nature plants

ARTICLES

https://doi.org/10.1038/s41477-020-0654-y

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

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Numerous studies have demonstrated that plant species diversity enhances ecosystem functioning in terrestrial ecosystems, including diversity effects on insects (herbivores, predators and parasitoids) and plants. However, 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 2,914 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 the 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 behaviour of their prey (including herbivores), thereby releasing the next lower trophic level (that is, plants) from predation or herbivory[12–14]. Several experiments have shown significant 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 also been 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].

A 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. Furthermore, these meta-analyses did not compare these diversity effects across different ecosystems, plant life forms or biomes on a global scale.

Here we conducted a meta-analysis of 351 published studies with 2,914 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 references and Supplementary Table 1). On the basis of 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. First, how does plant species diversity affect the abundance and diversity of arthropod communities

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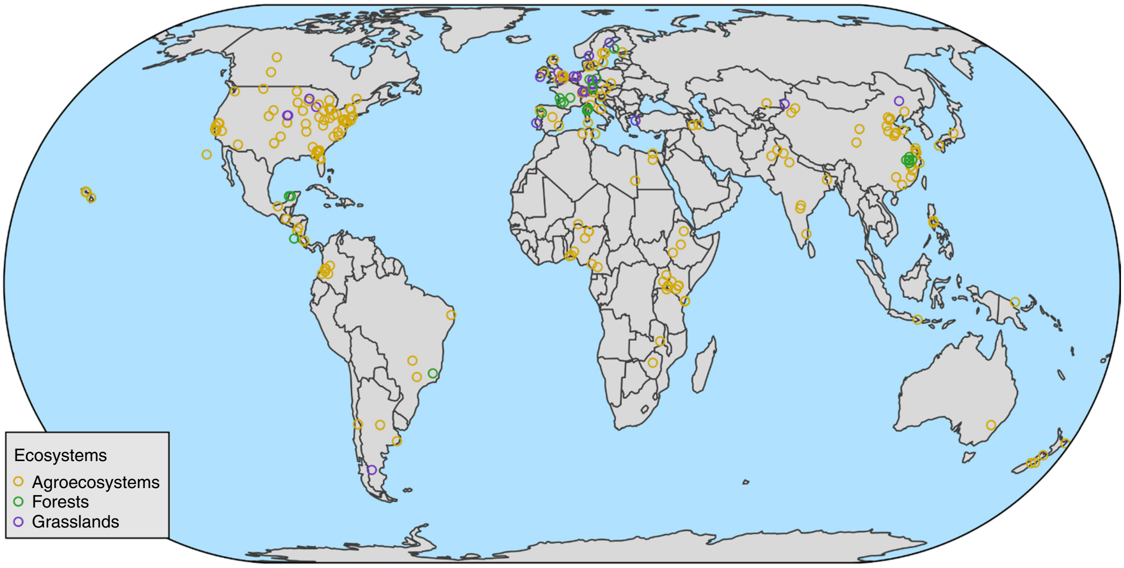

Fig. 1 | Global distribution of study locations. A literature search identified 226, 25 and 22 study locations for agroecosystems, forests and grasslands, respectively, from a total of 351 published articles. Twelve articles included more than one study location (range 2–11).

(predators, parasitoids and herbivores) and plant performance (growth, reproduction and quality)? Second, do the effects differ among ecosystems (agroecosystems, grasslands and forests), plant life forms (herbaceous and woody plants) or biomes (tropical and temperate biomes)? Third, 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 (2,914 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 and 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 and 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 and 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 and 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 and 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 and 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, predator performance included abundance of predators and predation, parasitoid performance included abundance of parasitoids and parasitism, herbivore performance included herbivore abundance and herbivory damage, and plant performance included growth, quality and reproduction of plants. In the meta-regression model, 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. = 1,039, $P < 0.001$; Extended Data Fig. 4). However, none of the relationships between predator, parasitoid, herbivore or plant performance and the number of plant species was significant for individual ecosystem types (Extended Data Fig. 5).

Effects of plant species diversity on bi-trophic associations

We used all paired observations of predator/parasitoid performance versus herbivore performance and of herbivore performance versus 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 versus herbivores: $r = -0.191$, $T = -2.650$, d.f. = 313, $P = 0.008$; parasitoids versus herbivores: $r = -0.240$, $T = -2.535$, d.f. = 100, $P = 0.013$; Fig. 3a). 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 and Supplementary Table 10). This was also the case when we analysed 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 and Supplementary Table 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: $r = -0.051$, $T = -1.198$,

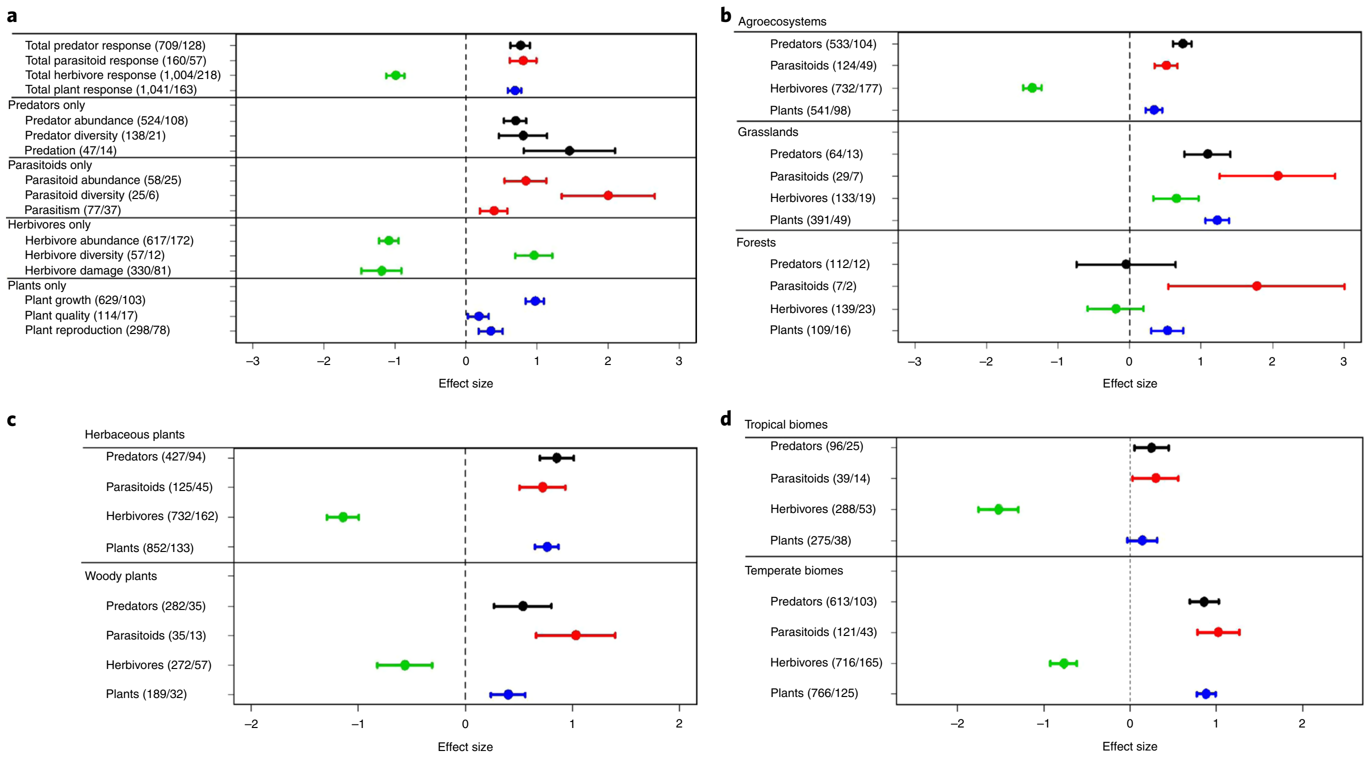

Fig. 2 | Responses of four trophic groups to plant species diversity. a, Across all studies. **b**, In three ecosystems. **c**, For two plant life forms. **d**, For two biome types. The response categories nested in each trophic level are also shown in **a**. The horizontal lines indicate the 95% confidence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

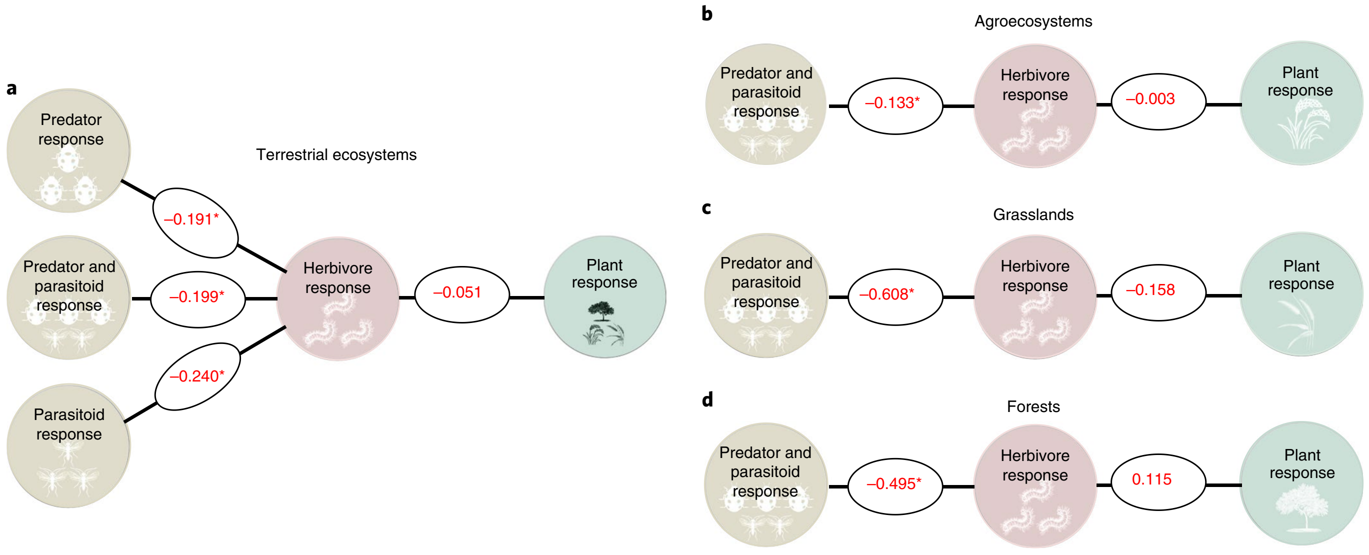

Fig. 3 | Pairwise (bi-trophic) correlations of trophic group responses to plant species diversity. a, In all analysed terrestrial ecosystems. **b**, In agroecosystems. **c**, In grasslands. **d**, In forests. Predator response (abundance and predation) and parasitoid response (abundance and parasitism) are shown in beige circles, herbivore response (abundance and plant damage) is shown in pink circles and plant response (growth, quality and reproduction) is shown in green circles. The red numbers in ellipses indicate the effect sizes of correlations between trophic groups. The asterisks indicate statistical significance at $\alpha = 0.05$. The number of observations, studies and statistical values for the association analysis are shown in Supplementary Table 10.

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 and Supplementary Table 10). Similarly, pairwise associations were mostly negative when the analyses were performed for each plant life form and biome, separately (Supplementary Table 10).

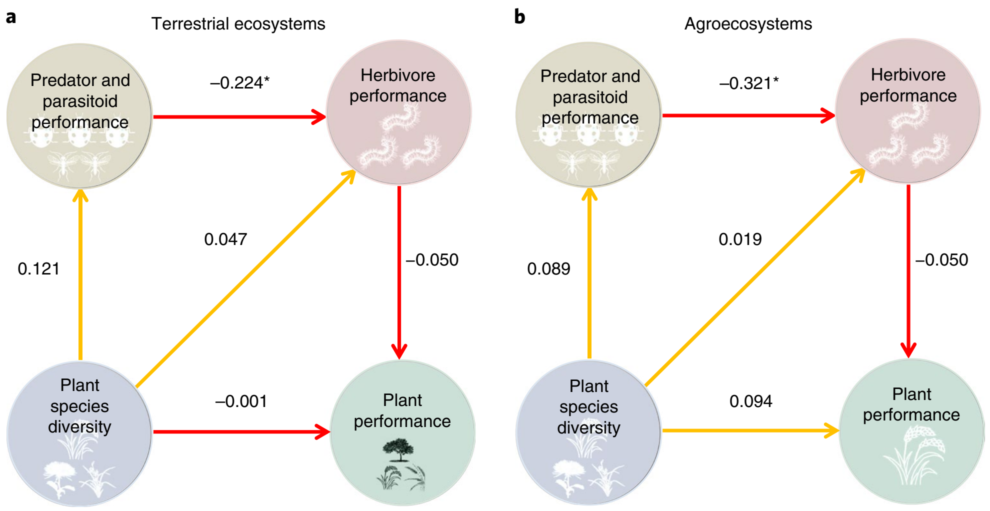

Fig. 4 | Path analysis for the effects of the increased plant species diversity on tri-trophic interactions. a, In all analysed terrestrial ecosystems. **b**, In agroecosystems. Predator performance (abundance and predation) and parasitoid performance (abundance and parasitism) are shown in beige circles, herbivore performance (abundance and plant damage) is shown in pink circles and plant performance (growth, quality and reproduction) is shown in green circles. The yellow and red arrows denote positive and negative relationships, respectively, and the numbers beside each arrow are the standardized estimate coefficients for the fitted path-analytic models (Supplementary Table 11). The asterisks indicate statistical significance at $\alpha = 0.05$.

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 nonsignificant for agroecosystems ($n = 119$; $P = 0.195$; Fig. 4b and 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: $P = 0.489$; Fig. 4a,b and 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: $P = 0.227$; Fig. 4a,b and 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 were 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 suggest 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 of the trophic groups (Supplementary Table 4 and Fig. 2a), the plant response to increased plant diversity differed among different ecosystems. This is probably related to the different number of plant species added to the experimental plots in the 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 biodiversity–ecosystem functioning experiment in China[4]). While it may not be practical to reach as high a 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 (Extended Data 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 benefited predator, parasitoid and plant performance in both agroecosystems and grasslands (Fig. 2b). However, while plant species diversity reduced herbivore performance in agroecosystems, it benefited 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 levels 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 a 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 nonsignificant 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 (Extended Data Fig. 1) may be explained by the fact that agroecosystems are typically diversified by fewer and specifically selected species and more intensively managed (for example, 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 and 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 references and 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 artefact 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 Table 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 probably 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 versus 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 reanalysis of raw data, future studies should pay greater attention to the effects of plant diversity on trophic interactions between generalist/specialist natural enemies versus 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 (that is, 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 the population density of the herbivorous 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 tri-trophic 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 3 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 versus observational). Owing to the limited number of landscape-scale studies (only 1 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) versus landscape scales. 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 40,000 papers were screened for relevance and 351 were finally selected on the basis of the following criteria: 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); the measurements of treatment and control groups were conducted at the same spatiotemporal scale; 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 versus different plant species were considered as independent observations. Data extraction from figures was conducted with Get Data Graph Digitizer 2.25 (ref. [44]). We first used the data for which the authors had presented the average values of multiple sampling dates and multiple sampling years 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 the Supplementary methods). In agroecosystems, farming of a single species (that is, monocultures) was considered as the control group, while diversified systems that involved planting two or more crops simultaneously (that is, mixed-cropping or polycultures) or a mix of species around the main crop were considered 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 (that is, the Jena experiment and the Cedar Creek experiment) and forests (that is, the biodiversity–ecosystem functioning 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 the Supplementary methods): trophic group (predators, parasitoids, herbivores or plants); 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); ecosystem type (agroecosystems (crops, ornamental plant plantations and orchards), grasslands and forests); plant life form (herbaceous or woody plants[47]); biome type (tropical or temperate biomes); and 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) ($\mathrm{SMD} = m_{1i} - m_{2i})/spi$. m_{1i} and m_{2i} were used to specify the means of the two groups, sd_{1i} and sd_{2i} the standard deviations of the two groups, and n_{1i} and n_{2i} the sample sizes of the two groups. $\mathrm{spi} = \sqrt{\frac{(n_{1i}-1)\times \mathrm{sd}_{1i} + (n_{2i}-1)\times \mathrm{sd}_{2i}}{(n_{1i}+n_{2i}-2)}}$ 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 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 (that is, 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 the 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 the paragraph below and the Supplementary methods). 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]. Before model fitting, we changed the signs of the herbivore-related SMDs (see Supplementary methods). 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 performed on the basis of different subsets of the data (Supplementary methods). To test whether 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 Extended Data 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 (see Supplementary Table 2).

Analysis of trophic interactions. For each trophic performance and response category, we first tested the pairwise comparisons considering all of the data together and then for each ecosystem separately (that is, agroecosystems, grasslands and forests). As there were several performance, pairwise comparisons for the plant species diversity moderator (that is, 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 analysing the bi-trophic associations among trophic performance levels, we first established a new datasheet including only the paired observations of predator/parasitoid performance versus herbivore performance and herbivore performance versus 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 analysed the associations of predator/parasitoid performance with herbivore performance, and 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 of the trophic levels (additional information on pairwise analysis is given in the Supplementary methods).

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 versus herbivore performance versus 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 the performance of all trophic groups, and to test whether there is a trophic cascade among these trophic groups, we performed a series of path analyses[50]. Owing to lack of studies, we analysed only the associations of predator/parasitoid performance with herbivore performance, and 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 a moderator variable (for more details, see Supplementary methods). 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, see Supplementary methods).

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's fail-safe number for the full dataset[53]. The fail-safe number for the full dataset of 351 cited articles was 101,836 (Supplementary methods).

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 (ref. [55]) in conjunction with the R package nlme (ref. [56]). The significance level 0.05 was used for all tests.

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

Data availability

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

Received: 21 August 2019; Accepted: 27 March 2020;
Published online: 4 May 2020

References

1. Li, L., Tilman, D., Lambers, H. & Zhang, F. S. Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol.* **203**, 63–69 (2014).
2. Tilman, D., Reich, P. B. & Knops, J. M. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).
3. Isbell, F. et al. Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* **105**, 871–879 (2017).
4. Huang, Y. et al. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* **362**, 80–83 (2018).
5. Cardinale, B. J., Ives, A. R. & Inchausti, P. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos* **104**, 437–450 (2010).
6. Bright, M. B. H. et al. Long-term *Piliostigma reticulatum* intercropping in the Sahel: crop productivity, carbon sequestration, nutrient cycling, and soil quality. *Agric. Ecosyst. Environ.* **242**, 9–22 (2017).
7. Damien, M. et al. Flowering crops in winter increases pest control but not trophic link diversity. *Agric. Ecosyst. Environ.* **247**, 418–425 (2017).
8. 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).
9. Macfadyen, S. et al. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecol. Lett.* **12**, 229–238 (2009).
10. Dainese, M. et al. A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* **5**, eaax0121 (2019).
11. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).
12. Frank, K. T., Petrie, B., Choi, J. S. & Leggett, W. C. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623 (2005).
13. Knight, T. M., Mccoy, M. W., Chase, J. M., McCoy, K. A. & Holt, R. D. Trophic cascades across ecosystems. *Nature* **437**, 880–883 (2005).
14. Start, D. & Gilbert, B. Predator personality structures prey communities and trophic cascades. *Ecol. Lett.* **20**, 366–374 (2017).
15. Scherber, C. et al. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556 (2010).
16. Ebeling, A. et al. Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. *Basic Appl. Ecol.* **26**, 50–63 (2018).
17. Bischoff, A. et al. Effects of spontaneous field margin vegetation and surrounding landscape on *Brassica oleracea* crop herbivory. *Agric. Ecosyst. Environ.* **223**, 135–143 (2016).
18. Wan, N. F. et al. Plant diversification promotes biocontrol services in peach orchards by shaping the ecological niches of insect herbivores and their natural enemies. *Ecol. Indic.* **99**, 387–392 (2019).
19. Hector, A. et al. Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127 (1999).
20. Seabloom, E. W. et al. Food webs obscure the strength of plant diversity effects on primary productivity. *Ecol. Lett.* **20**, 505–512 (2017).
21. Litsinger, J. A., Hasse, V., Barrion, A. T. & Schmutterer, H. Response of *Ostrinia furnacalis* (Guenée) (Lepidoptera: Pyralidae) to intercropping. *Environ. Entomol.* **20**, 988–1004 (1991).
22. Hooks, C. R. R. & Johnson, M. W. Lepidopteran pest populations and crop yields in row intercropped broccoli. *Agric. Forest Entomol.* **4**, 117–125 (2002).
23. Nitschke, N. et al. Plant diversity has contrasting effects on herbivore and parasitoid abundance in *Centaurea jacea* flower heads. *Ecol. Evol.* **7**, 9319–9332 (2017).
24. Moreira, X. et al. Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. *Curr. Opin. Insect Sci.* **14**, 1–7 (2016).
25. Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. Meta-analysis and the science of research synthesis. *Nature* **555**, 175–182 (2018).
26. Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J. & Kremen, C. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* **14**, 922–932 (2011).
27. Shackelford, G. et al. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* **88**, 1002–1021 (2013).
28. Letourneau, D. K. et al. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* **21**, 9–21 (2011).
29. 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).
30. Greenstone, M. H., Cornelius, M. L., Olsen, R. T. & Payton, M. E. Test of a natural enemy hypothesis on plant provenance: spider abundance in native and exotic ornamental landscapes. *J. Entomol. Sci.* **52**, 340–351 (2017).
31. Novais, S. M. A., Macedo-Reis, L. E. & Neves, F. S. Predatory beetles in cacao agroforestry systems in Brazilian Atlantic forest: a test of the natural enemy hypothesis. *Agroforestry Syst.* **91**, 201–209 (2017).
32. 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).
33. Long, Z. T., Mohler, C. L. & Carson, W. P. Extending the resource concentration hypothesis to plant communities: effects of litter and herbivores. *Ecology* **84**, 652–665 (2003).
34. Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W. & Tscharntke, T. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* **117**, 1808–1815 (2008).
35. Ebeling, A. et al. Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. *PLoS ONE* **9**, e106529 (2014).
36. Bernays, E. A., Bright, K. L., Gonzalez, N. & Angel, J. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* **75**, 1997–2006 (1994).
37. Srivastava, D. S. & Lawton, J. H. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.* **152**, 510–529 (1998).
38. Janssen, A., Sabelis, M. W., Magalhães, S., Montserrat, M. & Van der Hammen, T. Habitat structure affects intraguild predation. *Ecology* **88**, 2713–2719 (2007).
39. Coll, M. & Bottrell, D. G. Effects of nonhost plant on an insect herbivore in diverse habitats. *Ecology* **75**, 723–731 (1994).
40. Petermann, J. S., Müller, C. B., Weigelt, A., Weisser, W. W. & Schmid, B. Effect of plant species loss on aphid–parasitoid communities. *J. Anim. Ecol.* **79**, 709–720 (2010).
41. Karp, D. S. et al. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl Acad. Sci. USA* **115**, 7863–7870 (2018).
42. Martin, E. A. et al. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecol. Lett.* **22**, 1047–1175 (2019).
43. Sirami, E. et al. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl Acad. Sci. USA* **116**, 16442–16447 (2019).
44. Lu, M. et al. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. *New Phytol.* **189**, 1040–1050 (2011).
45. Treseder, K. K. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecol. Lett.* **11**, 1111–1120 (2008).
46. Liu, L. L. & Greaver, T. L. A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecol. Lett.* **13**, 819–828 (2010).
47. Liao, C. et al. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* **177**, 706–714 (2008).
48. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48 (2010).
49. Nakagawa, S. & Santos, E. S. Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253–1274 (2012).
50. Shipley, B. Confirmatory path analysis in a generalized multilevel context. *Ecology* **90**, 363–368 (2009).
51. Begg, C. B. & Mazumdar, M. Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101 (1994).
52. 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).
53. Rosenberg, M. S. The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* **59**, 464–468 (2005).
54. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2018).
55. Lefcheck, J. S. piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2015).
56. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team nlme: Linear and nonlinear mixed effects models. R package version 3.1–137 https://CRAN.R-project.org/package=nlme (2018).

Acknowledgements

We thank M. van Kleunen, E. Siemann, X. Chen and Z.-W. Ren for useful suggestions on early versions of this paper, J. Weiner for providing the inspiration for this study, and all of the people whose data and work have been included in this meta-analysis. This study was financially supported by the Agriculture Research System of Shanghai, China (grant no. 201908), the National Natural Science Foundation of China (31401751 and 11971117), the Shanghai Academy of Agricultural Sciences Program for Excellent Research Team (2018[B-01]) and the European Union's Horizon 2020 research and innovation programme (grant no. 727284).

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. 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. analysed 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 interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41477-020-0654-y.

Supplementary information is available for this paper at https://doi.org/10.1038/s41477-020-0654-y.

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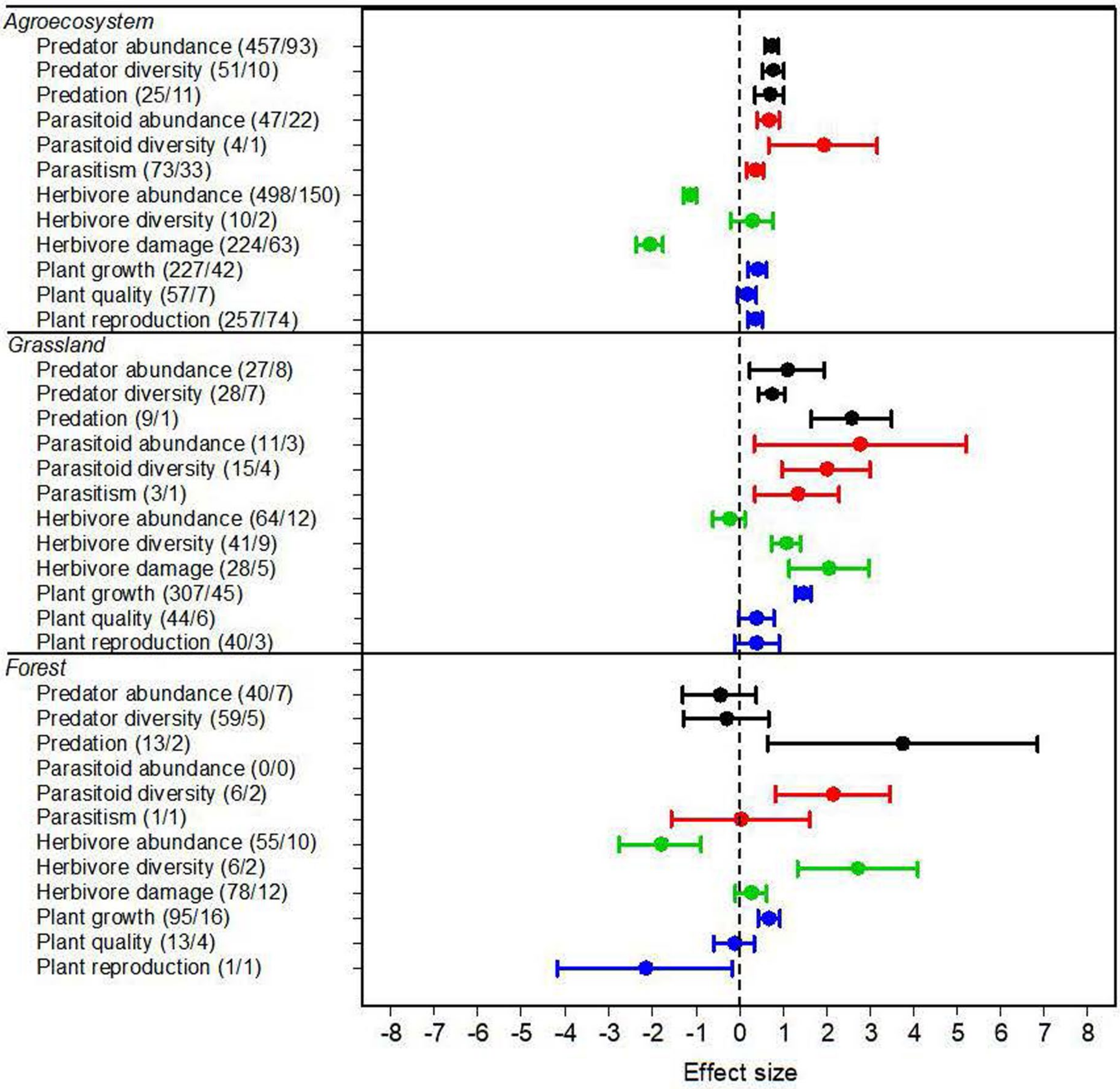
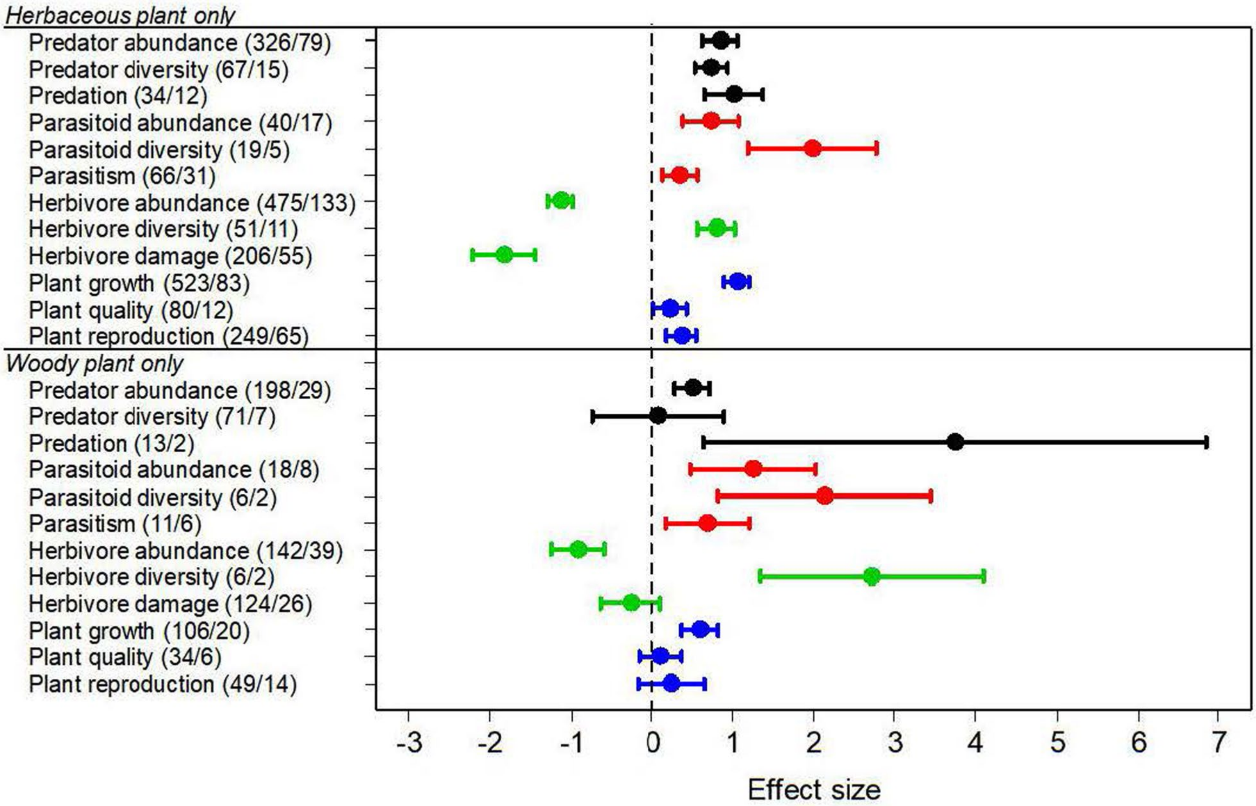
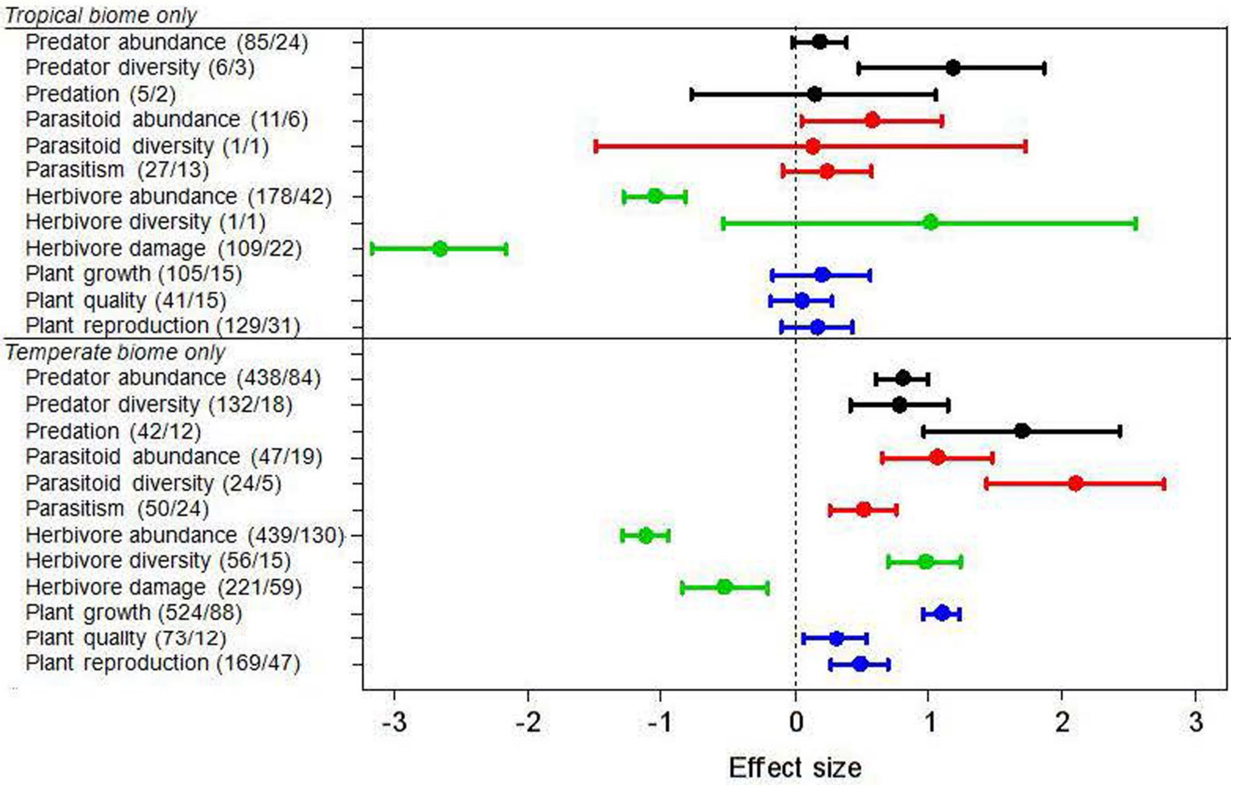
Peer review information *Nature Plants* thanks Forest Isbell and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.



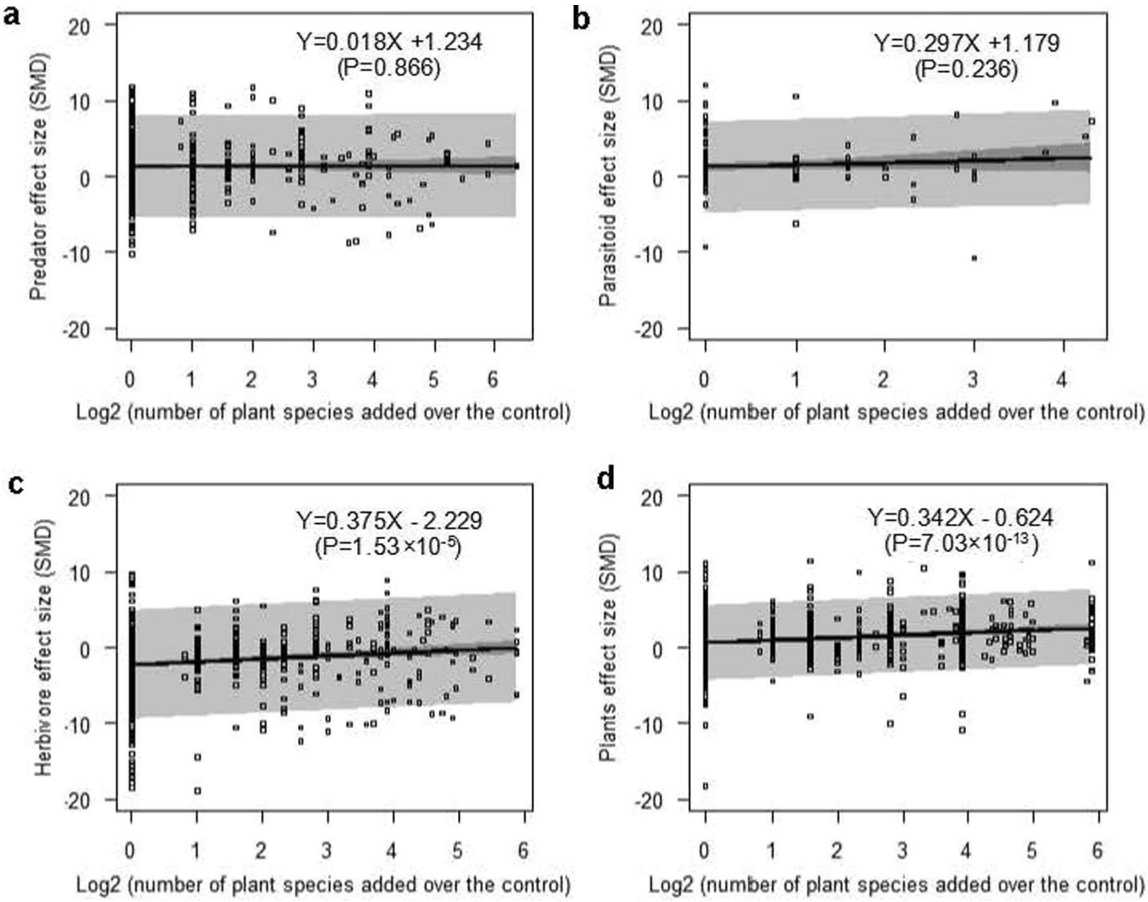
Extended Data Fig. 1 | Mean effect sizes of 12 response categories for the 4 trophic groups in agroecosystems, grasslands and forests, separately. Numbers in brackets indicate the numbers of observations and studies, respectively. The horizontal lines indicate the 95% confidence intervals around the means. Black, red, green, and blue lines represent predators, parasitoids, herbivores and plants, respectively.



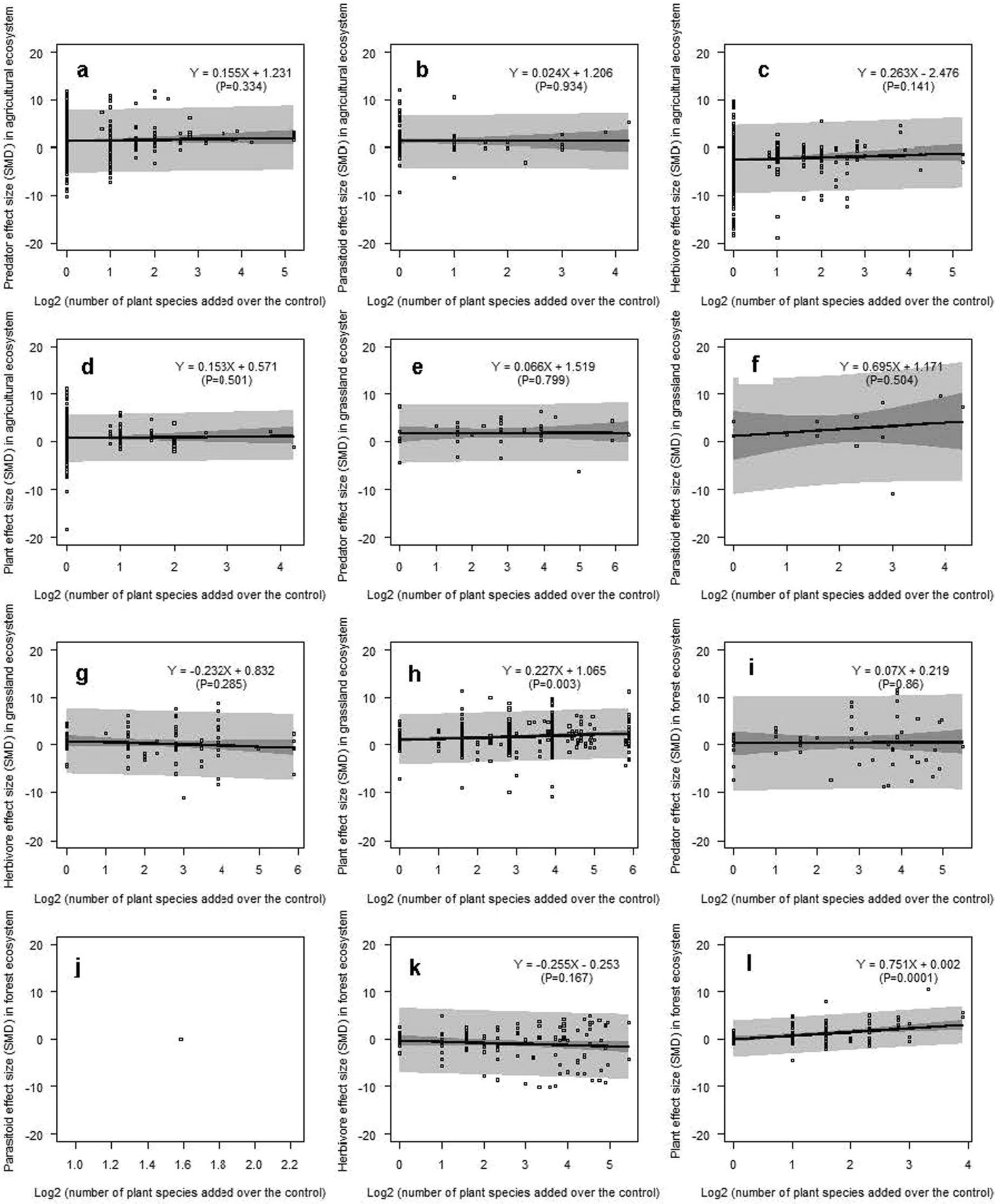
Extended Data Fig. 2 | Response of 12 response categories for 4 trophic groups to herbaceous and woody plants. Numbers in brackets indicate the numbers of observations and studies, respectively. The horizontal lines indicate the 95% confidence intervals around the means. Black, red, green, and blue lines represent predators, parasitoids, herbivores and plants, respectively.



Extended Data Fig. 3 | Response of 12 response categories for 4 trophic groups to tropical and temperate biomes. Numbers in brackets indicate the numbers of observations and studies, respectively. The horizontal lines indicate the 95% confidence intervals around the means. Black, red, green, and blue lines represent predators, parasitoids, herbivores and plants, respectively.



Extended Data Fig. 4 | Scatter plots showing the relationship between log-transformed number of added species in the plant species diversity treatment over the control and the effect sizes along with the fitted meta-regression line. a, Scatter plot for predator performance (571 observations/122 studies). **b**, Scatter plot for parasitoid performance (135 observations/57 studies). **c**, Scatter plot for herbivore performance (947 observations/214 studies). d, Scatter plot for plant performance (1041 observations/161 studies). Predator performance included predator abundance and predation, parasitoid performance included parasitoid abundance and parasitism, herbivore performance was involved in herbivore abundance and herbivore damage and plant performance was related with plant growth, quality and reproduction. The dark and light shaded regions indicate respectively the 95% confidence interval for the predicted average SMD and the 95% credible/prediction interval. The regression model intercepts, slopes and the P-values for the slopes are presented.



Extended Data Fig. 5 | Scatter plots showing the relationship between number of added plant species over control and effect sizes for predator, parasitoid, herbivore and plant performances. a–d, Scatter plots for agroecosystems. **e–h**, Scatter plots for grasslands. **i–l**, Scatter plots for forests. Sample sizes for Fig. S5a-5l are 533, 124, 732, 541, 64, 29, 133, 391, 112, 7, 139 and 109, respectively. The fitted meta-regression lines are also presented. The dark shaded and the light shaded regions indicate the 95% confidence interval for the predicted average SMD and the 95% credible/prediction interval respectively. The regression model intercepts, slopes, and the P-values for the slopes are presented.

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Policy information about availability of computer code

Data collection	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. Means, standard errors (or standard deviations) and sample sizes of the selected variables could be extracted from tables, figures, the main text or supporting information. Data extraction from figures was conducted with Get Data Graph Digitizer 2.25.
Data analysis	R version 3.5.0 was used for all statistical analyses. The R package ‘metafor’ was used for performing meta-regression and analysis of publication bias. The path analyses were performed using the R package ‘piecewiseSEM’ in conjunction with the R package ‘nlme’. The significance level 0.05 was used for all tests.

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Study description	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. Means, standard errors (or standard deviations), and sample sizes of the selected variables could be extracted from tables, figures, the main text or supporting information. Data extraction from figures was conducted with Get Data Graph Digitizer 2.25. When we obtained the data, we analyzed the effect size of response to plant species diversity for trophic groups, the effect of plant species diversity on bi-trophic associations and finally analyzed the effect of plant species diversity across tri-trophic levels.
Research sample	2914 observations from 351 studies were finally selected to conduct this global meta-analysis.
Sampling strategy	We collected all available studies matching the inclusion criteria to ensure the largest possible sample size for the analyses. More than 40000 papers were reviewed 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. 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.
Data collection	First, we (mainly from Nian-Feng Wan, Xiang-Rong Zheng and Li-Wan Fu) selected the papers through a search on the Web of Science (last accessed in May 2019) , and then extracted the data from the papers. Second, we established a datasheet for trophic groups (herbivores, predators, parasitoids and plants). In this datasheet, we included (i) herbivory abundance, diversity and its damage, (ii) predator abundance, diversity and predation rate, (iii) parasitoid abundance, diversity and parasitism rate, and (iv) plant growth, reproduction and quality.
Timing and spatial scale	The start and stop dates of data collection was in November 2017 and May 2019, respectively.
Data exclusions	When we collected the data, the data were excluded in this meta-analysis if they did not reach 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.
Reproducibility	The readers can extract the data from the 351 papers which were selected in this paper to reproduce the results.
Randomization	We used a mixed-effects meta-regression to account for between-study, within-study and sampling variances.
Blinding	Our study were based on existing data, therefore blinding is not relevant to our study.

Did the study involve field work? ☐ Yes ☒ No

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