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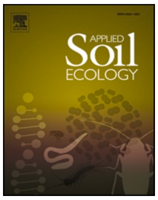

Plant species richness enhances aboveground primary productivity via net biodiversity effects and bacterial community interactions

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ABSTRACT

The multifunctionality of grassland ecosystems is significantly affected by dominant and subdominant species, particularly in terms of aboveground primary productivity. Few studies have explored how various dominant and subdominant plant species control the interactions between several trophic levels, driving aboveground productivity. To investigate the direct and indirect drivers of productivity in dominant and subdominant plant communities, we selected three dominant and seven subdominant species from the Ningxia northern Yanchi Desert steppe for monoculture and mixture experiments to establish the richness of plant species (monoculture and 4-, 6-, 8-, and 10-species mixtures). We examined the aboveground biomass, soil properties, insect diversity, and microbial diversity of different plant species combinations, linking biotic and abiotic factors with aboveground primary productivity. We found: (1) a significant positive correlation between species richness and net biodiversity effects. Higher aboveground relative productivity was achieved for mixed species than for monoculture, particularly for *Elymus dahuricus*, and the selection effect had a unimodal relationship with increased species richness, with the highest productivity observed in the 8-species mixture. (2) The co-dominant insect groups in various plant species were the phytophagous Miridae, Agromyzidae, and Cicadellidae families, constituting 69.5 % of all insects collected. Plant species richness had an encouraging influence on phytophagous insect diversity, but the effects on predatory, omnivorous, and parasitic insects remained insignificant. Additionally, insect similarity indices for different plant species richness values were lower than 0.5. (3) Stoichiometric analyses of soil enzymes revealed a reduction in microbial metabolism primarily by the relative limitation of nitrogen and phosphorus, with nitrogen limitations being significantly stronger in the monoculture than in the 8-mixture species; the dominant bacterial phyla, Actinobacteria and Ascomycetes, played essential roles in promoting plant growth in desert steppes, and bacterial biodiversity influenced primary productivity more prominently than fungal biodiversity. Our findings underscore the importance of conserving species diversity and its potential benefits for ecosystem restoration and sustainability.

1. Introduction

Since the year 1500, approximately 30 % of species globally (within a 16–50 % uncertainty range) have been endangered or extinct (Díaz et al., 2019; Isbell et al., 2023), resulting in a 10–70 % reduction in the contribution of ecosystem functioning to society (Isbell et al., 2023). The decline in species diversity has been progressively amplified owing to globalization, including climate change. A reduction in plant species threatens ecosystems by directly reducing ecosystem functions or indirectly affecting other trophic-level compositional changes through abiotic factors (de Vries et al., 2012; Cardinale, 2012; Liang et al., 2016). Serious impacts include biodiversity loss, habitat loss, reduced productivity, and imbalanced nutrient cycling. Grasslands account for approximately 40.5 % of the plant species diversity; therefore, changes in this biome affect human development.

The association between biodiversity and ecosystem function is a well-researched topic (Tilman et al., 1996; Hector et al., 1999; Xu et al., 2022). Ecosystem functions and services after biodiversity loss rely

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Abbreviations: PCoA, Principal coordinate analysis; SEM, Structural Equation Modeling; EC, electrical conductivity.

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heavily on the relationship between plant species richness and productivity (Fraser et al., 2015). However, because species-rich communities have a greater likelihood of containing highly productive plant species, their higher biomass may be simply a "selection effect" rather than a positive interaction between species (complementary effect). The relationship between the observed biomass (productivity) of a multispecies plant community and the productivity of a single cultivated species, as well as the distinction between the observed and expected yields (biodiversity effect), is currently under-research. Studies have found a range of relationships between plant community diversity and productivity, including linear positive correlations (Maestre et al., 2012), nonlinear positive correlations (Liang et al., 2016), linear negative correlations (Grace et al., 2016), neutral non-correlations (Adler and Bradford, 2002), and single-peak correlations (Fraser et al., 2015). In 2007, Hector and Bagchi (2007) assessed the impact of biodiversity on several ecosystem processes, and subsequent research suggested that single-species study findings underestimate the significance of biodiversity in the context of ecosystem operations. Therefore, biodiversity research has evolved from focusing on the regulation and maintenance of diversity to investigating the impacts of biodiversity gradients on ecosystem multifunctionality and services. This shift underscores the importance of biodiversity (Mace, 2014).

Insects play essential roles as vegetative feeders, pollinators, and predators in ecosystems. Changes in diversity can have cascading effects within food webs, affecting the functioning and services of the entire ecosystem (van Klink et al., 2020; Wagner et al., 2021). Changes in plant species richness primarily affect insect communities by indirectly influencing insect food sources and microenvironments (Wan et al., 2022), thereby forming a synergistic evolutionary relationship between mutual constraints and interdependence. Zhu et al. (2023) showed that various regulatory mechanisms differentially affect the trophic level of insects. Specifically, phytophagous insects exhibit the greatest sensitivity to changes in plant mass, surface predators to variations in plant species, and canopy predators to changes in plant biomass. The resource monophagy theory suggests that the diversity of phytophagous insects increases with the increased diversity of plant species and that predatory insect diversity increases with increased plant-predator diversity. The individual hypothesis suggests that plant communities that are more productive can provide richer food resources for consumers, supporting a greater number of consumers and leading to greater overall species richness (Srivastava and Lawton, 1998). Wagg et al. (2014) established soil fauna and microbial communities with varying species compositions and diversities in typical grasslands and examined their roles in different ecosystem functions. Reductions in biodiversity and the simplification of the soil community structure reduced ecosystem functioning and showed an increasingly strong inhibitory effect over time, indicating the importance of soil community structure in regulating ecosystem functionality. Plant diversity has declined in conjunction with a decline in soil biodiversity and microorganism community simplification. Thus, declining soil biodiversity and changes in soil community components have implications for a range of ecological processes that maintain ecosystem function. Van der Heijden et al. (2015) analyzed early experimental data using a function–species substitution approach and found that clumped mycorrhizal fungi and ectomycorrhizal fungi correlated with plant productivity and contributed significantly to many ecosystem processes (e.g., P uptake by plants), up to 90 % of the total for some processes. They also verified the experimental results of Wagg et al. (2014) who reported a positive correlation between soil biodiversity and ecosystem functionality. Previous studies have shown that soil biodiversity has both positive and negative effects on ecosystem functions and processes (Bradford et al., 2002; Heemsbergen et al., 2004; Nielsen et al., 2011), but whether a reduction in soil community biodiversity affects the integrated performance of an ecosystem remains poorly understood. Therefore, it is necessary to examine the regulation of ecosystem structure and function, in conjunction with aboveground and belowground ecological processes.

The important role of abiotic factors in driving ecosystem multifunctionality was emphasized in the theoretical framework of Giling et al. (2019), in which biotic and abiotic factors individually and effectively combine to drive ecosystem multifunctionality. Plant diversity responds to soil environmental factors through its effects on microorganisms, which can either affect microorganisms individually or drive microbial community changes in conjunction with plant community changes, affecting ecosystem processes (Yang et al., 2022). Jing et al. (2015) found that the combined effects of aboveground and belowground biodiversity contributed to 45 % of the changes in ecosystem multifunctionality, and biotic and abiotic variables accounted for up to 86 % of the changes in ecosystem multifunctionality. Therefore, understanding the major biotic and abiotic factors that regulate ecosystem function is essential for the conservation and management of natural and human-dominated grassland ecosystems.

Most research on the correlation between biodiversity and ecosystem functionality has considered only one trophic level and has concentrated on the influence of changes in plant and soil biodiversity on ecosystem functionality. However, this approach neglects the significant role of insect diversity in ecosystem functionality. Thus, determining the independent and combined effects of plant species richness, biomass, and other plant traits on insect communities is critical for elucidating the mechanisms by which changes in plant communities affect insect communities. Notably, most studies have focused on species culling, and relatively few experimental studies have explored combinations of native dominant and subdominant plant species. Desert steppes are sparsely vegetated in unstable soil environments, with an undetermined relationship between changes in plant diversity, productivity, and other ecosystem functions.

Therefore, in this study, we selected three dominant and seven subdominant species from the Ningxia northern Yanchi desert steppe for monoculture and mixture experiments to establish the richness of plant species (monoculture and 4-, 6-, 8-, and 10-species mixtures), and measured and explored multiple trophic levels and aboveground primary productivity of different plant communities. We aimed to test two hypotheses: (1) different plant species richness positively affects aboveground primary productivity through different ecological niches or species-specific traits and (2) different plant communities directly or indirectly affect the aboveground production of the community through biotic and abiotic factors. Our study enhances the understanding of the links between biodiversity and ecosystem functionality, and provides evidence for a theoretical framework for preserving grassland biodiversity and sustaining the health of grassland ecosystems.

2. Materials and methods

2.1. Study sites

This research was conducted in the northern region of the Yanchi desert steppe (37°76′ N, 107°28′ E), near Mu Us Sandy Land, and the Loess Plateau in the south. This region serves as a transitional zone from the hilly slopes of the Loess Plateau to the Ordos Platform and extends from south to north. This represents an intersection of the agricultural and pastoral areas in northern China (Fig. 1a and b). The experimental area features a consistent flat topography with an average altitude of 1600 m. The climate is temperate continental with a mean annual temperature of 8.7 °C. The annual precipitation is approximately 294 mm (1981–2023), with over 60 % occurring between July and September (Fig. 1c). The annual evaporation was considerably high at 2132 mm. The typical zonal vegetation includes desert steppes. The main soil type is calcareous, sandy, and silty with relatively low fertility. The vegetation is mainly xerophytic and mesoxerophytic, with three dominant species, *Astragalus melilotoides*, *Agropyron mongolicum,* and *Lespedeza potaninii*; seven subdominant species, *Glycyrrhiza uralensis, Sophora alopecuroides, Agropyron cristatum, Cleistogenes squarrosa, Artemisia desertorum, Astragalus austrosibiricus,* and *Elymus dahuricus*; and

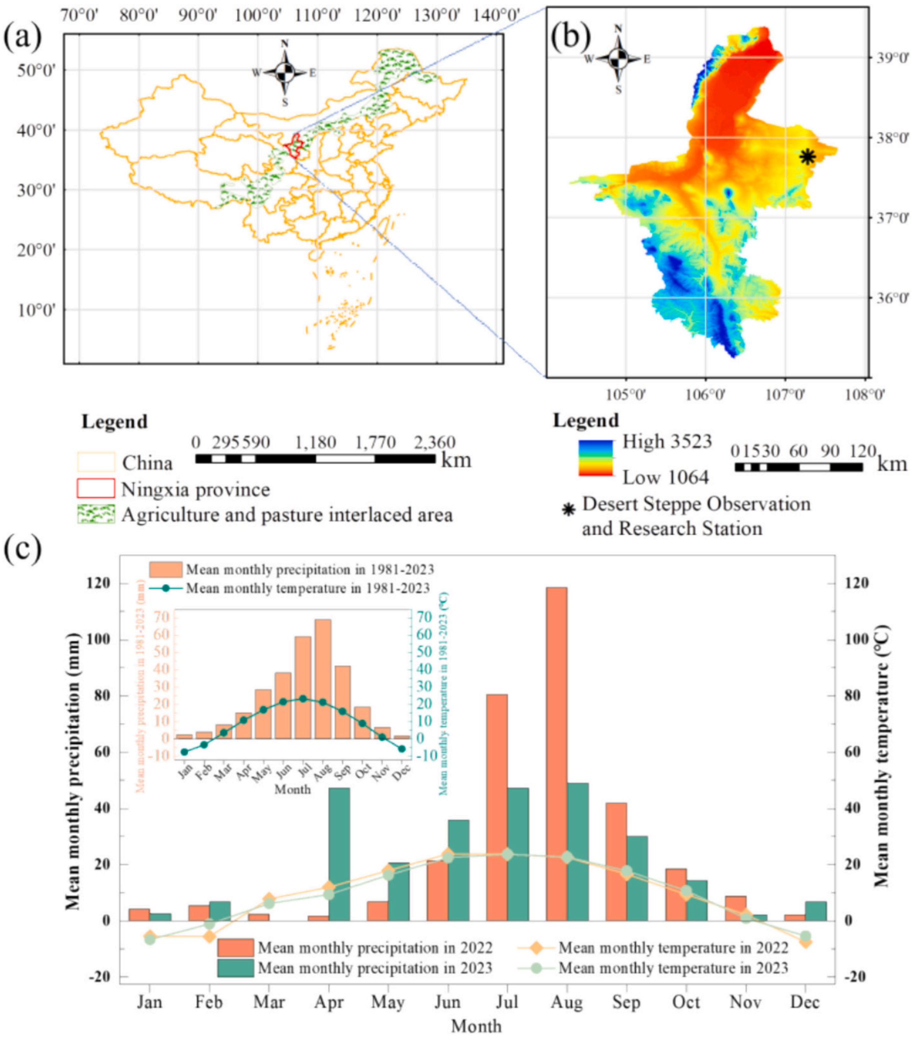

Fig. 1. Profile of the study area.

other companion species, such as *Achnatherum splendens, Leymus secalinus, Pennisetum centrasiaticum, Setaria viridis, Salsola collina, Polygala tenuifolia,* and *Allium mongolicum.*

2.2. Manipulated experiment

Three dominant and seven subdominant species from the Ningxia northern Yanchi desert steppe were selected for monoculture and mixture experiments to establish the richness of the plant species (monoculture and 4-, 6-, 8-, and 10-species mixtures). Species combinations were monocultures of ten species, three groups of 4-species mixes, three groups of 6-species mixes, three groups of 8-species mixes, and one group of 10-species mixes. The total number of treatments was 20 (species combinations in Table S1), with seven replicates for each treatment and an additional 12 plots without planting, totaling 152 plots. A completely randomized experimental design was used, with plots measuring 5 m × 5 m and an aisle width of 1.5 m (see Fig. S1 for the sample plot schematic and aerial images, respectively). The quantity of seeds sown in the monoculture sowing was the maximum environmental capacity, and the proportion of mixed sowing was calculated as the actual price of the seeds used (i.e., the product of seed purity and germination) as a proportion of the weight of the monoculture sowing (sowing seed quantities in Table S2).

The seeds for the experiment were planted from May 16 to 18, 2022, and approximately 6500 m^2 of homogeneous habitat cultivated for agricultural production in the early period around the Ningxia northern Yanchi desert steppe observatory and research station were investigated. First, deep plowing was conducted using a rotary tiller to break up the native vegetation, and plant roots, apoplastic materials, and plant residues were manually collected. The seeds were sown by hand, mulched, and collected from local seed suppliers and in the field. The uniformity of the sprinkled seeds was ensured by thoroughly mixing them into the fine soil of the sample plot; this combination of seeds and fine soil was then evenly sprinkled on the plots by the same worker, with a mulch thickness of approximately 2 cm. All sample plots were weeded regularly to ensure that plant species richness was maintained at the planned levels or slightly below the planned levels where communities were not established. Eight weeks after sowing, the stubble was mowed, leaving approximately 10 cm of stubble, and the biomass was removed to support the establishment of the sown species. Unestablished species were re-cropped in mid-August 2022 using the following criteria: (1) species richness below 50 seedlings per m^2 and (2) monoculture species coverage of <5 % (see Table S3 for seed pretreatment methods). Plots that did not fulfill seedling emergence requirements were replanted in the bare area at the same rate as in the first sowing. No fertilizer was used in the experiment. After planting, water was added from time to time based on soil moisture to ensure proper seed germination and emergence. No watering of the test sample plots was performed since 2023.

2.3. Sample collection and measurement

Sample collection was conducted in mid-August 2023. For plant canopy insects, an ordinary net with a diameter of 28 cm, mesh diameter of approximately 0.5 mm, and length of 50 cm was used. During sampling, the end of the sweeping net handle was held, and the net was swept back and forth evenly in the shape of an "8" once. The opening of the net to be swept was perpendicular to the ground, pointing in the direction of swinging, and swung ten times for each sample. Insects below the plant canopy used polyvinyl chloride plastic cups with an opening diameter of 8 cm and depth of 10 cm. A 30 mL solution was poured into the cup, and the ratio of sugar:acetic:acid:ethanol:water was 3:1:3:80. One trap cup was placed at the center of each plot to be tested and traps were collected by setting them for 72 h. The captured insects were individually placed in vials containing ethyl acetate to kill them. Next, all insects were poured into polyvinyl chloride plastic cups containing a 75 % alcohol solution. The cups were labeled and immediately transported to the laboratory for identification by experts. A morphological classification method was adopted to classify the insect specimens collected from sweep nets and traps according to their order, family, and species, and then into four functional groups, phytophagous, predatory, omnivorous, and parasitic insects, according to their feeding characteristics.

The Margalef, Simpson, Pielou, and Shannon–Wiener insect diversity indices were calculated using the following formulas (Pielou, 1966):

$$\text{Margalef} = (S-1) \div lnN$$

$$\text{Simpson} = -\sum_{i=1}^{s} (P_{\text{i}})^2$$

$$\text{Shannon}-\text{Wiener} = H' = -\sum_{i=1}^{S} P_i lnP_i$$

$$\text{Pielou} = J' = H' \div ln\text{S}$$

where S represents the number of species, N_{i} represents the number of individuals of the ith species at the sample site, N represents the total number of individuals of all species at the sample site, and P_{i} represents the ratio of the number of individuals of the ith species to the total number of individuals, given as N, formulated as $P_{\text{i}} = N_{\text{i}}/\text{N}$.

Productivity measurements were conducted from August 15 to August 20, 2023, and a 1 m × 1 m sample plot was randomly selected, avoiding the edge of the plot (1.5 m). The aboveground biomass of the plants was harvested to denote the community aboveground primary productivity, with a stubble height of 3 cm. Three replicates of each of *A. melilotoides*, *A. mongolicum*, *A. cristatum*, *A. desertorum*, and L. *potaninii* were harvested from the monoculture, and seven replicates of the 10-species mixture were harvested. The remaining treatments were sampled in three replicates, totaling 49 samples, all of which were dried (48 h, 65 °C) to a constant weight and weighed.

The net biodiversity formula is as follows (Roscher et al., 2005):

$$\Delta Y = Y_O - Y_E \qquad = \sum_i RY_{O,i}M_i - \sum_i RY_{E_i}M_i = \sum_i \Delta RY_iM_i$$
$$= N\overline{\Delta RYM} + Ncov(\Delta RY, M)$$

where N represents the total number of species. The total observed yield of the mixture is expressed as $Y_O = \Sigma_i Y_{\text{O},i}$, and the total expected yield of the mixture is denoted by$Y_{\text{E}} = \Sigma_i Y_{E,i}$. $Y_{\text{O},i}$ refers to the computed yield of species i within the mixture, and M_i represents the yield of species i when it is grown in monoculture. The observed relative yield of species i in the mixture was given by $RY_{O,i} = Y_{\text{O},i}/M_i$, and the expected relative yield was denoted by $\text{RY}_{E,i}$. The discrepancy between the expected and observed relative yields for species i in the mixture was indicated by $\Delta RY_i = RY_{\text{O},i} - RY_{E,i}$. The terms $N\overline{\Delta RYM}$ and $Ncov(\Delta RY, M)$ represent the complementarity and selection effects, respectively.

Soil respiration was measured using an LI-8100 (LI-COR Inc., Lincoln, NE, USA). Total soil respiration was measured by burying a soil respiration ring (inner diameter: 20 cm; height: 6 cm) 3 cm into the soil, and soil heterotrophic respiration was determined by burying another PVC ring (inner diameter: 20 cm; height: 40 cm) 37 cm into the soil. Soil temperature and moisture were accurately measured at depths of 0–10 cm near the PVC ring, using a highly reliable portable temperature and moisture probe connected to an LI-8100 instrument. Measurements were collected during sunny daylight hours in August, with the first set of replicates measured precisely from 09:00 to 11:00, the second from 11:00 to 13:00, and the third from 13:00 to 15:00. Three random soil samples of 0–10 cm were collected and thoroughly mixed to create a single representative soil sample using a soil in situ soil sampler (Australia Cote VD51) within the sample plots where plant aboveground production was determined. One sample was passed through a 2 mm sieve and promptly transferred to a 5 mL centrifuge tube, preserved in liquid nitrogen, and transported to the laboratory for storage at −80 °C. The diversity of bacteria and fungi was evaluated using Illumina-based absolute quantification sequencing, while the initial bacterial and fungal sequencing data were processed in QIIME 2 (Yang et al., 2023b), and the soil microbial sequences were analyzed using the GENESCLOUD Platform (https://www.genescloud.cn). The microbial diversity index is calculated in detail at https://www.genescloud.cn/microbiomeProcess/AppendixPage/Schedule.Soil enzyme activity was ascertained using the 96-micropore enzyme plate method (Qi et al., 2016), and the level of soil organic matter was measured by external heating using potassium dichromate. The soil pH and electrical conductivity (EC) were analyzed using a pH-3c meter (Leici, Shanghai, China).

Soil enzyme $E_{\text{C:N}}$, $E_{\text{C:P}}$, and $E_{\text{N:P}}$ were calculated using log-transformed enzyme activities using the following equations (Sinsabaugh et al., 2008):

$$E_{\text{C:N}} = ln(\beta G + CBH)/lnLAP$$

$$E_{\text{C:P}} = ln(\beta G + CBH)/lnAKP$$

$$E_{\text{N:P}} = lnLAP/lnAKP$$

where *βG* denotes β-1,4-Glucosidase, *CBH* denotes cellobiose hydrolase, *LAP* denotes leucine aminopeptidase, and *AKP* denotes alkaline phosphatase, respectively.

The evaluation of the relative limits of carbon, nitrogen, and phosphorus for microbial metabolism was based on a vector analysis model (Zhang et al., 2022).

$$\text{Vector length} = \left(x^2 + y^2\right)^{0.5}$$

$$\text{Vector angle} = \text{Degrees}\left[\text{ATAN2}(x, y)\right]$$

where x denotes $E_{\text{C:N}}$, and y denotes $\text{E}_{\text{C:P}}$.

2.4. Statistical analysis

One-way analysis was used to identify significant variances in insect abundance across various functional groups. Tukey's multiple comparison method was used to determine the microbial α-diversity among plant species richness (Yang et al., 2023b). A general linear model was used to analyze community biomass; the additive partition of biodiversity effects was used to calculate the complementarity, the selection, and the net biodiversity effects (Loreau and Hector, 2001); a constrained principal coordinate analysis (PCoA) employing the Bray–Curtis dissimilarity matrix was conducted using the "vegan" package of R 4.3.3, which was used to analyze the microbial β-diversity (Yang et al., 2023b); and the "rarestR" package was used to analyze the insect β-diversity (Zou et al., 2023) among different plant species richness.

Random forest modeling and correlation analysis were performed using the “randomForest” and “rfPermute” packages of R 4.3.3 and the “Correlation Plot” app of Origin 2024 to identify drivers of aboveground productivity (Ma et al., 2022). The “piecewise SEM,” “nlme,” and “lme4” packages were used to conduct the piecewise structural equation modeling (Tian et al., 2022), which was used to determine how insects, soil physical properties, soil enzyme activity, and microorganisms affected the aboveground biomass of plant communities and its driving effect on the aboveground productivity among the plant species richness.

3. Results

3.1. Aboveground biomass of individual species in monocultures and mixtures

In the second year of the experiment, based on aboveground biomass production in monocultures, *A. melilotoides* was the most productive species, with approximately twice the productivity of *A. desertorum, A. cristatum,* and *A. mongolicum*; *L. potaninii* and *S. alopecuroides* had very low productivity (Fig. 2a). However, in mixtures containing the complete pool of ten species, the aboveground biomass of *A. melilotoides* and *E. dahuricus* was much higher than that of the other species (Fig. 2b). The greatest differences in productivity were between the monoculture and the 10 species mixture of *A. desertorum*, confirming the rationale for selecting five monoculture species for monoculture data collection (*A. melilotoides*, *A. mongolicum*, *A. cristatum*, *A. desertorum*, and L. *potaninii*).

The aboveground biomass production in the mixtures ranged from 155 to 1173 g m^{-2}, with *A. melilotoides* exhibiting the most substantial relative increase among the species present. In the eight-species mixture, *A. melilotoides* , *A. mongolicum* , *L. potaninii* , *G. uralensis* , *A. cristatum* , *C. squarrosa* , *A. desertorum* , *A. austrosibiricus* , *E. dahuricus* species were located above or close to the line, and their biomass in the mixture was predicted based on their yield in the monoculture (Fig. 3). In the mixtures, most species demonstrated relative yields greater than anticipated. Some of the least productive monoculture species reached high relative yields in mixtures (e.g., *E. dahuricus* in 10-species mixtures).

3.2. Species richness–aboveground biomass relationships, overyielding, and niche complementarity

Statistical analysis of the aboveground biomass suggested a positive relationship between species richness and aboveground biomass production (Fig. 4a, Table S4). The additive partitioning method established by Roscher et al. (2005) (Loreau and Hector, 2001), allowed the analysis of the relative contributions of the selection and complementarity effects to the positive net biodiversity effect (Fig. 4b–d). A significant surge was observed in the net biodiversity effect with growth in species richness ($F = 30.04$, $P < 0.001$; Fig. 4b, Table S4). The selection effects tended to increase and then decrease with increasing species richness, with selection effects reaching a maximum for the 8-species mixtures (Fig. 4c), and the complementarity effect was positive across the entire range of species richness levels (Fig. 4d, Table S4).

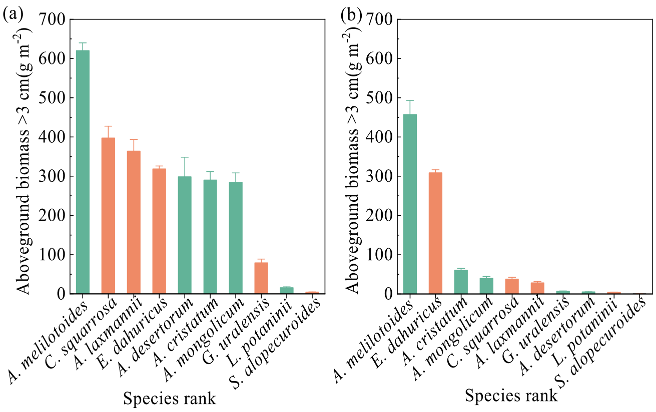

Fig. 2. Rank–dominance relationship of monocultures and 10-species mixtures in the experiment. The values represent the mean aboveground biomass with a standard error (±SE). For the monocultures (a), means were calculated from three identical replicates, and the means for the 10-species mixture (b) were derived from seven congruent replicates. The green bars indicate species for which data were collected in the monoculture plots.

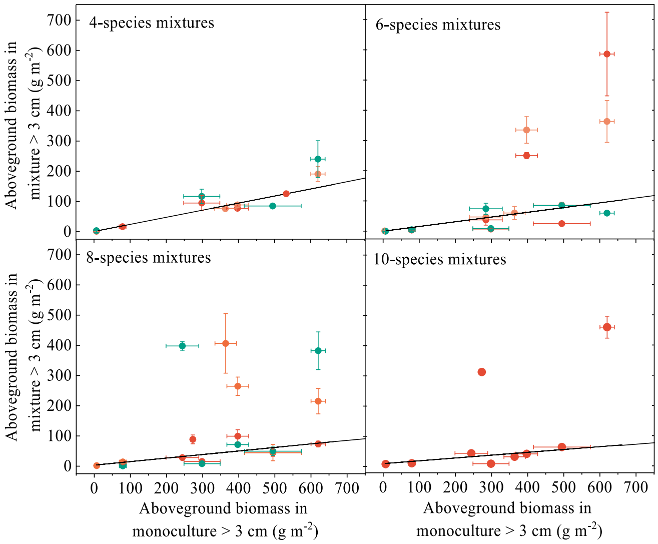

Fig. 3. Aboveground biomass, specific to each species either in monoculture or mixture, is represented by the mean values with the standard error (±SE). These values were calculated from a selection of three replicates originating from five distinct monoculture species and various mixtures at each diversity level. The dots with different colors are used to indicate the unique combinations of species within the same plant richness level. The black line symbolizes the predicted biomass from each species in the mixture, which is derived from the yield of monoculture biomass divided by the species richness level.

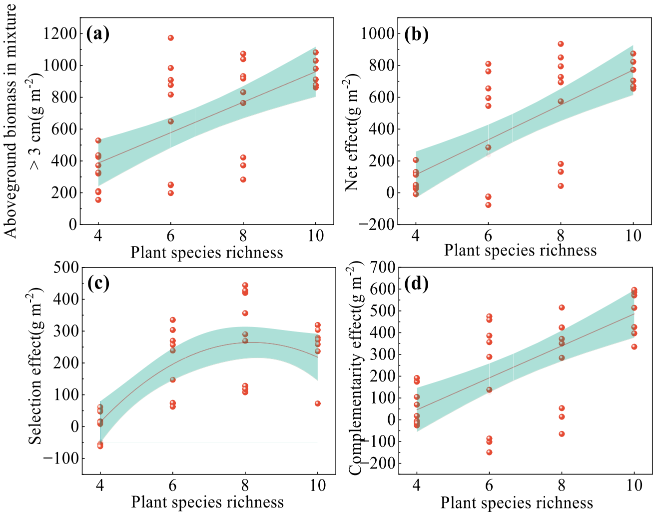

Fig. 4. Aboveground productivity (a), net biodiversity effect (b), selection effect (c), complementarity effect (d), as functions of sown species richness. The dots indicate identical replicates of the same species richness.

3.3. *Changes in insect community composition and abundance among plant species richness*

A total of 16,561 insects belonging to nine orders and 34 families were collected for different plant species richness (Fig. 5, Table 1). The dominant families (I) were Miridae, Agromyzidae, and Cicadellidae, which accounted for 27.09 %, 24.79 %, and 17.67 % of the total number of individuals, respectively. In total, 2338 specimens (14.12 % of the total number of individuals) were found in rich families (II). Common family (III) comprised six families, representing 9.14 % of the total number of individuals. Occasional family (IV) comprised 15 families, representing 6.91 % of all individuals. Eight rare families (V) accounted for 0.28 % of the total number of individuals.

Among the functional groups of insect communities with different plant species richness, phytophagous insects were the most abundant, with 13,074 specimens in seven orders and 22 families, accounting for 78.95 % of the total number of individuals. Omnivorous insects were the second most abundant, with 1885 specimens from two orders and three families, accounting for 11.38 % of the total number of individuals. Predatory insects were the third most abundant, with 1126 specimens from three orders and seven families, representing 6.80 % of the total number of individuals. The lowest abundance was observed for parasitic insects, with 476 specimens from one order and three families, representing 2.87 % of the total number of individuals (Table 1). The order of magnitude of the number of families in the functional groups of insect communities treated with different levels of plant species richness was Ph > Pr > Om > Pa.

Different levels of plant species richness significantly affected the total insect and phytophagous insect population, showing consistent trends (Fig. 5). The total number of insects significantly increased in the 4-species and 6-species mixtures. Compared with the 4- and 6-species mixtures, which exhibited low species richness, the 8-species mixture significantly reduced the number of phytophagous insects ($P < 0.05$). The number of predatory insects was in the order of monoculture >10 > 6 > 8 > 4. The 8-species mixture had the lowest number of omnivorous and parasitic insects, and there were no significant differences ($P > 0.05$) among the plant species gradients.

3.4. *Changes in insect diversity among plant species richness*

No significant differences were observed in the α diversity of the insect community associated with plant species richness ($P > 0.05$; Fig. S2). The Pielou index of the predatory insect monoculture was significantly lower than that of the 10-species mixtures, and the Simpson index was significantly higher than that of all mixtures ($P < 0.05$). The Simpson index of phytophagous insects was appreciably higher in the four-species mixtures than in the six-species mixtures. The Pielou index of parasitic insects was lower in the four-species mixture than in the monoculture and six-species mixtures. Additionally, the Shannon–Wiener index of predatory insects in the 4- and 10-species mixtures showed a significant increase compared to those in the monoculture ($P < 0.05$). The Shannon–Wiener index was significant for mixtures comprising 6-species mixtures compared to those with 4-species mixtures ($P < 0.05$). The Margalef index was significantly higher in the 8-species insect mixtures for omnivorous species than in the monoculture and the 4- and 10-species mixtures. Similarly, a significant increase was observed in the Margalef index for parasitic insects when present in 8-species mixtures compared with their presence in 4- and 6-species mixtures. The Simpson index for omnivorous insects in the 8-species mixtures was significantly lower than that in the monoculture and 4-species mixtures, and the Shannon–Wiener index for omnivorous insects in the 8-species mixtures was higher than in the 4-species mixtures ($P < 0.05$) (Fig. 6).

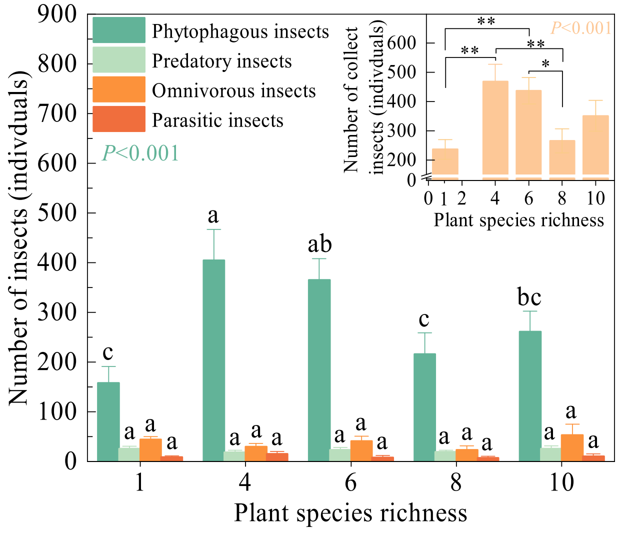

Fig. 5. Changes in insect functional groups and abundance along plant species richness. The lowercase letters within the same insect functional group indicate significant differences among plant species richness at the 0.05 level.

We analyzed the β-diversity of insect communities, separately assessing all and dominant species across various levels of plant species richness. The similarity coefficients for the insect species were below 0.5 (Tables 2 and S5). In comparison, monoculture and the 8- and 10-species mixtures, as well as the 4-species mixtures with the 6-, 8-, and 10-species mixtures, and the 6-species mixtures with the 8- and 10-species mixtures consistently showed reduced similarity for dominant species compared with those favoring all species. The similarity of four- and 8-species mixtures favoring the dominant species and six- and 8-species mixtures favoring all species was the lowest at 0.1590 and 0.2654, respectively. The similarity between the 4- and 10-species mixtures exceeded 0.42, regardless of whether they favored dominant or all species.

3.5. *Changes in microbial community composition and abundance among plant species richness*

The composition (Fig. 7a and b) and absolute numbers (Fig. 7c and d) of bacteria and fungi in the soil linked to plant species richness were analyzed at the phylum level. Actinobacteria, Acidobacteria, Proteobacteria, and Gemmatimonadota were the dominant bacterial phyla associated with the plant species richness. There were only two dominant phyla in the fungal community: Ascomycota and Basidiomycota. The quantity of bacterial copies in the soil showed a unimodal variation pattern with increased plant species richness, and the absolute copy number of bacteria in the 8-species mixtures was higher than that in the other mixtures. In all mixtures, except for the 8-species mixtures, the absolute copy number of soil fungi decreased with increasing plant species richness.

3.6. *Changes in soil microbial diversity among plant species richness*

The Chao 1 index for bacteria showed no significant differences, whereas for fungi, both Shannon and Simpson indices remained constant ($P > 0.05$). In contrast, measuring bacteria under the Shannon, Simpson, and Good coverage indices revealed a highly significant difference ($P < 0.01$) between monocultures and 8-species mixtures (Fig. 8). However, the PCoA analyses based on the Bray–Curtis dissimilarity matrix demonstrated poor segregation in the bacterial and fungal community structures associated with different plant species richness (Fig. 9).

3.7. *Potential drivers of aboveground biomass among plant species richness*

To identify the main soil physical characteristics, insect functional groups, and soil microbial drivers of the aboveground biomass of different plant species, we employed random forest analysis (Fig. S3a). It

Table 1
Composition of the insect community among plant species richness.

Functional group	order	Species	Number of individuals					Class
			1	4	6	8	10	
Ph	Diptera	Agromyzidae	637	1351	995	814	308	I
		Chloropidae	31	60	72	78	36	III
		Drosophilidae	9	20	19	38	13	IV
		Scaeva selenitica	10	13	9	2	9	IV
		Anthomyia	32	8	24	4	20	IV
	Homoptera	*Psammotettix striatus*	402	648	906	384	565	I
		Cicadella viridis	4	6	8	2	2	
		Aphididae	100	64	–	–	–	IV
	Hemiptera	*Trigonotylus caelestialium*	536	706	796	370	499	I
		Polymerus cognatus	183	64	87	45	98	
		Lygus pratensis	227	72	20	4	–	
		Stenodema turanica	40	358	188	57	136	
		Stictopleurus abutilon	8	28	32	44	36	
		Coranus hammarstroemi	–	1	–	–	–	V
		Nysius ericae	2	136	–	1	–	IV
		Carpocoris purpureipennis	2	4	–	–	–	V
		Aelia sibirica Reuter	1	–	–	–	–	
	Coleoptera	*Monolepta hieroglyphica*	57	64	80	36	48	III
		Gonocephalum reticulatum	6	5	14	6	6	IV
		Pentodon mongolicus	2	2	–	2	3	V
		Meteutinopus mongolicus	1	2	–	1	1	V
		Chrysolina aeruginosa	–	–	–	–	1	V
	Hymenoptera	*Halictus*	2	1	2	8	4	IV
		Apis mellifera ligustica	4	1	3	1	1	IV
	Orthoptera	*Oedaleus infernalis*	6	1	4	7	5	IV
		Acrida cinerea	2	2	8	7	5	IV
	Lepidoptera	Noctuidae	36	22	10	16	18	III
		Lepidoptera	26	6	11	18	16	
Pr	Coleoptera	*Harpalus griseus*	297	62	121	88	68	II
		Harpalus calceatus	40	34	29	36	27	
		Cymindis binotata	17	4	14	3	19	
		Harpalus pallidipennis	8	5	27	16	2	
		Carabus brandti	–	2	–	–	–	
		Merohister jekeli	–	3	5	7	2	IV
		Ocypus (Pseudocypus) graeseri	1	1	–	–	–	V
		Coccinellidae	–	–	–	–	12	V
	Neuroptera	Myrmeleontidae	7	32	4	14	12	IV
		Chrysopa sinica	12	14	14	7	37	IV
	Hemiptera	*Nabis palifer*	11	12	–	–	–	IV
Om	Hymenoptera	*Cataglyphis aenescens*	497	222	272	132	296	II
		Formica cunicularia	91	42	60	55	58	III
	Dermaptera	*Labidura riparia*	76	5	36	23	20	IV
Pa	Hymenoptera	*Dacnusa*	113	116	44	16	–	III
		Cynipinae	14	20	24	48	72	III
		Cremastinae	1	2	1	3	2	V

Note: Ph, Phytophagous insects; Pr, predator insects; Om, Omnivorous insects; Pa, Parasitic insects. Class I, dominant families ($D \geq 10$ %); II, rich families ($5 \% \leq D < 10 \%$); III, common families ($1 \% \leq D < 5 \%$); IV, occasional families ($0.1 \% \leq D < 1 \%$); V, rare families ($D < 0.1$ %).

($R^2 = 0.10$, $P < 0.01$) showed that good bacterial coverage and alkaline phosphatase were the most critical drivers regulating the aboveground biomass of the plant community ($P < 0.01$), followed by soil autotrophic respiration ($P < 0.05$). Correlation analyses (Fig. S3b) revealed that bacterial diversity, fungal diversity, soil physical characteristics, and the activities of soil enzymes involved in the cycling of carbon, nitrogen, and phosphorus significantly influenced aboveground biomass. The predominant bacterial taxa, Actinobacteria, and the preeminent fungal taxa, Ascomycota, were identified as significant determinants ($P < 0.05$), highlighting their critical role in influencing plant productivity.

Piecewise segmented structural equation modeling (SEM) analysis was used to establish an integrated pathway of aboveground biomass impacts among different plant species richness (Fisher's C = 2.48, $P = 0.29$, df = 2, AIC = 68.29) (Fig. 10a and b), and the final model explained 46 % of the aboveground biomass. The results showed that soil physical characteristics and carbon-, nitrogen-, and phosphorus-related soil enzyme activities indirectly affected plant community aboveground biomass by altering the bacterial diversity and community structure. C-, N-, and P-related soil enzyme activities had direct and significant positive effects on the bacterial diversity.

4. Discussion

4.1. Direct and indirect responses of plant community aboveground productivity to plant species richness

Biodiversity is fundamental to ecosystem processes, particularly primary production (Cardinale et al., 2006). We ascertained a net biodiversity gain that embodied the consequence of advantages gleaned from selection and complementarity, one reason for which can be observed by visually comparing the biomass of monocultures to that of mixtures, especially the 8-species mixtures (Fig. 3). The findings show that complementarity and selection effects contribute to net biodiversity effects. Another study demonstrated a positive correlation between biodiversity and productivity, attributable to selection effects (Roscher et al., 2005). This phenomenon suggests that the increased incorporation of dominant and productive species is associated with an increased number of species. Our experiments showed a trend where the selection effects initially increased with species richness and then decreased; the peak of this selection effect was evident in 8-species mixtures. Aggregating data from highly productive species within low-diversity

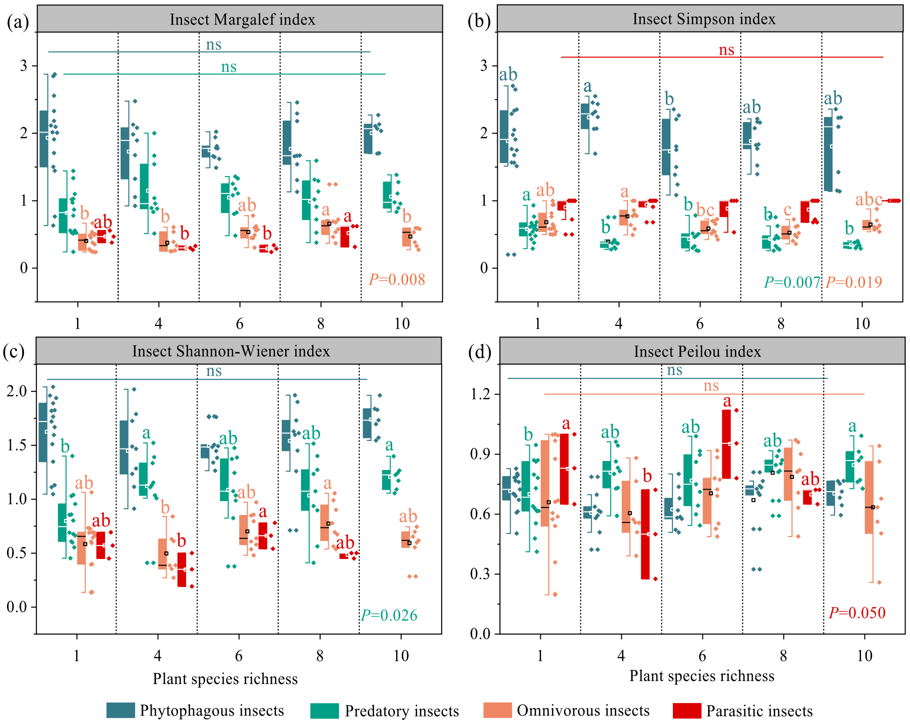

Fig. 6. Changes in the α diversity of functional groups of insects among plant species richness. The values represent the mean (±SE). Within the same insect functional group, distinct lowercase letters signify statistically significant differences in richness among various plant species, with a significance level set at 0.05.

Table 2
Comparison of insect species similarity among the plant species richness gradient (favoring all species).

Plant species richness	1	4	6	8
4	0.3163			
6	0.3006	0.3416		
8	0.4022	0.3946	0.2654	
10	0.4036	0.4337	0.2847	0.2735

mixtures leads to greater productivity than aggregating data from monocultures of both dominant and subdominant species (Roscher et al., 2005). Even when considering the delayed establishment of L. *potaninii*, the relative yields of *E. dahuricus* and *A. mongolicum* tended to be higher in mixtures than in monocultures, indicating a stronger intraspecific than interspecific competition (Roscher et al., 2005). We also observed that complementary effects were most pronounced with high species richness in our selected desert steppe-dominant and steppe-subdominant species combinations, which was the primary factor driving the observed enhancement in productivity with an increase in plant diversity.

4.2. Direct and indirect responses of plant community aboveground productivity to insect diversity

In this study, 45 insect species belonging to nine orders and 34 families were collected. The three dominant families are Miridae, Agromyzidae, and Cicadellidae. The total number of insects was higher in low plant species richness than in monocultures and high plant species richness because moderate plant species richness increases the resources available to insects (e.g., food and habitats, which attract additional insects to migrate to the plot) (La Pierre and Smith, 2016; Streitberger and Fartmann, 2016). In this study, we captured various insect species, including phytophagous, predatory, omnivorous, and parasitic. The majority of captured insects were phytophagous, probably because high temperatures and rainfall during the summer months promote plant and insect growth and reproduction. Additionally, some phytophagous insects (e.g., bees) are known to visit flowering plants (Pfisterer et al., 2003), which may have contributed to the high number of phytophagous insects observed. Most phytophagous insects feed on plants of a single genus or family; therefore, an increase in plant species richness may contribute to an increase in the abundance of these insects. However, in the present study, plant and insect diversity did not show a consistent trend, indicating that consumer (primary or secondary) species richness may not be attributable to plant species richness (Pellissier et al., 2013). Environmental variables are stronger predictors of insect diversity than of plant diversity (Kemp and Ellis, 2017). Additionally, estimates of insect species richness in a given community may be biased when sampling omnivorous species that can move between sampling plots with different species richness values. Omnivorous species may also be influenced by a cascading bottom-up effect, which is affected by plant diversity through variations in herbivore abundance and diversity (Haddad et al., 2009; Scherber et al., 2010). The cascading effect of insect diversity reduces phytophagous insect diversity as the number of natural enemies increases, which has potential implications for plant abundance (Pearson and Dyer, 2006). The 8-species mixtures significantly reduced the number of phytophagous insects ($P < 0.05$), probably because the sample plots had only meiofauna (insects), which were few in number and low in feeding and did not have a significant weakening effect on biomass. Analyses of insect diversity indices for different plant species richness showed that different plant species richness could alter the characteristics of plant communities, affecting insect survival conditions, and ultimately, insect diversity. Insect similarity indices at different plant species richness levels were all below 0.5, and the 4- and 8-species mixtures yielded the lowest similarity, favoring the dominant species. The 6- and 8-species mixtures showed benefits for all species, with 0.1590 and 0.2654, respectively. Insects collected from different habitats showed different results, but all showed low similarity. These findings indicate that insects tend to select for different plant communities.

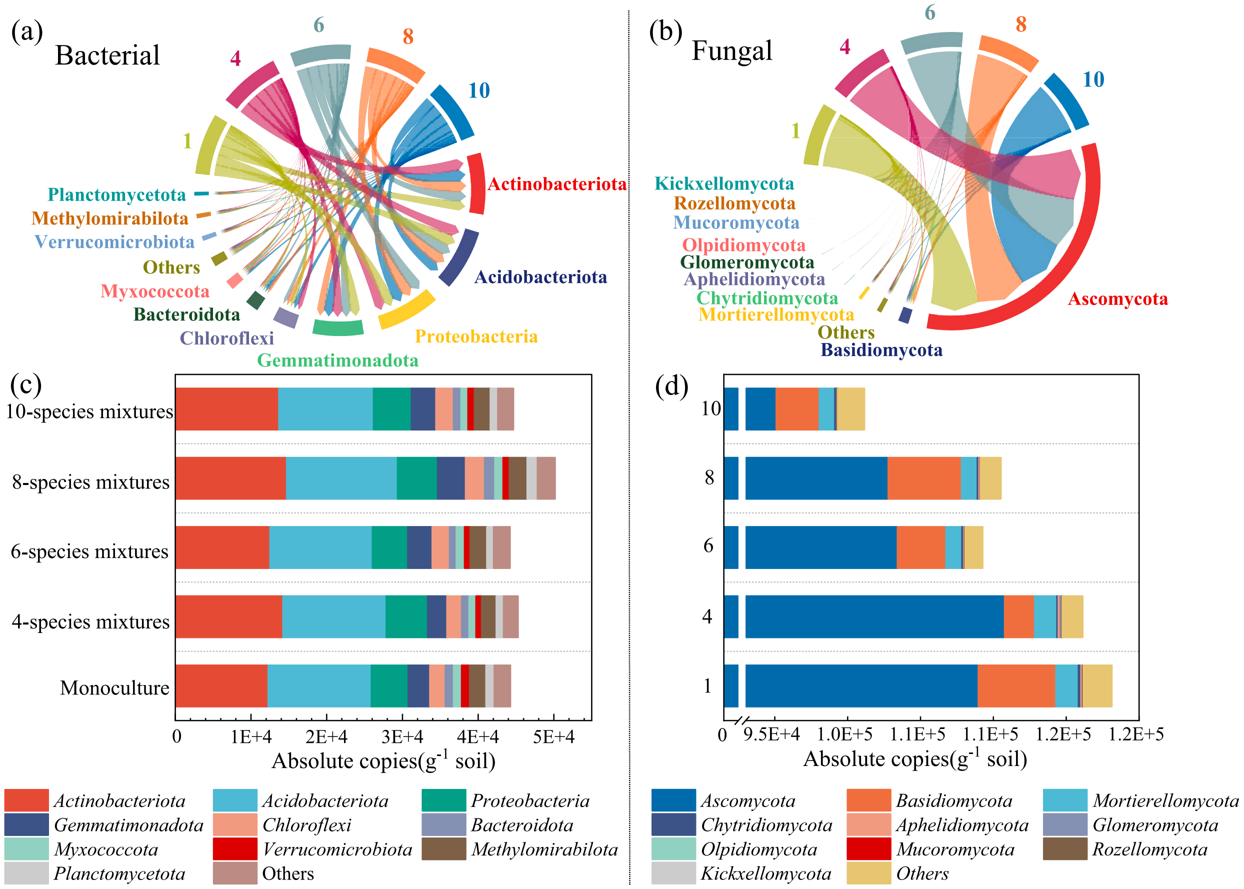

Fig. 7. The contrast of soil bacterial (a) and fungal (b) community composition among plant species richness. Absolute copies of predominant taxonomic groups (Abundance top 10) at the level of bacterial (c) and fungal (d) phyla.

4.3. Direct and indirect responses of plant community aboveground productivity to soil and soil microbial diversity

Plant-induced changes in soil properties may occur through root secretion (Dukunde et al., 2019; Pan et al., 2023). Stoichiometric analyses of soil enzymes for different plant species showed that microbial metabolism was consistently constrained by carbon, and phosphorus (Fig. S4). The relative limitation of microbial metabolic carbon was significantly smaller ($P < 0.05$) in the 8-species mixtures than in the monoculture (Fig. S4a). Soil enzyme activity is regulated by resource demand and supply. When microorganisms are limited by a particular resource, to access enzymes preferentially, they increase the amount of energy and nutrients they invest because of the shortage of resources. In this study, a significant negative correlation was observed between soil respiration and the enzymes involved in nitrogen and phosphorus acquisition and soil respiration ($P < 0.001$), suggesting that microorganisms can regulate resource acquisition strategies through resource allocation (Wang et al., 2023). Soil total respiration and heterotrophic respiration related to microbial respiration differed significantly between the monoculture and the 6-species mixtures (Table S6). Additionally, soil enzyme activity was significantly positively correlated with soil temperature, moisture, and pH (Fig. S3b). Members of the phylum Actinomycetes that coexist under different plant species richness conditions form hyphae to access water and scarce nutrients, which enables survival strategies in dry environments and may increase drought resistance in desert plants (Řeháková et al., 2015; Yang et al., 2023b). Some Ascomycetes phyla have nitrogen-fixing capacity and can increase nutrient effectiveness by solubilizing phosphates and degrading residues (Yang et al., 2023a), thereby promoting the growth of desert steppe plants. The 8-species mixtures significantly increased the number of ascomycete phyla in the soil compared to that of other mixtures. Ascomycete fungi are primarily saprophytic and tend to utilize readily decomposable carbon components. In contrast, Basidiomycota prefer organic substances that are difficult to degrade, such as lignin and cellulose (Yang et al., 2023b). Microbial α-diversity does not exhibit discernible or U-shaped patterns in species richness, particularly for fungi. This phenomenon can be attributed to the different shaping variables of the bacterial and fungal communities. Typically, bacterial communities are influenced by their ecological niche, whereas fungal communities exhibit comparatively high plant specificities (Urbanová et al., 2015; de Vries et al., 2018).

Analysis using piecewise SEM revealed that soil properties (i.e., temperature, pH, and EC) were the most important abiotic drivers of aboveground primary productivity, influencing combinations of dominant and non-dominant desert steppe species, and that certain elements within the soil biomass, particularly bacterial diversity and taxa, had a greater impact on primary productivity than other elements. In summary, different combinations of dominant and subdominant species lead to variations in the composition and diversity of plant, insect, and microbial communities as well as changes in soil properties, which are direct and indirect drivers of net primary productivity.

5. Conclusions

This study is one of the few that have examined the combined effects of plant species richness on soil factors, insect diversity, and microbial diversity, and their impact on the productivity drivers of dominant and subdominant plant communities. Our findings provide clear empirical evidence that variations in plant species richness drive aboveground primary productivity through soil variables, biome structure, and

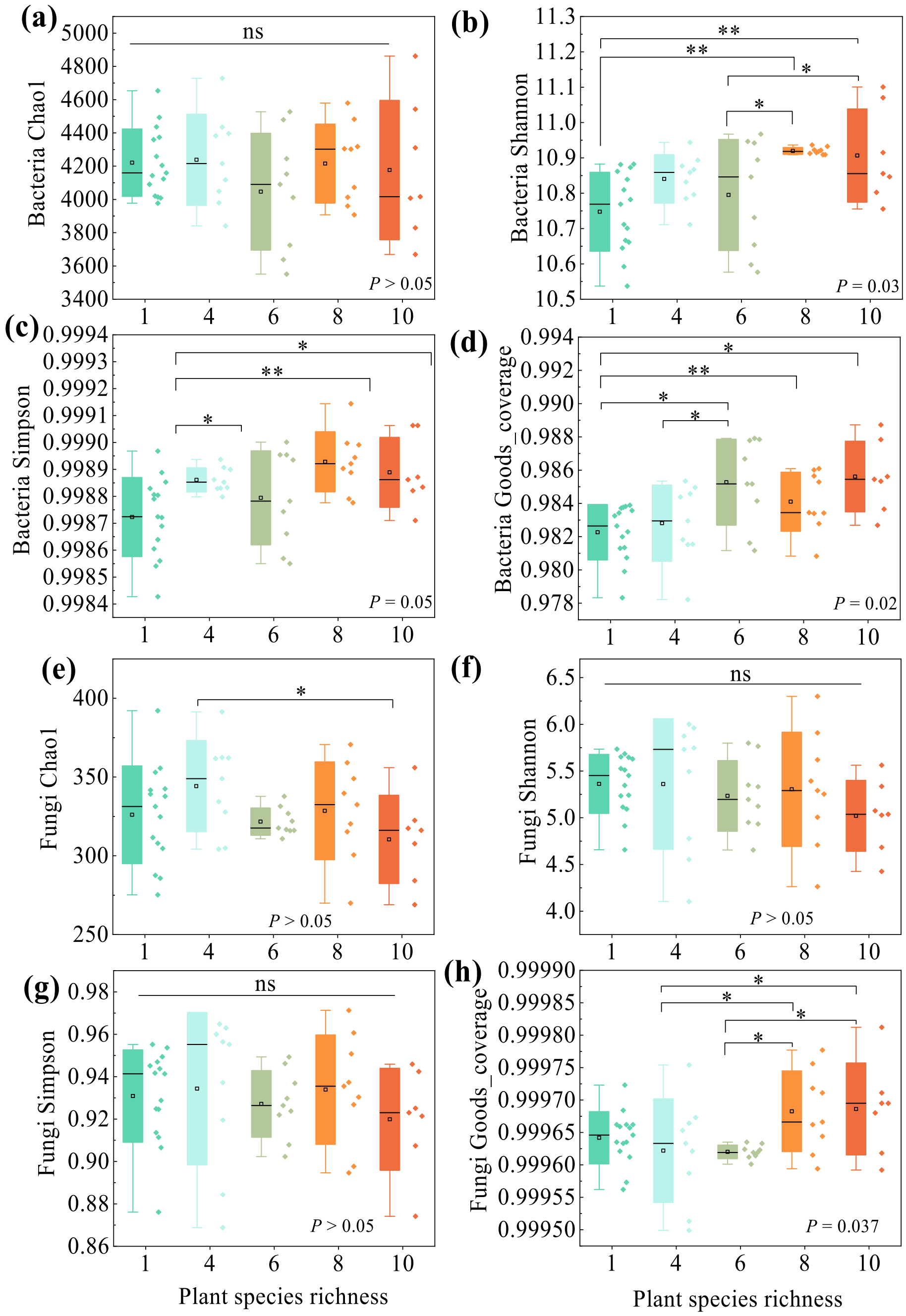

Fig. 8. Bacterial and fungal α diversity in soil among plant species richness. The values represent the mean (±SD). For bacteria, Chao1 (a), $F = 0.68$, $P = 0.611$, Shannon (b), $F = 4.85$, $P = 0.003$, Simpson (c), $F = 4.33$, $P = 0.005$, Goods_coverage (d), $F = 5.15$, $P = 0.002$; for fungi, Chao1 (e), $F = 1.61$, $P = 0.188$, Shannon (f), $F = 0.70$, $P = 0.597$, Simpson (g), $F = 0.44$, $P = 0.781$, Goods_coverage (h), $F = 2.81$, $P = 0.037$, FDR corrected. * and ** represent significant differences at $P < 0.05$ and $P < 0.01$, respectively.

diversity and that selection and complementary effects make important positive contributions to aboveground primary productivity. Plant species richness significantly influenced the diversity of phytophagous insects. However, its impact on the overall insect diversity decreased as trophic levels increased. The composition and diversity of plant, insect, and microbial communities vary depending on the combination of dominant and subdominant species, and these variations affect soil properties, forming direct and indirect drivers of net primary productivity. These variations can be used to predict the long-term effects of future biodiversity loss. Because of the decline in biodiversity, bolstering efforts to conserve arid and semiarid grassland ecosystems, with particular emphasis on dominant or subdominant species, is essential. In future research, we will continue to maintain and monitor dominant and subdominant plant communities and further explore their relationships with soil and ecosystem functions to improve the assessment of the multiple functions and overall services of ecosystems under the species richness gradient and the understanding of the relationships between biodiversity and ecosystem functions, and the potential mechanisms.

CRediT authorship contribution statement

Xu Luo: Writing – original draft, Visualization, Software, Methodology, Data curation. **Yingzhong Xie:** Writing – review & editing, Supervision, Resources, Project administration, Methodology,

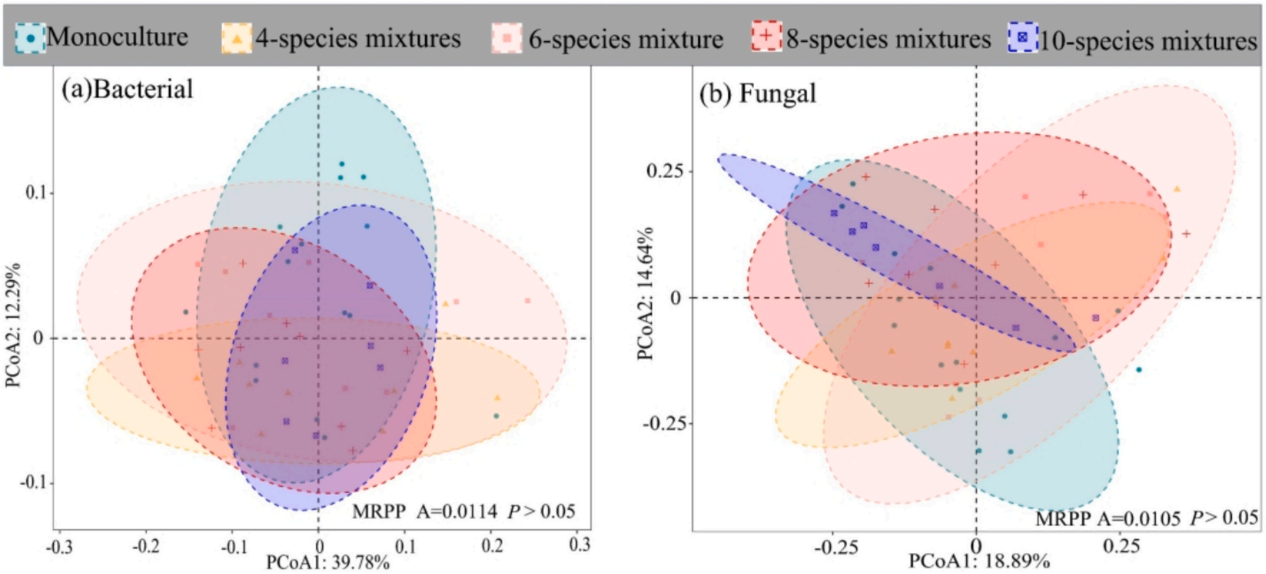

Fig. 9. A constrained principal coordinate analysis (PCoA), underpinned by the Bray–Curtis dissimilarity matrix, represents alterations in bacterial (a) and fungal (b) genus communities. Each point on this graphical representation shows an independent replicate, with distinct colour-coding denoting variations in plant species richness.

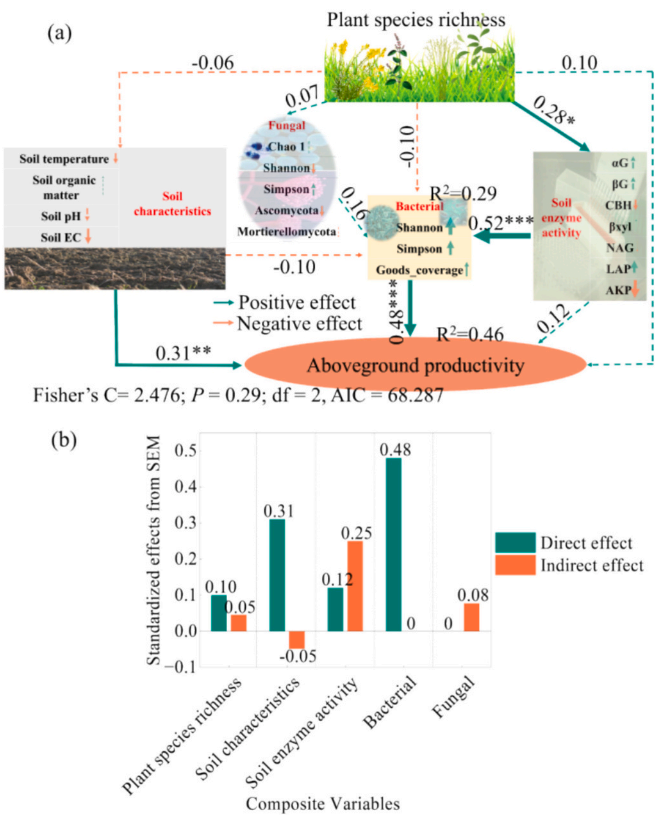

Fig. 10. Main pathways of plant aboveground biomass among plant species richness. Piecewise structural equation modeling (a) accounting for the direct and indirect effects (b) of soil indicators and microbiological characteristics on plant aboveground biomass. The green and orange arrows indicate the positive and negative influences, respectively. The solid lines indicate the significant coefficients ($P < 0.05$) and the dotted lines indicate the nonsignificant ($P > 0.05$) coefficients ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$). The numbered arrows between composite elements typify direct pathways and standardized path coefficients. The breadth of the arrows is proportionate to the strength of the path coefficient.

Conceptualization. **Shaoli Yue:** Investigation. **Mingfan Yang:** Investigation. **Cui Han:** Software, Investigation. **Yaxin Zhao:** Investigation, Data curation. **Ying Zhao:** Investigation, Data curation. **Jianping Li:** Writing – review & editing, Supervision, Methodology, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106052.

Data availability

Data will be made available on request.

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