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Global synthesis of effects of plant species diversity on trophic groups and interactions

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Abstract: Numerous studies have demonstrated that plant species diversity enhances ecosystem functioning in terrestrial ecosystems, including diversity effects on insect arthropods (herbivores, predators and parasitoids) and plants. Yet, the effects of increased plant diversity across trophic levels in different ecosystems and biomes have not yet been explored on a global scale. Through a global meta-analysis of 2914 observations from 351 studies, we found that increased plant species richness reduced herbivore abundance and damage but increased predator and parasitoid abundance, predation, parasitism, and overall plant performance. Moreover, increased predator/parasitoid performance was correlated with reduced herbivore abundance and enhanced plant performance. We conclude that increasing plant species diversity promotes beneficial trophic interactions between insects and plants, ultimately contributing to increased ecosystem services.

Plant species diversity can influence and provide multiple ecosystem services in terrestrial ecosystems [1-4]. In managed ecosystems, plant diversity can be increased by adding more plant species within and around the managed areas or by increasing structural variation of vegetation in the surrounding landscapes. Such increases in plant species diversity can increase primary production[5] and crop yields[6], promote natural pest and disease control[7], and reduce the use of chemical pesticides[8]. Many studies have documented the detrimental effects of monoculture intensification on farmland biodiversity[9, 10], and reported the identity effects of a single or few plant species on community-level diversity[11]. However, the effects of increasing plant species diversity across trophic levels in different ecosystems or biomes have not yet been explored on a global scale.

Trophic interactions are ubiquitous in nature, and one type of interaction of great interest to society occurs when predators and parasitoids in a food web suppress the abundance or alter the behavior of their prey (including herbivores), thereby releasing the next lower trophic level (i.e. plants) from predation or herbivory[12-14]. Several experiments have shown major bottom-up effects, in which an increase in plant species diversity can intensify trophic interactions at higher trophic levels[15,16]. This can manifest through increases in the abundance and diversity of predators and parasitoids[17], decreases in the abundance of insect herbivores[8,18], and increases in primary productivity and reproductive output[19, 20]. Opposite results, however, have been also reported in other studies. For instance, plant species diversity decreased predatory ladybird abundance [21], increased herbivorous cabbage worm abundance [22] and reduced plant biomass and production [23]. We still lack a comprehensive understanding of these relationships because most studies of plant diversity effects on associated consumers have not taken into account the potential for dynamic feedbacks across trophic levels[24].

Generalized understanding often requires synthesis of the literature, to elucidate broad trends and to identify research gaps. Meta-analysis has become a common approach to improving the overall understanding of scientific problems and identifying sources of variation in study outcomes across independent studies[25-27]. Previous meta-analyses have shown that crop species diversity enhances natural pest control by predators[28, 29]. However, these syntheses covered only bi-trophic interactions of predators/parasitoids and insect herbivores or herbivores and plants, but not the tri-trophic interactions involving all three. Additionally, these meta-analyses did not investigate these diversity effects on a global scale, comparing across different ecosystems, plant life forms or biomes.

We here conducted a meta-analysis of 351 published studies with 2914 observations on the effects of plant species diversity on trophic groups (plants, herbivores, predators and parasitoids) in terrestrial ecosystems around the world (Fig. 1; Supplementary Note 1; Supplementary Table 1). Based on the mean effect sizes of responses to plant species diversity for these trophic groups across all studies, we examined pairwise interactions and tri-trophic interactions using path analysis. Through these approaches, we asked three questions: (1) How does plant species diversity affect abundance and diversity of arthropod communities (predators, parasitoids and herbivores) and plant performance (growth, reproduction and quality)? (2) Do the effects differ among ecosystems (agroecosystems, grasslands forests), plant life forms (herbaceous and woody plants) or biomes (tropical and temperate biomes)? and (3) What are the direct and indirect effects of plant species diversity across trophic interactions? The meta-analysis allowed us to address the first two questions, by testing for the effects of plant species diversity on the four individual trophic groups, while pairwise association and path analysis were used to answer the third question, advancing our understanding of trophic interactions, and the combination of these methods provides insights into future priorities for research and management.

Trophic group responses to increased plant species diversity

Across the 351 studies (2914 data points in total) synthesized here, increased plant diversity significantly affected all trophic groups, with predators, parasitoids and plants responding positively and herbivores negatively (Supplementary Tables 2-4; Fig. 2a). Similar patterns emerged when the trophic groups were subdivided into 12 response categories ($\mathbf{X}^2$ = 152.601, d.f. = 8, P<0.001; Fig. 2a; Supplementary Table 2). Increased plant diversity positively affected all response categories of predators, parasitoids and plants, and negatively affected herbivore abundance and herbivory damage (Fig. 2a; Supplementary Table 4). Herbivore diversity, on the other hand, increased in response to addition of plant species.

When considering ecosystems separately, increased plant species diversity was also found to significantly affect all four trophic groups in both agroecosystems and grasslands, while in forests, only plants were significantly affected by increased plant diversity (Supplementary Table 5; Fig. 2b). Additionally, plant species diversity significantly affected all trophic groups when the two life forms of herbaceous and woody plants were considered separately (Supplementary Table 6; Fig. 2c). All trophic groups were significantly affected in temperate biomes, whereas predators, parasitoids and herbivores, but not plants, were significantly affected in tropical biomes (Supplementary Table 7; Fig. 2d).

We then further examined the relationship between plant species diversity and the different trophic groups and tested the direct and indirect effects of plant species diversity across trophic interactions by considering the performance of each trophic group separately. Specifically, (1) predator performance included abundance of predators and predation, (2) parasitoid performance included abundance of parasitoids and parasitism, (3) herbivore performance included herbivore abundance and herbivory damage, and (4) plant performance included growth, quality and reproduction of plants. In the meta-regression model (model 1), the addition of plant species had significantly different effects on different trophic groups ($\mathbf{X}^2$ = 115.186, d.f. = 1, P < 0.001; Supplementary Table 2). Separate meta-regressions for each trophic group showed that herbivore performance and plant performance increased with the increasing number of additional species, while predator performance and parasitoid performance were not significantly affected by plant species diversity (predators: T= 0.169, d.f.=569, P=0.866; parasitoids: T =1.190, d.f.=133, P=0.236; herbivores: T=4.347, d.f.=944, P < 0.001; plants: T =7.271, d.f.=1039, P<0.001) (Supplementary Fig. 4). However, none of the relationships between predator, parasitoid, herbivore or plant performance and the number of plant species were significant for individual ecosystem types (Supplementary Fig. 5).

Effects of plant species diversity on bi-trophic associations

We used all paired observations of predator/parasitoid performance vs. herbivore performance and of herbivore performance vs. plant performance, respectively, to test how interactions among these trophic groups responded to the increase in plant species diversity (Supplementary Table 8). Overall, herbivore responses to plant species diversity were significantly negatively correlated with both predator and parasitoid responses to increased plant species diversity (predators vs. herbivores: r = -0.191, T = -2.650, d.f. = 313, P = 0.008; parasitoids vs. herbivores: r = -0.240, T = -2.535, d.f. = 100, P = 0.013) (Fig. 3a; Supplementary Fig. 10). Accordingly, herbivore responses were correlated negatively with predator and parasitoid responses when these guilds were included in a unique 'natural enemy' group (r = -0.199, T = -3.365, d.f. = 415, P < 0.001) (Fig. 3a; Supplementary Fig. 10). This was also the case when we analyzed the ecosystems separately (agroecosystems: r = -0.133, T = -1.972, d.f. = 359, P = 0.049; grasslands: r = -0.608, T = -4.416, d.f. = 28, P < 0.001; forests: r = -0.495, T = -2.316, d.f. = 24, P = 0.029) (Fig. 3b-d; Supplementary Fig. 10). Herbivore responses to increased plant species diversity were not significantly correlated with plant responses to increased plant species diversity in any of the ecosystems (across ecosystems: r = -0.051, T = -1.198, d.f. = 292, P = 0.232; agroecosystems: r = -0.003, T = -0.068, d.f. = 239, P = 0.946; grasslands: r = -0.158, T = -0.934, d.f. = 10, P = 0.372; forests: r = 0.115, T = 0.764, d.f. = 39, P = 0.450) (Fig. 3a-d; Supplementary Fig. 10). Similarly, pairwise associations were mostly negative when the analyses were performed for each plant life form and biome, separately (Supplementary Table 10).

Effects of plant species diversity on trophic interactions

For the subset of studies where data for all tri-trophic levels were provided (N = 136; Supplementary Table 9), path analyses showed that plant diversity increased predator and parasitoid performance, but the effect was only marginally significant across all ecosystems (P=0.065) (Fig. 4a) and non-significant for agroecosystems (N = 119; P=0.195) (Fig. 4b; Supplementary Table 11). Increases in predator and parasitoid performance significantly reduced herbivore performance in all ecosystems combined

(P=0.002), notably in agroecosystems (P<0.001). Herbivore performance had no significant effects on plant performance (across ecosystems: P=0.425; agroecosystems: P=0.489) (Figs. 4a, b; Supplementary Table 11), and nor did increased plant species diversity impact herbivore performance (across ecosystems: P=0.401; agroecosystems: P=0.740) or plant performance (terrestrial ecosystems: P=0.985; agroecosystems: P=0.227) (Figs. 4a, b; Supplementary Table 11). Overall, the full model provided a reasonable fit to the data (d-separation test, P =0.294).

Our meta-analysis showed that increasing plant diversity generally enhanced predator abundance and predation, increased parasitoid abundance and parasitism, decreased herbivore abundance and damage, and promoted plant performance across major terrestrial ecosystems. Path analysis revealed that natural enemy effects on herbivores was the strongest of these relationships, although the reduced set of studies measuring all three trophic levels might not have had the predictive power to detect these effects in the larger set of studies with pairwise comparisons. These findings clearly support that plant species diversity can help farmers, decision-makers, and society to take advantage of the important ecosystem services provided by beneficial insects in agricultural and other systems.

Effects of plant species diversity on trophic groups

While plant diversity significantly affected all the trophic groups (Supplementary Table 4; Fig. 2a), the plant response to increased plant diversity differed among different ecosystems. This is likely related to the different number of plant species added to experimental plots in different ecosystems. In agroecosystems, for example, intercropping and cover vegetation are commonly applied and the number of crop species used is often smaller (2-3 in general) [8, 18] than in grasslands and forests, where species counts ranged from a maximum of 60 (in the Jena Experiment in Germany) [23] to 16 (in the Cedar Creek Experiment in Minnesota[2] and the BEF Experiment in China[4]). While it may not be practical to reach as high number of plant species in agroecosystems as in unmanaged systems, our results show that intercropping and cover cropping measures are also beneficial practices for increasing predators/parasitoids, reducing herbivory damage to crops and improving crop yield. The fact that there were no significant differences between adding one and adding more than one species in agroecosystems (Supplementary Fig. 5) implies that trophic interactions can be triggered just by adding a single species and that additional species may not be so important in agroecosystems.

Plant species diversity significantly benefitted predator, parasitoid and plant performance in both agroecosystems and grasslands (Fig. 2b). However, while plant species diversity reduced herbivore performance in agroecosystems, it benefitted herbivores in grasslands. In agroecosystems, the decline in herbivore performance due to higher plant species diversity could be explained by the 'Natural Enemy Hypothesis', which predicts that natural enemy diversity is positively correlated with plant species diversity, resulting in lower herbivore level in fields with greater plant species diversity[30, 31]. However, this result could be also explained by the 'Resource Concentration Hypothesis', which predicts that specialist arthropod herbivores attain higher density per unit mass of the host-plant species when their food plants grow in high-density patches in mono-cultivated fields[32, 33]. In grasslands, the increased herbivore performance could instead be due to greater availability of nutritionally more balanced or temporally less variable food resources[34, 35], while the non-significant effects on predator and herbivore in forests (Fig. 2b) might be due to contrasting diversity effects. On the one hand, tree species diversity can increase the abundance of generalist herbivores and predators by providing a higher diversity of resources that allows for optimized nutrient uptake or increases host or prey biomass[36, 37]. On the other hand, an increased tree species diversity and generally higher structural heterogeneity[38] can reduce the abundance of specialist herbivores by decreasing host availability[32], and can decrease the abundance of predators by reducing their rate of encountering herbivore prey. Diversification of food sources might also be the main cause of higher herbivore diversity with increased plant species diversity (Fig. 2a), which determines an accumulation of consumers specializing on different resources as indicated by the 'Resource Specialization Hypothesis'. The finding that an increase in herbivore diversity was higher in natural grasslands and forest ecosystems (Supplementary Fig. 1) may be explained by the fact that agroecosystems are typically diversified by fewer and specifically selected species and more intensively managed (e.g. pesticides) than less disturbed ecosystems.

Increased plant species diversity significantly affected the four trophic groups in both herbaceous species- and woody species-dominated systems ($P<0.001$; Supplementary Table 6; Fig. 2c), as indicated by a positive effect of plant species diversity on predators, parasitoids and plants, and a negative effect on herbivores. Both herbaceous species- and woody species -dominated systems were effective in benefiting predators, parasitoids and plants and in suppressing herbivores, but there were fewer studies documenting the responses of multiple trophic groups to plant diversity in woody species-dominated systems (Supplementary Note 1; Supplementary Table 6). Likewise, we found that such increased plant diversity significantly affected the four trophic groups in temperate biomes. These responses were only marginally significant in tropical biomes (P=0.115), but this might be an artifact of fewer studies documenting plant responses to increased plant diversity in tropical biomes (Supplementary Table 7), Thus, more studies are needed to test the effect of increasing plant species diversity on trophic groups in woody species-dominated systems and in the tropics.

Effects of plant species diversity on trophic interactions

Our results indicated that plant species diversity significantly promoted bi-trophic interactions between predators/parasitoids and herbivores in agroecosystems, grasslands and forests (correlation coefficient from -0.608 to -0.133; P=0.000-0.049; Supplementary 10). In agroecosystems and forests, the positive responses of predator and parasitoid performance and the negative responses of herbivore performance to plant species diversity might suggest a negative bi-trophic association (Predator and parasitoid performance: agroecosystems, effect size=0.820, P<0.001; forests, effect size=0.759, P=0.091. Herbivore performance: agroecosystems, effect size= -1.147, P<0.001; forests, effect size= -0.959, P=0.001) (Supplementary Table 8). The even stronger negative bi-trophic association in grasslands was likely a result of the stronger responses of both natural enemy and herbivore performance to plant species diversity (predator and parasitoid performance: effect size=2.363, P<0.001; herbivore performance: effect size= -1.768, P<0.001) (Supplementary Table 8).

The effects of plant diversity on specialist vs. generalist arthropods have been shown to be of high importance[27]. For example, generalist predators and generalist herbivores had strong positive responses to plant diversity, while such response was not significant for specialist herbivores[27]. While our meta-analysis was unable to cover this important aspect without a re-analysis of raw data, future studies should pay greater attention to the effects of plant diversity on trophic interactions between generalist/specialist natural enemies vs. generalist/specialist herbivores to better understand the underlying effects of increased plant diversity on trophic interactions.

The bi-trophic interactions between herbivores and plants were not very strong in individual ecosystems (i.e., the correlation coefficient was lower or not significant: *r*=-0.003-0.115; P=0.372-0.946; Supplementary Table 10). Although the correlations between herbivore performance and plant performance were negative in both agroecosystems and grasslands, the mechanism explaining this link could be different. In agroecosystems, herbivore performance and plant performance responses to plant diversity were negative and positive, respectively (herbivore: effect size=-1.269, P<0.001; plant: effect size=0.902, P<0.001; Supplementary Table 8). The conclusions in agroecosystems were exemplified by the effects of maize intercropped in snap bean (*Phaseolus vulgaris*) fields that led to a reduction in population density of herbivore--Mexican bean beetle (*Epilachna varivestis*) and a greater growth of snap bean[39]. However, in grasslands, herbivore performance and plant performance responses were opposite (herbivore: effect size=0.308, P=0.374; plant: effect size= -0.106, P=0.745). A similar result reported by Petermann and colleagues showed that increasing plant species richness had the potential to increase herbivore abundance as an increased plant species richness could be advantageous for aphids, with negative consequence for plant biomass[40]. However, we are unable to explain the slightly positive correlations between herbivore performance and plant performance in forests (r=0.115, P=0.450), as herbivore performance response to plant diversity was negative (effect size=-0.231, P=0.136) while plant performance response was positive (effect size=0.316, P=0.027) (Supplementary Table 8).

In the path analysis for multiple trophic levels, we found that the responses of both predator and parasitoid performance and plant performance to plant diversity were significantly positive, and that the response of herbivore performance was negative in both terrestrial and agricultural ecosystems (Supplementary Table 9). However, we found that only six papers included in our meta-analysis tested tri-trophic interactions in grasslands and forests, and thus we had to discard the comparison among different ecosystems in the trophic cascade. Yet, 39 studies from all ecosystems and 33 studies from agroecosystems showed that plant diversity had the potential to trigger a tritrophic cascade with increased predator and parasitoid performance, which may have led to the observed decrease in herbivore performance, and, in turn, may explain the enhanced plant performance. However, as not all coefficients were statistically significant (Supplementary Table 11), it is likely that more studies are needed to explore this tri-trophic cascade.

Database limitations, implications and future directions

The data used in our meta-analysis were obtained mainly from agroecosystems, and hence the results of other ecosystems must be interpreted with caution. The limited number of studies (only 39) that included data from all three trophic levels limited our power for those analyses. To better understand the mechanisms driving top-down pest control, which could enhance the specificity of science-based management recommendations, we strongly encourage more biodiversity experiments that account for trophic cascades in the future. As there were only 5 observational papers in this meta-analysis, we did not classify the 351 papers into different study types (manipulative vs. observational). Due to the gap of landscape scale studies (only one study used plots larger than ≥500 m radius), we failed to distinguish effects of plant species diversity on trophic groups at local (field or plot-scale) vs. landscape scales. Up to date, large, cross-taxonomic and cross-regional studies have explored the effects of increasing landscape heterogeneity on pest control as a trophic interaction in agroecosystems[41-43]. Thus, we encourage more studies to focus on the effects of landscape composition and configuration on trophic interactions in agroecosystems, as well as in other ecosystems.

Conclusions

Our synthesis indicates that plant diversity enhances ecosystem services by strengthening trophic interactions, conserving beneficial arthropods, regulating herbivores and enhancing plant productivity. These results also help to reveal the context dependence of the mechanisms by which increasing plant diversity influences different trophic groups and their interactions. From an applied perspective, we highlight the importance of promoting plant diversification practices to enhance ecosystem functioning and its services.

Methods

Study Selection. Studies were selected through a search on the Web of Science (last accessed in May 2019) using the boolean search string: [“plant diversity” OR “plant richness” OR “mix crop*” OR “polyculture” OR “trap crop*” OR “ground cover” OR “vegetation” OR “intercrop*” OR “interplant*”] AND [“predat*” OR “herbivor*” OR “parasit*” OR “wasp*” OR “yield” OR “biomass*” OR “biological control” OR “pest control” OR “natural enem*” OR “pest”]. Reference lists of selected studies were also checked for relevant studies. In total, more than 40000 papers were screened for relevance and 351 were finally selected based on the following criteria: (1) the study included a treatment that increased the number of plant species, and the use of pesticides was the same for the control (single/lowest plant species) and the treatment (diverse plant species); (2) the measurements of treatment and control groups were conducted at the same spatiotemporal scale; (3) the means, standard errors (or standard deviations), and sample sizes of the selected variables could be extracted from tables, figures, the text or supporting information. When a study included different levels of plant species, measurements for lowest plant species vs. different plant species were considered as independent observations. Data extraction from figures was conducted with Get Data Graph Digitizer 2.25[44]. We first used the data that the authors had presented the average values of multiple sampling date and multiple sampling year in a cited study. If these average values were not given in a certain paper, we used the data of the latest sampling date when a study took measurements at different points in time[45, 46] (more details are provided in Supplementary Note 2). In agroecosystems, farming of a single species (i.e., monocultures) was considered as the control group, while diversified systems that involved planting two or more crops simultaneously (i.e. mixed-cropping or polycultures) or a mix of species around the main crop as the treatment group. In grasslands and forests, monocultures and various mixtures of species were considered as the control and the treatment groups, respectively. In these studies, plant species diversity has relied on randomized species composition in grasslands (i.e., Jena Experiment and Cedar Creek Experiment) and forests (i.e., BEF Experiment) but controlled compositions in agroecosystems.

Predictor variables. As predictor variables, we used five categorical variables and one continuous variable (a detailed description is presented in Supplementary Note 2): (1) Trophic group: predators, parasitoids, herbivores or plants. (2) Response category: abundance and diversity of predators and predation rate; abundance and diversity of parasitoids and parasitism rate; abundance and diversity of herbivores and herbivory damage; growth, quality and reproduction of the plants. (3) Ecosystem type: agroecosystems (crops, ornamental plant plantations, and orchards), grasslands, and forests. (4) Plant life form: herbaceous or woody plants[47]. (5) Biome type: tropical or temperate biomes. (6) Number of added plant species: the number of species added by manipulated plant diversity in experimental designs or by non-manipulated plant diversity in observational studies compared to a control group.

Effect size measures. We used the Standardized Mean Difference (SMD) (SMD=m_{1i} - m_{2i})/spi. m_{1i} and m_{2i} were used to specify the means of the two groups, sd_{1i} and sd_{2i} the standard deviations of in the two groups, and n_{1i} and n_{2i} the sample sizes of the two groups. $spi= \sqrt{\frac{(n_{1i}-1)\times sd_{1i}+(n_{2i}-1)\times sd_{2i}}{(n_{1i}+n_{2i}-2)}}$) as effect size to quantify the effects of plant species diversity on the various responses considered, with sampling variance of each SMD being estimated using the unbiased method[48]. Note that for predators, parasitoids, plants and their associated response categories, a positive SMD and T-test statistic (used for inference of statistical significance) indicated that plant species diversity increased, on average, the value of the response variable of the trophic group. In contrast, for herbivores, a negative SMD and T-test statistic indicated that plant species diversity has decreased, on average, the value of the response variable of the trophic group.

Meta-regression models. We used meta-regression[49] to examine whether variation in the effects of plant species diversity on the different trophic groups (i.e. whether variation in the effect sizes) could be explained by response categories, ecosystem types, plant life forms, biome types and number of added plant species over control. This was achieved by treating trophic groups and the interactions between the trophic group and the other variables as moderators in the model (see below paragraph and Supplement Note 3). To account for heterogeneity in the design among studies and non-independence of data from the same study, we included study identity as a random effect. We also included within-study and sampling variances as random effects[50]. Prior to model fitting, we changed the signs of the herbivore-related SMDs (see Supplementary Note 3). However, to facilitate a correct interpretation of the results, the signs of the herbivore-related model estimates were back-transformed before being presented. To explore the data in more detail, meta-regression was done based on different subsets of the data (Supplementary Note 3). To test if the mean effect sizes for the different categories differed significantly from zero, we used t-distribution-based 95% confidence intervals, derived from the fitted meta-regression models. Here we report only results based on ≥ 3 studies in the text (results based on < 3 studies are reported in Supplementary Figs. 1-3).

As a base model, we started with a mixed-effects model with the trophic group (herbivores, predators, parasitoids and plants) as the only variable. Then, we tested whether the base model could be improved by adding the interaction term between the trophic group and other moderator variables (ecosystem types, plant life forms, biome types and $\log_2$ (added plant species over control)). After that, we tested whether adding the trophic group response category (nested within the trophic group) improved the model. Finally, we tested the significance of interaction effects of the response category with the ecosystem types, plant life forms and biome types. The significance of various moderator variables was determined with a likelihood-ratio test (LRT) (see Supplementary Table 2).

Analysis of trophic interactions. For each trophic performance and response category, we first tested the pairwise comparisons considering all the data together and then for each ecosystem separately (i.e.

agroecosystems, grasslands and forests). As there were several performance, pairwise comparisons for the plant species diversity moderator (i.e. predator/parasitoid performance, herbivore performance and plant performance), we used a Bonferroni correction, with multiplication factor 3, to determine the critical P-values of these pairwise comparisons.

Before analyzing the bi-trophic associations among trophic performance levels, we first established a new datasheets including only the paired observations of predator/parasitoid performance vs. herbivore performance and herbivore performance vs. plant performance. We then used a meta-regression model to calculate the effect sizes for the responses of each performance to increased plant species diversity across ecosystems and in agroecosystems, grasslands and forests, respectively (Supplementary Table 8). The R function "factanal" was used to perform the factor analysis. Next, we analyzed the associations of predator/parasitoid performance with herbivore performance, herbivore performance with plant performance for different ecosystems (Supplementary Table 10). For each association analysis, we used only observations from the study that exactly assessed all the trophic levels (additional information on pairwise analysis is given in Supplementary Note 4).

The above approach was then employed to explore other connections in the tri-trophic interactions. In detail, we first established a new datasheet including paired observations of tri-trophic-levels of predator and parasitoid performance vs. herbivore performance vs. plant performance, and used a meta-regression model to calculate the effect sizes for the responses of each performance to increased plant species diversity across ecosystems and in agroecosystems (Supplementary Table 9). To elucidate the complex relationships between plant species diversity and all the performance of the trophic groups, and to test whether there is a trophic cascade among these trophic groups, we performed a series of path analyses[50]. Due to of lack of studies, we only analyzed the associations of predator/parasitoid performance with herbivore performance, herbivore performance with plant performance across ecosystems and in agroecosystems (Supplementary Table 11). The connections between predator and parasitoid performance and herbivore performance and between herbivore performance and plant performance were investigated through three meta-regression models. All models used herbivore performance as moderator variable (for more details, see Supplementary Notes 2, 4). We used the $\log_2$-transformed number of added plant species over the control as a measure of the increase in plant species diversity (for more details on the path analysis in Supplementary Note 5).

Publication bias test. Publication bias was assessed using both a regression test based on the number of fitted models and the rank-correlation test[51]. Then, the impact of publication bias was assessed with the trim-and-fill method with the R_0 estimator[52]. These tests were performed on the residuals from the various models, which, as suggested by Nagakawa and Santos[49], is a more appropriate approach for publication bias assessment in mixed-effects meta-regression analysis. We additionally report the Rosenthal fail-safe number for the full dataset[53]. The fail-safe number for the full dataset of 351 cited articles was 101836 (Supplementary Note 7).

R version 3.5.0 was used for all statistical analyses[54]. The R package 'metafor' was used for performing meta-regression and analysis of publication bias[48]. The path analyses were performed using the R package 'piecewiseSEM' [55] in conjunction with the R package 'nlme' [56]. The significance level 0.05 was used for all tests.

Data availability

All data generated or analysed during this study are included in this Article and its Extended data, Supplementary tables and Supplementary notes.

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Author contributions

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

Competing interests

The authors declare no competing financial interests.

Figures

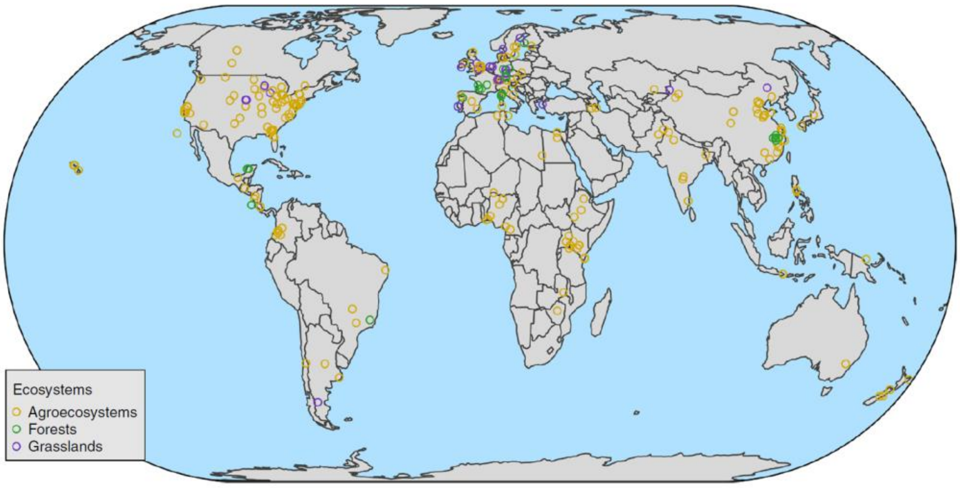

Fig. 1 | Global distribution of study locations. A literature search identified 226, 25 and 22 study locations for agroecosystems, forests and grasslands, respectively, from a total of 351 published articles. Twelve articles included more than one study location (range 2-11).

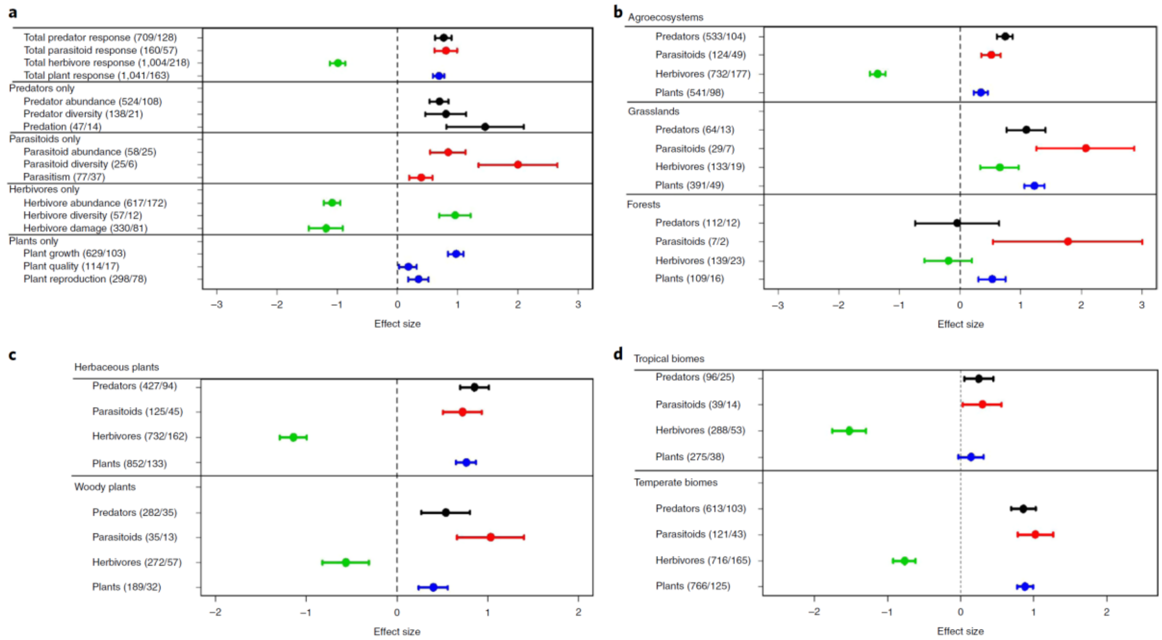

Fig. 2 | Responses of four trophic groups to plant species diversity. a, Across all studies. **b**, In three ecosystems. **c**, For two plant life forms; **d**, For two biome types. Response categories nested in each trophic level are also shown in Fig 2a. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the number of effect sizes behind each meta-response. Black, red, green and blue lines represent predator, parasitoid, herbivore and plant responses, respectively. Estimates based on less than three effect sizes are not shown, but can be seen in Supplementary Figures. 1, 2 and 3.

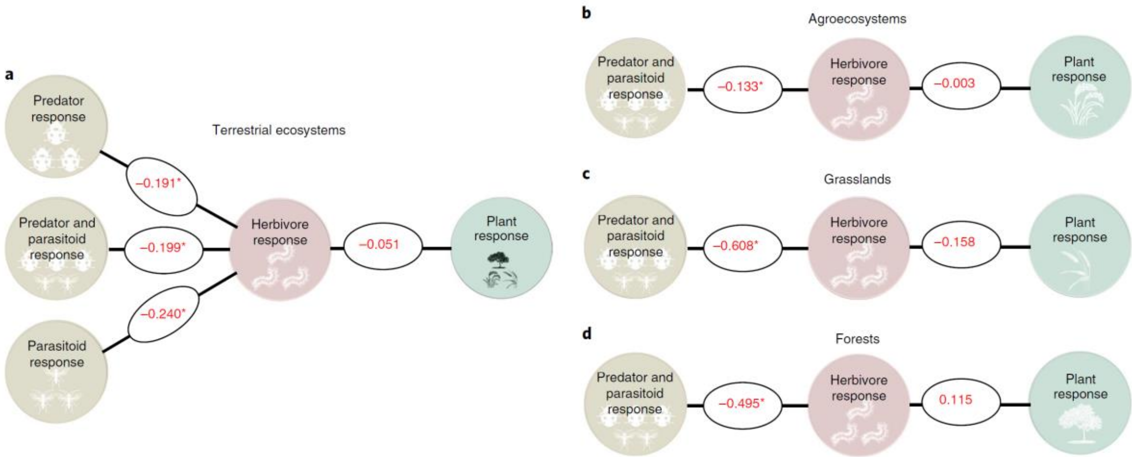

Fig. 3 | Pair-wise (bi-trophic) correlations of trophic group respones to plant species diversity. a, In all analyzed terrestrial ecosystems. **b**, In agroecosystems. **c**, In grasslands. **d**, In forests. Predator response (abundance and predation) and parasitoid response (abundance and parasitism) are shown in beige circles, herbivore response (abundance and plant damage) in pink circles, and plant response (growth, quality and reproduction) in turquoise circles. Asterisks indicate statistical significance at α = 0.05. Red numbers in ellipses indicate the effect sizes of correlations between trophic groups. The number of observations, studies and statistical values for the association analysis are shown in Supplementary Table 10.

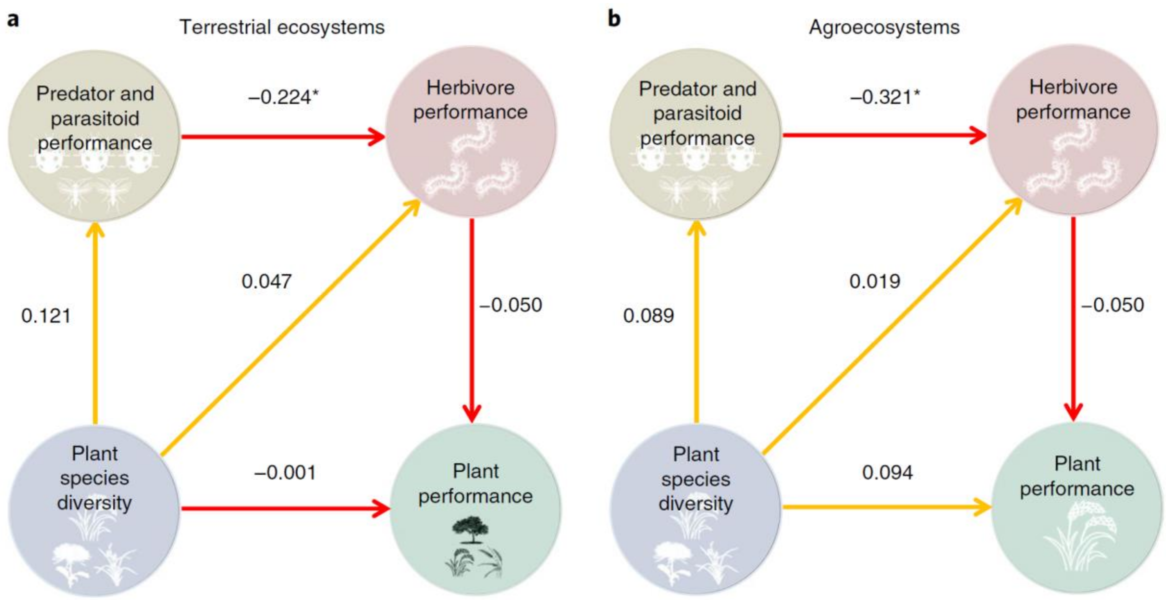

Fig. 4 | Path analysis for the effects of the increased plant species diversity on tri-trophic interactions. a, In all analyzed terrestrial ecosystems. **b**, In agroecosystems. Predator performance (abundance and predation) and parasitoid performance (abundance and parasitism) are shown in beige circles, herbivore performance (abundance and plant damage) in pink, and plant performance (growth, quality and reproduction) in teal. The yellow and red arrows denote positive and negative relationships, respectively, and numbers beside each arrow are the standardized estimate coefficients for the fitted path-analytic models (Supplementary Table 11).