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RESEARCH ARTICLE

Plant species composition and key-species abundance drive ecosystem multifunctionality

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Abstract

1. Global biodiversity loss has generated great interest in the role of plant communities in driving ecosystem functions. There is limited understanding of how soil properties, plant richness and plant community composition interact to affect ecosystem multifunctionality.
2. We conducted a constructed ecosystem experiment by simultaneously manipulating soil origin (i.e. fertile farmland soil and relatively infertile bare land soil), plant richness and community composition (one-species monoculture, and all possible two-, three- and four-species combinations of five plants) to evaluate their influence on ecosystem multifunctionality related to the accumulation of biomass, carbon (C) and nitrogen (N) in plants, greenhouse gas emissions, soil nutrients, soil N fixation and mineralization of N and phosphorus (P).
3. We found that ecosystem multifunctionality was significantly affected by soil origin, plant community composition and the community-weighted mean (CWM) of plant biomass, but not by plant richness.
4. We grouped the community composition into the N-fixing group (including N-fixing plants) and the non-N-fixing group (excluding N-fixing plants). The N-fixing plant group exhibited significantly higher multifunctionality than the non-N-fixing species group in both soil origins. For bare land soil, multifunctionality increased with the increasing relative abundance and biomass ratio of *Albizia julibrissin* (N-fixing species) in communities, but decreased with the biomass ratio of *Platycladus orientalis* (non-N-fixing species). For farmland soil, multifunctionality increased with the abundance of *Toona sinensis* (non-N-fixing species) and the biomass ratio of *Albizia julibrissin*, but decreased with the abundance and biomass ratio of *Morus alba* (non-N-fixing species). These results indicate that the key species determining ecosystem multifunctionality vary under different soil conditions.

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5. *Synthesis and applications*: We propose that plant community composition and the relative abundance and biomass ratio of key species drive ecosystem multifunctionality. We suggest that selecting the appropriate plant combination under different soil conditions should be emphasized in ecological restoration projects. Our study highlights the differentiated roles of key species on ecosystem functions under different resource conditions. The N fixation in general plays a crucial role in driving ecosystem multifunctionality and the N-fixing plants can serve as restoration tools in nutrient-poor degraded lands.

KEYWORDS
biomass, ecological restoration, ecosystem multifunctionality, soil microbes, soil nutrients, species composition, species diversity

1 | INTRODUCTION

Global biodiversity loss has sparked great interest in how plant communities drive ecosystem functions (Beugnon et al., 2021; Craven et al., 2018). In recent decades, the relationship between biodiversity and ecosystem functioning (i.e. BEF) has become a prominent research topic (Feng et al., 2022; Hector et al., 1999). There is widespread evidence that plant diversity affects ecosystem functions such as productivity, nutrient cycling, microbial respiration, chemical interactions and soil carbon (C) sequestration (Beugnon et al., 2021; Chen et al., 2022; Huang et al., 2018; Lange et al., 2015; Liang et al., 2016; Ristok et al., 2023). Early research on BEF mainly focused on evaluating individual ecosystem functions, while more recent studies have emphasized ecosystem multifunctionality, that is, the ability of ecosystems to simultaneously provide multiple ecosystem functions (Maestre, Quero, et al., 2012; Manning et al., 2018). Although many studies have provided evidence that ecosystem multifunctionality generally increases with plant diversity (Meyer et al., 2018; van der Plas, 2019), some studies have reported negative or neutral (i.e. non-significant) relationships between plant diversity and ecosystem multifunctionality (van der Plas, 2019). Furthermore, a few studies have shown that species richness is not the only community attribute driving multifunctionality and the specific combinations of community attributes may be required to maximize functioning (Liu et al., 2021; Maestre, Quero, et al., 2012). To date, it is still debated how plant species combine to control overall ecosystem multifunctionality (Liu et al., 2021).

The mass ratio hypothesis and diversity hypothesis have been proposed to explain the influence of plant communities on ecosystem functioning (Grime, 1998; Tilman, 1997). The mass ratio hypothesis postulates that the extent to which a plant species affects ecosystem functions is closely related to its contribution to the total plant biomass (Grime, 1998), and thus, it explicitly considers the number, relative abundance and identity (through quantitative traits) of the species present (Garnier et al., 2004). It suggests that the instantaneous functioning of ecosystems is controlled to a great extent by the trait values of the dominant contributor to the plant biomass (Garnier et al., 2004; Grime, 1998; Grman et al., 2010). The 'diversity hypothesis' proposes that a high diversity level can enhance resource utilization among species and reduce negative biotic interactions, thereby improving ecosystem functioning (Tilman, 1997). These hypotheses have been supported by some results from experimentally manipulated communities or naturally assembled communities (Liu et al., 2021; Manning et al., 2015). However, the linkages among plant community attributes (e.g. richness, composition and relative abundance of species), soil properties, microbial properties and ecosystem multifunctionality have rarely been explored.

Soil properties closely interlink with ecosystem processes and functions by influencing the activities and interactions of plants and soil microorganisms (Beugnon et al., 2021; Wardle, 2013). For instance, soil fertility strongly affects plant growth rate, C allocation, leaf and root biomass, nutrient absorption and nutrient accumulation. Fertile soils may exhibit rapid, leaky nutrient cycles with less C accumulation, whereas relatively infertile soils are likely to support slow nutrient cycles in which nutrients are conserved and C sequestration is promoted (Wardle, 2013). In addition, soil microbial biomass, community structure and functions are also affected by soil properties (Beugnon et al., 2021; Delgado-Baquerizo et al., 2017; Pei et al., 2016). Since ecosystem multifunctionality is determined by the combination of biotic and abiotic factors, the interactions among soil, plant and soil microbes may drive ecosystem multifunctionality in complex ways. To the best of our knowledge, no prior experiment has simultaneously manipulated the soils, plant richness and plant community composition to test their interactions on ecosystem multifunctionality.

We conducted a constructed ecosystem experiment by simultaneously manipulating soil origin (i.e. fertile farmland soil and relatively infertile bare land soil), plant richness (from one to four species) and community composition (one-species monoculture, all possible two-, three- and four- species combinations of five typical indigenous plants). The goal was to assess how each manipulation drives ecosystem multifunctionality related to the C and N accumulation, greenhouse gas emissions, soil nutrients, soil N-fixing and mineralization rates of N and P. We hypothesized that (1) soil origin and plant richness would affect ecosystem multifunctionality, and plant richness would be the most important factor driving

multifunctionality; (2) the effects of plant community attributes on ecosystem functions would depend on soil origin and soil microbial properties.

2 | MATERIALS AND METHODS

2.1 | Experiment design

Farmland soil and bare land soil were collected from two adjacent locations (111°19′ E, 32°79′ N, a.s.l. 345 m) in Danjiangkou County, central China (Figure 1). These locations share the same parent material but are characterized by different land use. These soil origins represent the initial soil conditions of two typical pathways of vegetation restoration in China, that is, farmland abandonment and bare land revegetation. The bare land soil originated from the degraded land caused by soil erosion and has remained unvegetated for approximately 20 years. Soils were collected from a 5–20 cm layer, mixed intensively and sieved using a 1-cm aperture sieve. The chemical properties of the soil were measured before planting (Table S1).

The constructed ecosystem experiment was conducted in an experimental field of Wuhan Botanical Garden (Figure 1). We used square PVC pots with a bottom inner area of 19 cm, upper area of 25 cm, height of 16 cm and small holes in the bottom. Each pot was filled with 5 kg of soil. The PVC pots were placed in waterproof plastic basins (Figure 1). Five plant species were selected for the experiment: *Albizia julibrissin* (AJ), *Toona sinensis* (TS), *Morus alba* (MA), *Platycladus orientalis* (PO) and *Pinus tabuliformis* (PT). The five species are typical indigenous plants in the study region, known to form communities together in abandoned farmlands and bare lands (Cheng et al., 2013). The broad-leaved *A. julibrissin* is an N-fixing plant. *T. sinensis* is a broad-leaved non-N-fixing plant. *M. alba* is a broad-leaved plant that hosts arbuscular mycorrhiza fungi. *P. orientalis* is a coniferous plant with endotrophic mycorrhiza. *P. tabuliformis* is a coniferous plant with ectomycorrhiza (Flora of China Editorial Committee, 2018).

There were 30 plant treatments (i.e. community composition) in each soil origin: one-species monoculture treatments (AJ, TS, MA, PO and PT), all possible two-species combination treatments (AJ+TS, AJ+MA, AJ+PO, AJ+PT, TS+MA, TS+PO, TS+PT, MA+PO, MA+PT and PO+PT), all possible three-species combination treatments (AJ+TS+MA, AJ+TS+PO, AJ+TS+PT, AJ+MA+PO, AJ+MA+PT, TS+MA+PO, TS+MA+PT, TS+PO+PT, MA+PO+PT and AJ+PO+PT) and all possible four-species combination treatments (AJ+TS+MA+PO, AJ+TS+MA+PT, TS+MA+PO+PT, AJ+MA+PO+PT and AJ+TS+PO+PT). In addition, a blank control (i.e. unplanted) was set for each soil origin. Totally, 248 constructed ecosystems, that is, 2 soil origins × 31 treatments (plant treatments + unplanted) × 4 replicates, were established in our experiment (Figure 1c, Figure S1). We grouped the community composition in two different ways according to plant traits: one is N-utilization-type, that is, the N-fixing plant group (including N-fixing plant) and non-N-fixing plant group (not including N-fixing plant), and the other is leaf type, that is, broad-leaved, coniferous, and mixed (mixed community of coniferous and broad-leaved species) groups. The seeds were surface sterilized with 0.5% NaClO solution and sown in September 2019. During the first month, the seeds were germinated, and the plants were thinned or replanted to ensure that there were 12 individuals in each pot (Table S2). Each experimental pot contained 12 individual plants arranged in three rows and four columns with a spacing of 5 cm (Figure 1b, Figure S1).

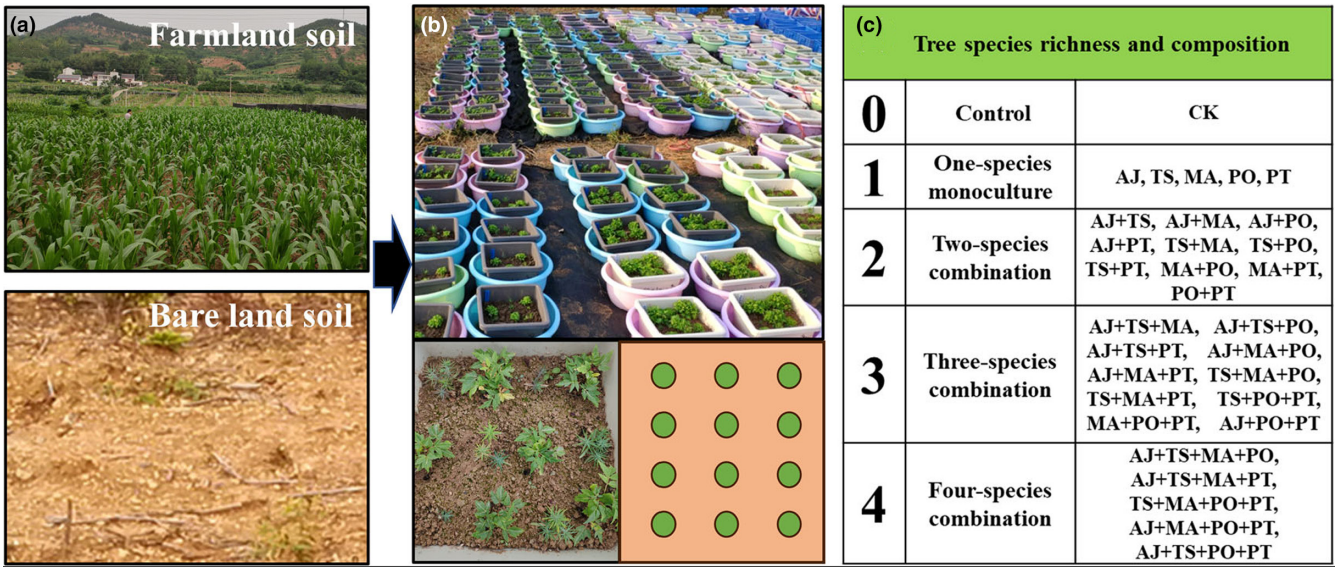


FIGURE 1 The experiment design and plant treatments. (a) Sampling sites of two origins of soil. (b) Image showing the constructed ecosystem experiment and the planting design. Except for the unplanted control, each ecosystem contained 12 individual plants arranged in three rows and four columns with a spacing of 5 cm (Figure S1). (c) Plant species richness and composition. AJ (*Albizia julibrissin*), TS (*Toona sinensis*), MA (*Morus alba*), PO (*Platycladus orientalis*), PT (*Pinus tabuliformis*).

2.2 | Measuring ecosystem properties and functions

Plant growth occurred from September 2019 to January 2021, and ecosystem properties and functions were measured thereafter. Prior to soil and plant sampling, greenhouse gas fluxes (CO_2, CH_4 and N_2O fluxes) were measured by static transparent chamber (Diameter = 70 cm, Height = 100 cm) and gas chromatography. All constructed ecosystems were moved to an artificial weather room to maintain a constant temperature for gas sampling. Gas samples were collected from the chamber every 10 min over a 40-min period.

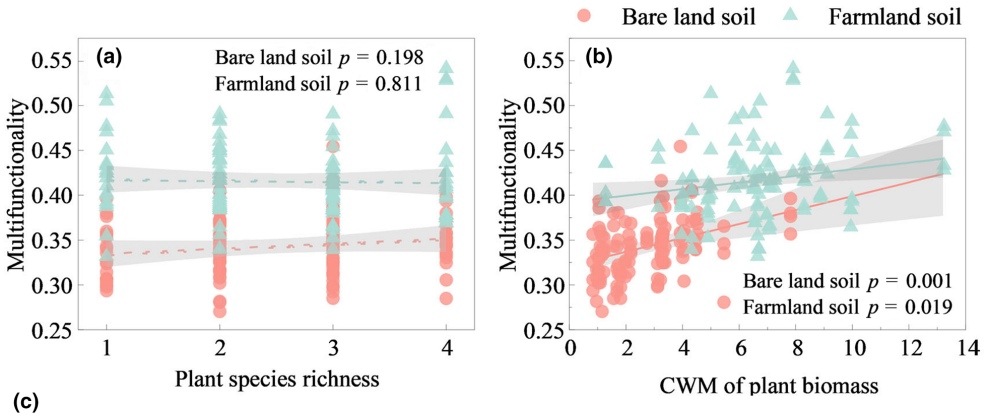
Harvested plants were sorted by species and the soil in each pot was collected and thoroughly mixed. The leaves, stems and roots of each species in each pot were oven-dried at 80°C and weighed to determine C and N concentrations (vario MACRO cube, Germany). Stocks were calculated by multiplying biomass and the C or N concentration in the leaves, stems and roots. Fresh soil samples from each pot were used for analyses including phospholipid fatty acid (PLFA) profile, N-fixation rates, rates of N and P net mineralization, microbial biomass C (MBC), microbial biomass N (MBN) and chemical properties. Freeze-dried soil (4 g) was used to extract the PLFAs following a standard protocol (Prasanna et al., 2016). The total microbial biomass for each soil sample was summed from all identified PLFAs. Soil MBC and MBN were determined using chloroform fumigation extraction (Vance et al., 1987). Soil pH was measured at soil water suspension (soil: water suspension = 1:2.5) with a pH electrode. Soil organic C (TOC) and total N (TN) concentrations were determined using an element analyser. The soil net mineralization rates of N (Nmin) and P (Pmin) were measured in a 28-day laboratory incubation procedure using the methods of Tian et al. (2017). Briefly, fresh soil equivalent to 30 g dry weight was incubated in a 250-mL glass bottle. Concentrations of NO_3^--N and NH_4^+-N and dissolved inorganic P were measured before and after incubation. Soil N-fixation rates were measured using the acetylene reduction method described by Li et al. (2018) with acetylene reduction activity (nmol $C_2H_4\,g^{-1}$ dry mass day^{-1}) representing soil N-fixation rates.

Ecosystem multifunctionality index was calculated using the method of Byrnes et al. (2014) and Maestre, Castillo-Monroy, et al. (2012) which standardizes the scale of a multifunctional index by a maximum value. Ecosystem multifunctionality was evaluated based on the unweighted average of 17 ecosystem function variables, including plant biomass, plant N stock, plant C stock, CO_2 emission, CH_4 emission, N_2O emission, soil net N mineralization rate, soil net P mineralization rate, soil N-fixation rate, soil microbial biomass, MBC, MBN and the concentrations of soil organic C, soil total N, NO_3^--N, NH_4^+-N and available P. We divided each function variable by its maximum value to scale all functions. Additionally, we employed the multiple threshold approach to investigate the effects of plant species richness on multifunctionality index across the full range of possible thresholds (from 5% to 99% at one percent intervals; Figure S2; as Chen et al., 2023).

2.3 | Statistical analyses

To test the diversity hypothesis and mass ratio hypothesis, the CWM (i.e. community-weighted mean) of plant biomass was calculated based on the abundance and biomass of each species under each soil origin using the R package 'FD' (as Mammola et al., 2021). Linear mixed-effects models were used to test the effect of soil origin, plant species richness, the CWM of plant biomass and their interactions on ecosystem multifunctionality (Figure 2), using the R packages 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017). Soil origin, plant species richness or the CWM of plant biomass and their interactions were included as fixed effects. Plant community composition (categorical variable, levels = 30) and spatial block (i.e. the replicate of plant community composition, Figure S1) were used as random effects, but the model results failed to converge. Therefore, the random effect structure was simplified (as Barr et al., 2013), including only plant community composition as a random effect, leading to a convergent model result. We tested the significance of fixed effects and interactions through model reduction using likelihood ratio tests and confirmed their importance using Akaike information criteria (AIC), inspected residual plots to ensure the assumptions of heteroscedasticity and normality were met, and fit the final model with restricted maximum likelihood (Mack et al., 2021). The conditional R^2_C and marginal R^2_M were used to represent the proportion of variance explained by the fixed effects with and without the random effects, respectively, using the package 'MuMIn' (Li et al., 2022). The pairwise comparison of marginal mean intercepts and slopes for soil origin was tested using a Bonferroni post hoc analysis in the 'emmeans' package (Mack et al., 2021). We also used nested ANOVA to test the effects of the soil origin, CWM of plant biomass, plant richness and plant community composition on ecosystem multifunctionality (Table S4; as Keith et al., 2008). The plant community composition was nested within species richness (Keith et al., 2008). We used one-way ANOVA to compare the mean values of individual functions and multifunctionality index under different soil origins, as well as the unplanted versus planted groups. To further explore the detailed effects of plant community composition, one-way ANOVA was used to assess how the different groups differed in individual ecosystem function and the multifunctionality index. The Bonferroni correction was applied for multiple comparisons among groups if the effect was significant. We used linear mixed-effects models to test the relationships between plant species relative abundance or the proportion of various species in total biomass and the multifunctionality index, as well as the relationship between soil microbial properties and the multifunctionality index (excluding unplanted pots) (package 'lme4').

A piecewise structural equation model (SEM) was used to evaluate the direct and indirect relationships among the plant species composition (principal component analysis was performed based on the plant abundance in each pot, and the scores from the first PCA axis were used to represent plant species composition; as Fukami et al., 2005), N-utilization-type (0 for non-N-fixing plant group and 1 for N-fixing



(c)

Model	Fix effects	Estimate	Std.Error	df	*t*-value	*p*-value
Multifunctionality~ Soil origin+ plant richness + (1|composition) R^2_M = 0.50 R^2_C = 0.59	Bare land (Intercept)	0.329	0.011	52.83	28.799	**<0.001**
	Farmland	0.090	0.012	208.00	7.417	**<0.001**
	Plant species richness	0.006	0.004	52.83	1.303	0.198
	Soil origin × plant species richness	−0.007	0.005	208.00	−1.460	0.146
Multifunctionality~ Soil origin + CWM of biomass + (1|composition) R^2_M = 0.54 R^2_C = 0.58	Bare land (Intercept)	0.321	0.007	74.70	44.118	**<0.001**
	Farmland	0.071	0.011	232.89	6.184	**<0.001**
	CWM of plant biomass	0.008	0.002	77.06	3.439	**<0.001**
	Soil origin × CWM of plant biomass	−0.004	0.002	231.99	−1.690	0.092

Note: See Table S3 for the intercept and slope of the fit lines.

FIGURE 2 Relationships of (a) plant species richness and (b) CWM (community- weighted mean) of plant biomass with multifunctionality index based on linear mixed effect model (LMM) in bare land soil and farmland soil, and (c) the linear mixed effect model results of multifunctionality. Fit lines represent the fixed effect. The significant fit lines are shown in solid lines and the non-significant fit lines are shown in dashed lines. The shaded area shows 95% confidence interval of the fit. The random intercept model includes plant species compositions (level = 30) as a random effect in both models. Estimates represent the effect size relative to the intercept or slope. Marginal $R^2(R^2_M)$ represents the variance explained by the fixed effects and conditional $R_2(R^2_C)$ represents the variance explained by fixed and random effects. The interaction between soil origin and plant richness or CWM of plant biomass for multifunctionality was included in the final model. The sum of squares type is type III.

plant group), soil properties (i.e. soil NH_4^+-N, NO_3^--N, available P, total N and total organic C were combined as composite variable), ecosystem processes (i.e. Plant C-stock, Nmin, Pmin, soil N-fixing rates, CO_2, CH_4 and N_2O emissions were combined as composite variable), soil microbial properties (i.e. total microbial biomass, microbial biomass C and N were combined as composite variable) and the multifunctionality index in two soil origins (Liu et al., 2022). Composite variables were calculated by the coefficients from multiple regressions: (i) using the maximum-likelihood fitting function to choose parameter estimates for each predictor (each composite variable) that maximize the likelihood of observing the response (multifunctionality index); (ii) those parameter values serve as the loadings for the indicators of the composite variable; (iii) the data for each indicator are multiplied by their loading and summed to generate the factor scores for the composite variable, which is then used in the structural model (Grace et al., 2010). The hypothetical SEM model was based on the results of our statistical analysis (i.e. linear mixed-effects models and ANOVA), the model structures of previous work (Beugnon et al., 2021; Liu et al., 2022) and the underlying hypotheses (Table S5). Then, the possible paths of the model were tried and simplified by eliminating the pathways with $p > 0.1$ (Figure S8; Zhang et al., 2021). The iterative model optimization was conducted to improve the goodness of the modelling results according to Fisher's C statistic, AIC and whole-model *p*-value (Lefcheck, 2016).

3 | RESULTS

3.1 | Effects of plant richness, composition and soil origin on ecosystem multifunctionality

Ecosystem multifunctionality was significantly affected by soil origin, plant species composition and the CWM of plant biomass, but not by plant richness (Figure 2; Tables S3 and S4). There was no significant

relationship between plant species richness and multifunctionality in both soil origins (Figure 2a). The ecosystem multifunctionality increased significantly with the increasing CWM of plant biomass in both soil origins (Figure 2b). The ecosystem multifunctionality of the N-fixing plant group was significantly higher than that of the non-N-fixing species group in both soil origins (Figure 3a). There was no significant difference among the broad-leaved, coniferous and mixed groups in either soil origins (Figure 3b). In bare land soil, ecosystem multifunctionality increased significantly with the abundance of the N-fixing species *A. julibrissin* (R^2_M=0.21, Figure 4a). Multifunctionality increased significantly with the increasing proportion of *A. julibrissin* biomass (i.e. Biomass of *A. julibrissin*/Total biomass of plant community; Figure 4k), but decreased with the proportion of *P. orientalias* biomass (Figure 4n). For farmland soil, multifunctionality increased significantly with the abundance of *T. sinensis* (Figure 4g), but decreased with the abundance of *M. alba* (Figure 4h). Ecosystem multifunctionality increased with the increasing proportion of *A. julibrissin* biomass (Figure 4p), but decreased with the proportion of *M. alba* biomass (Figure 4r) in farmland soil.

The results of the multiple threshold approach confirmed that the effects of increasing plant richness on ecosystem multifunctionality were not significant in farmland soil, and the influences of the plant richness manipulation were significant only when considering low and moderate levels of functioning in bare land soil (Figure S2).

3.2 | Response of individual function to plant community composition and soil origin

The total plant biomass and C and N stock in plants were greater in the N-fixing group than those in the non-N-fixing group in both soil origins (Figure S4a,c,e). The plant N stock in the coniferous group was lower than that in the broad-leaved and mixed groups in farmland soil (Figure S4f). The plant biomass and plant C stock in the coniferous group was lower than that in the mixed group in farmland soil (Figure S4b,d).

The presence of plants increased the total microbial biomass, bacteria biomass, fungal biomass and arbuscular mycorrhizal fungi biomass, and their values in farmland soil were significantly higher than those in bare land soil (Figure S5c,f,i,l). Bacterial biomass, fungal biomass and arbuscular mycorrhizal fungal biomass of the N-fixing plant group were higher than those of the non-N-fixing species group in bare land soil (Figure S5d,g,j), whereas there was no significant difference between the two groups in farmland soil. For the farmland soil, total microbial biomass and bacterial biomass were higher in the coniferous and mixed groups than those in the broad-leaved group (Figure S5b,e), whereas for the bare land soil, bacterial biomass was higher in the broad-leaved group than those in the coniferous and mixed groups (Figure S5e).

In farmland soil, the net N mineralization rate of the non-N-fixing species group was significantly higher than that of the N-fixing plant group (Figure S6a), and the net N mineralization rate of the coniferous group was significantly higher than that of broad-leaved and mixed groups (Figure S6b). In bare land soil, the net N mineralization rate of the coniferous group was significantly lower than that of the broad-leaved and mixed groups (Figure S6b). The NH_4^+-N concentration of the N-fixing species group was higher than that of the non-N-fixing plant group in the bare land soil (Figure S7a).

3.3 | Pathways of N-utilization-type and plant species composition mediating multifunctionality

The N-utilization-type indirectly affected multifunctionality by mediating ecosystem progresses. In addition, the N-utilization-type directly affected multifunctionality and indirectly influenced it by mediating soil properties in bare land soil (Figure 5a). Plant species composition indirectly affected multifunctionality by mediating soil properties in farmland soil (Figure 5b).

Microbe indirectly affected multifunctionality by influencing ecosystem processes in bare land soil (Figure 5a). Ecosystem multifunctionality was positively correlated with soil microbial biomass (R^2_M=0.39, Figure 6a) and the biomasses of bacteria, fungi and arbuscular mycorrhizal fungi (Figure S5b–d), and negatively correlated with ratios of bacteria/fungi and Gram-positive/gram-negative bacteria (Figure S5e,g).

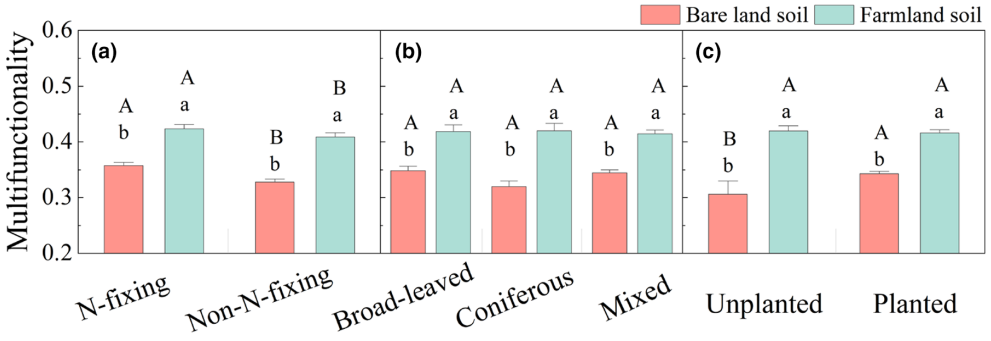


FIGURE 3 Effects of the N-utilization-type (i.e., N-fixing plant group and non-N-fixing plant group) (a), leave-type (i.e., broad-leaved, coniferous, and mixed groups) (b), and planting (c) on ecosystem multifunctionality based on one-way ANOVA.

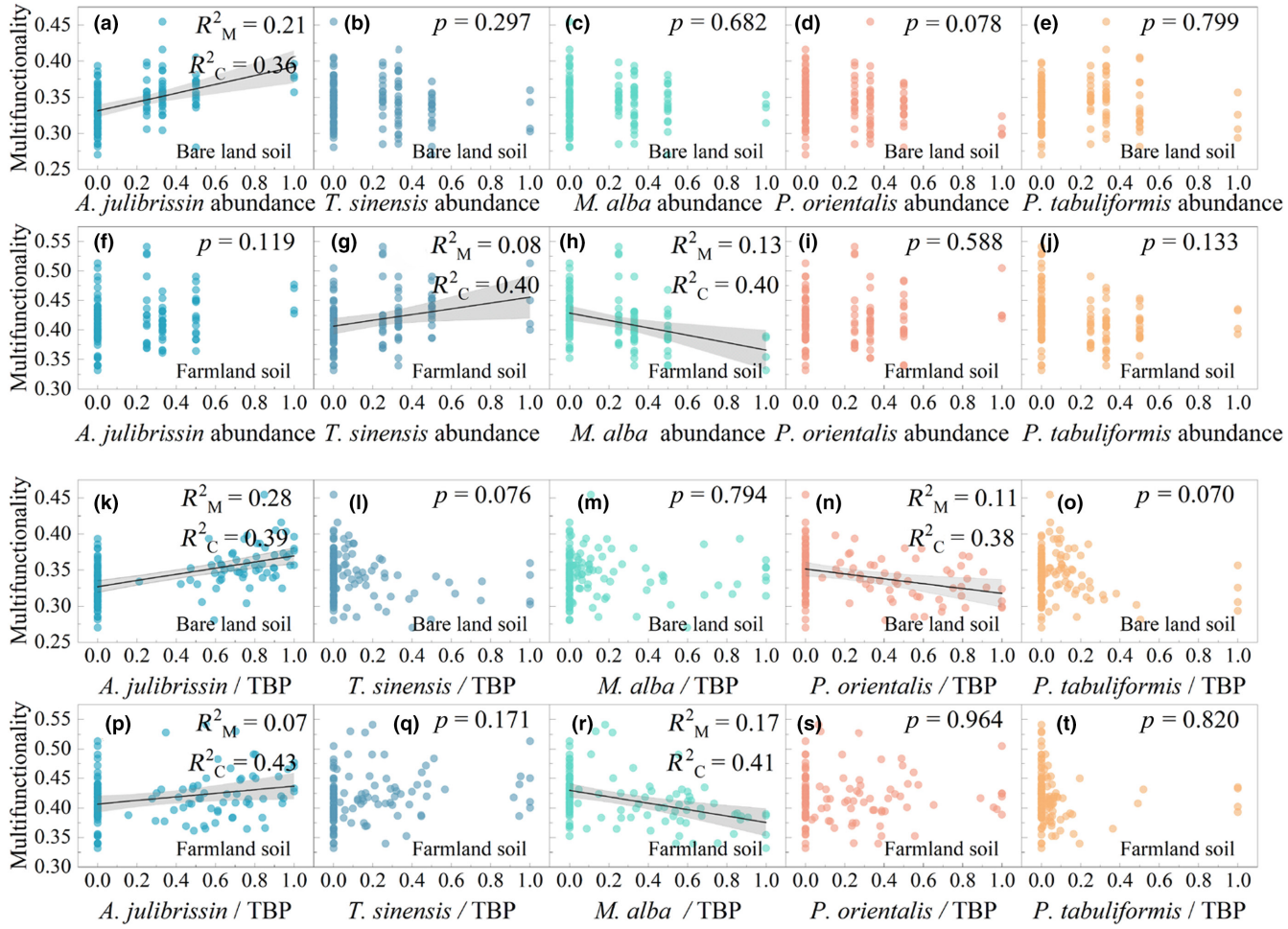


FIGURE 4 Relationships of plant species relative abundance (a–j) and the proportion of various species in total biomass (k–t) with multifunctionality index in bare land soil (a–e, k–o) and farmland soil (f–j, p–t). Only significant fitted lines are displayed on the graphs. The shaded area shows 95% confidence interval of the fit. TBP, total biomass of plant community.

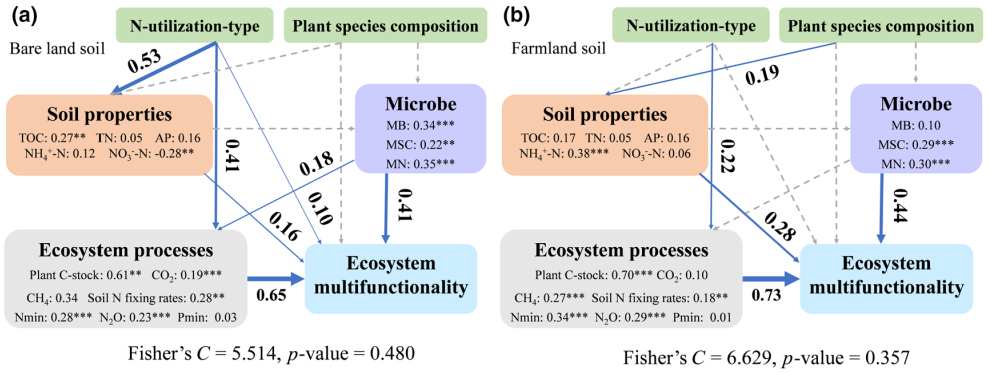


FIGURE 5 Direct and indirect drivers of ecosystem multifunctionality. (a) Bare land soil, (b) farmland soil. Piecewise SEM accounting for the direct and indirect effects of N-utilization-type, species composition, soil properties, microbe and ecosystem processes as predictors of ecosystem multifunctionality (Figure S8, Table S5). Solid blue arrows represent positive paths ($p < 0.05$), solid red arrows represent negative paths ($p < 0.05$) and dotted grey arrows represent non-significant paths ($p > 0.05$).

4 | DISCUSSION

We provide the first evidence that ecosystem multifunctionality is significantly affected by soil origin, plant species composition and the CWM of plant biomass, but not by plant richness (Figure 2; Tables S3 and S4). Ecosystem multifunctionality of the N-fixing plant group was higher than that of the non-N-fixing species group in both soil origins, and multifunctionality increased significantly

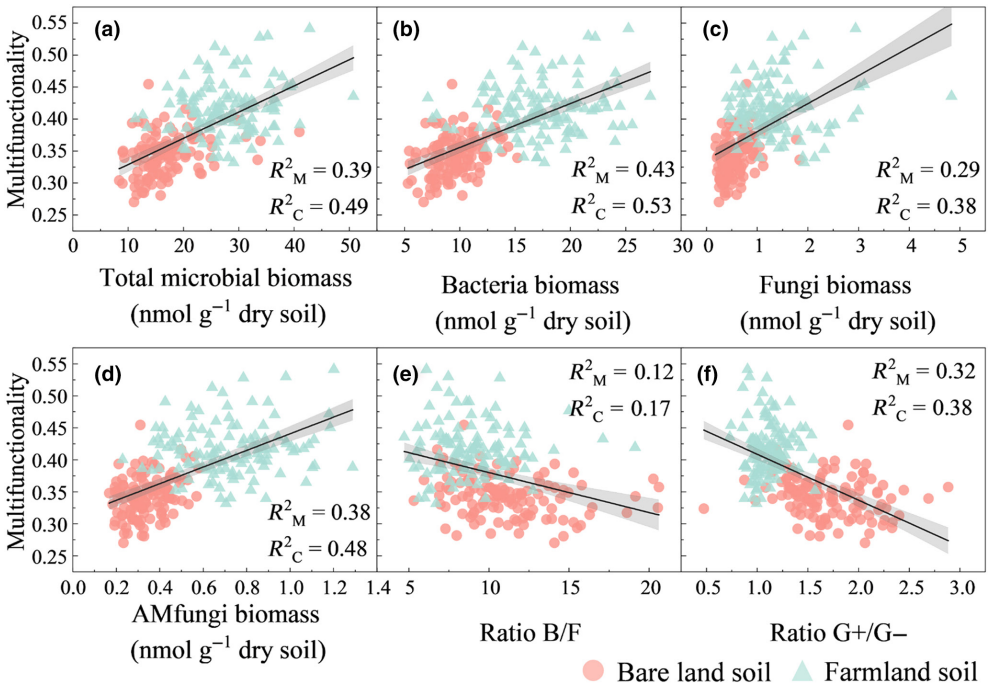


FIGURE 6 Ecosystem multifunctionality in relation to the microbial biomass (a), bacteria biomass (b), fungi biomass (c), arbuscular mycorrhizal (AM) fungi biomass (d), ratio B/F (e) and ratio G+/G− (f). Light green points represent farmland soil in experiment, and light red points represent bare land soil. Shaded area shows 95% confidence interval of the fit.

with the increasing relative abundance and biomass ratio of *A. julibrissin* (N-fixing species) in communities (Figures 3 and 4). This partly supports the mass ratio hypothesis that more dominant species will have a greater impact on the ecosystem, proportional to their biomass (Grime, 1998). We found that ecosystem multifunctionality increased significantly with the increasing CWM of plant biomass in two soil origins (Figure 2b), which is consistent with the prediction of the mass ratio hypothesis. In bare land soil, characterized by low N and low SOC, the N-fixing species *A. julibrissin* emerged as the key-species determining multifunctionality (Figure 4). These results demonstrated that N-fixing plants play important roles in driving ecosystem multifunctionality and have the potential to serve as ecological restoration tools in nutrient-poor degraded lands. Our results also indicated that the key-species determining ecosystem multifunctionality varied under different soil conditions. For example, *M. alba* was the key-species influencing multifunctionality in the farmland soil, but was not in the bare land soil (Figure 4m,h).

Interestingly, we found that species richness did not affect ecosystem multifunctionality (Figure 2b), which is in contrast to the diversity hypothesis. Specifically, broad-leaved and coniferous species are capable of partitioning space within the canopy structure (Ishii & Asano, 2010), and broad-leaved and evergreen species can segregate along temporal gradients (Lu et al., 2016). Thus, these partitioning strategies can alleviate competition for resources and promote ecosystem functions. However, we found that there was no significant difference in multifunctionality among the broad-leaved, coniferous and mixed groups in both soil origins (Figure 3b).

Plant species composition and N-utilization-type regulate multifunctionality through different pathways in different soils (Figure 5), and the relationships between the abundance of key-species and multifunctionality showed different patterns under different soil origins (Figure 4), indicating that the linkages between plant community and ecosystem multifunctionality depend on soil origin or soil properties. Our findings emphasize the importance of selecting the appropriate plant combinations for different soil conditions in ecological restoration projects. In our study, farmland soil is fertile, while bare land soil is relatively infertile; thus, the two soils represented different resource conditions and may have different impacts on the relationships between plant community and multifunctionality. There are two potential explanations for the impacts of soil conditions (Agren et al., 2012). The first is that, when soil is in deficient in a particular element, the growth and functions of all plants in the community may be limited by that element (Agren et al., 2012; Chaer et al., 2011), thus reducing the role of plant biodiversity. The second explanation is that some plant species have a greater capacity for absorbing or utilizing certain elements, allowing them to grow well under low-concentration conditions and thus dominate plant community function (Chaer et al., 2011). Our results showed that ecosystem multifunctionality was regulated by the relative abundance and biomass ratio of *A. julibrissin* (N-fixing species) in communities in low-N bare land soil (Figure 4), supporting the second explanation. Previous studies have shown that soil N availability and total carbon increased with the proportion of *Albizia falcataria* (Kaye et al., 2000), which is similar to our findings (Figure S7a,j).

Our results show that the N-fixing plant group had higher plant N-stock in both soil origins (Figure S4e,f), indicating the important role of the N-fixing plant in driving N accumulation in ecosystems. This was expected as N-fixing plants are known to provide large quantities of

new N to ecosystems (Menge et al., 2019; Zhang et al., 2020). We also found that the plant N-stock of the coniferous group was lower than that of the broad-leaved and mixed groups in farmland soil (Figures S4f), suggesting that coniferous species had lower N accumulation rates. This result supports the conclusion of previous meta-analyses showing that conifers and broad-leaved trees display different N accumulation patterns and the coniferous trees are characterized by lower N/biomass ratio (Zhang et al., 2018, 2020). In addition, the mixed group displayed higher plant biomass and C-stock than that of the coniferous group in farmland soil (Figure S4b,d,f), indicating that the mixing of coniferous and broad-leaved plants can increase the accumulation of biomass and C-stock in ecological restoration. However, this pattern was not observed for the bare land soil (Figure S4b,d,f), suggesting that the mixing effect depends on soil conditions.

Our results showed that soil microbial properties differed among N-utilization-type groups and leaf-type groups (Figure S5). This pattern is expected as previous studies showed that plant species identity and neighbouring plant species can shape microbial richness and composition (Hu et al., 2023; Yang et al., 2019). Microbes indirectly affected multifunctionality by influencing ecosystem processes in bare land soil (Figure 5a), demonstrating the importance of soil microbes in driving ecosystem multifunctionality (Beugnon et al., 2021). Previous studies have reported that microbes can directly or indirectly drive ecosystem processes such as productivity (Van Der Heijden et al., 2008), soil N mineralization and N availability (Li et al., 2019). In addition, we found that microbes mediated ecosystem processes in bare land soil, suggesting that microorganisms have the potential to drive the ecological restoration of degraded lands (Coban et al., 2022).

5 | CONCLUSIONS

Plant community composition and the relative abundance and biomass ratio of key species drive ecosystem multifunctionality. Plant species composition indirectly affects ecosystem multifunctionality by mediating soil properties. Our study highlights the differentiated roles of key species on ecosystem functions under varying resource conditions and has implications for optimizing ecological restoration strategies. Our findings suggest that selecting the appropriate plant combination for different soil conditions should be emphasized in ecological restoration projects. For fertile lands, the mixing of coniferous and broad-leaved plants can increase the accumulation of plant biomass, C- and N-stocks. For infertile lands, the introduction of N-fixing species is a key step. The N fixation in general plays a role in driving ecosystem multifunctionality and N-fixing plants have the potential to serve as ecological restoration tools in nutrient-poor degraded lands.

AUTHOR CONTRIBUTIONS

Kerong Zhang designed the research, conducted analysis and wrote the manuscript. Xinshuai Li and Youchao Chen collected samples, measured samples, conducted analysis and wrote the manuscript. Xinshuai Li, Youchao Chen, Feng Liu, Xiaoli Cheng, Quanfa Zhang and Kerong Zhang conducted analysis and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The original data were archived in the Dryad Digital Repository https://doi.org/10.5061/dryad.63xsj3v86 (Li et al., 2024).

STATEMENT ON INCLUSION

Our study fails to include scientists based in the country where the study was carried out. We recognize that more could have been done to engage local scientists with our research as our project developed, and to embed our research within the national context and research priorities. We are planning to address these caveats in future research.

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REFERENCES

Agren, G. I., Wetterstedt, J. A. M., & Billberger, M. F. K. (2012). Nutrient limitation on terrestrial plant growth-modeling the interaction between nitrogen and phosphorus. *New Phytologist*, *194*, 953–960.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*, 255–278.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Beugnon, R., Du, J., Cesarz, S., Jurburg, S. D., Pang, Z., Singavarapu, B., Wubet, T., Xue, K., Wang, Y., & Eisenhauer, N. (2021). Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning. *ISME Communications*, *1*, 41.

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., & Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*, 111–124.

Chaer, G. M., Resende, A. S., Campello, E. F., de Faria, S. M., & Boddey, R. M. (2011). Nitrogen-fixing legume trees species for the reclamation of severely degraded lands in Brazil. *Tree Physiology*, *31*, 139–149.

Chen, W., Wang, J., Chen, X., Meng, Z., Xu, R., Duoji, D., Zhang, J., He, J., Wang, Z., Chen, J., Liu, K., Hu, T., & Zhang, Y. (2022). Soil microbial network complexity predicts ecosystem function along elevation gradients on the Tibetan Plateau. *Soil Biology and Biochemistry*, *172*, 108766.

Chen, Y., Chi, J., Lu, X., Cai, Y., Jiang, H., Zhang, Q., & Zhang, K. (2023). Fungal-bacterial composition and network complexity determine soil multifunctionality during ecological restoration. *Catena*, *230*, 107251.

Cheng, X., Yang, Y., Li, M., Dou, X., & Zhang, Q. (2013). The impact of agricultural land use changes on soil organic carbon dynamics in the Danjiangkou reservoir area of China. *Plant and Soil*, *366*, 415–424.

Coban, O., De Deyn, G. B., & van der Ploeg, M. (2022). Soil microbiota as game-changers in restoration of degraded lands. *Science*, *375*(6584), abe0725.

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J., Cerabolini, B., Cornelissen, J., Craine, J., De Luca, E., Ebeling, A., Griffin, J., Hector, A., … Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*, *2*, 1579–1587.

Delgado-Baquerizo, M., Reich, P. B., Khachane, A. N., Campbell, C. D., Thomas, N., Freitag, T. E., AlSoud, W. A., Sorensen, S. J., Bardgett, R. D., & Singh, B. K. (2017). It is elemental: soil nutrient stoichiometry drives bacterial diversity. *Environmental Microbiology*, *19*, 1176–1188.

Feng, Y., Schmid, B., Loreau, M., Forrester, D. I., Fei, S., Zhu, J., Tang, Z., Zhu, J., Hong, P., Ji, C., Shi, Y., Su, H., Xiong, X., Xiao, J., Wang, S., & Fang, J. (2022). Multi species forest plantations out yield monocultures across a broad range of conditions. *Science*, *376*, 865–868.

Flora of China Editorial Committee. (2018). *Flora of China*. Flora of China.

Fukami, T., Martijn Bezemer, T., Mortimer, S. R., & van der Putten, W. H. (2005). Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, *8*(12), 1283–1290.

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J. P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*, 2630–2637.

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, *80*(1), 67–87.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910.

Grman, E., Lau, J. A., Schoolmaster, D. R., Jr., & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, *13*, 1400–1410.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitaset, H., Giller, P., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P., Loreau, M., Minns, A., … Lawton, J. H. (1999). Plant diversity and productivity experiments in European Grasslands. *Science*, *286*, 1123–1127.

Hu, J., Ricono, C., Fournier, P., Mondy, S., Vandenkoornhuyse, P., & Mony, C. (2023). Neighbourhood effect of weeds on wheat root endospheric mycobiota. *Journal of Ecology*, *111*(5), 994–1008.

Ishii, H., & Asano, S. (2010). The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecological Research*, *25*, 715–722.

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Haerdtle, W., Oheimb, G. V., Yang, X., Liu, X., Pei, K., Both, S., Yang, B., Eichenberg, D., Assmann, T., Bauhus, J., Behrens, T., Buscot, F., … Schmid, B. (2018). Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, *362*, 80–83.

Kaye, J. P., Resh, S. C., Kaye, M. W., & Chimner, R. A. (2000). Nutrient and carbon dynamics in a replacement series of Eucalyptus and Albizia trees. *Ecology*, *81*(12), 3267–3273.

Keith, A. M., van der Wal, R., Brooker, R. W., Osler, G. H. R., Chapman, S. J., Burslem, D. F. R. P., & Elston, D. A. (2008). Increasing litter species richness reduces variability in a terrestrial decomposer system. *Ecology*, *89*(9), 2657–2664.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26.

Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., Gleixner, G., Mellado-Vázquez, P. G., Malik, A. A., Roy, J., Scheu, S., Steinbeiss, S., Thomson, B., Trumbore, S., & Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, *6*, 6707.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Li, D., Zhang, Q., Xiao, K., Wang, Z., & Wang, K. (2018). Divergent responses of biological nitrogen fixation in soil, litter and moss to temperature and moisture in a karst forest, southwest China. *Soil Biology and Biochemistry*, *118*, 1–7.

Li, S. P., Jia, P., Fan, S. Y., Wu, Y., Liu, X., Meng, Y., Li, Y., Shu, W., Li, J., & Jiang, L. (2022). Functional traits explain the consistent resistance of biodiversity to plant invasion under nitrogen enrichment. *Ecology Letters*, *25*, 778–789.

Li, X., Chen, Y., Liu, F., Chen, X., Zhang, Q., & Zhang, K. (2024). Data from: Plant species composition and key-species abundance drive ecosystem multifunctionality. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.63xsj3v86

Li, Z., Tian, D., Wang, B., Wang, J., Wang, S., Chen, H. Y. H., Xu, X., Wang, C., He, N., & Niu, S. (2019). Microbes drive global soil nitrogen mineralization and availability. *Global Change Biology*, *25*, 3.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E. D., Mcguire, A. D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C., Glick, H., Hengeveld, G., Nabuurs, G., Pfautsch, S., … Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*, aaf8957.

Liu, D., Chang, P. H. S., Power, S. A., Bell, J. N., & Manning, P. (2021). Changes in plant species abundance alter the multifunctionality and functional space of heathland ecosystems. *New Phytologist*, *232*, 1238–1249.

Liu, S., García-Palacios, P., Tedersoo, L., Guirado, E., van der Heijden, M. G. A., Wagg, C., Chen, D., Wang, Q., Wang, J., Singh, B. K., & Delgado-Baquerizo, M. (2022). Phylotype diversity within soil fungal functional groups drives ecosystem stability. *Nature Ecology & Evolution*, *6*, 900–909.

Lu, H., Mohren, G. M. J., Ouden, J. D., Goudiaby, V., & Sterck, F. J. (2016). Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in The Netherlands. *Forest Ecology and Management*, *376*, 321–332.

Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., & Miller, S. N. (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. *Science*, *372*(6539), 280–283.

Maestre, F. T., Castillo-Monroy, A. P., Bowker, M. A., & Ochoa-Hueso, R. (2012). Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. *Journal of Ecology*, *100*, 317–330.

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A. N., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M. A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., … Zaady, E. (2012). Plant species richness and ecosystem multifunctionality in Global Drylands. *Science*, *335*, 214–218.

Mammola, S., Carmona, C. P., Guillerme, T., & Cardoso, P. (2021). Concepts and applications in functional diversity. *Functional Ecology*, *35*, 1869–1885.

Manning, P., de Vries, F. T., Tallowin, J. R. B., Smith, R., Mortimer, S. R., Pilgrim, E. S., Harrison, K. A., Wright, D. G., Quirk, H., Benson, J., Shipley, J., Cornelissen, J., Kattge, J., Bönisch, G., Wirth, C., & Bardgett, R. D. (2015). Simple measures of climate, soil properties and plant traits predict national-scale grassland soil carbon stocks. *Journal of Applied Ecology*, *52*, 1188–1196.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., Whittingham, M. J., & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, *2*, 427–436.

Menge, D. N. L., Chisholm, R. A., Davies, S. J., Salim, K. A., Allen, D., Alvarez, M., Bourg, N., Brockelman, W., Bunyavejchewin, S., Butt, N., Cao, M., Chanthorn, W., Chao, W., Clay, K., Condit, R., Cordell, S., Silva, J., Dattaraja, H. S., Andrade, A., … Fung, T. (2019). Patterns of nitrogen-fixing tree abundance in forests across Asia and America. *Journal of Ecology*, *107*, 2598–2610.

Meyer, S. T., Ptacnik, R., Hillebrand, H., Bessler, H., Buchmann, N., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Halle, S., Klein, A., Oelmann, Y., Roscher, S., Rottstock, T., Scherber, C., Scheu, S., Schmid, B., Schulze, E., Temperton, V. M., … Weisser, W. W. (2018). Biodiversity–multifunctionality relationships depend on identity and number of measured functions. *Nature Ecology & Evolution*, *2*, 44–49.

Pei, Z., Eichenberg, D., Bruelheide, H., Kröber, W., Kühn, P., Li, Y., Oheimb, G. V., Purschke, O., Scholten, T., Buscot, F., & Gutknecht, J. L. M. (2016). Soil and tree species traits both shape soil microbial communities during early growth of Chinese subtropical forests. *Soil Biology and Biochemistry*, *96*, 180–190.

Prasanna, R., Kanchan, A., Ramakrishnan, B., Ranjan, K., Venkatachalam, S., Hossain, F., Shivay, Y. S., Krishnan, P., & Nain, L. (2016). Cyanobacteria-based bioinoculants influence growth and yields by modulating the microbial communities favourably in the rhizospheres of maize hybrids. *European Journal of Soil Biology*, *75*, 15–23.

Ristok, C., Weinhold, A., Ciobanu, M., Poeschl, Y., Roscher, C., Vergara, F., Eisenhauer, N., & van Dam, N. M. (2023). Plant diversity effects on herbivory are related to soil biodiversity and plant chemistry. *Journal of Ecology*, *111*(2), 412–427.

Tian, Q., Wang, X., Wang, D., Wang, M., Liao, C., Yang, X., & Liu, F. (2017). Decoupled linkage between soil carbon and nitrogen mineralization among soil depths in a subtropical mixed forest. *Soil Biology and Biochemistry*, *109*, 135–144.

Tilman, D. (1997). Distinguishing between the effects of species diversity and species composition. *Oikos*, *80*, 185.

Van Der Heijden, M. G., Bardgett, R. D., & Van Straalen, N. M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, *11*(3), 296–310.

van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, *94*, 1220–1245.

Vance, E. D., Brookes, P. C., & Jenkinson, D. S. (1987). An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry*, *19*, 703–707.

Wardle, D. A. (2013). *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press.

Yang, T., Tedersoo, L., Soltis, P. S., Soltis, D. E., Gilbert, J. A., Sun, M., Shi, Y., Wang, H., Li, Y., Zhang, J., Chen, Z., Lin, H., Zhao, Y., Fu, C., & Chu, H. (2019). Phylogenetic imprint of woody plants on the soil mycobiome in natural mountain forests of eastern China. *The ISME Journal*, *13*(3), 686–697.

Zhang, D., Peng, Y., Li, F., Yang, G., Wang, J., Yu, J., Zhou, G., & Yang, Y. (2021). Changes in above-/below-ground biodiversity and plant functional composition mediate soil respiration response to nitrogen input. *Functional Ecology*, *35*(5), 1171–1182.

Zhang, K., Cheng, X., Dang, H., & Zhang, Q. (2020). Biomass:N:K:Ca:Mg:P ratios in forest stands world-wide: Biogeographical variations and environmental controls. *Global Ecology and Biogeography*, *29*, 2176–2189.

Zhang, K., Song, C., Zhang, Y., Dang, H., Cheng, X., & Zhang, Q. (2018). Global-scale patterns of nutrient density and partitioning in forests in relation to climate. *Global Change Biology*, *24*, 536–551.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The schematic figure of the plant treatments in the experiment.

Figure S2. Relationships between plant species richness and multifunctionality when measured as the number of functions exceeding threshold levels of maximum process rates.

Figure S3. Figure of normal distribution and residuals.

Figure S4. Effects of the N-utilization-type (i.e. N-fixing plant group and non-N-fixing plant group) and leave-type (i.e. broad-leaved, coniferous, and mixed group) on plant properties (i.e. biomass, total C- and N- stocks in plants) based on one-way ANOVA.

Figure S5. Effects of the N-utilization-type (i.e., N-fixing plant group and non-N-fixing plant group), leave-type (i.e. broad-leaved, coniferous, and mixed groups), and planting on microbial properties based on one-way ANOVA.

Figure S6. Effects of the N-utilization-type (i.e., N-fixing plant group and non-N-fixing plant group), leave-type (i.e. broad-leaved, coniferous, and mixed groups), and planting on soil net N mineralization rate (Nmin) and soil P mineralization rate (Pmin) based on one-way ANOVA.

Figure S7. Effects of the N-utilization-type (i.e. N-fixing plant group and non-N-fixing plant group), leave-type (i.e. broad-leaved, coniferous, and mixed groups), and planting on soil properties based on one-way ANOVA.

Figure S8. Schemes of tested structural equation model.

Table S1. The soil chemical properties before planting.

Table S2. Number of different plant species in the plant species compositions.

Table S3. Marginal mean intercept, slope estimates, and standard errors of as multifunctionality a function of plant species richness or CWM of plant biomass for bare land soil and farmland soil.

Table S4. Summary results of the nested ANOVA analyses of ecosystem multifunctionality.

Table S5. Potential relations between the considered variables in the structural equation model (Figure S8). Arrows indicate the direction of the paths.

Table S6. The normalization coefficient of the composite variables obtained from multiple regression.

Table S7. Model summaries of piecewiseSEM for bare land soil and farmland soil (Figure 5).

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