Article (refereed) – postprint

Wan, Nian-Feng ; Wang, Yu-Quan ; Fu, Liwan ; Liu, Jie; Woodcock, Ben A. ; Hu, Yue-Qing ; Eskelinen, Anu ; Hector, Andy ; Loreau, Michel ; Hautier, Yann ; Bardgett, Richard D.; Kardol, Paul ; Zuppinger-Dingley, Debra ; Fraser, Lauchlan H. ; Bullock, James M. ; Nakagawa, Shinichi; Shen, Siyuan; Xin, Fengfei ; Shi, Da-Peng; Li, Zhong; Zhou, Jia; Scherber, Christoph. 2026. **Global evidence that plant diversity suppresses pests and promotes plant performance and crop production**.

The definitive version was published in Nature Ecology & Evolution, 10. 293-307.
10.1038/s41559-025-02964-5.

Global evidence that plant diversity suppresses pests and promotes plant performance and crop production

Nian-Feng Wan[1†,*], Yu-Quan Wang[2†], Liwan Fu[3†], Jie Liu[1†], Ben A. Woodcock[4], Yue-Qing Hu[2], Anu Eskelinen[5], Andy Hector[6], Michel Loreau[7,8], Yann Hautier[9], Richard D. Bardgett[10], Paul Kardol[11], Debra Zuppinger-Dingley[12], Lauchlan H. Fraser[13], James M. Bullock[4], Shinichi Nakagawa[14], Siyuan Shen[2], Fengfei Xin[15], Da-Peng Shi[16], Zhong Li[1], Jia Zhou[1], Christoph Scherber[17,18]

[1] Shanghai Key Laboratory of Chemical Biology, State Key Laboratory of Bioreactor Engineering, School of Pharmacy, East China University of Science and Technology, Shanghai 200237, China.
[2] State Key Laboratory of Genetic Engineering, Institute of Biostatistics, School of Life Sciences, Fudan University, Shanghai 200438, China.
[3] Center for Non-communicable Disease Management, Beijing Children's Hospital, Capital Medical University, National Center for Children's Health, Beijing 100045, China.
[4] UK Centre for Ecology and Hydrology, Wallingford, OX10 8BB, UK.
[5] Department of Ecology and Genetics, University of Oulu, Oulu, Finland.
[6] Department of Biology, University of Oxford, Oxford, UK.
[7] Theoretical and Experimental Ecology Station, CNRS, 2 route du CNRS, Moulis, 09200 France.
[8] Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China.
[9] Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.
[10] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK.
[11] Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, 750 07, Uppsala, Sweden.
[12] Department of Evolutionary Biology and Environmental Studies, University of Zurich, 170 Winterthurerstrasse 190, CH-8057, Switzerland.
[13] Department of Natural Resource Science, Thompson Rivers University, Kamloops, BC V2C 0C8, Canada.
[14] Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Building, Edmonton, Alberta, T6G 2E9, Canada.
[15] Wetland Research Department, Shanghai Wildlife and Protected Natural Areas Research Center, Shanghai 202150, China.
[16] Shanghai Center for Mathematical Sciences, Fudan University, Shanghai, China.
[17] Centre for Biodiversity Monitoring and Conservation Science, Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Adenauerallee 127, 53113 Bonn, Germany.
[18] Bonn Institute for Organismic Biology, University of Bonn, Bonn, Germany.

† These authors contributed equally to this work.

[*]Correspondence: Prof. & Dr. Nian-Feng Wan (nfwan@ecust.edu.cn)

Abstract: The diversity-productivity relationship suggests that increasing plant species could increase primary productivity, with this effect being explained in part by the suppression of plant antagonists. We conducted a global synthesis of 609 studies to investigate how plant diversity affects plants and their antagonists. Here we show that increasing plant species consistently promotes plant performance and suppresses antagonist performance in agroecosystems, grasslands and forests, for herbaceous and woody plants, across tropical and temperate zones, and for replacement series and additive experimental design studies. Crop diversification (e.g., intercropping and cover cropping) indirectly promotes crop production through the suppression of pests. This demonstrates that diversifying planting systems can increase productivity while reducing reliance on synthetic pesticides, offering a sustainable pathway for agriculture from subsistence to large scale agriculture. Overall, these results suggest crop diversification has considerable potential to support sustainable agroecosystems that benefit productivity while reducing reliance on synthetic pesticides.

Monocultures have been the heart of intensive agricultural and forestry systems since before the green revolution of the 1960's[1]. While monocultures can be high yielding[2], they have had negative consequences, including loss of co-occurring native biodiversity[3] with nock-on consequences for biological pest control[4] and crop pollination[5]. Monocultures are linked to the heavy use of often synthetic pesticides and fertilizers, which contribute to impacts on agroecosystem biodiversity as well as having negative consequences in terms of wider diffuse pollution[6,7]. Increasing plant diversity can mitigate these negative effects by promoting multiple ecosystem functions and services[8–11.] This can be achieved though crop diversification (e.g., intercropping, cover cropping and sown field margins) in arable and horticultural systems, diversified grasslands, and mixed forest plantations. For example, intercropping has been shown to increase crop yield under low nitrogen availability[12,13], to reduce pesticide and nitrogen fertilizer reliance while maintaining gross margins[14], and to decrease pests[15].

Mechanisms such as the resource-use complementarity hypothesis, based on negative interspecific interactions (competition theory), have been proposed to explain why increasing plant species can promote primary productivity[8,16]. However, an increase in productivity with increasing plant diversity may be explained by complementarity in top-down control. Here, the impact of specialist consumers (e.g. pest herbivores) on plants would be lessened as, thereby promoting overall productivity[8]. Individual experiments have demonstrated that increasing plant diversity can suppress plant antagonists, as evidenced by decreases in the abundance or biomass of insect herbivores[17,18], plant-feeding nematodes[19] and rodents[20], decreases in competitive weeds (i.e. both agricultural as well as invasive non-native plants in natural ecosystems)[21], and reductions in plant disease spread or damage[22,23]. Where the abundance of soil pathogens is not linearly related to the density of susceptible plant species there may also be a complementarity effect whereby plant-soil feedbacks negatively affect the growth of plants to a greater extent in monocultures than in diverse communities[24–26]. However, opposite results have also been reported in a few studies. For example, increasing plant species was shown to increase damage from herbivorous thrips[27]. If antagonists are suppressed, plant productivity may be enhanced indirectly by plant species richness resulting in increased yields in production systems such as crops, timber or fibre. The suppression of antagonists by plant diversity in agroecosystems (i.e., crop diversification) has significant potential to contribute to pesticide reduction strategies by maintaining antagonist populations below the threshold for economic injury[6,28]. However, there remains considerable debate over how generalized these plant diversity-antagonist relationships are as we currently lack a comprehensive understanding of their context dependence[29].

Meta-analysis is an effective tool to support evidence-based practice by resolving seemingly contradictory research outcomes across the broader literature[29]. Previous meta-analyses have shown that plant species diversity has variable effects on invertebrate herbivore abundance and damage[30–33]. They have also shown that increasing plant species diversity can decrease arthropod pests[34], and increase plant productivity[33] and crop yield[34,35]. In addition, past meta-analyses focusing on agroecosystem intercropping have also identified this can increase crop yields[15,36–42] and decrease pests[43–46], including plant diseases[15,47], weeds[36,48,49], and pest nematodes[15]. Intercropping has also been shown to increase natural enemies of arthropod pests (i.e., predators and parasitoids)[43–46]. However, these previous meta-analyses have only considered specific plant antagonists or pests, and did not distinguish specific types of plant diversity or experimental designs. Further, they did not consider the indirect (mediation) effects of plant antagonists on the diversity-productivity relationship and how such mediation effects can vary globally across different ecosystems, plant diversity types, experimental design types (replacement series vs. additive), plant forms (herbaceous vs. woody), climatic zoness (temperate vs. tropical), or types of experimental study (plot vs. pot).

Here, we conducted a global synthesis of 609 biodiversity experiments from which we derived 5,712 effect size observations on the impact of plant species diversity (i.e., intercropping, cover cropping, sown field margins, diversified grasslands, and mixed forest plantations) on plant performance. We assessed the effects of plant species diversity on a wide range of antagonist groups, i.e., invertebrate herbivores, plant diseases (bacteria, fungi, and viruses), weeds, plant-feeding nematodes, and plant-consuming rodents (Fig. 1a; Extended Data Fig. 1; Supplementary Data 1). We focused on the consequences of increasing plant species on overall measures of: (i) plant growth, reproduction, and quality; (ii) invertebrate herbivore growth, reproduction, and damage that herbivores cause to plants; (iii) disease reproduction, spread and damage; (iv) weed growth, reproduction, and diversity; (v) nematode reproduction, and damage; (vi) rodent reproduction, and damage; and (vii) aggregate performance indicators[29] for each of these categories. From these response variables, we derived log ratio response (lnRR) effect sizes comparing diverse plant communities (i.e., high plant species richness) and simple plant communities or monocultures (i.e., low species richness). Piecewise structural equation modeling was then used to analyze the effects of plant species diversity on plant performance as mediated though plant antagonists across different levels of plant diversity. We hypothesized that plant species richness within agricultural (arable and horticulture), grassland, and forestry ecosystems (Fig.1b): (i) increases plant performance directly through either increased complementarity or decreased competition among different plant species (H1); (ii) decreases plant antagonist performance directly (H2), and (iii) increases plant performance indirectly by reducing the performance of plant antagonists (H3). We also propose that this diversity-antagonist-productivity relationship varies across different ecosystems, plant diversity types, experimental design types, plant life forms, and climatic zones. Together, we recommend a plant antagonist hypothesis and suggest that mediation effects of plant antagonists on plants can be another mechanism by which plant diversity influences plant performance both directly and indirectly.

Results and Discussion

Direct effect of plant species richness on plant performance

Our results were based on 5,712 observations from 609 articles and confirmed the biodiversity-productivity relationship (Supplementary Tables 1−3). However, agroecosystems (arable and horticulture; N=2,583) datasets were considerably larger than those for forests (N=118) and grasslands (N=65). Overall, we found that increased plant species richness promoted plant performance across global terrestrial ecosystems, for metrics including plant growth, quality, and reproduction (Fig.1c) (CI=0.148 to 0.221, df=2390, ES (effect size)=0.184, P<0.001) (Supplementary Table 3). When we split the aggregate indicator of plant performance into plant growth, reproduction and quality, we also found each showed positive responses to increasing plant species (plant growth: CI=0.165 to 0.271, df=1160, ES=0.218, P<0.001; plant reproduction: CI=0.072 to 0.169, df=956, ES=0.120, P<0.001; plant quality: CI=0.068 to 0.170, df=272, ES=0.119, P<0.001; see Supplementary Table 3). All responses of plant performance to plant diversity were positive across different ecosystem types, with the largest effect size found in grasslands (Fig. 2a) (grasslands: CI=0.271 to 0.535, df=467, ES=0.403, P<0.001; agroecosystems: CI=0.107 to 0.179, df=1784, ES=0.143, P<0.001; forests: CI=0.041 to 0.208, df=137, ES=0.124, P=0.004) (Supplementary Table 4). We explain this pattern through five mechanisms by which increasing plant species could promote productivity: i) mixed planting (e.g., intercropping but not cover cropping) resulting in a complementarity effect (i.e., direct niche partitioning or facilitation between plants)[8,16] that impacts trophic interactions with other non-plant species[24,25]. This is relevant to our H1: complementarity or decreased competition hypothesis; ii) reduced pressure of plant antagonists (e.g., herbivores[18,50], plant disease[22] and weeds[21]) indirectly facilitating plant productivity[4,6]. This has implication for our hypotheses H2: directly decreased plant antagonist performance, and H3: indirectly decreased plant antagonist performance; iii) strengthening of the top-down effects of natural enemies on crops by providing additional resources for natural enemies supporting increased population sizes[35,51]; iv) improved soil fertility[13], field micro-climate[52], and increasing nutrient use efficiency[53]; and v) direct positive effect on plant-plant interactions though the release by one or more plant species in a mixture of beneficial plant secondary compounds like allelochemicals[54]. We also found positive responses of plant performance in response to plant diversity for herbaceous and woody plants (Fig. 2b), temperate and tropical zones (Fig. 2c), plot and pot experiments (Fig. 2d), and additive design and replacement series designs (Fig. 2f).

When we classified plant diversity in agroecosystems (i.e., crop diversification) into intercropping, cover cropping, and sown field margins, we found that intercropping increased plant performance through its action on plant growth, quality, and reproduction (growth: CI=0.034 to 0.159, df=517, ES=0.097, P=0.003; reproduction: CI=0.061 to 0.153, df=758, ES=0.107, P<0.001; quality: CI=0.054 to 0.198, df=201, ES=0.126, P=0.001; see Fig. 2e and

Supplementary Table 4). Increased crop production in intercropping might be due to a more efficient use of available resources though complementarity in niches, leading to a reduced reliance on external inputs that may be important in the context of sustainable crop production[55,56]. Likewise, we found that cover cropping increased plant performance (growth: CI=0.103 to 0.338, df=100, ES=0.220, P<0.001; reproduction: CI=0.080 to 0.402, df=148, ES=0.241, P=0.004; quality: CI=0.175 to 0.248, df=8, ES=0.212, P<0.001). Cover crops promote the production of main crops either by acting as green manures when incorporated into soils or directly though nitrogen release in the case of legumes[57].

Possibly due to low sample sizes, the evidence for increased plant performance in response to sown field margins was equivocal with effect sizes more or less symmetrical around zero (growth: CI=−0.458 to 0.545, df=13, ES=0.044, P=0.853; reproduction: CI=−0.010 to 0.246, df=32, ES=0.118, P=0.069; quality: N=0; see Fig. 2d and Supplementary Table 4). However, field margins increase diversity at the scale of the whole field, and so direct interactions leading to and king of complementarity with crop species are limited. Indeed, field margins likely principle role in increasing crop productivity is via a reduction in pest populations through spill over from invertebrate natural enemies or in the case of flowering crops though increased pollination[4,6].

Direct effects of plant species richness on plant antagonists

Across all studies, plant species richness decreased the overall performance of plant antagonists (CI=−0.490 to −0.388, df=3318, ES=−0.439, P<0.001) as well as when considered as subgroups of herbivores (CI=−0.522 to −0.379, df=1809, ES=−0.451, P<0.001), plant diseases (CI=−0.465 to −0.323, df=601, ES=−0.394, P<0.001), weeds (CI=−0.632 to −0.396, df=600, ES=−0.514, P<0.001), plant-feeding nematodes (CI=−0.461 to −0.134, df=284, ES=−0.298, P<0.001) and plant-consuming rodents (CI=−0.677 to −0.270, df=20, ES=−0.474, P<0.001). This pattern of responses largely held when these aggregate performance indicators for each antagonist group were partitioned into individual components, i.e., when plant disease performance was considered in terms of its component metrics of plant disease reproduction, spread and damage (see Supplementary Table 3). When sample sizes were small, differences in the response to increased plant species richness tended to be not significant (i.e., herbivore growth: CI=−0.403 to 0.122, df=48, ES=−0.141, P=0.287, but for other cases see Supplementary Table 3.

We also tested whether responses differed among ecosystems. The responses of plant antagonist performance to increasing plant species was negative for agroecosystems (CI=−0.538 to −0.423, df=2777, ES=−0.481, $P<0.001$) and grasslands (CI=−0.466 to −0.147, df=315, ES=−0.306, $P<0.001$), but only marginally significant in forests (CI=−0.213 to 0.013, df=224, ES=−0.100, P=0.083). When plant antagonists were split into different subgroups (i.e., invertebrate herbivores, plant diseases, nematodes, rodents, and weeds) and into different response categories (e.g., invertebrate herbivore growth, reproduction, and damage), the overall pattern described above was maintained in agroecosystems (Fig. 2a; Extended Data Fig. 2a), but these responses varied in grasslands and forests (Extended Data Fig. 2b, c; Supplementary Table 4). We found that plant species richness reduced herbivore performance (i.e., herbivore growth, reproduction and damage) only in agroecosystems (CI=−0.602 to −0.443, df=1436, ES=−0.523, $P<0.001$) (Supplementary Table 4). This finding supports several key hypotheses, including: 1) the Enemies Hypothesis that suggests herbivore natural enemy performance is positively related to plant species richness[6,33,58], 2) the Resource Concentration Hypothesis (RCH) which argues that the density of insect herbivores increases with monoculture host density and patch size[58], and, finally, 3) the Insurance Hypothesis (IH) whereby more diverse crops provide insurance against pest damage[59]. However, there was little support for these hypotheses in grasslands (CI=−0.316 to 0.065, df=171, ES=−0.126, P=0.195) and forests (CI=−0.162 to 0.067, df=200, ES=−0.048, P=0.413) as the negative response of herbivores to plant species richness had confidence intervals that overlapped zero.

The observed differences may be due to the more common outbreaks (i.e., more severe impacts) of specialist herbivores in agroecosystems than grasslands, although for monospecific forest destructive outbreaks of specialist herbivore do occur. The prevalence of this effect may be exacerbated by lower crop diversity in arable or horticultural cropping systems (~2-3 plant species in general)[18,23] than would be seen in many grasslands (e.g. the Jena experiment in Germany[10,11] and Cedar Creek experiment in the USA[9,11]; both consider 60 plant species), and to a lesser extent for forests (e.g. a maximum of 24 tree species in a Chinese forestry study[33]). Increased plant species richness may also provide greater access to nutritionally superior or more variable food resources for insect herbivores in grasslands, particularly for oligophagous or polyphagous specie[60].

Across all studies, we found that increased plant species richness decreased symptomatic disease expression in plants in agroecosystems (CI=−0.458 to −0.301, df=514, ES=−0.379, P<0.001), grasslands (CI=−0.696 to −0.358, df=70, ES=−0.527, P<0.001) and forests (CI=−0.689 to −0.100, df=15, ES=−0.395, P=0.012), as well as weed performance in agroecosystems (CI=−0.610 to −0.369, df=547, ES=−0.490, P<0.001) and grasslands (CI=−1.411 to −0.072, df=52, ES=−0.742, P=0.031). As to different groups of plant anatagonists in the three ecosystems, nematode performance only in agroecosystems (CI=−0.511 to −0.117, df=266, ES=−0.314, P=0.002), and rodent performance in both agroecosystems (CI=−0.712 to −0.428, df=10, ES=−0.570, P<0.001) and grasslands (CI=−0.924 to −0.160, df=6, ES=−0.542, P=0.013) also decreased with plant species richness. These finding strongly suggest that enhancing plant species richness is an effective method to promote antagonist control services in managed systems, such as agro-ecosystems, managed grasslands and production forest. Increased control of antagonists might be explained by the effects of plant species diversity on disease performance, resulting from altered wind and vector dispersal, modified microclimate, dilution of host density, decreased vectors of plant diseases (e.g., aphids and planthoppers), changes in host morphology and physiology and direct pathogen inhibition[22]. Suppressed weed growth in diverse mixtures may be linked to the spatio-temporal continuity of ground cover provided by the agricultural plants in diverse assemblages, with this providing little bare ground for weeds to establish[61]. It may also be related to the allelopathic effects of diversified plant species on weed growth and germination[62], and to the physical and chemical properties of the mulches[63]. Decreased growth of nematodes in diverse plant communities may be a by-product of a greater diversity of allelopathic chemicals[64]. Alternatively, this may be due to many plant parasitic nematodes being relatively specialized such that a diverse assembly of crop plants is likely to result in a dilution of suitable plants across space and time[65]. Finally, increased rodent dispersal in monocrop plots may be driven by a response to limited habitat and resource diversity availability[20]. Overall, physical barriers, allelopathic chemicals, plant species resistance, natural enemies and dilution effects may be responsible for the negative effects of plant species richness on herbivores, plant diseases, nematodes and weeds[22].

Next, we tested whether these responses of plant antagonists and their subgroups differed among plant life forms, climatic zones, experimental types, plant diversity types and experiment design types. We found qualitatively similar negative responses for both herbaceous and woody plants (Fig. 2b; Extended Data Fig. 3; Supplementary Table 5), for both temperate and tropical zones (Fig. 2c; Extended Data Fig. 4; Supplementary Table 6), and in both additive (i.e. the densities of plant species increases as more species are added) and replacement series (i.e. plant density remains constant, even as more plant species are added) designs (Fig. 2f; Supplementary Table 7). Across types of experimental studies, we found stronger responses from the subgroup of plant antagonists to plant species richness in plot than in pot experiments, possibly due to smaller sample sizes in pot experiments (Fig. 2d; Extended Data Fig. 5; Supplementary Table 7). This would restrict below-ground components of these communities as well as dispersal parameters that would be encountered under field-based experiments. Consequently, they do not incorporate the intricate biotic interactions existing in natural communities.

Finally, we tested whether these responses of plant antagonists (i.e., pests in agroecosystems) and their subgroups differed among intercropping, cover cropping, and sown field margins. We found qualitatively similar negative responses for these crop diversification modes (Fig. 2e; Supplementary Table 4). The mechanisms to explain the decreased pests are proposed to be like those described above. Funnel plots for each trophic group was presented in Extended Data Fig. 6.

Mediation analysis of plant species richness on plants and their antagonists

We used mediation analysis (i.e., path analysis) to test our proposed diversity-antagonist-productivity relationship (Supplementary Tables 8−13). For our analysis, we collected 2,766 estimates of interactions between pairs of plants and plant antagonists derived from 240 articles. First, we tested the effects of plant species richness (i.e., a binary variable) on plants and plant antagonists using multilevel piecewise structural equation models. In these models, we aggregated different plant antagonists together, i.e., invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes, and plant-consuming rodents (Supplementary Methods). We found that plant species richness directly suppressed plant antagonists and increased plant performance across terrestrial ecosystems and in agroecosystems, grasslands, and forests (Fig. 3). increasing plant species also increased plant performance indirectly by reducing the performance of plant antagonists across terrestrial ecosystems (supplementary Table 11) and specifically in agroecosystems (Fig. 3a). However, this indirect effect on plant performance via suppression of antagonists was less pronounced in grasslands (Fig. 3b) or forests (Fig. 3c).

When we classified plant diversity in agroecosystems into different types, we found that intercropping, cover cropping, and sown field margins directly suppressed plant antagonists (i.e., pests) and increased plant performance (i.e., crop production) (Figs. 3d−f). Intercropping and cover cropping also increased crop production indirectly by reducing pests (Figs. 3d, e). The effect of sown field margins on crop production via the suppression of pests were not as clear as was seen for intercropping and cover crops (supplementary Table 11; Fig. 3f). Similarly, the direct effects of plant species richness on plant performance and plant antagonist performance were consistent in herbaceous-species dominated and woody-species dominated systems, temperate and tropical zones, and in plot and pot experiments. The mediation effects of plant antagonists on plant performance were significant for herbaceous plants (P=0.019, N=2,514), plot experiments (P=0.027, N=2,513), and temperate zones (P=0.027, N=1524). This finding may in part be a product of the well-studied effects of intercropping research in field crops. However, mediation effects were not significant for woody plants (P=0.593, N=252) or pot experiments (P=0.211, N=253), or in tropical zones (P=0.101, N=936) (Extended Data Figs.7; Supplementary Table 13). Indirect positive effects of plant species richness on plant performance were found to be mediated through a reduction of plant antagonist pressure when we separately tested for the effects of invertebrate herbivores, plant diseases and weed performance, although such an indirect effect was not evident for the nematodes (Fig. 4).

Our meta-analysis identifies that plant species richness enhances plant performance while suppressing the performance of various groups of plant antagonists, including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents. Further, across all studies our analysis indicated that in a comparison of low vs high plant diversity we see an increase in plant performance by 24.31% in agroecosystems, 69.59% in grasslands and 28.75% in forests. This can be explained by the decrease in plant antagonist performance by 30.18% in agroecosystems, 19.98% in grasslands and 8.85% in forests (Extended Data Fig. 8). Increased plant performance resulting from decreasing plant antagonist performance can be realized by adding only one plant species in agroecosystems, grasslands and forests (Tables 1, 2). These results highlight the negative effects of plant diversity on the plant antagonists, and in doing so contributes to the positive effects of the biodiversity-productivity relationship. The diversity-antagonist-productivity relationship for terrestrial ecosystems is highly dependent on the results from agroecosystems (studies from agroecosystems accounted for 93.38% of those from terrestrial ecosystems).

Piecewise structural equation model indicated that plant diversity can promote crop production through indirect effects (i.e., suppressing pests) in agroecosystems, as well as indirect mediation effects driven by factors such as improved soil fertility[13], field micro-climate[52] and increasing nutrient use efficiency[53]. While the data does not differentiate between specialist and generalist antagonists, theoretical predictions show that it is likely that specialists are mostly responsible for the observed effects.

From an applied perspective, our findings suggest that crop diversification, whether from intercropping, cover cropping, or sown field margins, can help to promote crop pest control and increase crop production[33]. Such crop diversification may also help to mitigate climate induced yield losses in the future by increasing system resilience[66]. Many other forms of crop diversification (e.g., crop rotations), landscape diversification, or cropping system diversification might also be beneficial for pest control and crop production[67–69]. It is important to note that this meta-analysis does not consider non-biological indicators (e.g., profitability, or access to specific markets via accreditation) which may alter the practical viability of more diversified systems. Rather, the results of this study have identified the general benefits across diverse production systems for suppressing plant antagonists though increasing plant diversity. However, for each systems the subtleties of which crops, varieties and unique traits to combine would need to be considered. This may include a need to consider other agronomic decisions such as the use of agrochemicals authorized for specific crops that may not be compatible with intercropping systems, as well as sowing density, timing and establishment patterns. This is beyond the scope of this analysis. Our results provide empirical support for more complex cropping systems that increase plant diversity in agricultural fields and management strategies that foster increased diversity species co-existence in grasslands and forests.

Methods

Definition of increasing plant species and number of added plant species

We considered "increasing plant species" as a binary variable (zero or one), indicating whether plant species richness was increased, but irrespective of the number of plant species added. Here "number of added plant species" is a continuous variable describing the increase in plant species richness between the control and the treatment. When comparing plant species richness of the control (i.e., pure, mono- or lowest plant species) with that of the treatment (i.e., higher plant species richness, $\geqslant 2$ plant species richness), we ensured that comparisons were also between the same trophic groups. Sensitivity analysis for "increasing plant species" is provided in Supplementary Table 14. Description for analyses of incresing plant species richness and number of added species richness is provided in Supplementary Table 15. Statistic values for the relationship between number of added species richness in the plant species richness treatment over the control is presented in Supplementary Table 16 and Supplementary Figs. 1–12. Detailed results for "increasing plant species" are shown in Fig. 1c, Figs. 2–4, Extended Data Figs. 2–8, Supplementary Tables 1–15, 17, and Supplementary Figs. 13–42. Detailed results for "number of added plant species" were shown in Tables 1 and 2, Supplementary Results, Supplementary Tables 9, 11, 13, 15 and 16.

Study selection

Studies were selected through a literature search of the Web of Science Core Collection, BIOSIS Previews, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE, Preprint Citation Index, ProQuest^{TM} Dissertations & Theses Citation Index, and SciELO Citation Index. We used the Boolean search string based on the "TOPIC" searching: ["plant diversity" OR "crop diversity" OR "crop diversification" OR "plant species richness" OR "polyculture" OR "ground cover vegetation" OR "flower strip" OR "strip crop*" OR "grassy field margin" OR "border crop" OR "intercrop*" OR "interplant*"] AND ["plant disease" OR "plant virus" OR "nematode" OR "weed" OR "herbivor*" OR "pest" OR "biological control" OR "rodent" OR "yield" OR "productivity" OR "biomass"]. This literature search was initiated in June 2019, and finalized in August 2023. In total, the search yielded 386,895 articles (see Extended Data Fig. 1 for a PRISMA diagram). Articles were screened by Y.Q.W., L.F., J.L., J.Z. and N.F.W.. Data were extracted from the articles by Y.Q.W., L.F., J.L. and N.F.W. during which regular cross-checking was performed to ensure consistency in extracted effect sizes.

We used data giving the mean values of multiple sampling dates or years. If these mean values were not presented, we used the data of the latest sampling period[33]. For articles that covered more than one experimental location, we considered these experimental results separately (see locations in Fig. 1a). When numeric values were not provided directly, we extracted them from figures using the "GetData Graph Digitizer" 2.26. However, where linear or non-linear relationships between plant species richness and one of the response variables was presented in a figure, we extracted the values by fitting regression equations[29].

To avoid pseudoreplication of data, we excluded multiple comparisons conducted within a single experiment[33]. Observations with the lowest plant species richness were considered as control groups, while those with higher plant species richness were considered as the treatment groups. When an article included different levels of plant species richness, measurements for the control groups (lowest plant species richness) were compared to all other treatments levels of plant species richness and treated as independent paired observations.

Predictor variables

We used eight categorical variables as predictor variables (see Supplementary Methods for details)—i) Trophic group: a categorical variable describing whether the target organisms were invertebrate herbivores, plant diseases (plant pathogenic viruses, fungi and bacteria that infested plants and cause damage to plants), weeds, plant-feeding nematodes, plant-consuming rodents (e.g., rats and mice that damage crops, pasture or trees), or plants (e.g., crops, fruits, grassland species and trees); and moreover, an aggregate categorical variable (i.e. plant antagonists) including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents. ii) Response category: growth, reproduction and damage of herbivores; reproduction, spread and damage of plant diseases; weed growth, reproduction and diversity (i.e., species richness and Shannon diversity of weeds); reproduction and damage of plant-feeding nematodes; reproduction and damage of plant-consuming rodents; and growth, reproduction and quality of plants. iii) Ecosystem type: agroecosystems, grasslands and forests. iv) Plant life form: herbaceous or woody plants. v) Climatic zone: temperate or tropical (data from greenhouse, indoor and laboratory experiments were removed from models including the climatic zone variable)[29]. vi) Experiment type: plots (i.e., field and common garden experiments) or pots (i.e., experiments with pots, containers, bottles, trays, boxes and tankers) (detailed description was presented in Supplementary Methods). vii) plant diversity types: crop diversification including intercropping, cover cropping and sown field margins in agroecosystems, mixed forest plantations, and diversified grasslands. viii) experimental design types: replacement series design and additive design. A replacement series design means that total plant density remains constant, even as more plant species are added.

Definition of effect size and its measures

To test the effect of plant species richness on the various groups (invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes, plant-consuming rodents, or plants; and moreover, an aggregate plant antagonists categorical variable including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents), we calculated the effect size and lnRR of these groups. The first proposed formula as follows:

$$lnRR_1 = \ln\left(\frac{m_1}{m_2}\right) \qquad \text{(Eq.1)}$$

$$v(lnRR_1) = \frac{sd_1^2}{n_1 m_1^2} + \frac{sd_2^2}{n_2 m_2^2} = \frac{CV_1^2}{n_1} + \frac{CV_2^2}{n_2} \qquad \text{(Eq.2)}$$

where m_1 and m_2 are the observed mean value in the treatment and control groups, sd_1 and sd_2 are the standard deviations (SDs) in the treatment and control groups, and n_1 and n_2 are the sample sizes in the treatment and control groups. m_1, m_2, sd_1, sd_2, n_1 and n_2 were extracted from original articles. Namely, mean value, SD and sample sizes of both treatment and control groups were included in our dataset to conduct meta-regression. This was done in order to deal with missing standard deviations (SDs) in dataset, using the approach of Nakagawa et al.[70] which is suited to accounting for missing SDs. Nakagawa et al.[70] proposed this new method weighting average coefficients of variation estimated from studies that do report SDs in the dataset. This is done by:

$$lnRR_2 = \ln\left(\frac{m_1}{m_2}\right) + \frac{1}{2}\left(\frac{CV_1^2}{n_2} - \frac{CV_2^2}{n_1}\right) \qquad \text{(Eq.3)}$$

$$v(lnRR_2) = \frac{CV_1^2}{n_1} + \frac{CV_2^2}{n_2} + \frac{CV_1^4}{2n_1^2} + \frac{CV_2^4}{2n_2^2} \qquad \text{(Eq.4)}$$

$$lnRR_3 = \ln\left(\frac{m_1}{m_2}\right) + \frac{1}{2}\left(\frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^2}{n_1} - \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^2}{n_2}\right) \qquad \text{(Eq.5)}$$

$$v(lnRR_3) = \frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^2}{n_1} + \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^2}{n_2} + \frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^4}{2n_1^2} + \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^4}{2n_2^2} \qquad \text{(Eq.6)}$$

where $CV=s_d/m$ is the coefficient of variation; s_d and n are the corresponding SDs and sample size, respectively; CV_{1i} and CV_{2i} are the CVs from the ith study (study: i=1,2,…,K). The proposed Eq.3 and Eq.5 can improve the accuracy and precision of the overall mean estimate.

We can use Eq.5 and 6 to calculate the effect sizes and sample variances when SDs are missing and use Eq.3 and 4 to calculate the effect size and sample variances when SDs are not missing. This paper uses Eq.5 to calculate effect regardless of whether SDs are missing or not, which was refer as "All Cases" method[70] We used lnRR as the response variable for different models except for path analyses described below.

Meta-regression

Meta-regression[71] was applied to test whether the effect sizes of different trophic groups could be explained by increasing plant species and the various predictor variables. Specifically, we fitted three-level mixed-effects meta-regression models, using the R package metafor (version 3.8-1). The effect size metric lnRR was calculated using the function "lnrr_laj()" in R.file implemented using the package "func.R" developed by Nakagawa et al.[70]. This was used to calculate the effect size metric lnRR for each observation as well as the unbiased sample variance estimates as defined under Eq.6 (using function "v_lnrr_laj()" in R.file "func.R"). Trophic groups, trophic group response categories, ecosystem types, plant life forms, climatic zones, types of experimental study, types of plant diversity, and experimental design types, were included as moderators whose effects were assumed to be fixed. In all models, we treated 'study' as a random effect (see Supplementary Tables 1.1, 1.3, 2.1, 2.3). To handle non-independence in effect sizes of each study, we added a random effect as a unique identifier for each effect size in every study (EsID) which allows true effect sizes to vary within studies, and to account for the within-study effect and quantify within-study heterogeneity. To obtain robust results and account for differences in precision across studies and effect sizes, we weighted effect sizes using the inverse of the addition of the variance-covariance matrix, which explicitly captured the non-zero covariance arising from correlation between sampling variance within the same original articles and random effect variance[72]. Phylogenetic correction for plants was also undertaken to investigate the effects of plant species richness on trophic groups. To do this, plant species phylogenies were included as a random effect with phylogenetic relatedness as part of the correlation structure. In addition, phylogenetic trees of all crop species in agroecosystems were drawn to investigate the evolutionary relationships among different crop species (Supplementary Fig. 43). Specifically, we matched the crop species included in our analysis with the available synthetic tree in R package "rotl", then the relationships between each matched crop species were returned so that they could be used to draw phylogenetic trees.

To adjust for repeated measurement of control values, we assigned the argument “V” in “rma.mv()” function with the sampling variance-covariance matrix estimated as follows[72]:

$$v_1 = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{1T,i}}{\sum_{i=1}^{K} n_{1T,i}}\right]^2}{n_{1T}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{1T,i}}{\sum_{i=1}^{K} n_{1T,i}}\right]^4}{2n_{1T}^2} \quad \text{(Eq.7)}$$

$$v_2 = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{2T,i}}{\sum_{i=1}^{K} n_{2T,i}}\right]^2}{n_{2T}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i,}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{2i}}{\sum_{i=1}^{K} n_{2T,i}}\right]^4}{2n_{2T}^2} \quad \text{(Eq.8)}$$

$$v_{12} = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2} \quad \text{(Eq.9)}$$

where the subscripts $1T$ and $2T$ represent the different treatment group who share the control value in a same group; the subscript $1C$ represents the 1st control group; n represents the number of observations, CV represents the coefficients of variance of observed value. Taking this approach 116 plant species defined the correlation structure based on the plant phylogeny (see Supplementary Tables 1.2, 1.4, 2.2, 2.4; Supplementary Methods)[73,74].

For each mixed-effects meta-regression model, we first fitted a base model by treating plant species richness and trophic group as the fixed effect terms. Second, the interactions between the trophic group and other predictor variables (types of ecosystems, plant life forms, climatic zones, experiment study types, plant diversity types, and experimental design types) were also included in the model to assess whether model fit was improved, using a likelihood-ratio test (LRT). Third, the trophic group response category (nested within trophic group) and the interactive effects between the response category and predictors were also included in the model (using a LRT to allow model comparisons) (Supplementary Table 1). For example, the model with “trophic group + ecosystem type” was compared to the base model with just trophic group, and the model with “trophic group + trophic group × ecosystem type” would be compared to a model with “trophic group + ecosystem type” (Supplementary Tables 1 and 2).

To examine whether the mean effect sizes of (added) plant species richness, response category and other predictors differed significantly from zero, we acquired estimations with their 95% confidence intervals, which were derived from the fitted meta-regression models. To assess the between-study heterogeneity in these models, I^2 statistics were calculated[72,75,76] (Supplementary Tables 1–7) and orchard plots[77] are presented in Supplementary Figs. 13–42.

Mediation analysis to test the effects of plant species richness

To explore the trophic interactions between plants and various groups of plant antagonists, we established a new data subset: 1) comprising paired trophic observations (e.g., plant performance vs. herbivore performance) (see Supplementary Fig. 12); 2) encompassing the paired observations of plant performance vs. plant antagonist performance in all ecosystems, and separately for agroecosystems, grasslands and forests, and the paired observations of plant performance vs. plant antagonist performance in intercropping, cover cropping and sown field margin farming systems (Fig. 4; Supplementary Figs. 11a–d); 3) and comprising the paired observations of plant performance vs. plant antagonist performance within different plant life forms, climatic zones, and experimental type, respectively (Extended Data Fig. 7; Supplementary Figs. 11e–j). The lnRR effect sizes were derived from these pairwise data sets.

To analyze the direct effect of plant antagonists on plant performance in path analysis, residual regression was applied (Fig. 4 and Extended Data Fig. 7). In this analysis we used the lnRR as the response variable. Specifically, the direct effects of increasing plant species on plant antagonist were estimated using linear mixed-effects model (See details in Supplementary Methods):

$$\text{plant antagonist performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij}$$

Following Emmenegger & Bühlmann[78]. The direct effect of plant species richness on plant performance were estimated by regressing the Pearson residuals of the linear mixed-effects model:

$$\text{plant performance lnRR}_{\text{ij}} = \beta \times \text{plant antagonist performance lnRR}_{ij} + r_i + \varepsilon_{ij}$$

on plant species richness. The direct effects of plant antagonists on plants were estimated by regressing the Pearson residuals extracted from the linear mixed-effects model:

$$\text{plant performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij}$$

on the Pearson residuals extracted from the linear mixed-effects model:

$$\text{plant antagonist performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij}$$

where β is the effect size, r_i is the random effect represents the heterogeneity between studies or the phylogenetic relatedness of the plant species within ith study, ε_{ij} is the random error term with variance equal to the lnRR's sample variance estimate.

In summary, for our path analyses, linear mixed-effects models were conducted with the R function "lme" of the package "nlme", with random intercepts for study IDs. Heteroscedasticity was accounted for by providing fixed variances based on lnRRs and setting sigma to 1 in the lme call.

We extracted the z-values of corresponding coefficients to test the effects of plant species richness on each of the interactions between performance values of plants and herbivores, plants and diseases, plants and weeds, and plants and nematodes, respectively. Likewise, we extracted the z-values of corresponding coefficients to test the effects of plant species richness on the interactions between performance values of plants and the aggregate indicator (i.e., plant antagonists) in different ecosystems (Fig. 4), as well as the effects of plant species richness on the interactions between plant performance and plant antagonist performance for different plant life forms, climatic zones, experiment types, plant diversity types in agroecosystems (intercropping, cover cropping and sown field margins), and experimental design types, respectively (Extended Data Fig. 7). The estimations and test statistics were extracted using the R function "coef()" (Supplementary Tables 8, 10 and 12). The relative goodness-of-fit analyses for path analyses of predictor variables (plant species richness), were conducted by extracting AIC (Akaike information criterion), AICc (corrected Akaike information criterion), BIC (Bayesian information criterion) and log-likelihood from the fitted models, using R functions "AIC()", "AICc()"[79], "BIC()" and "logLik()" (Supplementary Table 15).

Publication bias test

We assessed publication bias using regression tests[80,81] (Supplementary Table 2) which employ a partial slope test of association between effect size and the sample size. Here, a significant relationship ($p<0.05$) suggests publication bias. The trim-and-fill method was not employed as this is inappropriate for models with moderators[82,83]. Instead, we adopted the method suggested by Nakagawa et al.[81], which uses a multilevel version of Egger regression to assess publication bias in mixed-effects meta-regression analysis. Here, we considered lnRR as a response variable. Different categories of trophic groups, ecosystems, plant life forms, climatic zones, experimental studies, plant diversity types and experimental design types were considered as predictors, respectively, and sampling sizes were considered as an additional moderator in the mixed-effect model and the test statistics for coefficients of sampling sizes were used to test for publication bias (see Supplementary Methods).

We used R version 4.3.1[84] to conduct all statistical analyses, and used R package "metafor" 3.8-1 to perform meta-regression and publication bias assessment[85]. In addition, we used R packages "nlme"[86] to residual regression in path analyses. A significance level of 0.05 was used for all tests. To test the lnRR is appropriate for our raw data, we conducted a Geary- Lajeunesse test[87]. The data and code used in this study are publicly available in Zenodo (https://doi.org/10.5281/zenodo.17568135) (ref. 88).

Data availability

The raw and processed data used in this study is available and is deposited to Zenodo (https://doi.org/10.5281/zenodo.17568135) (ref. 88).

Code availability

The code that supports the findings of this study has been deposited in Zenodo (https://doi.org/10.5281/zenodo.17568135) (ref. 88).

Acknowledgments

We thank all of the researchers whose data and work have been included in this meta-analysis. N.F.W. was supported by Shanghai Agriculture Applied Technology Development Program, China (Grant No. 2023-02-08-00-12-F04586), Natural Science Foundation of Shanghai (22ZR1417200), National Natural Science Foundation of China (32172484), Fundamental Research Funds for the Central Universities (JKY01231718), Shanghai Science and Technology Innovation Action Plan from Shanghai Municipal Science and Technology Commission of China (22015821000) and National Ten Thousand Plan-Young Top Talents of China. L.F. was supported by the National Natural Science Foundation of China (82204063). Y.Q.H. was supported by National Key R&D Program of China (2023YFF1205101) and

National Natural Science Foundation of China (11971117). B.A.W is funded though the Natural Environment Research Council RestREco (NE/V006444/1) and AgZero+ (NE/W005050/1) projects. D.Z.D. was supported by the University of Zurich Research Priority program on Global Change and Biodiversity.

Author contributions

N.F.W. conceived the idea. N.F.W., Y.Q.W., L.F. and J.L. collected and analyzed data and drafted the article. N.F.W., Y.Q.W., L.F., J.L., B.A.W., Y.Q.H., A.E., A. H., M.L., Y.H., R.D.B., P.K., D.Z.D., L.H.F., J.M.B., S.N., S.S., F.X., D.P.S., Z.L., J.Z. and C.S. wrote the manuscript. All authors prepared and edited the final drafts.

Competing interests

The authors declare no competing financial interests.

Correspondence and requests for materials should be addressed to N.F.W.

Table 1 | Quantified effects of number of added plant species on plant performance in different ecosystems. Increased percentage of plant performance = (data of plant performance in treatment－data of plant performance in control) / data of plant performance in control×100%.

Number of added plant species over the control	Ecosystem types	Number of observations	Number of studies	Increased percentage of plant performance	Lower of 95% CI	Upper of 95% CI	t value	P value
1	Agroecosystem	1568	250	23.45%	23.42%	23.47%	12.5760	1.2657×10^{-34}
1	Grassland	96	40	35.02%	35.00%	35.04%	5.5417	2.6722×10^{-7}
1	Forest	39	13	5.71%	5.71%	5.72%	2.9297	0.0057
2	Agroecosystem	148	32	23.57%	23.56%	23.58%	9.2958	1.8594×10^{-16}
2	Grassland	14	9	14.87%	14.86%	14.88%	1.7463	0.1043
2	Forest	33	9	19.32%	19.31%	19.33%	3.2803	0.0025
3	Agroecosystem	51	15	44.60%	44.59%	44.62%	6.6179	2.3776×10^{-8}
3	Grassland	97	47	56.35%	56.30%	56.39%	4.6000	1.2903×10^{-5}
3	Forest	29	11	12.89%	12.89%	12.90%	3.6276	0.0011
4	Agroecosystem	6	5	20.21%	20.19%	20.23%	0.9271	0.3964
4	Grassland	10	3	61.86%	61.82%	61.90%	1.6249	0.1386
4	Forest	6	4	45.74%	45.71%	45.77%	1.2981	0.2509
5	Agroecosystem	5	3	77.77%	77.74%	77.79%	2.4287	0.0721
5	Grassland	9	7	227.52%	227.31%	227.72%	1.1663	0.2771
5	Forest	13	5	17.06%	17.05%	17.07%	2.5149	0.0272
6	Agroecosystem	2	2	9.87%	9.86%	9.88%	0.3540	0.7834
6	Grassland	2	2	95.62%	95.58%	95.67%	1.0300	0.4906
6	Forest	1	1	71.67%	NA	NA	NA	NA
7	Agroecosystem	1	1	226.93%	NA	NA	NA	NA
7	Grassland	72	34	61.98%	61.96%	62.00%	8.0216	1.5251×10^{-11}
7	Forest	6	3	61.79%	61.78%	61.80%	7.4426	0.0007
8	Grassland	7	5	27.22%	28.00%	27.23%	1.3044	0.2399
8	Forest	6	2	28.03%	28.01%	28.04%	1.7293	0.1443
9	Agroecosystem	1	1	89.47%	NA	NA	NA	NA
9	Grassland	5	2	195.45%	195.39%	195.51%	2.3752	0.0764
9	Forest	1	1	108.83%	NA	NA	NA	NA
10	Grassland	2	2	138.75%	138.72%	138.78%	2.2653	0.2646
10	Forest	1	1	120.35%	NA	NA	NA	NA
11	Grassland	4	3	69.81%	69.80%	69.81%	10.4638	0.0019
11	Forest	1	1	1217.65%	NA	NA	NA	NA
12	Grassland	5	1	-2.97%	-2.98%	-2.97%	-0.4319	0.6881
13	Agroecosystem	2	1	16.03%	16.01%	16.04%	0.6265	0.6437
13	Grassland	2	2	161.86%	161.82%	161.89%	2.1674	0.2752
14	Grassland	5	2	211.66%	211.58%	211.75%	1.9149	0.1280
15	Grassland	67	34	107.33%	107.29%	107.37%	7.9595	3.1282×10^{-11}
15	Forest	2	1	89.91%	89.90%	89.91%	7.6283	0.0830
19	Agroecosystem	1	1	-18.91%	NA	NA	NA	NA
20-56	Grassland	38	5	35.72%	35.71%	35.74%	4.4491	7.6204×10^{-5}
59	Grassland	33	12	138.53%	138.47%	138.60%	4.1016	2.6306×10^{-4}

Table 2 | Quantified effects of number of added plant species on plant antagonist performance in different ecosystems. Decreased percentage of plant antagonist performance = (data of plant antagonist performance in control − data of plant antagonist performance in treatment) / data of plant antagonist performance in control×100%.

Number of added plant species over the control	Ecosystem types	Number of observations	Number of studies	Decreased percentage of plant antagonist performance	Lower of 95% CI	Upper of 95% CI	t value	P value
1	Agroecosystem	2468	381	29.54%	29.55%	29.52%	-31.0030	1.6622×10^{-178}
1	Grassland	94	36	6.76%	6.79%	6.73%	-0.7847	0.4346
1	Forest	50	21	12.28%	12.29%	12.26%	-2.4477	0.0180
2	Agroecosystem	183	49	38.35%	38.36%	38.34%	-16.3881	1.1383×10^{-37}
2	Grassland	8	3	38.77%	38.79%	38.75%	-1.7762	0.1190
2	Forest	29	14	10.48%	10.50%	10.46%	-1.0285	0.3125
3	Agroecosystem	57	25	25.95%	25.97%	25.94%	-4.3253	6.3300×10^{-5}
3	Grassland	64	33	20.67%	20.68%	20.65%	-3.7826	0.0003
3	Forest	41	19	12.74%	12.75%	12.73%	-2.7906	0.0080
4	Agroecosystem	27	11	27.75%	27.76%	27.74%	-3.6813	0.0011
4	Grassland	7	2	41.32%	41.33%	41.31%	-3.6973	0.0101
4	Forest	17	7	23.65%	23.66%	23.64%	-4.2638	0.0006
5	Agroecosystem	11	7	58.54%	58.55%	58.53%	-7.3694	2.3990×10^{-5}
5	Grassland	9	6	51.11%	51.12%	51.10%	-4.2763	0.0027
5	Forest	18	7	17.44%	17.45%	17.43%	-2.3623	0.0303
6	Agroecosystem	17	7	41.94%	41.96%	41.91%	-2.8634	0.0113
6	Grassland	4	1	0.75%	0.75%	0.74%	-0.1155	0.9153
7	Agroecosystem	4	3	-36.44%	-36.41%	-36.47%	0.7764	0.4941
7	Grassland	49	25	12.97%	12.99%	12.95%	-1.6799	0.0995
7	Forest	7	6	-23.22%	-23.21%	-23.23%	1.7877	0.1241
8	Agroecosystem	2	2	39.70%	39.71%	39.69%	-2.0239	0.2922
8	Grassland	6	3	72.18%	72.19%	72.18%	-9.3168	0.0002
8	Forest	2	2	39.89%	39.91%	39.87%	-1.0375	0.4883
9	Agroecosystem	1	1	38.76%	NA	NA	NA	NA
9	Grassland	4	1	35.55%	35.55%	35.54%	-3.4948	0.0396
9	Forest	2	2	37.52%	37.52%	37.52%	-42.1868	0.0151
10	Forest	6	3	-17.58%	-17.56%	-17.60%	0.7334	0.4962
11	Grassland	9	5	62.86%	62.87%	62.85%	-5.0456	0.0010
11	Forest	1	1	12.86%	NA	NA	NA	NA
12	Agroecosystem	3	1	19.44%	19.43%	19.43%	-135.4130	5.4531×10^{-5}
12	Forest	1	1	83.73%	NA	NA	NA	NA
13	Agroecosystem	2	1	86.00%	86.00%	86.00%	-39.8020	0.0160
13	Forest	4	2	27.24%	27.26%	27.23%	-1.3453	0.2712
14	Grassland	4	1	26.45%	26.46%	26.44%	-1.5537	0.2181
14	Forest	6	2	17.87%	17.88%	17.86%	-1.2576	0.2641
15	Agroecosystem	1	1	48.65%	NA	NA	NA	NA
15	Grassland	34	19	19.51%	19.54%	19.48%	-1.4517	0.1560
15	Forest	9	5	-49.00%	-48.98%	-49.01%	3.2985	0.0109
16	Forest	2	2	32.17%	32.18%	32.15%	-1.1270	0.4620
19	Agroecosystem	2	1	41.25%	41.26%	41.24%	-1.9508	0.3016
19	Forest	4	2	31.47%	31.49%	31.46%	-1.6193	0.2038
20-31	Grassland	9	6	45.85%	45.87%	45.83%	-2.3252	0.0485
21-44	Forest	26	6	-4.35%	-4.33%	-4.36%	0.4334	0.6684
59	Grassland	17	8	22.11%	22.13%	22.08%	-1.0508	0.3090

Figure legends

Fig. 1 | Global distribution of 636 study locations of the responses of plants and their antagonists to plant species richness. a, Study locations across global terrestrial ecosystems (world map in World Robinson projection; a literature search identified 536, 49 and 45 study locations for agroecosystems, grasslands and forests, respectively, from a total of 609 published articles; seven articles included more than one study location (range 2–11)). **b**, Hypotheses (H1: direct effects of plant diversity on plant productivity; H2: direct effects of plant diversity on plant antagonists; H3: mediation effects of plant antagonists on plant diversity-productivity relationships). **c**, Responses of plants and their antagonists across all studies. Plant antagonists include invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents. Weeds in forests were not found. Estimates for rodent damage (n<3) can be found in Supplementary Table 3. In Fig. 1c, horizontal lines indicate the 95% confidence intervals around the means; numbers in brackets indicate the numbers of observations and articles; and the lines represent plant antagonist (black), invertebrate herbivore (red), plant disease (green), weed (blue), plant-feeding nematode (turquoise), plant-consuming rodent (purple), and plant (orange) performance responses, respectively. Map © ARCGIS Software.

Fig. 2 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness. a, In agroecosystems, grasslands and forests. **b**, For herbaceous and woody plants. **c**, In temperate and tropical zones. **d**, For plot and pot experiments. **e**, In agroecosystems with intercropping, cover cropping and sown field margins. **f**, In additive design and replacement series design. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles. All analyses used two-tailed t-tests, and no corrections for multiple comparisons were applied.

Fig. 3 | Piecewise structural equation model for the effects of plant species richness on the performances of plants and plant antagonists. a, In agroecosystems (N=2583). **b**, In grasslands (N=65). **c**, In forests (N=118). **d**, In intercropping (N=2051). **e**, In cover cropping (N=396). **f**, In sown field margins (N=136). Plant performance includes the growth, reproduction and quality of plants. Plant antagonists includes: i) invertebrate herbivores (herbivore growth and reproduction, and herbivory damage to plants); ii) plant diseases (reproduction, spread, and damage to plants; iii) weeds (growth, reproduction, and diversity); iv) nematodes (reproduction, and damage to plants); and v) rodents (reproduction, and damage to plants). *$P<0.05$, **$P<0.01$, ***$P<0.001$. The R^2 was the proportion of variance of response explained by the corresponding predictor in each linear mixed model. Blue and red arrows denote positive and negative relationships, respectively. Numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients (Supplementary Tables 10, 11). The R^2 measures the proportion of variance explained by the corresponding predictor in each linear mixed model. All analyses used two-tailed t-tests, and no corrections for multiple comparisons were applied.

Fig. 4 | Piecewise structural equation model for the effects of plant species richness on the performances of plants and different groups of plant antagonists in global terrestrial ecosystems. a, Effects on plant and antagonist performance (N=2766). **b**, Effects on plant and invertebrate herbivore performance (N=1218). **c**, Effects on plant and plant disease performance (N=638). **d**, Effects on plant and weed performance (N=642). **e**, Effects on plant and plant-feeding nematode performance (N=268). Plant performance includes the growth, reproduction and quality of plants. Herbivore performance includes growth, reproduction and damage of invertebrate herbivores. Plant disease performance includes reproduction, spread and damage to plants. Weed performance includes growth, reproduction and diversity. Plant-feeding nematode performance includes reproduction and damage to plants. The data on the relationships between plant and plant-consuming rodent performances was not found. *$P<0.05$, **$P<0.01$, ***$P<0.001$. The R2 was the proportion of variance of response explained by the corresponding predictor in each linear mixed model. Blue and red arrows denote positive and negative relationships, respectively. Numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients (Supplementary Tables 8, 9). The R^2 measures the proportion of variance explained by the corresponding predictor in each linear mixed model. All analyses used two-tailed t-tests, and no corrections for multiple comparisons were applied.

References

1. Reckling, M., Watson, C. A., Whitbread, A. & Helming, K. Diversification for sustainable and resilient agricultural landscape systems. *Agron. Sustain. Dev.* **43**, 44 (2023).
2. Ray, D. K., Ramankutty, N., Mueller, N. D., West, P. C. & Foley, J. A. Recent patterns of crop yield growth and stagnation. *Nature Commu.* **3**, 1292 (2012).
3. Priyadarshana, T. S. et al. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. *Ecol. Lett.* **27**, e14412 (2024).
4. Gurr, G. M. et al. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nat. Plants* **2**, 1–4 (2016).
5. Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C. & Dicks, L. V. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecol. Lett.* **20**, 673–689 (2017).
6. Wan, N. F. et al. Increasing plant diversity with border crops reduces insecticide use and increases crop yield in urban agriculture. *eLife* **7**, e35103 (2018).
7. van der Werf, H. M. G., Knudsen, M. T. & Cederberg, C. Towards better representation of organic agriculture in life cycle assessment. *Nat. Sustain.* **3**, 419–425 (2020).
8. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).
9. Tilman, D., Reich, P. B. & Knops, J. M. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).
10. Scherber, C. et al. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556 (2010).
11. Isbell, F. et al. High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).
12. Tilman, D. Benefits of intensive agricultural intercropping. *Nat. Plants* **6**, 604–605 (2020).
13. Li, X. F. et al. Long-term increased grain yield and soil fertility from intercropping. *Nat. Sustain.* **4**, 943–950 (2021).
14. Yan, E., Munier-Jolain, N., Martin, P. & Carozzi, M. Intercropping on French farms: Reducing pesticide and N fertiliser use while maintaining gross margins. *Eur. J. Agron.* **152**, 127036 (2024).
15. Chadfield, V. G. A., Hartley, S. E. & Redeker, K. R. Associational resistance through intercropping reduces yield losses to soil-borne pests and diseases. *New Phytol.* **235**, 2393–2405 (2022).
16. Prieto, I. et al. Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. *Nat. Plants* **1**, 1–5 (2015).
17. Abdala-Robert, L. et al. Comparison of tree genotypic diversity and species diversity effects on different guilds of insect herbivores. *Oikos* **124**, 1527–1535 (2015).
18. Alarcon-Segura, V., Grass, I., Breustedt, G., Rohlfs, M. & Tscharntke, T. Strip intercropping of wheat and oilseed rape enhances biodiversity and biological pest control in a conventionally managed farm scenario. *J. Appl. Ecol.* **59**, 1513–1523 (2022).

19. El-Hamawi, M. H., Youssef, M. M. A. & Zawam, H. S. Management of *Meloidogyne incognita*, the root-knot nematode, on soybean as affected by marigold and sea ambrosia (damsisa) plants. *J. Pest Sci*. **77**, 95–98 (2004).
20. Larsen, A. L. et al. Effects of habitat modification on cotton rat population dynamics and rodent community structure. *Forest Ecol. Manage.* **376**, 238–246 (2016).
21. Boetzl, F. A. et al. Undersowing oats with clovers supports pollinators and suppresses arable weeds without reducing yields. *J. Appl. Ecol.* **60**, 614–623 (2023).
22. Boudreau, M. A. Diseases in intercropping systems. *Annu. Rev. Phytopathol.* **51**, 499–519 (2013).
23. Brooker, R. W. et al. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytol.* **206**, 107–117 (2015).
24. Kulmatiski, A., Beard, K. H. & Heavilin, J. Plant-soil feedbacks provide an additional explanation for diversity-productivity relationships. *P. Roy. Soc. B-Biol. Sci.* **279**, 3020–3026 (2012).
25. van Ruijven, J., Ampt, E., Francioli, D. & Mommer, L. Do soil-borne fungal pathogens mediate plant diversity-productivity relationships? Evidence and future opportunities. *J. Ecol.* **108**, 1810–1821 (2020).
26. Forero, L. E., Kulmatiski, A., Grenzer, J. & Norton, J. Plant-soil feedbacks help explain plant community productivity. *Ecology* **103**, e3736 (2022).
27. Ziaie-Juybari, H., Pirdashti, H., Abo-Elyousr, K. A. M. & Mottaghian, A. Abiotic benefits of intercropping legumes and maize to reduce pests. *Arch. Phytopathol. Plant Prot.* **54**, 17–18 (2021).
28. Guinet, M. et al. Fostering temporal crop diversification to reduce pesticide use. *Nat. Commu.* **14**, 7416 (2023).
29. Wan, N. F. et al. Plant genetic diversity affects multiple trophic levels and trophic interactions. *Nat. Commu.* **13**, 7312 (2022).
30. Dassou, A. G. & Tixier, P. Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. *Ecol. Evol.* **6**, 1143–1153 (2016).
31. Vehviläinen, H., Koricheva, J. & Ruohomäki, K. Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. *Oecologia* **152**, 287–298 (2007).
32. Letourneau, D. K. et al. Does plant diversity beneft agroecosystems? A synthetic review. *Ecol. Appl.* **21**, 9–21 (2011).
33. Wan, N. F. et al. Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nat. Plants* **6**, 503–510 (2020).
34. Iverson, A. L. et al. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *J. Appl. Ecol.* **51**, 1593–1602 (2014).
35. Wan, N. F., Dainese, M., Wang, Y. Q. & Loreau, M. Cascading social-ecological benefits of biodiversity for agriculture. *Curr. Biol.* **34**, R587–R603 (2024).
36. Verret, V. et al. Can legume companion plants control weeds without decreasing crop yield? A meta-analysis. *Field Crop. Res.* **204**, 158–168 (2017).
37. Himmelstein, J., Ares, A., Gallagher, D. & Myers, J. A meta-analysis of intercropping in africa: impacts on crop yield, farmer income, and integrated pest management effects. *Int. J. Agric. Sustain.* **15**, 1–12 (2018).
38. Li, C. et al. Syndromes of production in intercropping impact yield gains. *Nat. Plants* **6**, 653–660 (2020a).
39. Li, C. et al. Yield gain, complementarity and competitive dominance in intercropping in China: A meta-

analysis of drivers of yield gain using additive partitioning. *Eur. J. Agron.* **113**, 125987 (2020b)

40. Li, C. et al. The productive performance of intercropping. *Proc. Natl Acad. Sci. USA* **120**, e2201886120 (2023).
41. Mudare, S. et al. Yield and fertilizer benefits of maize/grain legume intercropping in China and Africa: a meta-analysis. *Agron. Sustain. Dev.* **42**, 81 (2022).
42. Viaud, P. et al. Sugarcane yield response to legume intercropped: A meta-analysis. *Field Crop. Res.* **295**, 108882 (2023).
43. Lopes, T. et al. Wheat (*Triticum aestivum* L.)-based intercropping systems for biological pest control. *Pest Manag. Sci.* **72**, 2193–2202 (2016).
44. Rakotomalala, A. A. N. A., Ficiciyan, A. M. & Tscharntke, T. Intercropping enhances beneficial arthropods and controls pests: A systematic review and meta-analysis. *Agric. Ecosyst. Environ.* **356**, 108617 (2023).
45. Yousefi, M. et al. The effectiveness of intercropping and agri-environmental schemes on ecosystem service of biological pest control: a meta-analysis. *Agron. Sustain. Dev.* **44**, 15 (2024).
46. Fernandez, A. R., Gleiser, G., Aizen, M. A. & Garibaldi, L. A. Intercropping functionally similar species reduces yield losses due to herbivory. A meta-analytical approach. *Agric. Ecosyst. Environ.* **361**, 108800 (2024).
47. Zhang, C. et al. Intercropping cereals with faba bean reduces plant disease incidence regardless of fertilizer input; a meta-analysis. *Eur. J. Plant Pathol.* **154**, 931–942 (2019).
48. Gu, C. F., Bastiaans, L., Anten, N. P. R., Makowski, D. & van der Werf, W. Annual intercropping suppresses weeds: A meta-analysis. *Agric. Ecosyst. Environ.* **322**, 107658 (2021).
49. Scott, D. & Freckleton, R. P. Crop diversification and parasitic weed abundance: a global meta-analysis. *Sci. Rep.* **12**, 19413 (2022).
50. Ramkat, R. C., Wangai, A. W., Ouma, J. P., Rapando, P. N. & Lelgut, D. K. Cropping system influences Tomato spotted wilt virus disease development, thrips population and yield of tomato (*Lycopersicon esculentum*). *Ann. Appl. Biol.* **153**, 373–380 (2008).
51. Wang, Y. Q. et al. Understanding biodiversity effects on trophic interactions with a robust approach to path analysis. *Cell Rep. Sustain.* **2**, 100362 (2025).
52. Wang, X. Y. et al. Microclimate, yield, and income of a jujube-cotton agroforestry system in Xinjiang, China. *Ind. Crop. Prod.* **182**, 114941 (2022).
53. Tang, X. Y. et al. Intercropping legumes and cereals increases phosphorus use efficiency; a meta-analysis. *Plant Soil* **460**, 89–104 (2021).
54. Inderjit, I. & Weiner, J. Plant allelopathic interference or soil chemical ecology? *Perspect. Plant Ecol. Evol. System.* **4**, 3–12 (2001).
55. Thorsted, M. D., Weiner, J. & Olesen, J. E. Above- and below-ground competition between intercropped winter wheat Triticum aestivum and white clover Trifolium repens. *J. Appl. Ecol.* **43**, 237–245 (2006).
56. Andersen, M. K., Hauggaard-Nielsen, H., Weiner, J. & Jensen, E. S. Evaluating competitive dynamics in two and three component intercrops. *J. Appl. Ecol.* **44**, 545–551 (2007).
57. dos Santos-Cordeiro, C. F., Rodrigues, D. R. & Echer, F. R. Cover crops and controlled-release urea decrease need for mineral nitrogen fertilizer for cotton in sandy soil. *Field Crop. Res.* **276**, 108387 (2022).
58. Root, R. B. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards

(*Brassica oleracea*). *Ecol. Monogr.* **43**, 95–124 (1973).

59. Loreau, M. et al. Biodiversity as insurance: from concept to measurement and application. *Biol. Rev.* **96**, 2333–2354 (2021).
60. Schuldt, A. et al. Tree diversity promotes insect herbivory in subtropical forests of south-east China. *J. Ecol.* **98**, 917–926 (2010).
61. Osipitan, O. A., Dille, J. A., Assefa, Y. & Knezevic, S. Z. Cover crop for early season weed suppression in crops: systematic review and meta-analysis. *Agron. J.* **110**, 2211–2221 (2018).
62. Weiner, J. Applying plant ecological knowledge to increase agricultural sustainability. *J. Ecol.* **105**, 865–870 (2017).
63. Kunz, C., Sturm, D. J., Varnholt, D., Walker, F. & Gerhards, R. Allelopathic effects and weed suppressive ability of cover crops. *Plant Soil Environ.* **62**, 60–66 (2016).
64. Hooks, C. R. R., Wang, K. H., Ploeg, A. & McSorley R. Using marigold (*Tagetes* spp.) as a cover crop to protect crops from plant-parasitic nematodes. *Appl. Soil Ecol.* **46**, 307–320 (2010).
65. Mishra, S. & DiGennaro, P. Root-knot nematodes demonstrate temporal variation in host penetration. *J. Nematol.* **52**, 1–8 (2020).
66. Costa, A. et al. Crop rotational diversity can mitigate climate-induced grain yield losses. *Global Change Biol.* **30**, e17298 (2024).
67. Tamburini, G. et al. Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci. Adv.* **6**, eaba1715 (2020).
68. Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V. & Makowski D. Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Global Change Biol.* **27**, 4697–4710 (2021).
69. MacLaren, C. et al. Long-term evidence for ecological intensification as a pathway to sustainable agriculture. *Nat. Sustain.* **5**, 770–779 (2022).
70. Nakagawa, S. et al. A robust and readily implementable method for the meta-analysis of response ratios with and without missing standard deviations. *Ecol. Lett*. **26**, 232-244 (2023).
71. van Houwelingen, H. C., Arends, L. R. & Stijnen, T. Advanced methods in meta-analysis: multivariate approach and meta-regression. *Statist. Med.* **21**, 589–624 (2002).
72. Nakagawa, S., Yang, Y., Macartney, E. L., Spake, R. & Lagisz, M. Quantitative evidence synthesis: a practical guide on meta-analysis, meta-regression, and publication bias tests for environmental sciences. *Environ. Evid.* **12**, 8 (2023).
73. Jin, Y. & Qian, H. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**, 1353–1359 (2019).
74. Jin, Y. & Qian, H. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Diversity* **44**, 335–339 (2022).
75. Ruppar, T. Meta-analysis: How to quantify and explain heterogeneity? *Eur. J. Cardiovas. Nur.* **19**, 646–652 (2020).
76. Nakagawa, S. et al. orchaRd 2.0: An R package for visualisingmeta-analyses with orchard plots. *Methods Ecol. Evol.* **14**, 2003–2010 (2023).

77. Nakagawa, S. et al. The orchard plot: Cultivating a forest plot for use in ecology, evolution, and beyond. *Res. Syn. Meth.* **12**, 4–12 (2021).
78. Emmenegger, C. & Bühlmann, P. Plug-in machine learning for partially linear mixed-effects models with repeated measurements. *Scand. J. Statist.* **50**, 1553–1567 (2023).
79. Bartoń K. MuMIn: Multi-Model Inference. R package version 1.47.5, https://CRAN.R-project.org/package=MuMIn (2023).
80. Egger, M., Davey, S. G., Schneider, M. & Minder C. Bias in meta-analysis detected by a simple, graphical test. *BMJ*. **315**, 629–634 (1997).
81. Nakagawa, S. et al. Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods Ecol. Evol.* **13**, 4–21 (2022).
82. Duval, S. & Tweedie, R. Trim and fill: A simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. *Biometrics* **56**, 455–463 (2000).
83. Nakagawa, S. & Santos, E. S. A. Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253–1274 (2012).
84. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (2023).
85. Viechtbauer, W. Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Soft*. **36**, 1–48 (2010).
86. Pinheiro, J., Bates, D. & R Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-163. https://CRAN.R-project.org/package=nlme (2023).
87. Lajeunesse, M. J. Bias and correction for the log response ratio in ecological meta-analysis. *Ecology* **96**, 2056–2063 (2015).
88. Wan, N. F. Data and code for "Global evidence that plant diversity suppresses pests and promotes plant performance and crop production". Zenodo https://doi.org/10.5281/zenodo.17568135 (2025).