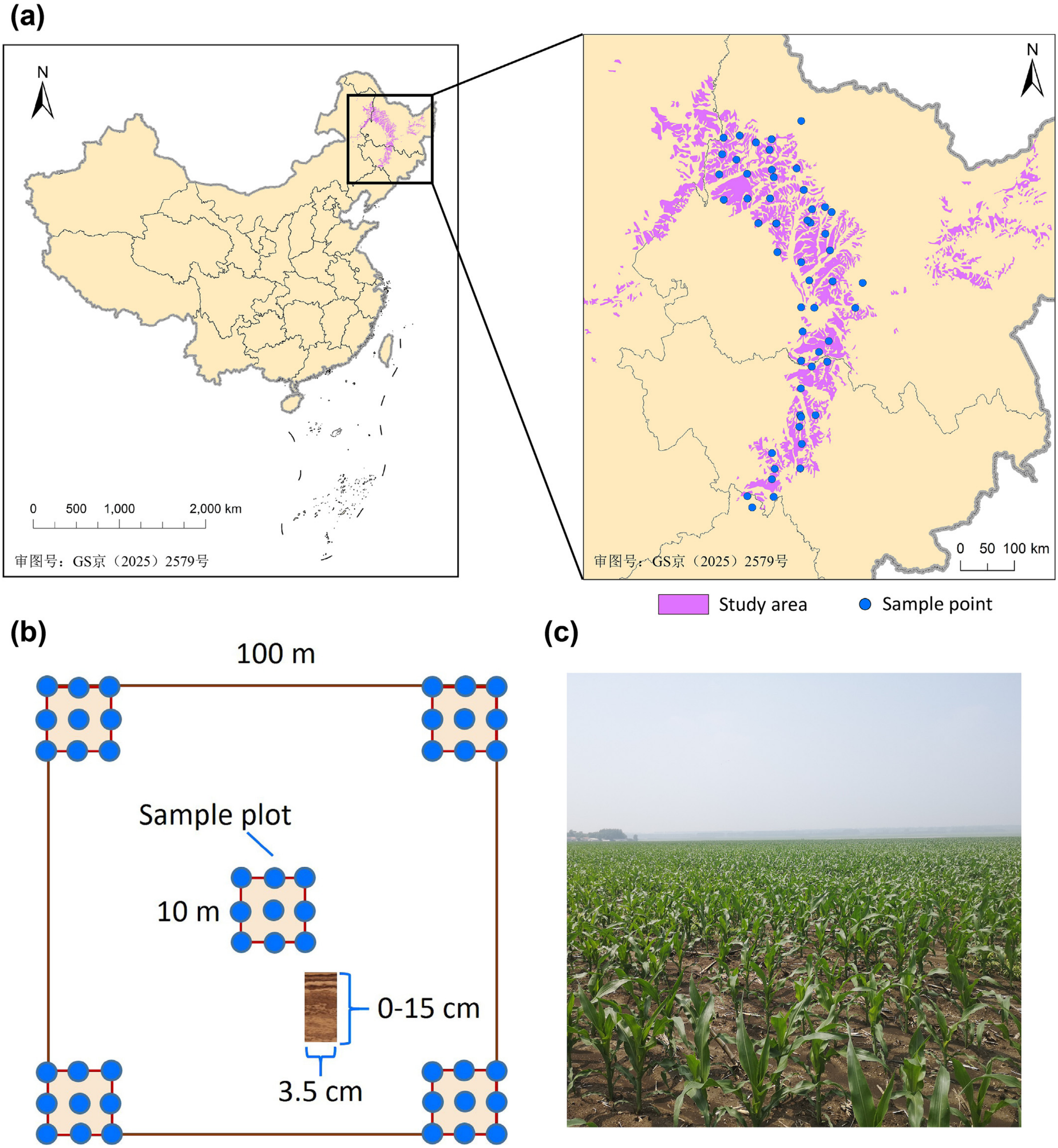

Fig. 1. Sample map and soil sampling protocols in the black soil region of Northeast China. (a) Distribution of 52 sample sites (100 m × 100 m) across the black soil region of Northeast China. (b) Soil sampling protocol at each site: five plots (10 m × 10 m) were established at the four corners and the center. Within each plot, nine soil cores (3.5 cm diameter, 0–15 cm depth) were collected and combined to form a composite sample. In total, 260 plots were surveyed. (c) Example of a sample site in Changchun, Jilin Province (latitude: 44.1857, longitude: 125.6013).

a suite of network parameters (Method S5 online). After accounting for environmental, geographic, and topographic factors, we evaluated the relative contributions of soil eukaryotic diversity and network structure to six key soil functions: soil organic C (SOC) content (soil fertility), SOC persistence (climate resilience), crop productivity, productivity stability, pathogen control, and soil biodiversity. These soil functions collectively represent essential components of soil health and agricultural sustainability [4].

SOC content was measured using an automatic elemental analyzer (Elemental Analyzer System Vario MACRO cube, Germany), and SOC persistence was expressed as mineral-associated organic C (MAOC) / (MAOC + particulate organic C, POC). Crop productivity was represented by the mean annual Normalized Difference Vegetation Index (NDVI) from 2002 to 2022, while productivity stability was calculated as the ratio of mean annual NDVI to its standard deviation. Annual NDVI was derived for the period from May 1st to October 1st, corresponding to the regional growing season. Pathogen control was quantified based on the relative abundances of plant pathogenic fungi (PPF), plant pathogenic bacteria, plant pathogenic protists, and plant-parasitic nematodes. Soil biodiversity was represented by the soil multidiversity index, calculated as the standardized average of the diversity of soil bacteria, archaea, and eukaryotes. Detailed calculation procedures are provided (Method S6 online).

A total of 59 diversity indices were calculated, including the richness, phylogenetic diversity, Chao1, Shannon, and evenness of soil eukaryotes, fungi, and saprotrophic fungi, as well as the richness of protists, algae, metazoa, and various taxonomic and functional groups within fungi, protists, algae, and metazoa (Fig. S1 online). In parallel, 16 network topological parameters were computed for statistical analyses, including average degree, modularity, average path length, diameter, positive cohesion, |negative cohesion|, within-kingdom edges, cross-kingdom edges, and multiple network motifs. After accounting for collinearity among candidate predictors, 43 soil eukaryotic biodiversity indices and 14 network parameters were retained for subsequent statistical analyses (Fig. S3 online).

In addition, to strengthen the robustness of our findings regarding the benefits of soil eukaryotic diversity for black soil health, we fully incorporated environmental, geographic, and topographic factors (elevation and slope) into our statistical models. Eighteen soil properties were measured, and ten climatic variables were compiled (Method S7 online). Geographic variables included the first 24 principal coordinates of neighbor matrix (PCNM) vectors showing positive spatial autocorrelation (Moran's I > 0; Fig. S4 online). In this study, we mainly employed three statistical approaches: Ordinary Least Squares (OLS) multiple regression models, Random Forest (RF) models, and piecewise structural equation modelling (SEM) (Method S8 online).

Among all soil eukaryotic biodiversity indices and network topological parameters, Rozellomycota richness (a basal fungal clade) emerged as the strongest predictor of both SOC content (Estimate = 0.205, $R^2_{\text{adj.partial}}$ = 0.362) and crop productivity (Estimate = 0.283, $R^2_{\text{adj.partial}}$ = 0.162). Meanwhile, the fungal Shannon and Chao1 indices were the strongest predictors of SOC persistence (Estimate = 0.281, $R^2_{\text{adj.partial}}$ = 0.275) and soil biodiversity (Estimate = 0.501, $R^2_{\text{adj.partial}}$ = 0.562), respectively (Figs. S5–S7; Table S2 online). To the best of our knowledge, this study is the first to report a positive linkage between Rozellomycota richness and both SOC content and crop productivity. Members of the Rozellomycota are fungal parasites of various eukaryotic hosts, including water molds, algae, amoebae, and metazoa [7]. They have been reported to efficiently transfer carbon and energy from their hosts (primary consumers) to grazing zooplankton and other higher-level consumers [8]. Therefore, increasing Rozellomycota richness in black soil may enhance overall eukaryotic richness, potentially by suppressing dominant taxa. This increase in eukaryotic diversity can accelerate the flow of matter and energy within the soil food web, thereby contributing to higher SOC content and increased crop productivity [9]. Specifically, a microbial diversity–gradient microcosm experiment demonstrated that soil microbial biodiversity—particularly eukaryotic Shannon diversity—enhances crop productivity and agroecosystem functioning, including decomposition and nutrient retention [9]. We propose that overall eukaryotic richness contributes to SOC accumulation and crop productivity mainly by: (i) accelerating litter and residue decomposition through complex food webs and energy channels, thereby promoting SOC formation; and (ii) enhancing nutrient (e.g., N and P) cycling, which improves plant nutrient uptake and increases yields. This hypothesis is supported by our SEM results (Fig. 2a). Furthermore, a recent meta-analysis reported a significantly positive effect of soil fungal diversity on SOC accumulation during natural restoration [10], and a review suggested that fungal diversity contributes to carbon stabilization through soil aggregation [11]. Across the Loess Plateau, a strong positive linear relationship was observed between soil fungal diversity and fungal necromass (R^2 = 0.55) [12]. Fungal necromass has also been identified as a primary source of mineral-associated organic C (MAOC) in black soil farmlands [13]. Together, these findings suggest that increasing fungal diversity in black soils may enhance SOC persistence by promoting soil aggregation and the stabilization of fungal necromass. Furthermore, fungal diversity was found to have the strongest positive effect on overall soil biodiversity, encompassing bacteria, archaea, and diverse eukaryotes (Figs. S5–S7 online). This highlights the critical role of fungal hyphal networks—often referred to as "underground highways"—in supporting the stability and maintenance of multi-kingdom communities in black soils, consistent with observations from other ecosystems [14]. In the future, black soil health could be enhanced through field management practices that promote fungal diversity, such as no-tillage, straw return, and the establishment of ecological corridors.

Nonetheless, not all diversity metrics contribute positively to soil functions. Among the soil eukaryotic biodiversity indices and network topological parameters, PPF richness emerged as the strongest negative predictor of both productivity stability (Estimate = –0.165, $R^2_{\text{adj.partial}}$ = 0.079) and pathogen control (Estimate = –0.256, $R^2_{\text{adj.partial}}$ = 0.350), exerting a significant negative influence on both functions (Figs. S5–S7; Table S2 online). At the global scale, soil PPF richness has also been reported to correlate negatively with productivity stability in grassland ecosystems [15]. To our knowledge, this study is the first to identify PPF richness as a sensitive biological indicator capable of predicting both the stability of agricultural productivity and the soil's suppressive capacity against a broad range of plant pathogens—including pathogenic fungi, bacteria, protists, and plant-parasitic nematodes—in black soils. A genus-level list of the identified PPF was compiled, with *Fusarium* and *Epicoccum* emerging as the dominant genera in this study (Table S3 online). These findings provide valuable insights for regional-scale assessments of soil health and agricultural sustainability, while also highlighting the trade-offs and complexity inherent in the relationships between biodiversity indices and soil functions [4].

Beyond the effects of soil eukaryotes, environmental, geographic, and topographic factors can also strongly influence soil functions. When these potential drivers were incorporated into the models (Fig. S8 online), cation exchange capacity (CEC) emerged as the strongest predictor of SOC content (Estimate = 0.357, $R^2_{\text{adj.partial}}$ = 0.642), while SOC itself was the strongest predictor of crop productivity (Estimate = 0.414, $R^2_{\text{adj.partial}}$ = 0.198). PCNM2 was the primary driver of SOC persistence (Estimate = 0.227, $R^2_{\text{adj.partial}}$ = 0.546). Correlation analyses further showed that BIO1 (mean annual temperature, MAT) was the environmental variable most strongly associated with PCNM2 (Pearson r = –0.84, Fig. S9 online), whereas fungal Shannon diversity was the biotic variable most strongly correlated with PCNM2 (Pearson r = 0.58, Fig. S10 online). Furthermore, univariate analyses indicated that SOC persistence declined significantly with increasing mean annual temperature ($R^2_{\text{adj.partial}}$ = 0.414) but increased markedly with higher fungal Shannon diversity (Fig. S11 online). Based on R^2 values, the integrated RF models outperformed OLS multiple regression models only in predicting SOC persistence and productivity stability (Table S4 online), with BIO12 (mean annual precipitation, MAP) emerging as the strongest predictor of productivity stability rather than PCNM2 (Fig. S12 online). Productivity stability increased strongly with MAP ($R^2_{\text{adj.partial}}$ = 0.307, Fig. S13 online). Notably, despite strong environmental constraints, fungal diversity indices consistently

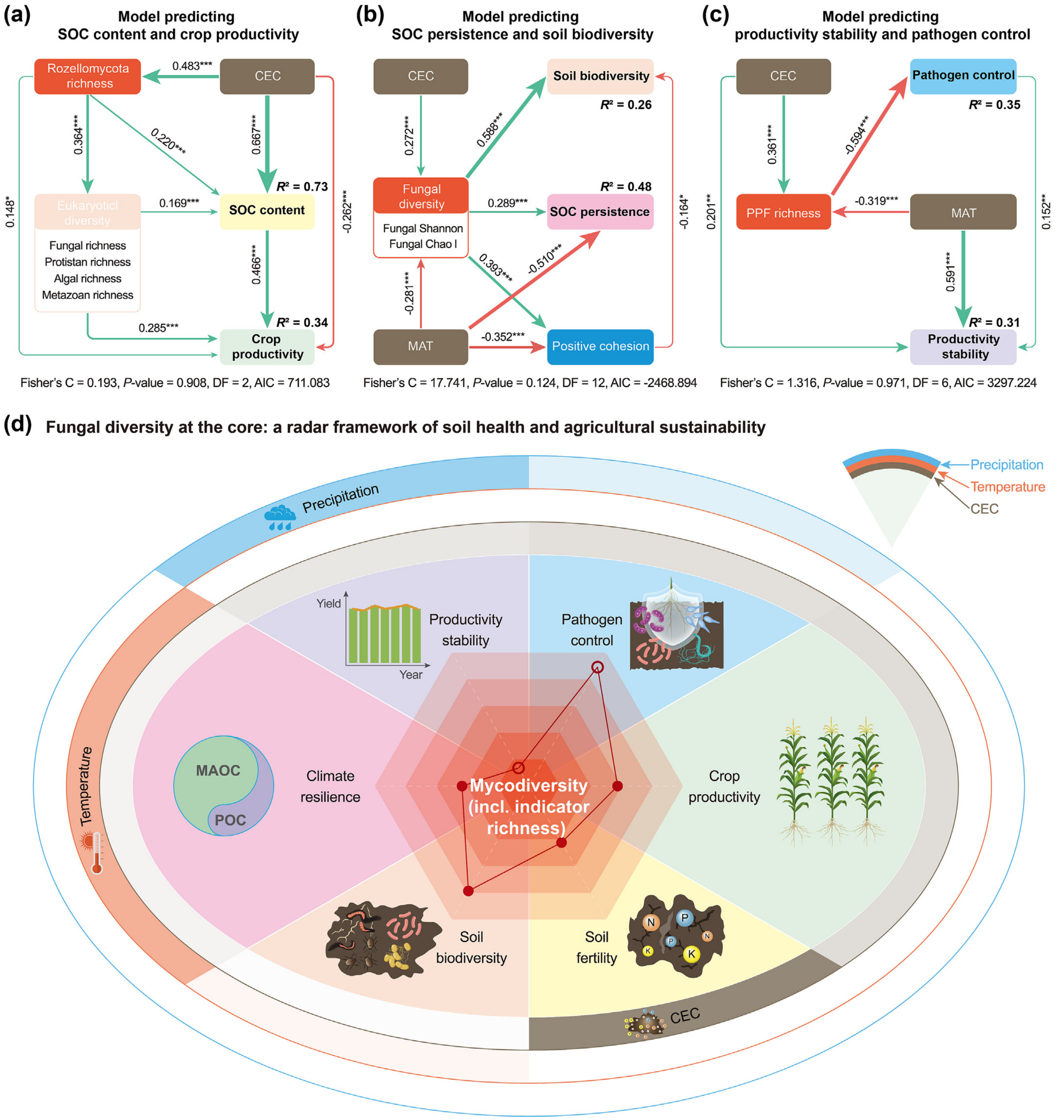

Fig. 2. Piecewise structural equation models illustrating the primary effects of fungal diversity on soil functions under the constraints of major climatic and soil predictors. (a) Model predicting SOC content and crop productivity. (b) Model predicting SOC persistence and soil biodiversity. (c) Model predicting productivity stability and pathogen control. Only significant paths are shown (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$), with standardized path coefficients (SPC) indicated alongside each path. Positive and negative paths are represented in light green and red, respectively, and line widths correspond to SPC values. $n = 260$. (d) Fungal diversity at the core: radar framework of soil health and agricultural sustainability. Fungal diversity is represented by the fungal Shannon and Chao1 indices, Rozellomycota richness (positive indicator), and PPF richness (negative indicator). SOC content and SOC persistence represent soil fertility and climate resilience, respectively. In the radar chart, each point's position reflects the magnitude of the total SPC, with solid and hollow points indicating positive and negative effects, respectively. Major environmental factors influencing these multiple soil health and agricultural sustainability objectives are shown on the outer ring, with varying levels of color transparency.

retained strong predictive power for key soil functions in the best integrated models (Figs. S8, S12; Table S4 online). For example, Rozellomycota richness exhibited positive effects on both soil organic carbon (SOC) content and crop productivity in OLS multiple regression models (Fig. S8a, d online), whereas fungal Shannon diversity significantly influenced SOC persistence in RF models (Fig. S12b online). Moreover, fungal Chao1 and PPF richness remained the strongest predictors of soil biodiversity

(Estimate = 0.451, $R^2_{\text{adj.partial}}$ = 0.562) and pathogen control (Estimate = –0.315, $R^2_{\text{adj.partial}}$ = 0.350), respectively, in the integrated models (Fig. S8c, f online).

Synthesizing the above results, piecewise SEM revealed that Rozellomycota richness strongly and positively influenced both SOC content and crop productivity, even after accounting for major environmental constraints (Fig. 2a). Specifically, Rozellomycota richness enhanced SOC content and crop productivity by regulating overall eukaryotic diversity. Fungal diversity, including Shannon and Chao1 indices, also strongly and positively drove SOC persistence and soil biodiversity (Fig. 2b). Conversely, PPF richness exerted strong negative effects on productivity stability and pathogen control: increased PPF richness impaired the soil pathogen suppression capacity, which in turn reduced the stability of agricultural productivity (Fig. 2c). Notably, CEC had significant effects on Rozellomycota richness, fungal diversity, PPF richness, and SOC content (Fig. 2a–c). As a commonly measured soil fertility indicator, CEC is closely related to nutrient retention, soil structural stability, and pH buffering capacity [16]. We infer that higher CEC promotes fungal niche differentiation by improving nutrient retention and soil buffering, thereby enhancing species richness across both taxonomic and functional guilds.

Overall, our findings highlight the critical role of fungal diversity—including key indicator guilds such as Rozellomycota richness and PPF richness—in shaping agricultural sustainability and soil health in black soils. Accounting for major environmental constraints, fungal diversity and Rozellomycota richness support soil multifunctionality, contributing to soil fertility, grain productivity, biodiversity conservation, and climate resilience, whereas increased PPF richness undermines pathogen control and reduces the stability of agricultural productivity (Fig. 2d). These results emphasize the importance of preserving soil fungal diversity as a strategy for achieving multiple SDGs in black soil regions and identify Rozellomycota and PPF richness as reliable biological indicators of black soil health.

Although advanced bioinformatic approaches and multiple statistical models were employed, accounting for environmental, biological, geographic, and topographic factors, the conclusions still rely mainly on mathematical and statistical analyses, including network analyses. The precise mechanisms through which fungal diversity supports the multi-objective goals of farmland health management remain to be elucidated, particularly via long-term field experiments, such as establishing soil fungal diversity gradients [9,11]. In addition to biodiversity and network structure, factors such as microbial activity, functional traits [17], biomass, and necromass [13] may also play key roles in determining the biological health of black soils. Therefore, future studies should incorporate these indicators into long-term or larger-scale field monitoring to develop a more comprehensive framework for evaluating black soil health.

Conflict of interest

The authors declare that they have no conflict of interest.

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Author contributions

Haiyan Chu, Teng Yang, and Jiabao Zhang designed the research. Teng Yang, Xiyuan Xu, Guifeng Gao, Kunkun Fan, Luyao Song, Dan Zhao, Yuying Ma, Li Nie, Di Wu, and Haiyan Chu conducted a field survey. Xiyuan Xu, Jingjing Liu, Luyao Song, Dan Zhao, and Qiuyan Tan carried out laboratory work. Teng Yang, Xu Liu, Ke Dong, Wu Xiong, Xiaofang Du, Liang Cheng, Lei Zhang, and Haiyan Chu analyzed data. The manuscript was written by Teng Yang, Xu Liu, Leho Tedersoo, Jiabao Zhang, and Haiyan Chu, with contributions from all co-authors.

Data availability

The sequence data of eukaryotes, bacteria, and archaea have been submitted to the Sequence Read Archive (SRA) under BioProject accession codes PRJNA1128872, PRJNA1313416, and PRJNA1313383, respectively. Additional information, such as geographic, topographic, climatic, edaphic, and vegetation variables, can be provided on request to the corresponding author. Custom scripts and codes in this study can be searched on GitHub (https://github.com/joshualiuxu/Fungal-diversity-drives-soil-health-and-agricultural-sustainability-in-black-soils). Figures are created using R software and Adobe Illustrator 2022.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scib.2026.01.005.

References

[1] Anthony MA, Tedersoo L, De Vos B, et al. Fungal community composition predicts forest carbon storage at a continental scale. Nat Commun 2024;15:2385.

[2] van der Heijden MGA, Klironomos JN, Ursic M, et al. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 1998;396:69–72.

[3] Crowther TW, Thomas SM, Maynard DS, et al. Biotic interactions mediate soil microbial feedbacks to climate change. Proc Natl Acad Sci USA 2015;112:7033–8.

[4] Lehmann J, Bossio DA, Kögel-Knabner I, et al. The concept and future prospects of soil health. Nat Rev Earth Env 2020;1:544–53.

[5] Zhao J, Li N, Yang XG, et al. For the protection of black soils. Nat Food 2025;6:119–20.

[6] Li R, Hu W, Jia Z, et al. Soil degradation: a global threat to sustainable use of black soils. Pedosphere 2025;35:264–79.

[7] Corsaro D, Walochnik J, Venditti D, et al. Solving an old enigma: *Morellospora* saccamoebae gen. Nov., sp. Nov. (rozellomycota), a *Sphaerita*-like parasite of free-living amoebae. Parasitol Res 2020;119:925–34.

[8] Gleason FH, Carney LT, Lilje O, et al. Ecological potentials of species of Rozella (cryptomycota). Fungal Ecol 2012;5:651–6.

[9] Romero F, Hilfiker S, Edlinger A, et al. Soil microbial biodiversity promotes crop productivity and agro-ecosystem functioning in experimental microcosms. Sci Total Environ 2023;885:163683.

[10] Zang ZF, Li YX, Wang YN, et al. Contrasting roles of plant, bacterial, and fungal diversity in soil organic carbon accrual during ecosystem restoration: a meta-analysis. Sci Total Environ 2024;930:172767.

[11] de Goede SPC, Hannula SE, Jansen B, et al. Fungal-mediated soil aggregation as a mechanism for carbon stabilization. ISME J 2025;19:wraf074.

[12] Yang Y, Gunina A, Chen J, et al. Unfolding the potential of soil microbial community diversity for accumulation of necromass carbon at large scale. Global Change Biol 2025;31:e70292.

[13] Kou XC, Morridn E, Tian YJ, et al. Exogenous carbon turnover within the soil food web strengthens soil carbon sequestration through microbial necromass accumulation. Global Change Biol 2023;29:4069–80.

[14] Yang T, Tedersoo L, Liu X, et al. Fungi stabilize multi-kingdom community in a high elevation timberline ecosystem. iMeta 2022;1:e49.

[15] Liu S, Garcia-Palacios P, Tedersoo L, et al. Phylotype diversity within soil fungal functional groups drives ecosystem stability. Nat Ecol Evol 2022;6:900–9.

[16] Nel T, Bruneel Y, Smolders E. Comparison of five methods to determine the cation exchange capacity of soil. J Plant Nutr Soil Sc 2023;186:311–20.

[17] Maynard DS, Bradford MA, Covey KR, et al. Consistent trade-offs in fungal trait expression across broad spatial scales. Nat Microbiol 2019;4:846–53.