Plant diversity enhances ecosystem multifunctionality via multitrophic diversity

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Ecosystem functioning depends on biodiversity at multiple trophic levels, yet relationships between multitrophic diversity and ecosystem multifunctionality have been poorly explored, with studies often focusing on individual trophic levels and functions and on specific ecosystem types. Here, we show that plant diversity can affect ecosystem functioning both directly and by affecting other trophic levels. Using data on 13 trophic groups and 13 ecosystem functions from two large biodiversity experiments—one representing temperate grasslands and the other subtropical forests—we found that plant diversity increases multifunctionality through elevated multitrophic diversity. Across both experiments, the association between multitrophic diversity and multifunctionality was stronger than the relationship between the diversity of individual trophic groups and multifunctionality. Our results also suggest that the role of multitrophic diversity is greater in forests than in grasslands. These findings imply that, to promote sustained ecosystem multifunctionality, conservation planning must consider the diversity of both plants and higher trophic levels.

Grasslands and forests cover half of the Earth's land surface[1], harbour nearly 60% of the world's known species[2], and are closely linked to six United Nations' Sustainable Development Goals[3]. However, both of these ecosystems are undergoing rapid biodiversity loss due to anthropogenic disturbance and climate change[4,5]. Biodiversity at multiple trophic levels provides ecosystem services in various ways, such as diverse pollinators ensuring plant production[6,7], while predators like spiders and birds control herbivore populations and prevent pest outbreaks[8]. Loss of biodiversity across trophic levels can thus impair ecosystem functions. Furthermore, complex interactions among trophic levels can also influence ecosystem functions[9–13]. Previous studies have shown that increased plant diversity and biomass may decrease light or soil nutrient availability if these resources are more completely consumed when niches are filled in diverse communities[14,15]. Likewise, increasing herbivore diversity is expected to increase herbivore biomass while decreasing plant biomass (given

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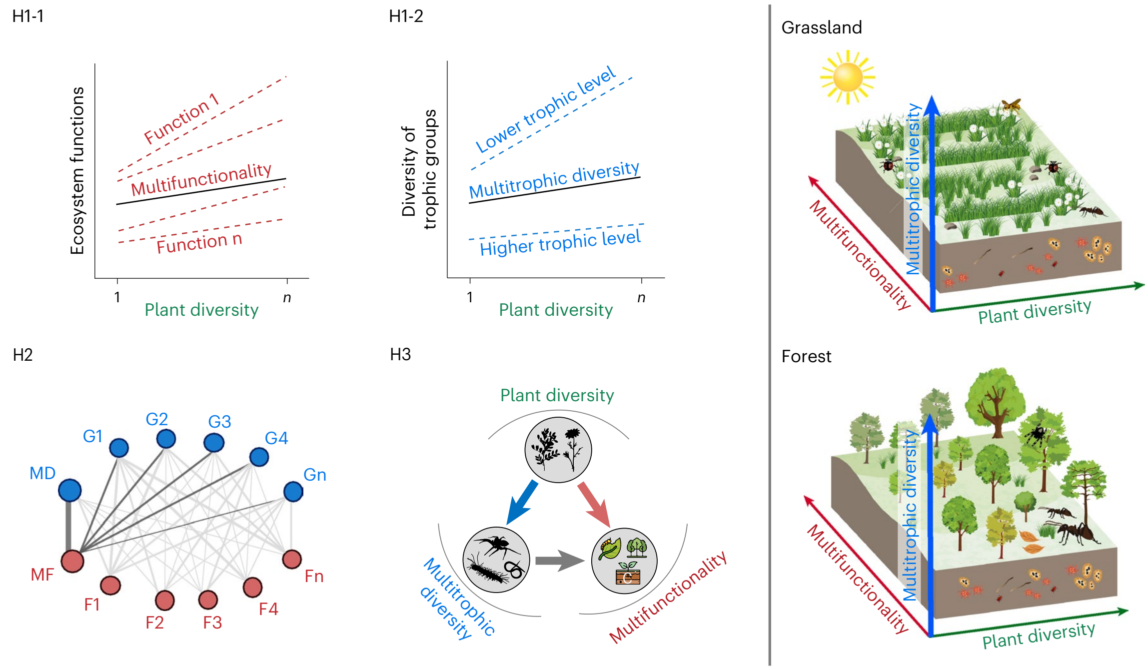

Fig. 1 | Graphical illustration of framework and hypotheses of this study. The study sites included the Jena Experiment, with grassland plots, and the BEF-China Experiment, with forest plots. We collected data on the diversity of 12 trophic groups and 13 ecosystem functions under varying plant diversities to test hypotheses H1 to H3. For both experiments, we hypothesized that: (1) plant diversity increases individual ecosystem functions and multifunctionality (H1-1) and plant diversity increases multitrophic diversity, with stronger effects on lower trophic levels than on higher trophic levels (H1-2); (2) the diversity of individual trophic groups and multitrophic diversity influence individual ecosystem functions and ecosystem multifunctionality, with multitrophic diversity having a stronger effect on multifunctionality than individual trophic groups (H2); and (3) plant diversity enhances multifunctionality both directly and indirectly via individual-group or multitrophic diversity (H3). Overall, multitrophic diversity plays a stronger role in maintaining multifunctionality in forests than in grasslands because trees have longer life cycles and higher structural complexity than herbaceous plants, thus supporting higher multitrophic diversity and more complex trophic interactions. MF, multifunctionality; MD, multitrophic diversity; F, ecosystem function; G, trophic group.

that plants are resources for herbivores[16–18]. Nevertheless, most recent research has either focused on individual trophic levels—often plants—ignoring the role of trophic complexity for ecosystem functioning[19–21], or did not consider whether these relationships vary across ecosystems[22–24]. These caveats make it unclear whether multitrophic diversity in general can be used to predict ecosystem multifunctionality. Grasslands and forests differ greatly in their demographic and structural characteristics, which also makes it unclear whether changes in multifunctionality are driven by similar mechanisms[4,25]. Understanding how biodiversity across trophic levels affects multifunctionality across these ecosystems assists in identifying common drivers and predicting the impacts of biodiversity loss on ecosystems and human well-being.

Multiple biodiversity experiments in which plant species richness was manipulated have shown that plant diversity not only enhances ecosystem functions, such as productivity, through complementarity in resource use[20,21,26], but also indirectly affects ecosystem functions by regulating diversity at higher trophic levels[27,28] and trophic interactions among species[29]. Further observational studies on natural ecosystems have found that the biodiversity of plants and higher trophic levels can enhance ecosystem functioning and multifunctionality[22,24]. However, there is a lack of large-scale, long-term biodiversity experiments investigating how ecosystem functions and multifunctionality depend on plant diversity and the diversity of all other trophic levels, that is, multitrophic diversity (hereafter, used in this sense, excluding plant diversity) in different types of ecosystems. Moreover, although biodiversity experiments on grasslands have demonstrated the importance of plant diversity for multifunctionality[30], it remains unknown how trophic groups other than plants affect this multifunctionality and how general such effects are across ecosystems such as grasslands and forests. If the effect of multitrophic diversity on multifunctionality were to be found to be stronger than that of individual trophic groups, this would suggest the need for a more holistic conservation approach across all trophic levels.

Here, we analysed how plant diversity, via multitrophic diversity, was related to ecosystem multifunctionality in two large-scale biodiversity experiments (Fig. 1 and Supplementary Fig. 1) in grassland (the Jena Experiment[31]) and forest (the Biodiversity–Ecosystem Functioning Experiment China (BEF-China)[32]). These two experiments cover plant species richness gradients from 1 to 60 (grassland) and 1 to 24 (forest) species, providing a large and robust dataset of multitrophic diversity to allow for causal analyses. In addition to the plants, we considered the species richness (hereafter, 'diversity') of the 12 above- and belowground trophic groups, including soil bacteria, arbuscular mycorrhizal fungi, nematodes, soil mites, the Cercozoa, the Oomycetes, leaflitter fungi, arthropod herbivores, herbivore-associated bacteria, arthropod pollinators, arthropod predators and arthropod parasitoids, together with 13 ecosystem functions related to multiple ecosystem services. We calculated both the average and threshold-based multifunctionality[22], as well as three types of average multifunctionality, based on provisioning (plant productivity and community stability), regulating (pathogen resistance, herbivory resistance, parasitism rate and predation rate) and supporting (leaf-litter production, leaf-litter carbon, extracellular enzyme activities in litter (β-glucosidase (BG) and polyphenol oxidase (PPO)), soil organic carbon, soil microbial biomass carbon and soil basal respiration) functions. Additionally, we calculated the above- and belowground multitrophic diversity and multifunctionality to compare the relative importance of the

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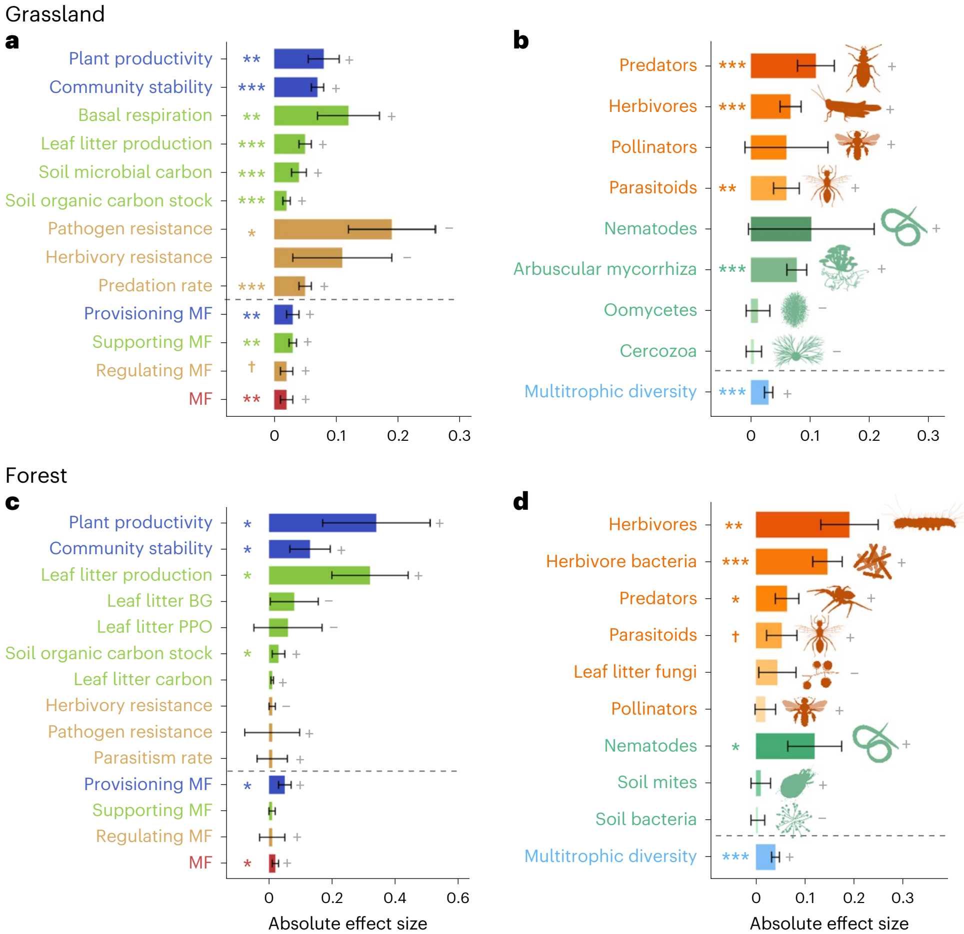

Fig. 2 | Effect size of relationships between plant diversity and individual ecosystem functions and multifunctionality, and between plant diversity and the diversity of individual trophic groups and multitrophic diversity. **a**,**c**, Effect size (standardized coefficients; mean ± s.e.m.) of plant diversity on individual ecosystem functions (provisioning in blue, supporting in green, regulating in orange) and multifunctionality in grassland (**a**, $n = 80$ plots) and forest (**c**, $n = 47$ plots) ecosystems. **b**,**d**, Effect size (standardized coefficients; mean ± s.e.m.) of plant diversity on the diversity of individual trophic groups and the multitrophic diversity in grassland (**b**) and forest (**d**) ecosystems. The slope, as an indication of effect size, and *P* values were calculated based on linear models, including plant diversity and site/block as predictors. All tests were two-sided. Here, we used the absolute effect size for comparison, where the + or − in grey indicates the direction of the corresponding effect. $^{\dagger}P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

aboveground, belowground and overall multitrophic diversity on the aboveground, belowground and average ecosystem multifunctionality. We fitted linear models and structural equation models to analyse the relationships between plant diversity, multitrophic diversity and ecosystem multifunctionality.

We hypothesized that, in both types of ecosystems: (1) plant diversity increases individual ecosystem functions and multifunctionality (H1-1)[30,33] and plant diversity increases multitrophic diversity[34,35], with stronger effects on lower than on higher trophic levels (H1-2) due to the increasing distance along the food chain[15,35,36]; (2) the diversity of individual trophic groups and multitrophic diversity influence individual ecosystem functions and ecosystem multifunctionality[22,24,37], with multitrophic diversity having a stronger effect on multifunctionality than individual trophic groups because multitrophic diversity considers the interactions and functional complementarity between different trophic groups (H2)[22,24,28,30,38]; and (3) plant diversity enhances multifunctionality both directly and indirectly via individual-group or multitrophic diversity (H3) (Fig. 1). Overall, we expected that multitrophic diversity would play a stronger role in maintaining the multifunctionality in forests rather than in grasslands because trees have longer life cycles and higher structural complexity than herbaceous plants, thus supporting higher multitrophic diversity and more complex trophic interactions[28].

Results and discussion

Plant diversity affects ecosystem multifunctionality and multitrophic diversity

Plant diversity increased the provisioning multifunctionality and average multifunctionality in both ecosystem types (we extracted *P* values and R^2 from linear models to show the relationship between plant diversity and ecosystem functions; Fig. 2a,c). In the grassland experiment, the plant diversity increased plant productivity ($P = 0.003$, $R^2 = 0.32$), community stability ($P < 0.001$, $R^2 = 0.36$), basal respiration ($P = 0.046$, $R^2 = 0.15$), leaf-litter production ($P < 0.001$, $R^2 = 0.30$), the soil organic carbon stock ($P < 0.001$, $R^2 = 0.50$), the soil microbial biomass carbon content ($P < 0.001$, $R^2 = 0.40$), the predation rate ($P = 0.004$, $R^2 = 0.27$) and the provisioning multifunctionality ($P = 0.002$, $R^2 = 0.22$), supporting multifunctionality ($P = 0.002$, $R^2 = 0.22$), regulating multifunctionality ($P = 0.07$, $R^2 = 0.10$) and average multifunctionality ($P = 0.005$, $R^2 = 0.20$), while decreasing pathogen resistance ($P = 0.01$, $R^2 = 0.10$) (Fig. 2a). In the forest experiment, the plant diversity promoted plant productivity ($P = 0.036$, $R^2 = 0.21$), community stability ($P = 0.047$, $R^2 = 0.09$), leaf-litter production ($P = 0.01$, $R^2 = 0.15$), the soil organic carbon stock ($P = 0.019$, $R^2 = 0.37$) and the provisioning multifunctionality ($P = 0.01$, $R^2 = 0.17$) and average multifunctionality ($P = 0.045$, $R^2 = 0.16$) (Fig. 2c). Plant diversity played a more important role in regulating the different types of multifunctionality in the

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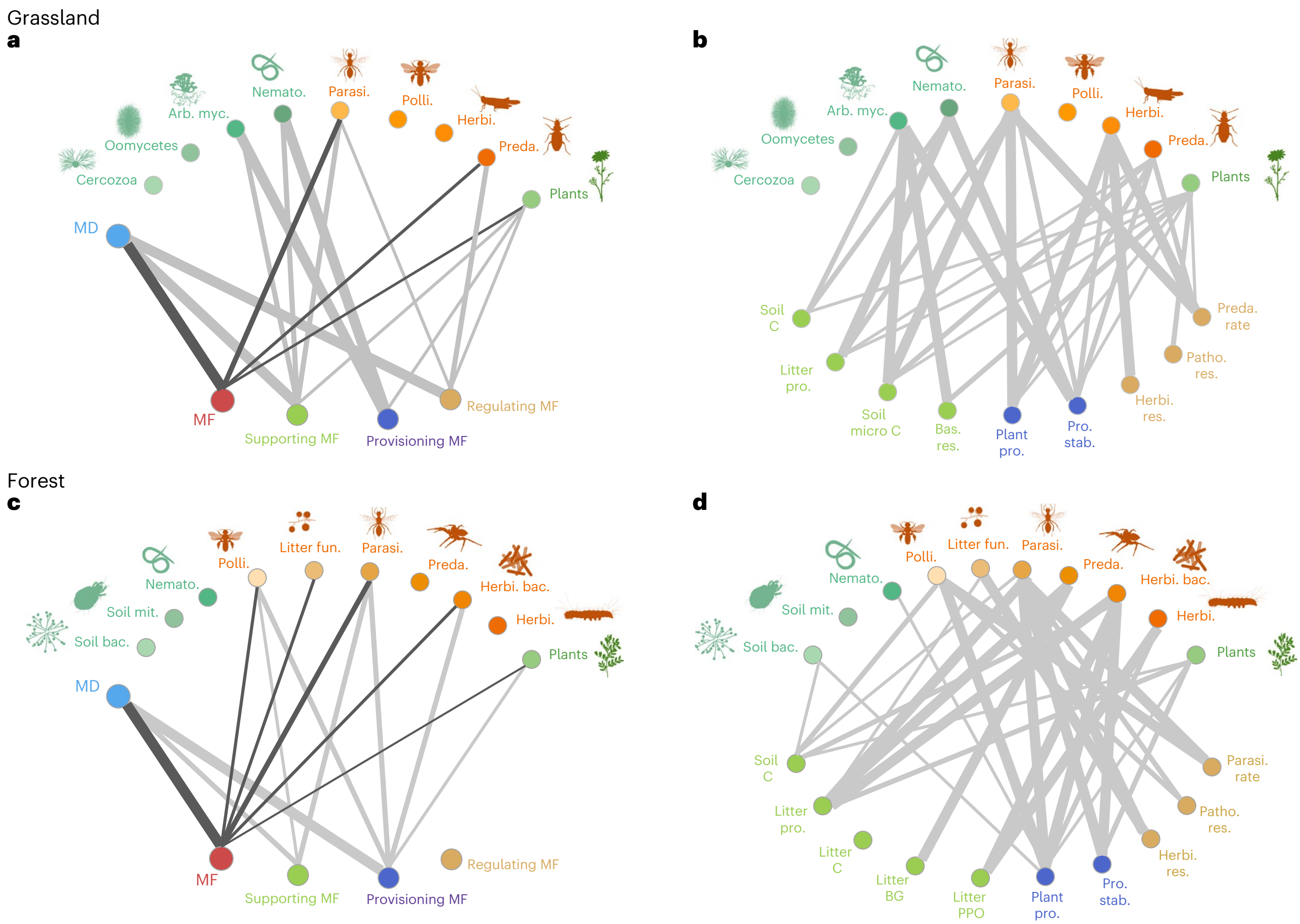

Fig. 3 | Relationships between multitrophic diversity or diversity of individual trophic groups and ecosystem multifunctionality, and between multitrophic diversity or diversity of individual trophic groups and individual ecosystem functions. a,**c**, Relationships between multitrophic diversity and the diversity of individual trophic groups and different types of multifunctionality in the grassland (**a**) and forest (**c**) experiments. **b**,**d**, Relationships between the diversity of individual trophic groups and ecosystem functions in the grassland (**b**) and forest (**d**) experiments. Dark grey lines show significant and marginally significant relationships between multitrophic diversity and the diversity of individual trophic groups and multifunctionality, with light grey lines showing significant and marginally significant relationships between the individual trophic groups and ecosystem functions. Non-significant relationships were omitted for clarity. The line widths are scaled by the absolute values of the standardized effect sizes, which were calculated based on linear models, including multitrophic diversity or the diversity of individual trophic groups and site/block as predictors. Arb. myc., arbuscular mycorrhizal fungi; bas. res., basal respiration; herbi., herbivores; herbi. bac., herbivore-associated bacteria; herbi, res., herbivory resistance; litter pro., leaf litter production; litter BG, litter β-glucosidase; litter C., leaf litter carbon; litter fun, leaf litter fungi; litter PPO, litter polyphenol oxidase; nemato., nematodes; parasi., parasitoids; parasi. rate, parasitism rate; patho. res., pathogen resistance; plant pro., plant productivity; polli., pollinators; preda., predators; preda. rate, predation rate; pro. stab., temporal stability of plant productivity; soil bac., soil bacteria; soil. C., soil organic carbon stock; soil micro. C., soil microbial biomass carbon; soil mit., soil mites.

grassland than in the forest experiment, including the supporting and regulating multifunctionality (Fig. 2a,c), possibly due to the more rapid turnover of aboveground plant biomass in the grassland. By identifying these key differences between forest and grassland ecosystems, our results expand previous findings on the relationship between plant diversity and ecosystem functions[21,39–44], including plant diversity and multifunctionality relationships[22,24,30].

Furthermore, plant diversity increased the multitrophic diversity in both ecosystem types (grassland: $P < 0.001$, $R^2 = 0.22$; forest: $P = 0.003$, $R^2 = 0.37$) (Fig. 2b,d). In the grassland experiment, plant diversity increased the diversity of predators ($P < 0.001$, $R^2 = 0.21$), arthropod herbivores ($P < 0.001$, $R^2 = 0.24$), arthropod parasitoids ($P = 0.005$, $R^2 = 0.30$) and the arbuscular mycorrhizae ($P < 0.001$, $R^2 = 0.39$), the strongest effect being on predator diversity (mean ± s.e.m. = 0.11 ± 0.03) and the weakest effect on arthropod parasitoid diversity (mean ± s.e.m. = 0.06 ± 0.02) (Fig. 2b). In the forest experiment, plant diversity increased the diversity of arthropod herbivores ($P = 0.002$, $R^2 = 0.22$), herbivore-associated bacteria ($P < 0.001$, $R^2 = 0.41$), arthropod predators ($P = 0.03$, $R^2 = 0.34$), arthropod parasitoids ($P = 0.08$, $R^2 = 0.13$) and nematodes ($P = 0.04$, $R^2 = 0.24$), with the strongest effect observed on herbivore diversity (mean ± s.e.m. = 0.19 ± 0.06) and the weakest effect on predator diversity (mean ± s.e.m. = 0.06 ± 0.02) (Fig. 2d). The latter findings suggest a predominance of bottom-up effects in forest ecosystems[35,36]. However, the results of the grassland experiment showed that plant diversity had a stronger effect on the diversity of predators than of herbivores, in contrast to an earlier study on the same experiment[35], possibly because of the young age of the plant and soil communities at the time of the earlier study, whereas we used data from the same ecosystem in the current study, but after nearly 20 years of development. Plant–soil interactions can affect subsequent biotic interactions, such as those between plants and aboveground arthropods like herbivores[45,46]. These findings suggest that legacy effects covered by long-term data[47] can improve our capacity to assess plant diversity–higher trophic group relationships[28].

Multitrophic diversity increases ecosystem multifunctionality

Multitrophic diversity was positively related to average multifunctionality (grassland: $P = 0.02$, $R^2 = 0.16$; forest: $P = 0.002$, $R^2 = 0.20$) (Fig. 3a,c) and threshold-based multifunctionality (Supplementary Figs. 3 and 4) in both ecosystem types. Moreover, changes in multitrophic diversity better predicted effects on average multifunctionality than changes in the diversity of any individual trophic group, including plants (despite the experimentally manipulated diversity) in both ecosystem types (grassland: mean ± s.e.m. = 0.20 ± 0.08; forest: mean ± s.e.m. = 0.31 ± 0.11) (Fig. 3a,c). The relationships between the diversity of individual trophic groups and threshold-based multifunctionality in both ecosystem types were contingent upon the trophic group (Supplementary Figs. 3 and 4). In the grassland, the diversities of the plants ($P = 0.01$, $R^2 = 0.20$), arthropod parasitoids ($P = 0.001$, $R^2 = 0.28$) and arthropod predators ($P = 0.02$, $R^2 = 0.18$) were positively related to average multifunctionality, whereas the diversities of arthropod herbivores, arthropod pollinators, arbuscular mycorrhizae, nematodes, the Cercozoa and Oomycetes were not related to average multifunctionality (Fig. 3a). In the forest, the diversities of the plants ($P = 0.01$, $R^2 = 0.17$), arthropod parasitoids ($P < 0.001$, $R^2 = 0.40$), arthropod pollinators ($P = 0.002$, $R^2 = 0.20$) and herbivore-associated bacteria ($P = 0.02$, $R^2 = 0.12$) were positively related to average multifunctionality, while the diversity of leaf-litter fungi ($P = 0.03$, $R^2 = 0.15$) was negatively related to average multifunctionality (Fig. 3c). Moreover, the effect size of the relationship between arthropod parasitoid diversity and average multifunctionality (grassland: mean ± s.e.m. = 0.11 ± 0.03, forest: mean ± s.e.m. = 0.12 ± 0.02) in both ecosystem types surpassed that of any other trophic group (Fig. 3c and Supplementary Fig. 4). These findings are consistent with available empirical evidence that indicates that multitrophic diversity and interactions among trophic groups are pivotal mechanisms maintaining high levels of ecosystem functioning across ecosystems, and expand previous findings on multitrophic diversity and multifunctionality relationships[22,24,48].

The comparison of ecosystem functions revealed that functions associated with resistance and regulation contributed more to the multitrophic diversity–multifunctionality relationship in the grassland ecosystems, whereas provision-related functions were more important in the forest ecosystems (Supplementary Tables 5 and 6). This difference may be attributed to the higher aboveground biomass in forests than in grassland, where a substantial part of primary production occurs belowground[49]. Moreover, the shorter longevity of primary producers in grasslands results in higher turnover rates, potentially explaining the more pronounced effects on resistance- and regulation-related functions in grasslands. In addition, by comparing the results from the two ecosystem types, we found that higher trophic groups in forest ecosystems play a more complex and important role in maintaining different types of ecosystem services than in grassland ecosystems (that is, the number of significant relationships between trophic groups and ecosystem functions in the forest was larger than in the grassland) (Fig. 3). This difference may be due to the longer life cycles and more complex structure of trees, which provide more abundant food resources and habitats to higher trophic groups, than of herbaceous plants.

When examining the relationships between the diversity of individual trophic groups and ecosystem functions, we found significant relationships between the diversity of individual trophic groups and at least one (and up to seven) of all considered ecosystem functions (Fig. 3b,d), with the exception of the diversity of arthropod pollinators, the Oomycetes and the Cercozoa in the grassland experiment and soil mites in the forest experiment. The direction of the relationship between the diversity at different trophic levels and individual ecosystem functions depended largely on both the trophic group and ecosystem function considered. In particular, we found that the diversity of arthropod parasitoids was positively associated with multiple ecosystem functions in both ecosystem types (Fig. 3b,d). Parasitoids can exert strong top-down forces on lower trophic levels (for example, herbivorous pests) and indirectly promote ecosystem functioning (for example, plant growth and community productivity)[28,50]. The increase in parasitoid diversity with plant diversity in both ecosystem types (Fig. 2b,d) suggests that combined bottom-up and top-down effects of diversity enhance ecosystem functions. This finding provides empirical evidence of the potential benefits of increasing parasitoid diversity to enhance the delivery of ecosystem services across ecosystem types. Nevertheless, the effects of multitrophic diversity or the diversity of individual trophic groups on individual ecosystem functions were not always positive in both ecosystem types[20,24,48]. Negative relationships may be attributed to species interference within a specific trophic group[51] (for example, intraguild competition) or shifts in composition that lead to a reduction in ecosystem functions[52,53].

When plant diversity was held constant—that is, within given levels of plant species richness—herbivore diversity was positively associated with plant biomass in the grassland experiment and negatively associated with plant biomass in the forest experiment (Supplementary Tables 3 and 4), suggesting bottom-up control in the grassland and top-down control in the forest when only plant biomass is considered[54]. When both plant and predator diversity were held constant, the effect of herbivore diversity in both the grassland and forest ecosystems was no longer significant (Supplementary Tables 3 and 4). These findings confirm the importance of higher trophic levels in regulating BEF relationships and of studying multiple trophic levels to understand BEF relationships and their underlying mechanisms[38].

Plant diversity increases ecosystem multifunctionality via multitrophic diversity

To investigate the underlying mechanisms of the effects of plant diversity on ecosystem multifunctionality, we mapped the hypothesized causal pathways from plant diversity to the diversity of different above- and belowground trophic groups or multitrophic diversity to ecosystem multifunctionality (Supplementary Fig. 5) using structural equation models (SEMs).

Plant diversity enhanced ecosystem multifunctionality primarily via aboveground trophic groups (except pollinators) (Fig. 4) in both the grassland and forest. Therefore, we computed additional SEMs focusing only on the aboveground trophic groups (that is, herbivores, predators and parasitoids). The models based only on the diversity of the aboveground trophic groups revealed that, in both grassland and forest, plant diversity increased average multifunctionality both directly and indirectly through the diversity of arthropod herbivores, predators and parasitoids (Supplementary Fig. 9). The interactions between the different trophic groups in the forest ecosystems explained a much larger proportion of the variation in average multifunctionality than in the grassland ecosystems (that is, $R^2 = 0.19$ versus 0.08 and $R^2 = 0.70$ versus 0.34 in Fig. 4; $R^2 = 0.46$ versus 0.20 in Supplementary Fig. 9). Our results suggest that the diversity of certain trophic groups can compensate for the effects of other groups on ecosystem functioning by providing functional redundancy or complementarity (Fig. 4)[55,56]. Additionally, interactions among higher trophic levels in the forest experiment accounted for a larger proportion of the variance in average multifunctionality than it did in the grassland experiment, suggesting that diversity at higher trophic levels and trophic interactions play a more important role in influencing multifunctionality in more complex ecosystems.

The direct path from plant diversity to average multifunctionality was not significant if the models contained multitrophic diversity as a

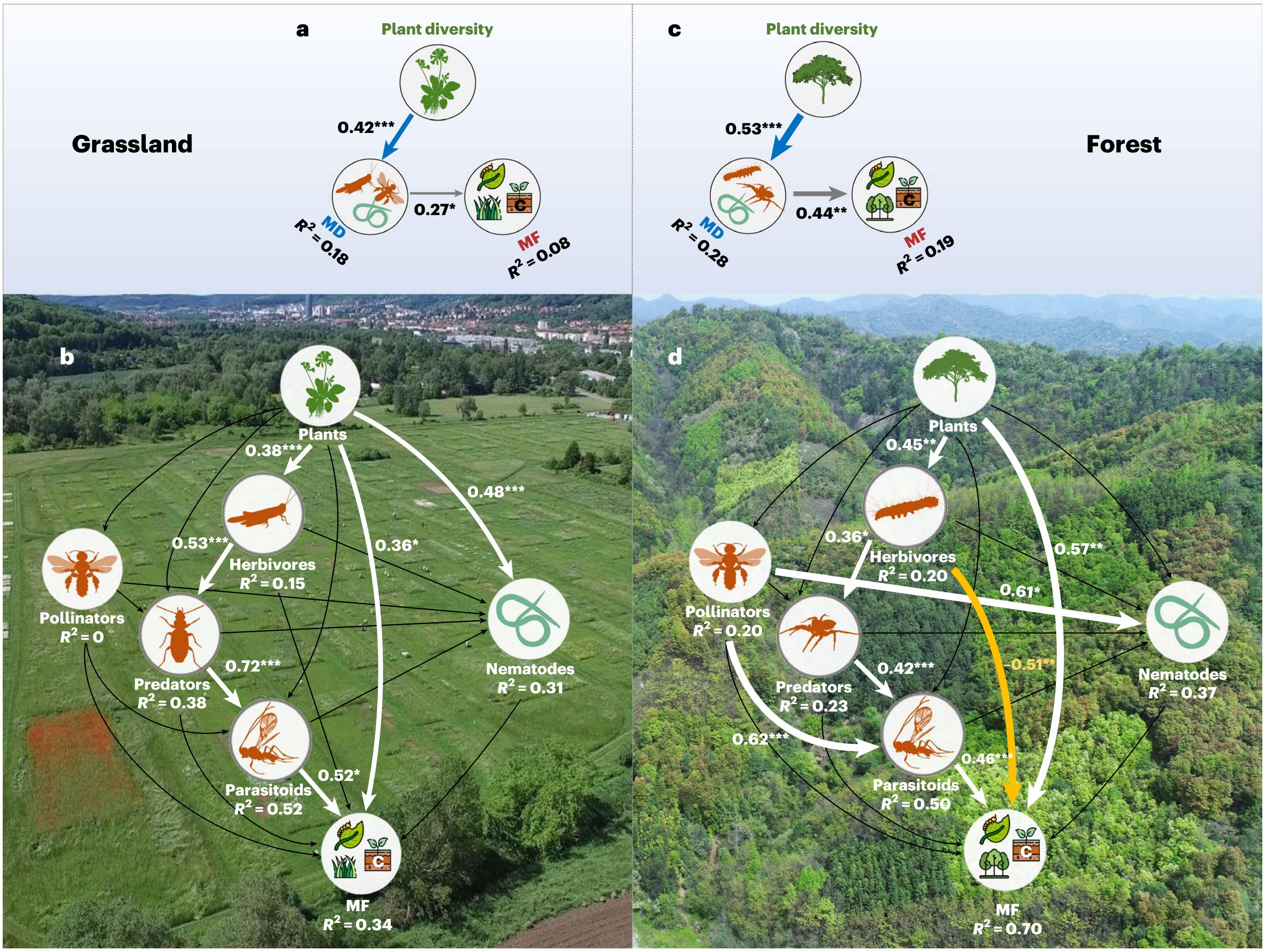

Fig. 4 | SEMs of plant diversity enhancing multifunctionality through multitrophic diversity or the diversity of multiple above- and belowground trophic groups. **a**,**c**, SEMs based on the multitrophic diversity in the grassland (**a**, Fisher's $C = 5.91$, $P = 0.052$, d.f. = 2, AIC = 17.91) and forest (**c**, Fisher's $C = 2.576$, $P = 0.276$, d.f. = 2, AIC = 14.576) ecosystems. Both the blue and grey lines in **a** and **c** show significant ($P < 0.05$) positive relationships. **b**,**d**, SEMs based on the diversity of multiple trophic groups in the grassland (**b**, Fisher's $C = 9.762$, $P = 0.045$, d.f. = 4, AIC = 71.762) and forest (**d**, Fisher's $C = 4.011$, $P = 0.405$, d.f. = 4, AIC = 60.011) ecosystems. The white (positive) and yellow (negative) lines in **b** and **d** show significant ($P < 0.05$) relationships, whereas the black lines show non-significant relationships. Models **a** and **c** include all trophic groups in both experiments, whereas models **b** and **d** only include the same trophic groups in both experiments (that is, aboveground trophic groups and nematodes). MF, multifunctionality; MD, multitrophic diversity. All tests were two-sided. Standardized path coefficients are shown in each path, with asterisks indicating significance (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Percentage values (marginal R^2) are shown next to the corresponding endogenous variables. The arrow widths are scaled by the absolute values of the standardized path coefficients. The full models of models **a** and **c** are shown in Supplementary Fig. 6, and the simplified models, including only the aboveground trophic groups, are shown in Supplementary Fig. 9.

mediator (Supplementary Fig. 6). Omitting this direct path from the models, the indirect path from plant diversity to multitrophic diversity, and from there to average multifunctionality, became significant, indicating an influence of plant diversity on average multifunctionality via multitrophic diversity (Fig. 4). Additionally, we found that this indirect effect of plant diversity on average multifunctionality via multitrophic diversity was driven by an association between aboveground multitrophic diversity and aboveground multifunctionality in forests (Supplementary Figs. 7 and 8). The findings from the forest experiment provide evidence for the critical role of higher aboveground multitrophic diversity in shaping both above- and belowground multifunctionality, which aligns with recent observational research on carbon–biodiversity relationships in a highly diverse subtropical forest[57].

The main effect of plant diversity on multifunctionality, which we observed in the models without additional covariates (that is, excluding potential mechanisms via multitrophic diversity) (Fig. 2a,c), and the residual direct effect of plant diversity on multifunctionality in the models including only mechanisms via aboveground trophic groups (Fig. 4b,d and Supplementary Fig. 9), disappeared when all trophic groups were included as the multitrophic diversity term in the models (Fig. 4a,c and Supplementary Fig. 6). This suggests that, when all trophic levels are considered, multitrophic diversity can explain all the effects of plant diversity on multifunctionality, leaving no unexplained direct effect of plant diversity on multifunctionality. Compared with previous studies on natural ecosystems[22,24], our findings further reveal the mechanisms underpinning the effect of plant diversity on multifunctionality—namely, the total of multitrophic diversity at all levels above plants.

How multitrophic diversity and interactions affect the BEF relationship is a central question in ecology, especially in the context of anthropogenic disturbance and climate change. Our findings offer a sign that, although differences in the food-web structure among ecosystems can lead to variability in specific taxon diversity–individual function relationships (bottom-up and top-down relationships between the plant biomass and herbivore diversity for a given plant diversity), the multitrophic diversity–multifunctionality relationship levels out this variability and, at least in the case of the two experiments used here, is overall positive. Furthermore, the comprehensive data presented here offer a unique opportunity to examine whether similar relationships between multitrophic diversity and multifunctionality are applicable across diverse ecosystems. Nevertheless, comparing one forest and one grassland may not necessarily provide the whole picture of actual differences between forests and grasslands. Therefore, the generality of our findings will need to be reassessed when more data on the two ecosystem types are available. Finally, these findings underscore the need for a multitrophic and multifunctional approach to advance our understanding of the mechanisms of BEF relationships[38], and by applying this approach, we have closed a knowledge gap, enabling better management of grasslands and forests, jointly comprising half of the land area on Earth. Importantly, these results should encourage relevant stakeholders, such as governmental and conservation agencies, to strengthen public understanding of the contribution of multitrophic diversity and to better integrate it in conservation strategies. They should ensure that the diversity of both plants and higher trophic groups, such as arthropods, are included when conducting global biodiversity assessments, setting global biodiversity goals and targets, and formulating the policies and other transformative changes needed to conserve biodiversity.

Methods

Study sites and experimental design

In this study, we used data from two large-scale plant-biodiversity experiments, representing two different ecosystems—the Jena Experiment on grasslands in Germany[31] and the BEF-China Experiment on the forests of southeastern China[32] (Fig. 1 and Supplementary Fig. 1).

The Jena Experiment is located on the Saale River floodplain near the city of Jena, Thuringia, Germany (50° 55′ N, 11° 35′ E)[31,58]. The average annual air temperature in the study region is 9.8 °C, with a mean annual precipitation of 571 mm. The main experiment of the Jena Experiment consists of 86 plots, completely and randomly distributed in four different blocks. The original plot size was 400 m^2, but in 2010, the subplot treatments were discontinued, reducing the plot size to 104.75 m^2, with a central area of 33 m^2 (6 × 5.5 m). The Jena Experiment includes 60 plant species from four typical grassland functional groups—grasses, small herbs, tall herbs and legumes. The plant diversity in these plots ranges from 1 to 2, 4, 8, 16 and 60 species. All species diversity treatments were replicated 16 times, with the exception of the 16-species and 60-species treatments, which were replicated 14 and 4 times, respectively. For this particular study, data were obtained from 80 grassland plots containing plants ranging from 1 to 60 species, excluding free succession and bare ground plots[58]. For more details on the design and previous results of the Jena Experiment, see refs. 31,58.

The BEF-China experiment is situated in Xingangshan, Jiangxi Province of China (29° 05′ 00″–29° 07′ 43″ N, 117° 54′ 19″–117° 55′ 53″ E)[32]. The region experiences an average annual temperature of 16.7 °C and an average annual precipitation of 1,821 mm. The experiment consists of two study sites, A and B, planted in 2009 and 2010, respectively. A total of 566 plots of 25.8 × 25.8 m^2 (equivalent to the Chinese area unit of 1 mu) were randomly distributed across these two sites, with 271 plots in site A and 295 plots in site B. Each plot contained 400 trees, arranged in a 20-row × 20-column grid. Using a 'broken-stick' design, 40 native deciduous and evergreen broadleaf tree species were planted to create gradients of species richness ranging from 1 to 24 tree species. For this study, data were collected from 47 plots (22 plots at site A and 25 plots at site B), encompassing a gradient from monocultures to plots with 24 species. Specifically, the number of plots sampled was 18, 13, 8, 4, 2 and 2 for the tree species richness levels of 1, 2, 4, 8, 16 and 24, respectively[32].

Diversity measures

In both ecosystems, we measured the species richness of various trophic groups (Supplementary Table 1). In the Jena Experiment, we collected aboveground arthropods, nematodes and microorganisms. Specifically, the data covered herbivores (Coleoptera, Hemiptera, Hymenoptera and Orthoptera), pollinators (Hymenoptera), predators (Araneae, Coleoptera, Geophilomorpha, Hemiptera, Hymenoptera, Opiliones, Orthoptera, Pseudoscorpiones and Strepsiptera), parasitoids (Hymenoptera), nematodes, arbuscular mycorrhizal fungi, Cercozoa and Oomycetes. The data for these trophic groups were obtained using taxon-specific methods[34,35,59–63] between 2017 and 2021.

For the BEF-China Experiment, we examined eight trophic groups, consisting of arthropods, soil nematodes, mites and microorganisms. These groups were divided into different functional groups based on their feeding ecology and trophic rank, including soil bacteria, nematodes, soil mites, leaf-litter fungi, arthropod herbivores (Lepidoptera caterpillars), herbivore-associated bacteria, arthropod pollinators (bees), arthropod predators (Araneae and Hymenoptera) and parasitoids (Hymenoptera and Strepsiptera). Here, we used herbivore-associated bacteria because bacteria are important symbionts of herbivores and a previous study on the same experiment found that herbivore-associated bacteria are probably from plant-leaf bacteria, which have been found to mediate relationships between plant diversity and ecosystem functions[27]. Data for these trophic groups were collected between 2015 and 2020 using taxon-specific methods, as documented in various studies[28,64–69]. For trophic groups collected in a single year, we directly used the species richness of that year, whereas for groups with data collected in more than one year, we calculated their average species richness before performing the subsequent analyses. Note that not all trophic groups were measured on all plots in the forest ecosystem. Therefore, we performed analyses using datasets of different sizes. For example, soil bacteria were collected from 28 plots. To ensure comparability between plots, we did not include this group in the calculation of multitrophic diversity in the forest ecosystem.

In both experiments, all samples were identified to at least a morphotype at the (sub)family level and, where possible, to the genus and species level. Data on the species richness of each trophic group were pooled per plot across sampling campaigns. For arthropods, it was quantified as the number of species or morphospecies (in cases where identification to species level was not possible), for nematodes as genus richness, and for microorganisms as the number of operational taxonomic units or amplicon sequence variants. Illumina MiSeq sequencing was performed to obtain the sequences of the 16S rRNA gene for bacteria or 18S rRNA gene for fungi. The Illumina MiSeq sequencing was performed at the Majorbio Bio-Pharm Technology Co. Ltd (Shanghai, China) and the Department of Soil Ecology, UFZ—Helmholtz Centre for Environmental Research in Halle (Saale), Germany, separately. Additionally, the abundance of each trophic group was measured at the plot level using different methods: the number of individuals for arthropods, the number of sequence reads assigned to operational taxonomic units (97% similarity) for soil bacteria and the number of amplicon sequence variants (100% similarity) for arbuscular mycorrhizal fungi. Given the strong correlation between species richness and abundance[28,34], and the dependence of abundance on sampling methods, our study focused only on the effects of species richness in the analyses.

Ecosystem functions

For the Jena Experiment (Supplementary Table 2), we focused on nine ecosystem functions, namely the soil organic carbon stock, soil microbial biomass carbon, soil basal respiration, leaf-litter production, plant productivity, temporal stability of plant productivity (hereafter referred to as 'community stability'), herbivory resistance, pathogen resistance and top-down control (that is, predation rate) by enemies. All measurements for the grassland experiment were carried out over the period from 2014 to 2021 using established methods[15,30,31,59,70,71]. Similarly, in the BEF-China Experiment, we conducted measurements of a comprehensive set of 10 ecosystem functions (Supplementary Table 2), including the soil organic carbon stock, leaf-litter production, leaf-litter carbon, extracellular enzyme activities in litter (BG and PPO), plant productivity, community stability, herbivory resistance, pathogen resistance and top-down control (that is, parasitism rate) by enemies. These measurements were carried out over the period from 2010 to 2022[21,41,69,72–75].

To estimate plant productivity in the forest, we used the aboveground accumulated stand volume measured in 2022[28], whereas in the grassland, this was estimated using the aboveground harvested (in 2020) dry biomass. The community stability was calculated as the inverse of the coefficient of variation[41], using plant biomass data collected from 2010 to 2020 for the forest ecosystem and from 2014 to 2020 for the grassland ecosystem. The herbivory and pathogen damage data were based on measurements of leaf-area damage by herbivorous insects and pathogens of plant leaves. Data on the herbivory and pathogen damage were multiplied by −1 before scaling to represent the herbivory and pathogen resistance[22]. The predation or parasitism rate was estimated based on the percentage of parasitism by parasitic wasps in the forest ecosystem and predation by enemy arthropods in the grassland ecosystem based on artificial caterpillar dummies. In the forest ecosystem, both soil organic carbon and leaf-litter carbon concentrations were estimated using a CHNOS elemental analyser. The soil organic carbon stock (0–20 cm belowground) was then calculated based on the equation: soil organic carbon stock = $H \times \text{BD} \times \text{OC} \times 10$, where H is soil depth (cm), BD is bulk density (g cm^{-3}) and OC is soil organic carbon concentration in bulk soil (g kg^{-1}). Extracellular enzyme activities in the leaf litter (BG and PPO) were measured using a microplate fluorometric assay. In the grassland ecosystem, the soil basal respiration was measured as the mean oxygen consumption per hour without the addition of any substrate, and the microbial biomass carbon was measured by substrate-induced respiration.

Statistical analysis

Calculation of multitrophic diversity and multifunctionality. We conducted all statistical analyses using R (http://www.R-project.org). Because of the large differences in diversity between the different taxonomic groups, we calculated the standardized multitrophic diversity (that is, the species richness of all trophic groups except plants) for each experimental plot using the method described in ref. 76. Specifically, we first performed a max-scaling for each trophic group in an experiment (plot-level richness divided by the maximum number of species occurring on a plot), and then we averaged the resulting values across all trophic groups.

Before calculating multifunctionality, we checked for collinearity between individual functions and ensured that Pearson's correlation coefficient, r, was less than 0.5 (that is, $r < 0.5$, Supplementary Fig. 2). Given the potential effects of extreme values (that is, outliers), we used the mean of the three largest values of each function as the observed maximum value. To calculate the ecosystem multifunctionality, we first standardized each individual ecosystem function (EF) between 0 and 1 using the formula $\text{SEF} = (\text{EF}_i - \text{EF}_{\min})/(\text{EF}_{\max} - \text{EF}_{\min})$, where EF_i is individual ecosystem function i and SEF is the standardized EF, and then calculated the multifunctionality using both the averaging approach and the multiple-threshold approach[77]. The averaging approach takes the average of the standardized values for each function. However, it does not consider potential trade-offs between functions. To address this limitation, we used the multiple-threshold approach, which estimates the association between trophic biodiversity and the number of functions (rate or availability) that simultaneously exceed a given threshold value. For this study, we used thresholds of 10%, 25%, 40%, 60% and 90% to analyse how diversity affects multifunctionality at different levels of thresholds of the observed maximum functioning, respectively[22,78]. In addition, we calculated the different facets of multifunctionality by categorizing the ecosystem functions according to the Millennium Ecosystem Assessment[79]: (1) provisioning services related to both forestry and agricultural values, including plant productivity and community stability; (2) regulating services associated with plant production, including resistance to plant pathogens, insect herbivory and top-down control by enemies; and (3) supporting services linked to nutrient capture and cycling, including leaf-litter production, leaf-litter carbon, extracellular enzyme activities in litter (BG and PPO), soil carbon, soil microbial biomass carbon and basal respiration. We also calculated the above- and belowground multitrophic diversity and multifunctionality so we could compare the relative importance of the aboveground, belowground and total multitrophic diversity to the aboveground, belowground and total ecosystem multifunctionality.

Relationships among plant diversity, multitrophic diversity and multifunctionality. Before the analysis, we checked the collinearity between different variables and transformed different variables to increase the normality (that is, the plant diversity was $\log_2$-transformed, and the data on the arthropods, nematodes, mites, soil bacteria, arbuscular mycorrhizal fungi and ecosystem functions were log-transformed). To test H1-1, we used linear models to assess the relationships between plant diversity and individual ecosystem functions and multifunctionality. For H1-2, we used linear models to examine the relationships between the plant diversity and species richness of different trophic groups and multitrophic diversity. In all cases of H1-1 and H1-2, we treated plant diversity as a predictor and included site (BEF-China Experiment) or block (Jena Experiment) as additional predictors. The model for H1-1 was 'lm (ecosystem function ~ plant diversity + site or block)', and the model for H1-2 was 'lm (trophic diversity ~ plant diversity + site or block)'. The effects of plant diversity on different trophic groups are reported as slopes, along with the partial R^2 from the linear regression models.

To test H2, we analysed the relationships between multitrophic diversity or species richness of different trophic groups and ecosystem multifunctionality, and between multitrophic diversity or species richness of different trophic groups and multiple individual functions using linear models. Similar to the previous models, we included the species richness of trophic groups and multitrophic diversity as predictors, along with sites or blocks. The model for H2 was 'lm (multifunctionality ~ trophic diversity + site or block)'. For the different trophic groups, we have reported their richness effects on multifunctionality or individual functions as slopes and partial R^2 values from the linear regression models. Furthermore, given that some functions were potentially more important than others in driving the observed patterns, we tested whether and how much excluding individual functions or each type of function from the multifunctionality measure could change our results. We also added further analyses to evaluate whether our results were consistent with multitrophic BEF theory. We tested the effect of herbivore diversity on plant biomass by keeping plant diversity constant. This was done by fitting plant diversity before herbivore diversity in a sequential model (type-I sum of squares or analysis of variance (ANOVA) short type-I) 'lm(plant biomass ~ plant diversity + herbivore diversity)'. We similarly tested the effect of herbivore diversity on plant biomass by holding the diversity of both plants and predators constant, fitting the model 'lm(plant biomass ~ plant diversity + predator diversity + herbivore diversity)' (again, type-I ANOVA). We conducted the same analyses for both the grassland and forest ecosystems.

To investigate whether plant diversity enhances multifunctionality via individual-group or multitrophic diversity (H3) (Supplementary Fig. 5), we used SEM (piecewiseSEM package[80]). To ensure comparability between the forest and grassland, we maintained a consistent structure for the models based on both ecosystem types. Specifically, we first used the diversity of multiple trophic groups to test how diversity at different trophic levels mediate the effects of plant diversity on multifunctionality (Fig. 4 and Supplementary Fig. 5). For these models, we included all trophic groups available for both the forests and grasslands (that is, plants, arthropod herbivores, arthropod pollinators, arthropod predators, arthropod parasitoids and nematodes) (Fig. 4). Herbivore-associated bacteria, soil mites, soil bacteria, arbuscular mycorrhizal fungi, the Cercozoa and Oomycetes were not included in the models because they were only collected from either forests or grasslands. We first included all potential interactions between the different trophic groups, including the pathways from plants to different trophic groups (herbivores, pollinators, predators, parasitoids, nematodes and soil bacteria), from herbivores and pollinators to predators (that is, predation), from pollinators and predators to parasitoids (that is, parasitism), from different trophic groups (herbivores, pollinators, predators and parasitoids) to nematodes (that is, decomposition), and from different trophic groups (plants, herbivores, pollinators, predators, parasitoids and nematodes) to multifunctionality. We then selected the major groups (that is, plants, herbivores, predators and parasitoids) that were associated with both plant diversity and ecosystem multifunctionality and constructed the SEM again (Supplementary Fig. 9). We checked the fitted models using Fisher's C statistics, and a model was considered to fit the data adequately if it had a Fisher's C statistic with $P > 0.05$ (ref. 80). The models were simplified by removing non-significant paths and compared using Akaike information criterion (AIC) values.

Subsequently, we analysed how overall multitrophic diversity mediates the plant diversity effects on ecosystem multifunctionality. We included in the models the paths from plant diversity to multitrophic diversity, from multitrophic diversity to multifunctionality, and from plant diversity to multifunctionality. Additionally, we performed the same analysis based on the aboveground multitrophic diversity and aboveground multifunctionality, aboveground multitrophic diversity and average multifunctionality, belowground multitrophic diversity and belowground multifunctionality, and belowground multitrophic diversity and average multifunctionality (that is, using aboveground multitrophic diversity or belowground multitrophic diversity to replace overall multitrophic diversity, and using aboveground multifunctionality or belowground multifunctionality to replace multifunctionality). We simplified and tested the models using the same procedure as above. For example, we removed the non-significant path from plant diversity to multifunctionality because the aim of our study was to determine whether multitrophic diversity mediates the effect of plant diversity on multifunctionality.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Biodiversity and ecosystem function data that support the findings of this study are available via Figshare at https://figshare.com/s/91cbc9f9aec78e2dced5 (ref. 81).

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Author contributions
X.L. and K.M. contributed to the conceptualization of the project. Yi Li, A.S., A.E., N.E., Y.H., G.A., C.A., A.A., M. Bonkowski, H.B., M. Bröcher, D.C., J.C., Y.C., J-T.C., M.C., X.D., F.F., G.G., L.G., P.-F.G., A.H., A.K., M.L., S.L., Q.L., Yingbin Li, A.L., S.M., G.O., G.R., T.S., M.D.S., M.S., M.-Q.W., N.Z. and C.-D.Z. contributed to the methodology and investigation. Yi Li and X.L. contributed to the visualization. The writing was led by Yi Li, X.L., A.S., A.E., N.E., B.S., K.M. and D.C., with reviewing and editing contributed to by all authors.

Competing interests
The authors declare no competing interests.

Additional information
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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
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☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	All analyses were conducted with R v 4.0.5. R packages we used include piecewiseSEM and ggplot2.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Biodiversity and ecosystem function data that support the findings of this study are available in figshare: https://figshare.com/s/91cbc9f9aec78e2dced5.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Here, we analyze how multidiversity is related to ecosystem multifunctionality in two large-scale biodiversity experiments in grasslands (Jena Experiment) and forests (BEF-China experiment). We considered species richness of 13 above- and below-ground trophic groups including soil bacteria, arbuscular mycorrhizae fungi, nematodes, soil mites, Cercozoa, Oomycetes, leaf-litter fungi, plants, arthropod herbivores, herbivore-associated bacteria, arthropod pollinators, arthropod predators, and arthropod parasitoids, as well as 13 ecosystem functions that are related to multiple ecosystem services. We calculated both average and threshold-based multifunctionality, as well as three types of average multifunctionality: provisioning (plant productivity and community stability), regulating (pathogen resistance, herbivory resistance, parasitism rate, and predation rate), and supporting multifunctionality (leaf litter production, leaf litter carbon, extracellular enzyme activities in litter [β-glucosidase BG and polyphenol oxidase PPO], soil organic carbon stock, soil microbial biomass carbon, and soil basal respiration).
Research sample	The study used data collected from two large-scale plant biodiversity experiments representing two different ecosystems: the Jena Experiment in grasslands in Germany and the Biodiversity–Ecosystem Functioning China (BEF-China) Experiment in forests of southeastern China.
Sampling strategy	The data for the grassland ecosystem were obtained from 80 grassland plots containing plant species ranging from 1 to 60 species (i.e. 1, 2, 4, 8, 16, 60), excluding free succession and bare ground plots. And the data for the forest ecosystem were collected from 47 plots (22 plots in site A and 25 plots in site B), encompassing a gradient from monocultures to plots with 24 species. Specifically, the number of plots sampled was 18, 13, 8, 4, 2, and 2 for the tree species richness levels of 1, 2, 4, 8, 16, and 24, respectively.
Data collection	In both ecosystems, we measured the species richness of various trophic groups. For the Jena Experiment, we collected aboveground arthropods, nematodes, and microorganisms. The data for these trophic groups were obtained using taxa-specific methods between 2017 and 2021. Furthermore, we focused on nine ecosystem functions, which were carried out over the period from 2014 to 2021 using established methods. In the BEF-China experiment, we examined eight trophic groups consisting of arthropods, soil nematodes, mites and microorganisms. These groups were categorized into different functional groups based on their feeding ecology and trophic rank. Data for these trophic groups were collected between 2015 and 2020 using taxa-specific methods as documented in various studies. Moreover, we conducted measurements of a comprehensive set of 10 ecosystem functions, which were carried out over the period from 2010 to 2022.
Timing and spatial scale	Data for higher trophic groups were collected between 2015 and 2021, and data for ecosystem functions were collected over the period from 2010 to 2022.
Data exclusions	N/A
Reproducibility	Detailed description of the methods are provided, all dataset are freely avaiable online and all analyses were performed in R. The results are fully reproducible using these data and packages.
Randomization	All species composition were randomized across plots.
Blinding	N/A

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The Jena Experiment is located in the Saale River floodplain near the city of Jena, Thuringia, Germany, with a mean annual temperature and precipitation of 9.8 °C and 571 mm, respectively. The BEF-China experiment is located in the subtropics of China with a mean annual temperature and precipitation of 16.7 °C and 1821 mm, respectively.
Location	The Jena Experiment is located in the Saale River floodplain near the city of Jena, Thuringia, Germany (50°55′N, 11°35′E). The BEF-China experiment is located in Xingangshan, Dexing, Jiangxi Province, China (29°05'00''–29°07'43'' N, 117°54'19''–117°55'53'' E).
Access & import/export	Both Jena and BEF-China experiments were established with permission of the local authorities in sites.
Disturbance	This study did not cause any environmental disturbance.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	N/A
Wild animals	The animals included in our study are nematodes, soil mites, arthropod herbivores, arthropod pollinators, arthropod predators, and arthropod parasitoids.
Reporting on sex	N/A
Field-collected samples	All samples were collected from the field i.e., the Jena Experiment (with a mean annual temperature and precipitation of 9.8 °C and 571 mm) and the BEF-China experiment (with a mean annual temperature and precipitation of 16.7 °C and 1821 mm).
Ethics oversight	This study was performed according to the international, national and institutional rules considering animal experiments, clinical studies and biodiversity rights.

Note that full information on the approval of the study protocol must also be provided in the manuscript.