Species richness promotes plant productivity by suppressing plant antagonists

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Abstract: The diversity-productivity relationship predicts a positive effect of plant species richness on primary productivity[1–7]. One key mechanism predicted to underlie this relationship is the effect of plant diversity on the suppression of plant antagonists, including invertebrate herbivores, plant diseases, antagonistic plants in an agricultural context (i.e., weeds), root-feeding nematodes, or plant-consuming rodents. Here, we conduct a global meta-analysis from 609 biodiversity manipulation studies and complementary path analyses, and show that increasing plant species richness promotes plant productivity by decreasing plant antagonist pressure in terrestrial ecosystems (especially in agroecosystems), with similar patterns seen for herbaceous and woody plants as well as in tropical and temperate zones. These results demonstrate how a key mechanism underpinning the diversity-productivity relationship can be explained via weakened effects of antagonists on plant productivity. Our findings provide new evidence supporting a multitrophic diversity-productivity relationship and highlight the importance of maintaining species diversity to promote productivity as an ecosystem function in both agricultural and more natural systems.

Higher plant species richness is associated with greater provision of multiple ecosystem functions and services across terrestrial ecosystems[1–7]. It is well known that plant diversity promotes productivity with increased crop yields[8,9], and increased biomass in grasslands[10–12] and forests[13–15]. Mechanisms such as the resource-use complementarity hypothesi, based on negative interspecific interactions (competition theory), have been proposed to explain these patterns[2,11,13,16]. Alternatively, increasing productivity with increasing plant diversity may also be explained by complementarity in top-down control, where each plant species is controlled by its own specialist consumer(s), leading to an increase in productivity with species richness[2]. However, the importance of antagonists for the diversity-productivity relationship has so far received only limited attention, and an overarching synthesis for different groups of consumers is lacking. Here we propose the 'antagonist hypothesis' as a framework to include all such relationships, although we note that the consequences of antagonists on the biodiversity-productivity relationship may be underpinned by multiple mechanisms discussed below.

Individual experiments have evidenced that increasing plant diversity may suppress plant antagonists, which is manifested through decreases in abundance or biomass of insect herbivores[17,18], plant-feeding nematodes[19] or rodents[20], decreases in biomass or densities of weeds (i.e. undesirable plants that are harmful in human-controlled settings such as agriculture, and invasive non-native plants in natural ecosystems)[21,22], and by reducing the spread or damage of plant diseases[23,24]. There may also be a complementarity effect whereby plant-soil feedback negatively affects the growth of plants to a greater extent in monocultures than in diverse communities, where species specific soil pathogens decrease in density with increased plant species richness[25–27]. While these effects of high plant diversity have been widely reported, there are studies that show opposite responses. As an example, increasing plant species richness was associated with increased damage of plants by herbivorous thrips (*Thrips tabaci*)[28]. If plant productivity is generally enhanced by the suppression of antagonists in species-rich systems, this could open new avenues for production systems such as crop, timber or fibre production. However, such generalized diversity-antagonist relationships are still under debate[29], and we lack a comprehensive assessment of their context dependency.

Meta-analysis is a key tool for evidence-based practice and for resolving seemingly contradictory research outcomes[30]. Previous meta-analyses which considered the effects of antagonists within the context of the diversity-productivity relationship have shown that increasing plant species diversity has variable effects on invertebrate herbivore abundance and damage[31–34], and may reduce the damage of plant-feeding nematodes and plant disease[35]. However, these global syntheses covered only selected plant antagonists or specific types of ecosystems, such as agroecosystems[35] or forests[32]. These syntheses did not generally consider how the impact of plant antagonists on the diversity-productivity relationship varies across different ecosystems, plant forms (herbaceous vs. woody), or climatic zones on a global scale.

Here, we conducted a global synthesis of 609 biodiversity experiments from which we derived 5,712 effect size observations on the impact of increasing plant species richness on plant productivity as well as effects on a wide range of antagonist groups, i.e., invertebrate herbivores, plant diseases (bacteria, fungi, and viruses), weeds, plant-feeding nematodes, and plant-consuming rodents (Fig. 1 and Supplementary Data 1). We focused on measures of: (i) plant growth, reproduction, and quality; (ii) invertebrate herbivore growth, reproduction, and damage that herbivores cause to plants; (iii) disease reproduction, spread and damage; (iv) weed growth, reproduction, and diversity; (v) nematode reproduction, and abundance; (vi) rodent reproduction, and damage; and (vii) aggregate performance indicators[29] for each of these categories. From these response variables, we derived standardized mean difference (SMD) effect sizes comparing diverse plant communities (i.e., high plant species richness) and simple plant communities or monocultures (i.e., low species richness). Piecewise structural equation modeling was then used to analyze the effects of plant species richness on plant productivity and plant antagonists. We build on previous research showing the role of plant antagonists and the need to consider them in studies on diversity-productivity relationships. We aim to test for overall effects of plant antagonists on plant productivity resulting from a variety of potential mechanisms, including increased diversity directly suppressing antagonists, as well as complementarity effects caused by a reduction in negative trophic interactions (i.e. predation in its widest sense). We also propose that this diversity-antagonist-productivity relationship is universal and consistent across different ecosystems, plant life forms, and climatic zones. Together, antagonistic interactions can be a powerful mechanism by which plant diversity influences plant productivity both directly and indirectly.

Results and Discussion

Direct effect of plant species richness on plant productivity

Our results from the 5,712 observations in 609 articles included in our study, confirm the biodiversity-productivity relationship, increased plant species richness within plant communities increased plant performance, across global terrestrial ecosystems (Fig. 1b) (CI= 0.629 to 0.877, df=2390, ES (effect size)= 0.753, $P<0.001$) (Fig. 1b). We split the aggregate indicator of plant performance into plant growth, reproduction, and quality and show that these responses to increasing plant species richness were consistent (see Supplementary Table 3). The positive effect of diversity on plant performance was consistent across ecosystem types, with the largest effect size found in grasslands (Fig. 2) (grassland: CI=0.828 to 1.516, df=467, ES=1.172, $P<0.001$; agroecosystem: CI=0.513 to 0.787, df=1784, ES=0.650, $P<0.001$; forest: CI=0.374 to 1.220, df=137, ES=0.797, $P<0.001$) (Supplementary Table 4). We explain this with two non-exclusive mechanisms: i) increasing plant species richness resulted in a complementarity effect (i.e., niche partitioning or facilitation)[2,11,13,16] as well as complementarity effects underpinned by trophic interactions[25,26,36] or reduced plant competition intensity among different plant species[37]; and ii) increasing plant species richness reduced the impact of plant antagonists (e.g., herbivores[18,38], plant disease[23] and weeds[22]) on plants and thus facilitated plant productivity indirectly[39,40].

Direct effects of plant species richness on plant antagonists

Across all studies, plant species richness decreased the performance of plant antagonists (CI= −1.475 to −1.196, df=3320, ES = −1.336, P<0.001) and their subgroups (i.e., herbivores (CI= −1.351 to −1.016, df=1809, ES= −1.184, P<0.001), plant diseases (CI= −2.075 to −1.416, df=601, ES= −1.746, P<0.001), weeds (CI= −2.251 to −1.473, df=600, ES= −1.862, P<0.001), plant-feeding nematodes (CI= −1.475 to −0.433, df=284, ES= −0.954, P<0.001) and plant-consuming rodents (CI= −1.037 to −0.283, df=22, ES= −0.660, P=0.002). This pattern of responses largely held when these aggregate performance indicators for each antagonist group were decomposed into individual components, e.g., weed performance into weed growth, reproduction, and diversity; see Supplementary Table 3). Where larger sample sizes were collected, differences in the responses of two categories were more likely to be significant (i.e., herbivore growth: CI= −1.181 to 0.168, df=48, ES= −0.506, P=0.138; rodent damage: CI= −6.912 to 6.064, df=1, ES= −0.424, P=0.559) with increased plant species richness (Supplementary Table 3).

In a second step, we tested whether these responses differed among ecosystems. As to the aggregate indicator, plant species richness decreased the performance of plant antagonists in agroecosystems (CI= −1.645 to −1.348, df=2777, ES= −1.496, P<0.001), grasslands (CI= −1.248 to −0.292, df=317, ES= −0.770, P<0.001) and forests (CI= −0.654 to 0.189, df=224, ES= −0.232, P=0.279). When plant antagonists were split into different subgroups (i.e., invertebrate herbivores, plant diseases, nematodes, rodents, and weeds) and into different response categories (e.g., invertebrate herbivore growth, reproduction, and damage), the overall pattern described above was maintained in agroecosystems (Fig. 2a; Extended Data Fig. 2a), but these responses varied in grasslands and forests (Extended Data Fig. 2b, c; Supplementary Table 4). Plant species richness reduced herbivore performance (i.e., herbivore growth, reproduction and damage) in agroecosystems (CI= −1.550 to −1.211, df=1436, ES= −1.380, P<0.001) (Supplementary Table 4), which is compatible with the: i) the Enemies Hypothesis that herbivore natural enemy performance is positively related to plant species richness[34,40,41]; ii) the Resource Concentration Hypothesis (RCH) that argues that the density of insect herbivores per plant increases with monoculture host density and patch size[41]; iii) the Insurance Hypothesis (IH) that suggests that habitats with greater plant species richness can provide insurance against pest damage in crop fields[42]. However, the negative effects of plant species richness on herbivores were comparatively weak both in grasslands (CI= −0.936 to −0.540, df=171, ES= −0.198, P=0.597) and forests (CI= −0.664 to 0.309, df=220, ES= −0.177, P=0.473). The observed differences may arise from increased plant species richness, which provides greater access to nutritionally superior or less variable food resources for insect herbivores in grasslands. Additionally, grasslands and forests are more likely to host specialist herbivores that selectively consume specific plant species leading to complementarity underpinned by changes in trophic interaction structure with increasing diversity[36]. Consequently, whether invertebrate herbivore performance increased or decreased will depend on the herbivore species and the specific plants they consume[43]. In forests, increased tree species richness may support greater abundances of generalist herbivores that benefit from a higher diversity of floral resources optimizing nutrient uptake[44].

We also found that increased plant species richness decreased: i) symptomatic disease expression in plants in agroecosystems (CI= −2.126 to −1.371, df=514, ES= −0.175, $P<0.001$), grasslands (CI= −2.712 to −1.272, df=70, ES= −1.992, $P<0.001$) and forests (CI= −2.462 to 0.196, df=15, ES= −1.133, P=0.089); ii) weed performance in agroecosystems (CI= −2.312 to −1.473, df=547, ES= −1.892, $P<0.001$) and grasslands (CI= −2.720 to −0.776, df=52, ES= −1.748, $P<0.001$); iii) nematode performance in agroecosystems (CI= −1.753 to −0.441, df=266, ES= −1.097, P=0.001); and iv) rodent performance in grasslands (CI= −1.306 to −0.144, df=8, ES= −0.725, P=0.021), indicating powerful antagonist control services.

Such increased antagonist control services might be explained by the effects of plant species diversity on i) decreased disease performance, including altered wind, rain and vector dispersal, modified microclimate, diluting the host density and preventing pathogen spread, changes in host morphology and physiology and direct pathogen inhibition[23], ii) suppressed weed growth in diverse mixtures which may include plant species that better compete against weeds, and iii) decreased growth of nematodes through allelopathic chemicals[45], and iv) increased rodent dispersal in monocrop plots due to high abundance and limited habitat availability[20]. Overall, physical barriers, allelopathic chemicals and plant species resistance may be responsible for the negative effects of plant species richness on herbivores, plant diseases, nematodes and weeds[23].

Finally, we tested whether these responses of plant antagonists and their subgroups differed among plant life forms, climatic zones, or experimental method. Similar patterns as described above were also found for both plant life forms (i.e., herbaceous and woody plants; Fig. 2b; Extended Data Fig. 3; Supplementary Table 5) and for both climatic zones (i.e., temperate and tropical; Fig. 2c; Extended Data Fig. 4; Supplementary Table 6). Across types of experimental studies, we found stronger responses of both plants and their antagonists to plant species richness in plot than in pot experiments (Fig. 2d; Supplementary Table 7), possibly because pot experiments often involve a restricted set of plant and antagonist species, omitting crucial below-ground components or varying dispersal parameters compared to field-based experiments. Consequently, they do not incorporate the intricate biotic interactions existing in natural communities.

Path analysis for the effects of plant species richness on plants and their antagonists

We used path analysis to test our proposed diversity-antagonist-productivity hypothesis. For our analysis, we collected 2,766 estimates of interactions between pairs of plants and plant antagonists derived from 240 articles. First, we tested the effects of plant species richness on plants and plant antagonists using multilevel piecewise structural equation models. In these models, different plant antagonists (i.e., invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes, and plant-consuming rodents) were aggregated together (Supplementary Methods). We found that plant species richness directly suppressed plant antagonists and increased plant performance across terrestrial ecosystems and in agroecosystems, grasslands, and forests (Fig. 2). Increasing plant species richness also increased plant performance indirectly by reducing the performance of plant antagonists across terrestrial ecosystems (Fig. 2a) and specifically in agroecosystems (Fig. 2b). Similarly, the direct and indirect effects of plant species richness on plants and plant antagonists were consistent in herbaceous-species-dominated systems, temperate and tropical zones, and in plot and pot experiments (Extended Data Figs.7a, c–f). However, this indirect effect on plant performance via suppressing antagonists was less pronounced in grasslands (Fig. 2c), forests (Fig. 2d), and for woody plants (Extended Data Fig. 7b). Indirect positive effects of plant species richness on plant performance were also found to be mediated through a reduction of plant antagonist pressure when we separately tested for the effects of invertebrate herbivores, plant diseases and weed performance, although such an indirect effect was not evident for the nematodes (Fig. 4).

Our meta-analysis indicates that plant species richness enhances crop production and plant productivity in terrestrial ecosystems by suppressing the performance of a broad range of plant antagonists, including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents. These results highlight the negative effects of increasing plant species richness on the plant antagonists included in this study and in so doing contribute to the positive effects of the biodiversity-productivity relationship. While our study does not allow differentiating between specialist vs. generalist antagonists, theoretical predictions show that it is likely that specialists are mostly responsible for the observed effects. From an applied perspective, increasing plant species richness in agroecosystems, for example by intercropping or increasing crop diversity, may help to promote crop pest control and increase crop productivity[34]. Our results provide empirical support for more complex cropping systems that increase plant diversity in agricultural fields and management strategies that foster the high diversity species co-existence in grasslands and forests.

Methods

Definition of plant species richness

In this paper, we considered "plant species richness" as *any* increase in the number of plant species in a plant community, relative to a monoculture or the lowest species control group. Thus, this is essentially a binary variable (zero or one), indicating whether plant species richness had been increased, but irrespective of the number of plant species added.

Study selection

Studies were selected through a literature search of the Web of Science Core Collection, BIOSIS Previews, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE, Preprint Citation Index, ProQuest^{TM} Dissertations & Theses Citation Index, and SciELO Citation Index. We used the Boolean search string based on the "TOPIC" searching: ["plant diversity" OR "crop diversity" OR "crop diversification" OR "plant species richness" OR "polyculture" OR "ground cover vegetation" OR "flower strip" OR "strip crop*" OR "grassy field margin" OR "border crop" OR "intercrop*" OR "interplant*"] AND ["plant disease" OR "plant virus" OR "nematode" OR "weed" OR "herbivor*" OR "pest" OR "biological control" OR "rodent" OR "yield" OR "productivity" OR "biomass"]. This literature search was initiated in June 2019, and finalized in August 2023. In total, the search yielded 386,895 articles (see Extended Data Fig. 1 for a PRISMA diagram). The titles and abstracts of this overall set of articles were first screened to determine whether the articles had measured a response variable relating to the effects of plant species richness on i) the growth, reproduction and damage of invertebrate herbivores; ii) the reproduction, spread and damage of plant disease; iii) the growth, reproduction and diversity of weeds; iv) the reproduction and damage of plant-feeding nematodes; v) the reproduction and damage of plant consuming rodents; and vi) the growth, reproduction and quality of plants. In total, 383,479 articles were excluded at this stage of title and abstract screening. From the remaining 3,416 papers, we obtained our final selection of 609 articles based on the following criteria: i) the means, standard deviations (or standard errors) and sample sizes of the selected variables could be extracted from the text, tables, figures or supporting files; ii) the measurements of the treatment (higher plant species richness, $\geqslant 2$) and control (single or lowest plant species richness) groups were conducted at the same spatiotemporal scale; and iii) the agricultural practice (e.g., pesticides and fertilizer input) should be the same for the control and the treatment. Articles were screened by Y.Q.W., L.F., J.L., J.Z. and N.F.W.. Data were extracted from the articles by Y.Q.W., L.F., J.L. and N.F.W.. during which regular cross-checking was performed to ensure consistency in extracted effect sizes. This protocol was developed using PRISMA-P (Preferred Reporting Items for Systematic review and Meta-Analysis Protocols) guidelines. The final protocols are published on the Zenodo open access data repository and is given the DOI of 10.5281/zenod.8333868 (https://zenodo.org/record/8333868).

We first used data giving the mean values of multiple sampling dates or years. If these mean values were not presented, we used the data of the latest sampling period[34]. For articles that covered more than one experimental location, we considered these experimental results separately (see locations in Fig. 1a). When numeric values were not provided directly, we extracted them from figures using the "GetData Graph Digitizer" 2.26. However, where linear or non-linear relationships between plant species richness and one of the response variables was presented in a figure, we extracted the values by fitting regression equations[29].

To avoid pseudoduplication of data, we excluded multiple comparisons within a single experiment[34]. Observations with the lowest plant species richness were considered as control groups, while those with higher plant species richness were considered as the treatment groups. When an article included different levels of plant species richness, measurements for the control groups (lowest plant species richness) were compared to all other treatments levels of plant species richness and treated as independent paired observations. For ecosystem type, we focused on agroecosystems (n=536 articles), grasslands (n=49), and forests (n=45) (Fig. 1a). Shrublands (n=2), arid ecosystems (n=2), and aquatic ecosystems (n=1) were not considered in this paper as they were poorly represented. Generally, in agroecosystems, the planting of a single main crop (e.g., monoculture of rice, wheat or maize) was regarded as the control group, and co-cultures of the main crop with other plants were regarded as treatment groups. However, experiments in grasslands and forests often focused on more complex plant communities necessitating mixtures with the lowest within-study plant species richness to be specified as the control[34].

Predictor variables

We used six categorical variables as predictor variables (see Supplementary Methods for details)—i) Trophic group: a categorical variable denoting whether the target organisms were invertebrate herbivores, plant diseases (plant pathogenic viruses, fungi and bacteria that infested plants and cause damage to plants), weeds (i.e. harmful plants in human-controlled settings such as farm fields, and invasive exotic plants in natural ecosystems; antagonistic plants that compete with crop plants for water and nutrients)[21,22], plant-feeding nematodes, plant-consuming rodents (e.g., rats and mice that damage crops, pasture or trees), or plants (e.g., crops, fruits, grass and trees); and moreover, an aggregate categorical variable (i.e. plant antagonists) including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents. ii) Response category: growth, reproduction and damage of herbivores; reproduction, spread and damage of plant diseases; weed growth, reproduction and diversity (i.e., species richness and Shannon diversity of weeds); reproduction and damage of plant-feeding nematodes; reproduction and damage of plant-consuming rodents; and growth, reproduction and quality of plants. iii) Ecosystem type: agroecosystems, grasslands and forests. iv) Plant life form: herbaceous or woody plants. vi) Climatic zone: temperate or tropical (data from greenhouse, indoor and laboratory experiments were removed from models including the climatic zone variable)[29]. and v)

Experiment type: plots (i.e., field and common garden experiments) or pots (i.e., experiments with pots, containers, bottles, trays, boxes and tankers) (detailed description was presented in Supplementary Methods).

Definition of effect size and its measures

To test the effect of plant species richness on the various groups (invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes, plant-consuming rodents, or plants; and moreover, an aggregate categorical variable (i.e. plant antagonists) including invertebrate herbivores, plant diseases, weeds, plant-feeding nematodes and plant-consuming rodents), we calculated the Standardized Mean Difference as $SMD_i = (M_{ti} - M_{ci})/sd_i, 1 \le i \le m$, in which M_{ti} and M_{ci} were the mean values in the treatment and control groups, respectively, and $sd_i = \sqrt{\frac{(n_{ti}-1) \times sd_{ti} + (n_{ci}-1) \times sd_{ci}}{n_{ti} + n_{ci} - 2}}$, in which n_{ti} and n_{ci} were the sample sizes and sd_{ti} and sd_{ci} were the standard deviations in the two groups, respectively. An unbiased approach was used to estimate the sampling variance[46]. We used SMD as the response variable for different models except for path analyses described below.

Meta-regression

Meta-regression[47] was applied to test whether the variances of different trophic groups could be explained by increasing plant species richness and the various predictor variables. Specifically, we fitted three-level mixed-effects meta-regression models, using the R package metafor (version 3.8-1). The effect size metric SMD was calculated with the function "escalc()" (argument "measure" set to "SMD"), and unbiased sample variance estimates were constructed with the function “escalc()” (argument “vtype” set to “UB”). Trophic group, response category, ecosystem type, plant life form, climatic zone, and types of experimental study were included as moderators whose effects were assumed to be fixed. In all models, we treated ‘study’ as a random effect (see Supplementary Tables 1.1, 1.3, 2.1, 2.3). Besides, we additionally performed a phylogenetic correction for plants to investigate the effects of plant species richness on trophic groups, where common phylogenies “plant species” was included as a random effect with phylogenetic relatedness as part of the correlation structure. Taking this approach 119 plant species defined the correlation structure based on the plant phylogeny (see Supplementary Tables 1.2, 1.4, 2.2, 2.4; Supplementary Methods)[48,49].

For each mixed-effects meta-regression model, we first fitted a base model by treating plant species richness and trophic group as the fixed effect terms. Second, the interactions between the trophic group and other predictor variables (type of ecosystem, plant life form, climatic zone, and experimental type) were also included in the model to assess whether model fit was improved, using a likelihood-ratio test (LRT). Third, the trophic group response category (nested within trophic group) and the interactive effects between the response category and predictors were also included in the model (using a LRT to allow model comparisons) (Supplementary Table 1). For example, the model with “trophic group + ecosystem type” was compared to the base model with just trophic group, and the model with “trophic group + trophic group × Ecosystem type” would be compared to a model with “trophic group + plant life forms” (Supplementary Tables 1 and 2). To examine whether the mean effect sizes of (added) plant species richness, response category and other predictors differed significantly from zero, we acquired estimations with their 95% confidence intervals, which were derived from the fitted meta-regression models.

Path analysis for plant species richness

To explore the trophic interactions between plants and various groups of plant antagonists, we established a new data subset comprising paired trophic observations (i.e., plant performance vs. herbivore performance, plant performance vs. plant disease performance, plant performance vs. weed performance, and plant performance vs. plant-feeding nematode performance (paired trophic observations of plants vs. rodents were not found) (see Fig. 4 and Supplementary Fig. 12). Next, we established another data subset encompassing the paired observations of plant performance vs. plant antagonist performance in different ecosystem types (i.e., all ecosystems, and separately for agroecosystems, grasslands, and forests (Fig. 3; Supplementary Figs. 11a–d). We then made three additional data subsets comprising the paired observations of plant performance vs. plant antagonist performance within different plant life forms, climatic zones, and experimental type, respectively (Extended Data Fig. 7; Supplementary Figs. 11e–j). Subsequently, we calculated the SMD effect sizes of the responses and tested whether the plant species richness (Fig. 3 and Extended Data Fig. 7) had effects on SMDs of different responses in newly built pairwised data. The estimations and test statistics were also extracted using the R function "coef()" (Supplementary Table 8, 10 and 12). A subsequent path analysis was conducted to explore how plant species richness influence the trophic interactions.

To analyze the direct effect of plant antagonists on plant performance in path analysis, residual regression was applied. In this analysis we used the log transformed ratio of means (ROM) as the response variable, which was calculated as $ROM_i = \log(M_{ti} / M_{ci}), 1 \le i \le m$,

and $sd_i = \sqrt{\frac{sd_{ti}^2}{n_{ti} M_{ti}^2} + \frac{sd_{ci}^2}{n_{ci} M_{ci}^2}}$.

Specifically, the direct effects of plant species richness on plant antagonist were estimated using linear mixed-effects model (See details in Supplementary Methods):

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

Following Emmenegger & Bühlmann[50]. The direct effect of plant species richness on plant performance were estimated by regressing the Pearson residuals of the linear mixed-effects model

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

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

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

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

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

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

We extracted the z-values of corresponding coefficients to test the effects of plant species richness on each of the interactions between performance values of plants and herbivores, plants and diseases, plants and weeds, and plants and nematodes, respectively (Fig. 4). Likewise, we extracted the z-values of corresponding coefficients to test the effects of plant species richness on the interactions between performance values of plants and the aggregate indicator (i.e., plant antagonists) in different ecosystems (i.e., all ecosystems, agroecosystems, grasslands and forests) (Fig. 3), as well as the effects of plant species richness on the interactions between plant performance and plant antagonist performance for different plant life forms (herbaceous, woody), climatic zones, (temperate, tropical) and experiment types (plot, pot), respectively (Extended Data Fig. 7). The relative goodness-of-fit analyses for path analyses of predictor variables (plant species richness), were conducted by extracting AIC (Akaike information criterion), AICc (corrected Akaike information criterion), BIC (Bayesian information criterion) and log-likelihood from the fitted models, using R functions "AIC()", "AICc()"[51], "BIC()" and "logLik()" (Supplementary Table 15).

Publication bias test

We assessed publication bias using regression tests[52] (Supplementary Table 2) which employ a partial slope test of association between effect size and the sample variance. Here, a significant relationship ($p<0.05$) suggests publication bias. The trim-and-fill method was not employed as this is inappropriate for models with moderators[53]. Instead, we adopted the method suggested by Nakagawa and Santos[54], in which the residuals from linear mixed-effects models were used to assess publication bias in mixed-effects meta-regression analysis. Here, we considered SMD as a response variable. Different categories of trophic groups, ecosystems, plant life forms, climatic zones, and experimental studies were considered as predictors, respectively, and sampling variances were considered as an additional moderator in the mixed-effect model and the test statistics for coefficients of sampling variances were used to test for publication bias. We also derived Rosenthal fail-safe number for the full datase[55] which represents the minimum number of studies averaging null results that would have to be added to a given set to change the conclusion of a meta-analysis. Using this approach we derive a fail-safe number of 2,326,601 for the full dataset from 609 articles (Supplementary methods).

We used R version 4.3.1[56] to conduct all statistical analyses, and used R package "metafor"

3.8-1to perform meta-regression and publication bias assessment[57]. In addition, we used R packages "nlme"[58] to residual regression in path analyses. A significance level of 0.05 was used for all tests.

Data availability

All data used in this analysis is deposited on Zenodo (https://zenodo.org/record/8328954). The data used for the overview of all the 609 studies is available as Supplementary Data 1.

Code availability

The code used to analyse data is deposited to Zenodo: https://zenodo.org/records/10069675.

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Author contributions

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

Competing interests

The authors declare no competing financial interests.

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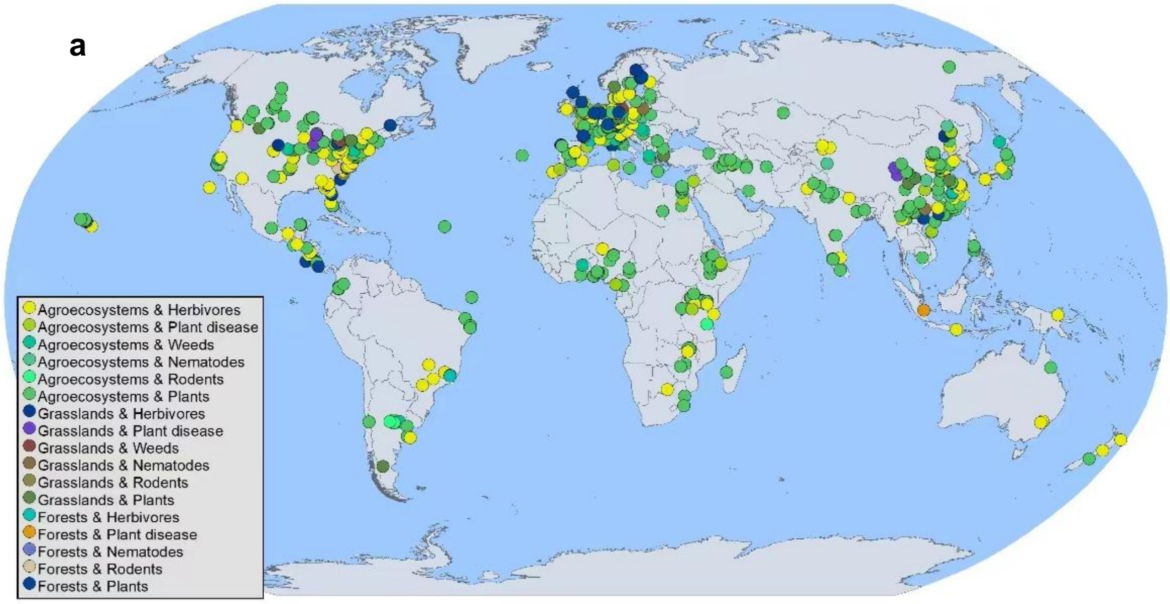


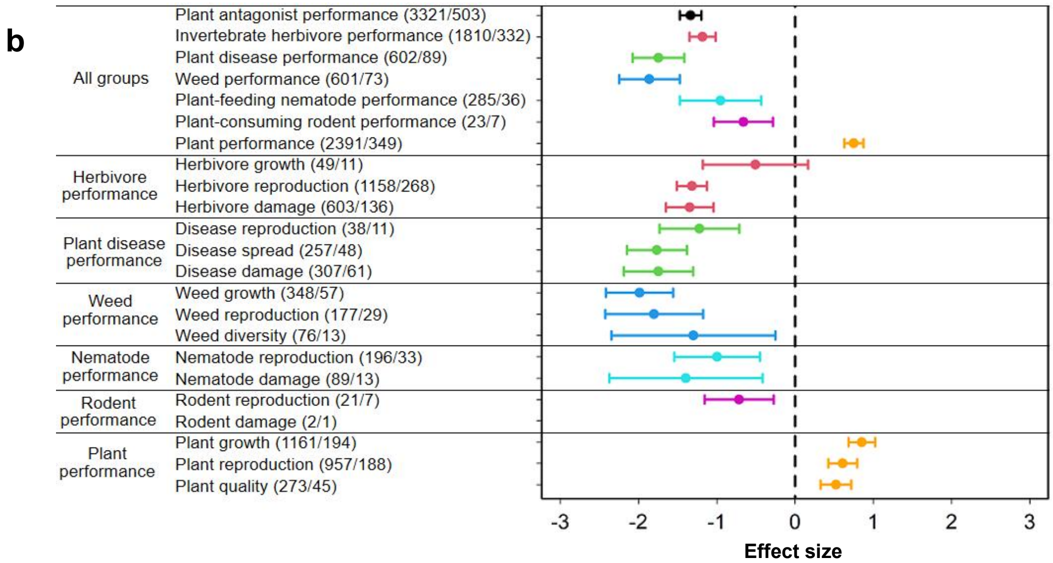


Fig. 1 | Global distribution of 636 study locations of the responses of plants and their antagonists to plant species richness. a, Study locations across global terrestrial ecosystems (world map in World Robinson projection; a literature search identified 536, 49 and 45 study locations for agroecosystems,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

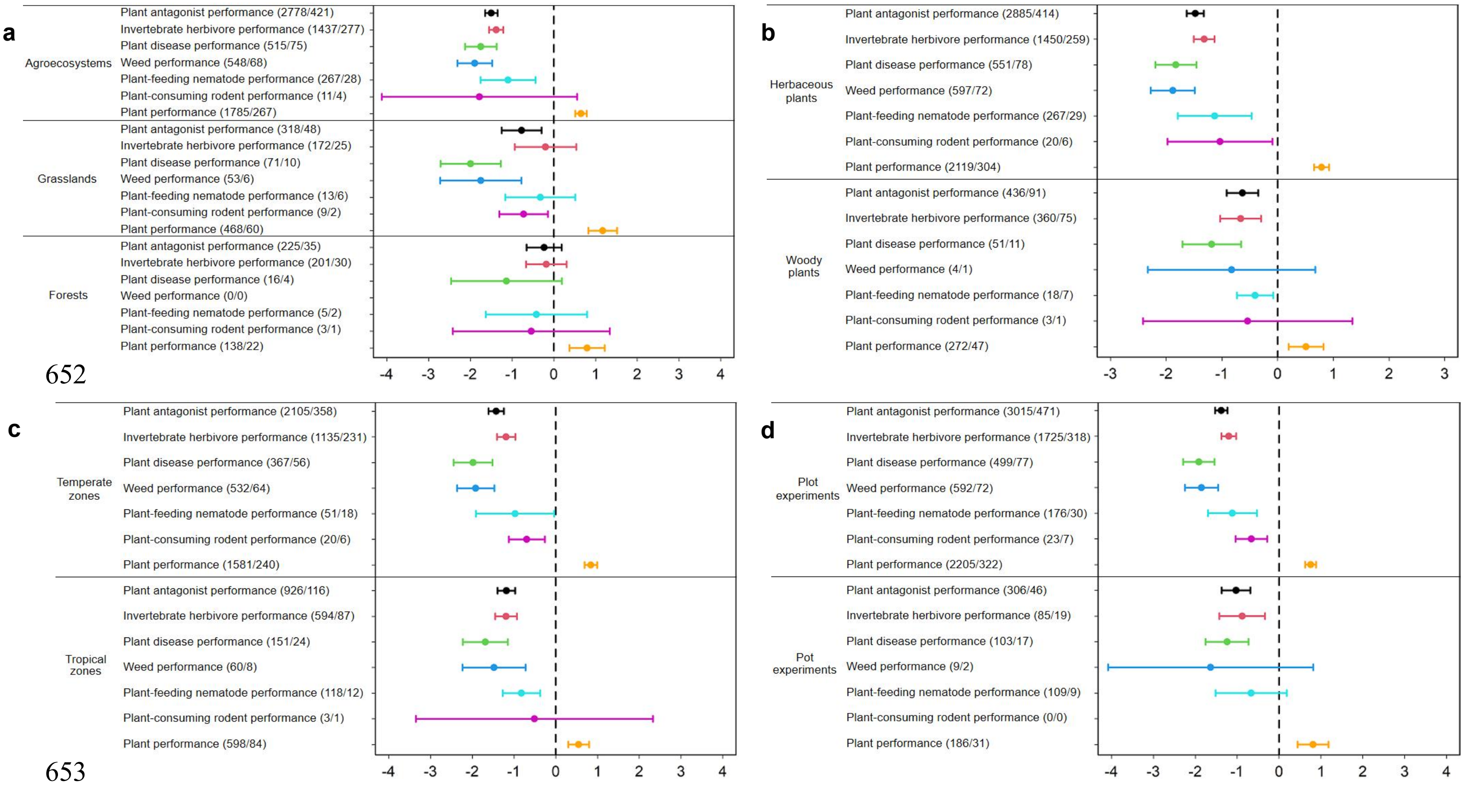


Fig. 2 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness. **a**, In agroecosystems, grasslands and forests. **b**, For herbaceous and woody plants. **c**, In temperate and tropical zones. **d**, For plot and pot experiments. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles.

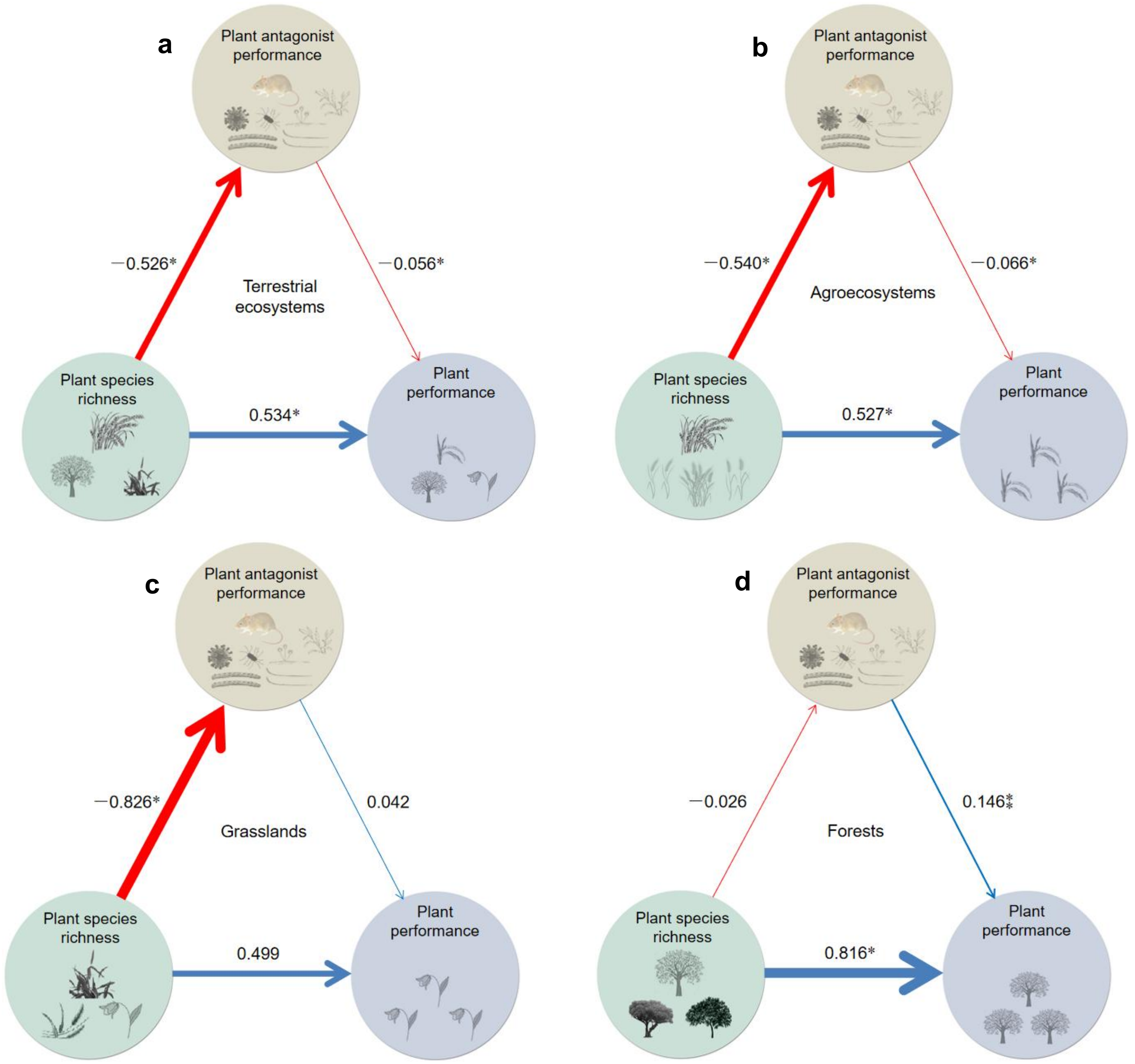


Fig. 3 | Piecewise structural equation model for the effects of plant species richness on the performances of plants and plant antagonists. a, In all analyzed terrestrial ecosystems (N=2766). **b**, In agroecosystems (N=2583). **c**, In grasslands (N=65). **d**, In forests (N=118). Plant performance includes the growth, reproduction and quality of plants. Plant antagonists includes: i) invertebrate herbivores (herbivore growth and reproduction, and herbivory damage to plants); ii) plant diseases (reproduction, spread, and damage to plants; iii) weeds (growth, reproduction, and diversity); iv) nematodes (reproduction, and damage to plants); and v) rodents (reproduction, and damage to plants). "*" denotes significance ($P<0.05$), and "⁑" denotes marginal significance ($0.05<P<0.10$). Blue and red arrows denote positive and negative relationships, respectively. Numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients (Supplementary Tables 10, 11).

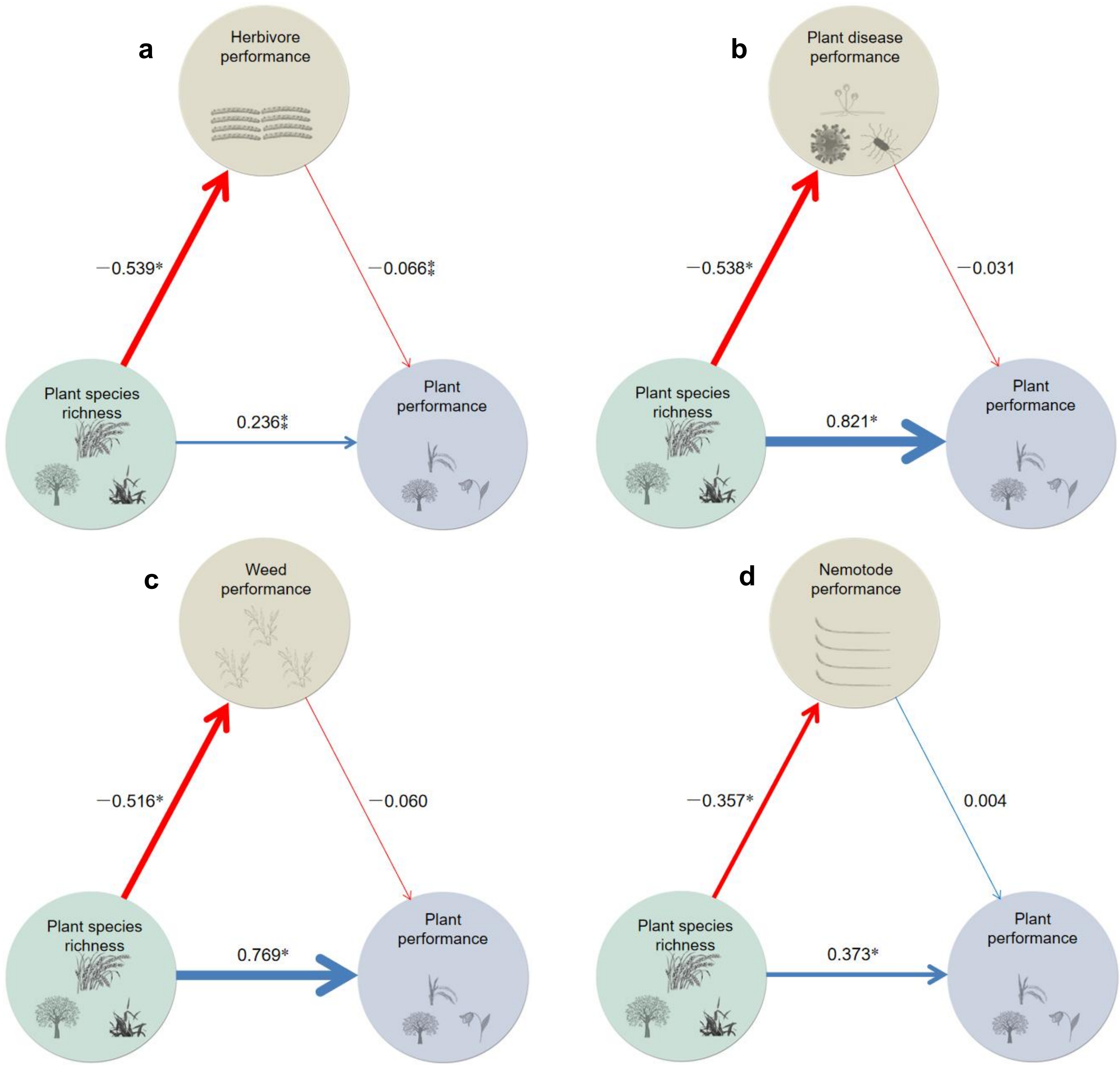
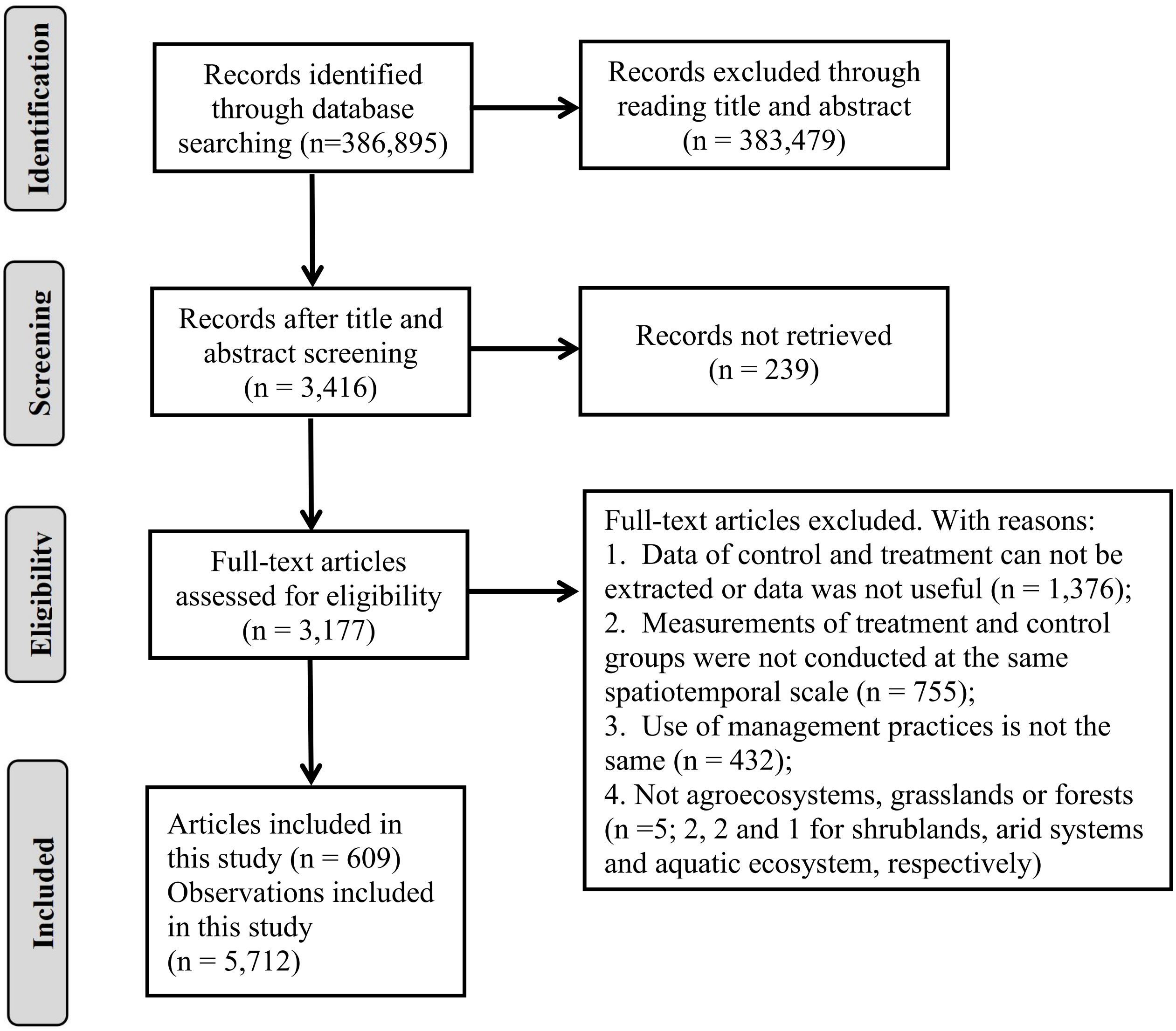
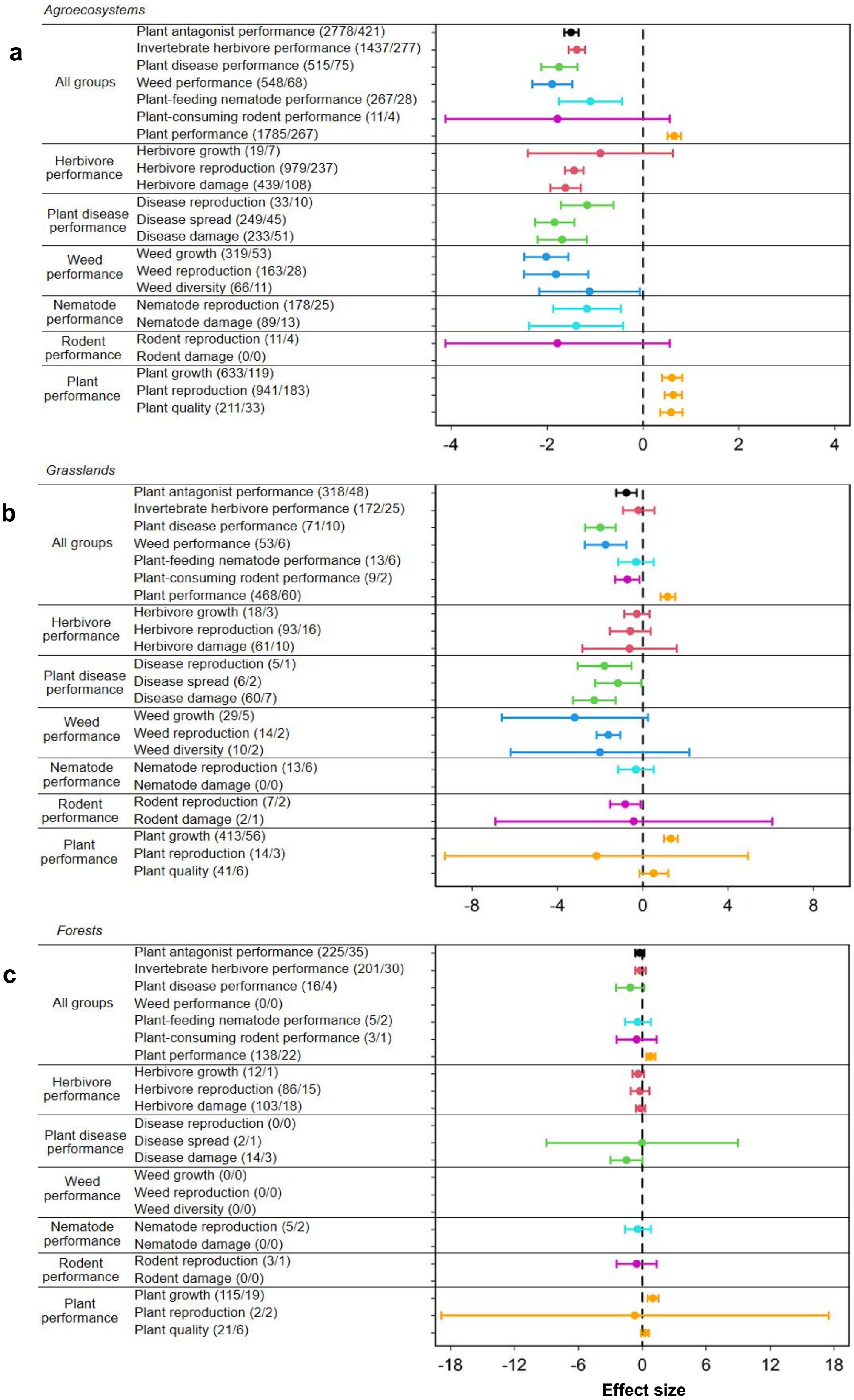


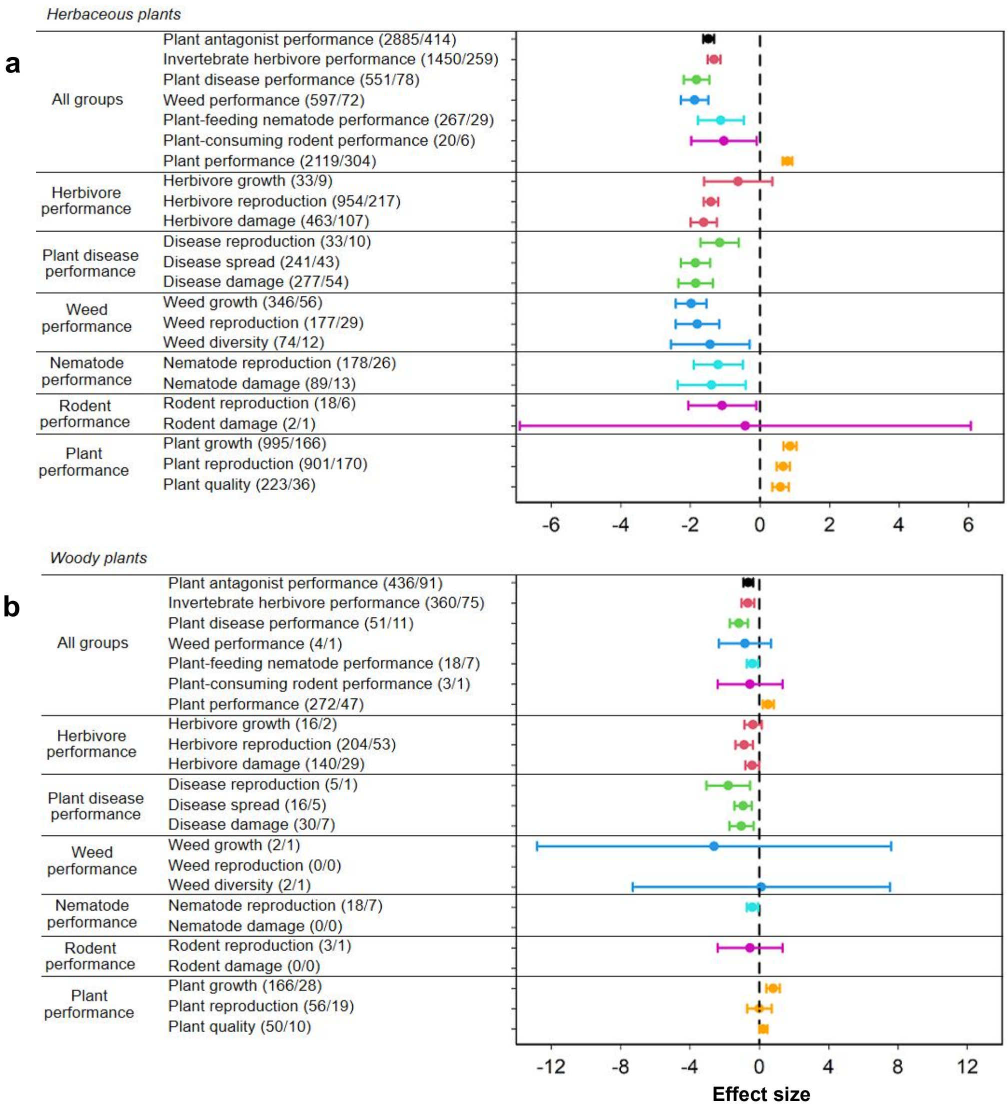
Fig. 4 | Piecewise structural equation model for the effects of plant species richness on the performances of plants and different groups of plant antagonists. a, Effects on plant and invertebrate herbivore performance (N=1218). **b**, Effects on plant and plant disease performance (N=638). **c**, Effects on plant and weed performance (N=642). **d**, Effects on plant and plant-feeding nematode performance (N=268). Plant performance includes the growth, reproduction and quality of plants. Herbivore performance includes growth, reproduction and damage of invertebrate herbivores. Plant disease performance includes reproduction, spread and damage to plants. Weed performance includes growth, reproduction and diversity. Plant-feeding nematode performance includes reproduction and damage to plants. The data on the relationships between plant and plant-consuming rodent performances was not found. "*" denotes significance ($P<0.05$), and "⁑" denotes marginal significance ($0.05<P<0.10$). Blue and red arrows denote positive and negative relationships, respectively. Numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients (Supplementary Tables 8, 9).



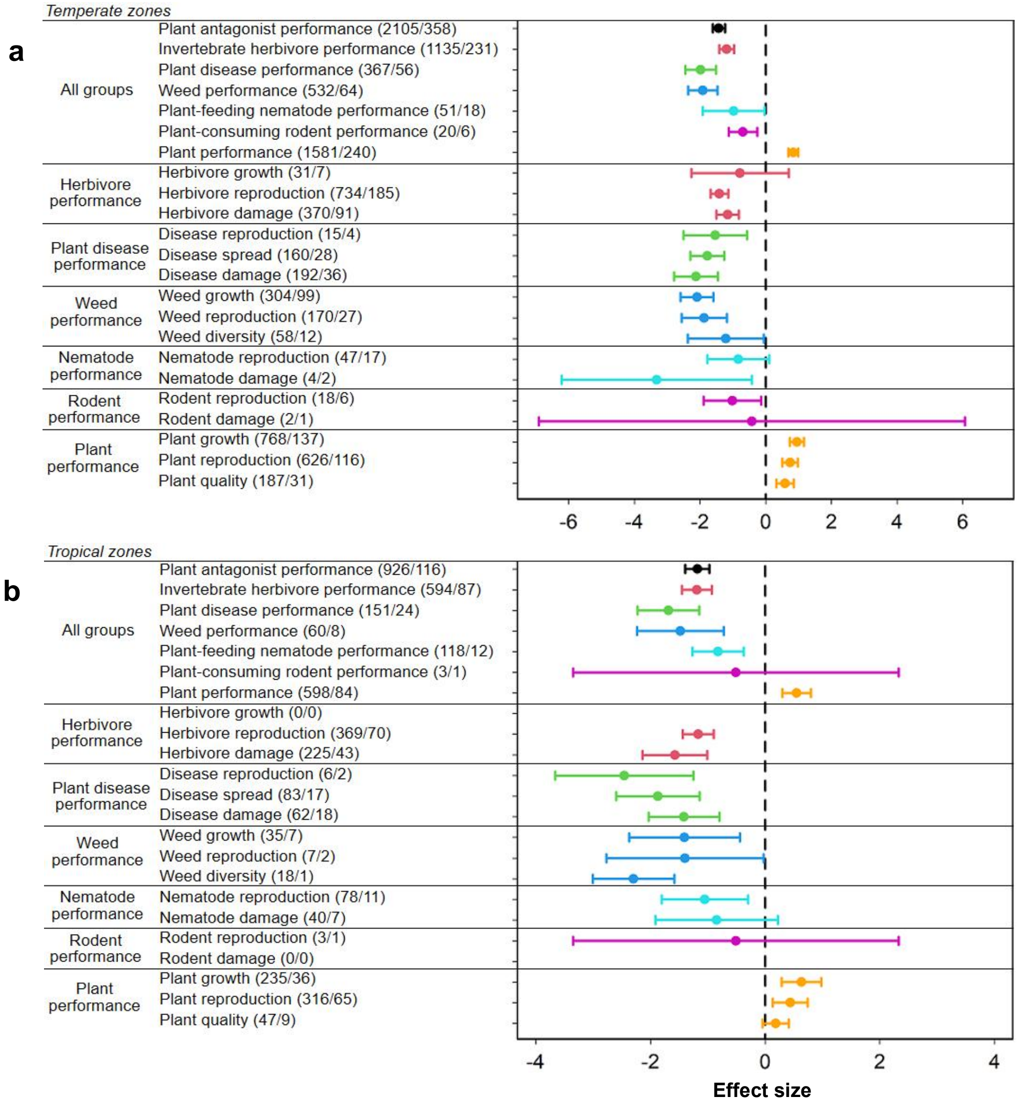
Extended Data Fig. 1 | A PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) describing the progress of data acquisition through the meta-analysis. It's the records identified in terms of numbers, and subsequent processed on inclusions and exclusions to derive the final data set used to assess the effects of plant species richness on the performance of plants and their antagonists.



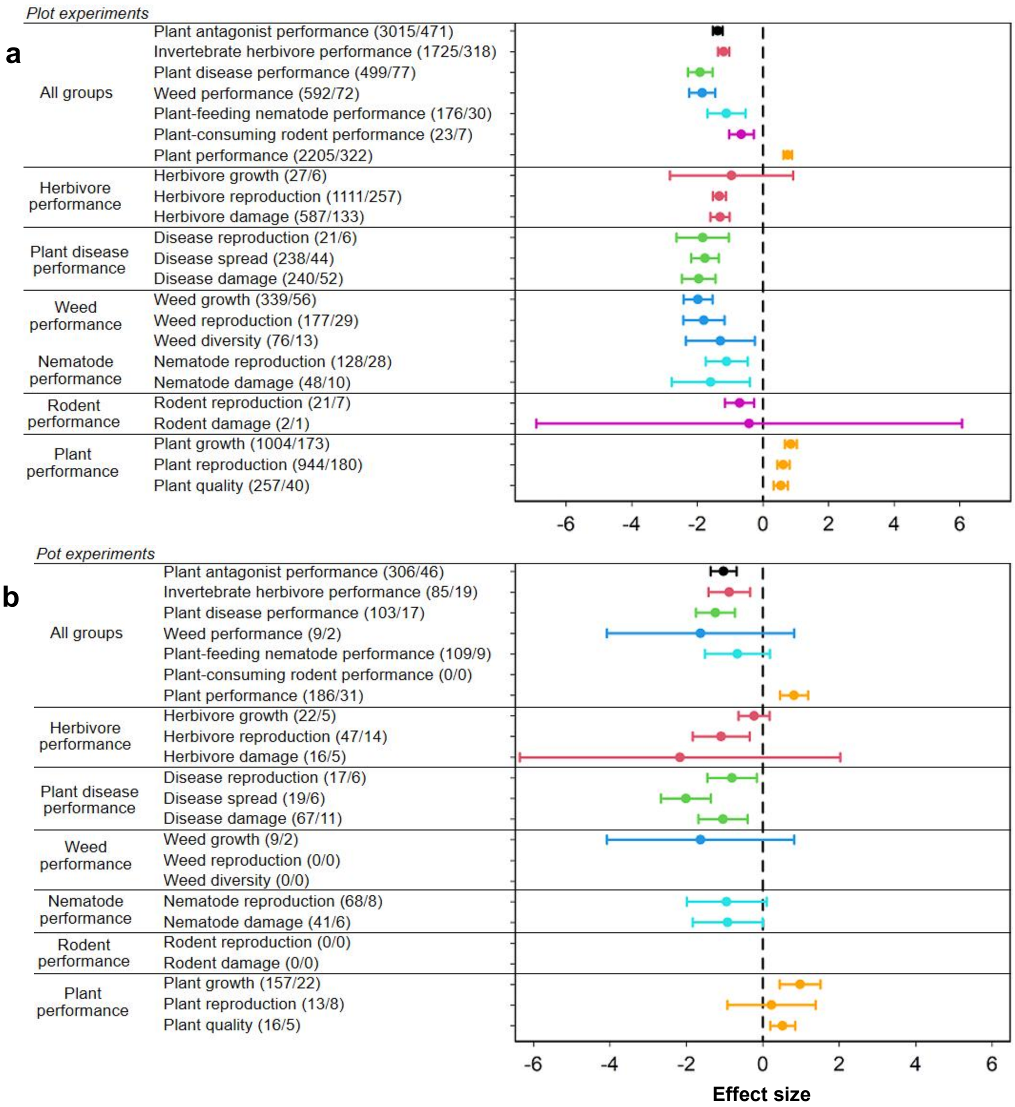
Extended Data Fig. 2 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness in different ecosystems. **a**, Agroecosystems. **b**, Grasslands. **c**, Forests. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles.



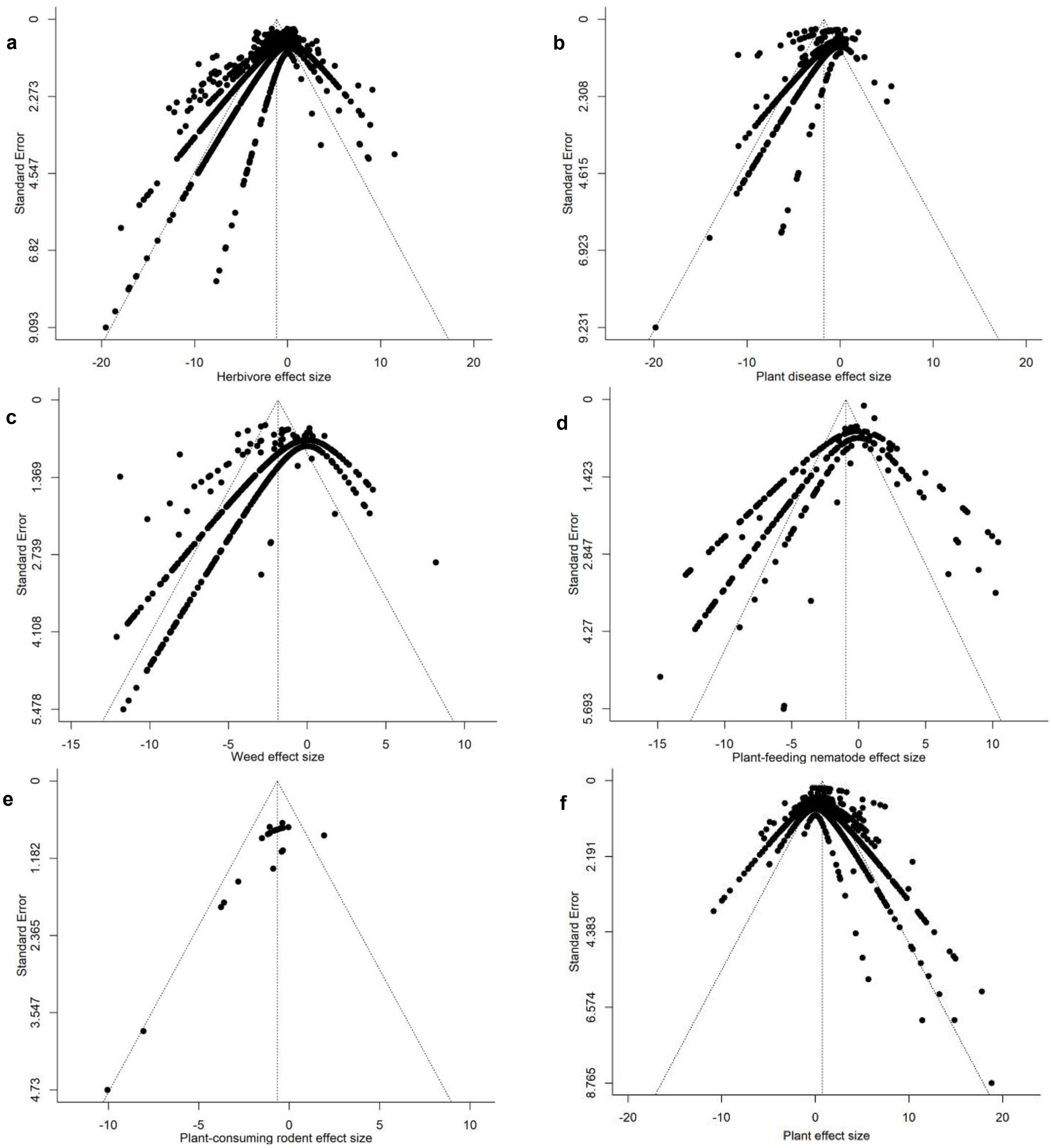
Extended Data Fig. 3 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness in different plant life forms. a, Herbaceous plants. **b**, Woody plants. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles.



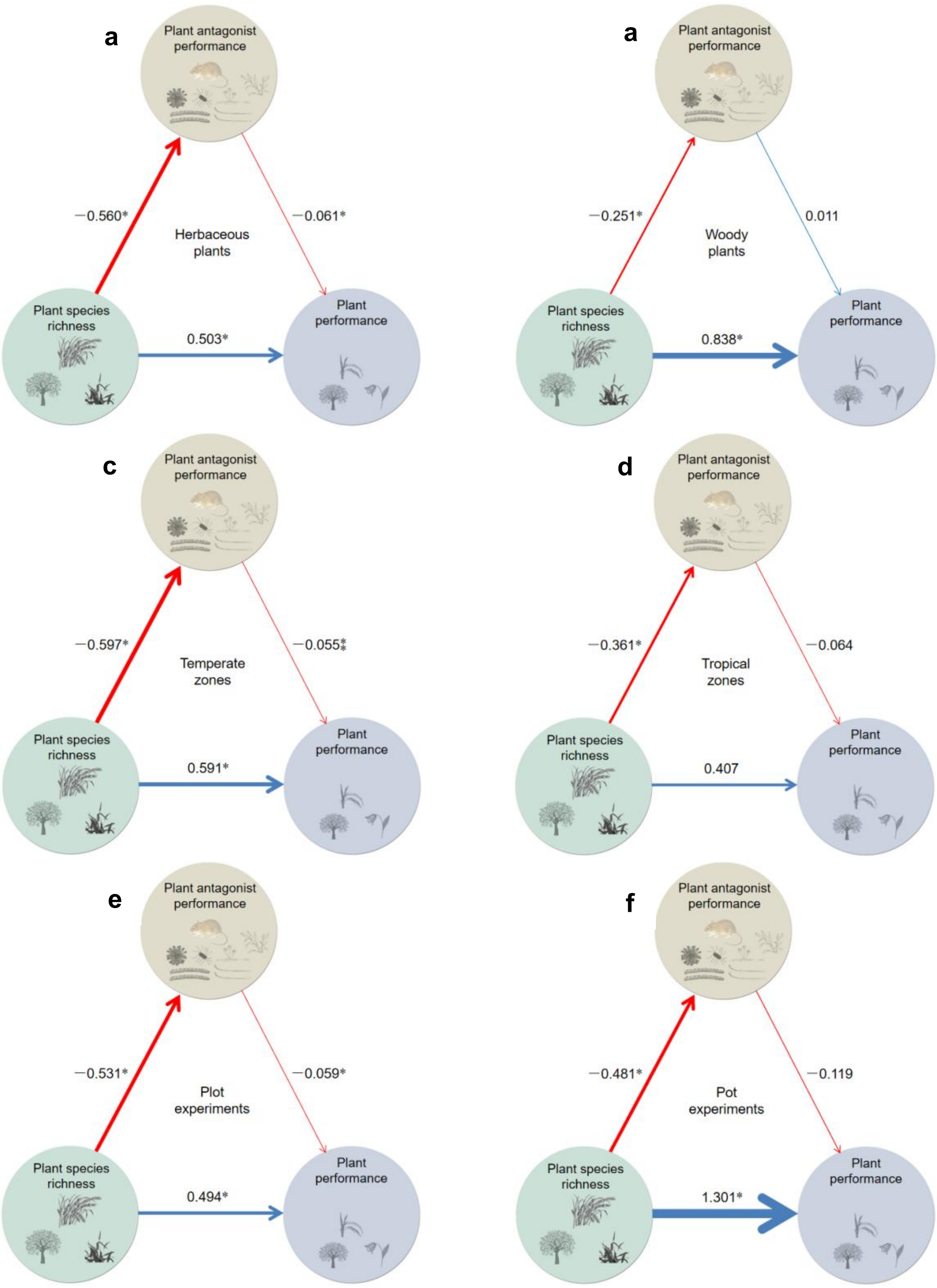
Extended Data Fig. 4 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness in different climatic zones. a, Temperate zones. **b**, Tropical zones. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles.



Extended Data Fig. 5 | Mean effect sizes of response categories of plants and plant antagonists to plant species richness in different experimental studies. **a**, Plot experiments. **b**, Pot experiments. Horizontal lines indicate the 95% confidence intervals around the means. Numbers in brackets indicate the numbers of observations and articles.



Supplementary Fig. 6 | Funnel plot showing of effect size standard errors plotted against effect size. a, Herbivore effect sizes include the responses of the growth, reproduction and damage of invertebrate herbivores to plant species richness. **b**, Plant disease effect sizes include the responses of the reproduction, spread and damage of plant diseases to plant species richness. **c**, Weed effect sizes include the responses of the growth, reproduction and diversity of weeds to plant species richness. **d**, Plant-feeding nematode effect sizes include the responses of the reproduction and damage of plant-feeding nematodes to plant species richness. **e**, Plant-consuming rodents effect sizes include the responses of the reproduction and damage of plant-consuming rodents to plant species richness. **f**, Plant effect sizes include the responses of the growth, reproduction and quality of plants to plant species richness.



Extended Data Fig. 7 | Piecewise structural equation model for the effects of plant species richness on the performances of plants and plant antagonists for different plant life forms, climatic zones and experimental studies. a, Herbaceous plants (N=2514). **b**, Woody plants (N=252). **c**, Temperate zones (N=1524). **d**, Tropical zones (N=936). **e**, Plot experiments (N=2513). **f**, Pot experiments (N=253). Plant performance composed of the growth, reproduction and quality of plants. Plant antagonist performance includes: i) herbivore performance composing of growth, reproduction and damage of invertebrate herbivores; ii) plant disease performance composing of reproduction, spread and damage of plant diseases; iii) weed performance composing of growth, reproduction and diversity of weeds; iv) nematode performance composing of the reproduction and damage of plant-feeding nematodes; and v) rodent performance composing of reproduction and damage of plant-consuming rodents to plants. “*” denotes significance ($P<0.05$), and “⁑” denotes marginally significance ($0.05<P<0.10$). Blue and red arrows denote positive and negative relationships, respectively. Numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients (Supplementary Tables 10, 11).

Supplementary Files

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