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Biocontrol enemies have stronger effects than non-biocontrol enemies on insect prey

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Abstract We used meta-analyses to examine the effects of different enemy taxa on insect prey populations as well as tri-trophic effects on their host plants. We also compared the effects of classical biocontrol, the use of biocontrol enemies for conservation biocontrol, and the use of naturally occurring enemies. Overall, there were strong negative effects of most enemy taxa on insect prey, but the effects of biocontrol enemies were significantly stronger than other naturally occurring enemies. There were differences in the strength of effects of enemy taxa with parasitoids, flying insect predators, ground insect predators other than ants, and spiders having stronger effects than ants or vertebrates such as birds, frogs, and bats. There were no significant differences between insect prey targets such as sucking insects, concealed feeders, leaf chewers, insect predators and detritivores. There were also no significant differences in the effects of enemies between insect prey of different origin, native or invasive, or host plant origin, native, invasive or introduced. However, the effects of enemies on their prey differed according to growth form of the prey host plant, with stronger effects of enemies or herbs and shrubs than on trees or grasses. There were no significant tri-trophic effects of enemies on the host plant morphometrics of their prey. There were also no significant difference in tri-trophic effects between biocontrol and non-biocontrol studies, enemy taxa, insect or plant origin, or plant growth form. However, the effects of enemies on prey were significantly negatively correlated with tri-trophic effects on plant morphometrics.

Keywords Classical biocontrol · Introduced insect enemies · Conservation biocontrol · Native insect enemies · Tri-trophic effects · Meta-analysis

Introduction

Many different native or naturally occurring animal taxa act as biocontrol agents of insect pests, including predatory insects, parasitoids, spiders, birds, bats, lizards, frogs and fish, and in many cases the reduction of insect pests benefit host plants because of so-called trophic cascades. Recently, Boldorini et al. (2024) examined the role of natural predators in the control of crop pests. They found that these naturally occurring vertebrates and invertebrates reduced pest populations by 73%, on average, and increased crop yield by 25%. However, there was taxonomic variation in

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the efficacy of these natural enemies, and variation in their effects depending on the habitats they occupied.

Other studies have also examined the strength of naturally occurring predators on insect pests and their host plants. Birds reduced insect abundance and plant damage in tropical agroforests and agricultural systems, and also in natural tropical and temperate forests (van Bael et al. 2008; Mäntylä et al. 2011; Diáz-Siefer et al. 2022). Bats have been found to reduce insect densities and defoliation in temperate forests (Beilke and O'Keefe 2022). Mooney et al. (2010) found that, together, birds, bats or lizards suppressed insect herbivores by 38% and increased plant biomass by 14%. For invertebrates, spiders were found to suppress agricultural pest species in 79% of cases studied (Michalko et al. 2018), but efficacy varied with crop type and increased slightly towards the tropics. For aphids, specialist natural enemies have stronger effects than generalist natural enemies (Diehl et al. 2013).

Conservation biocontrol focuses on landscape changes which enhance the effects of naturally occurring predator communities rather than introducing new ones. Such landscape changes may involve planting wildflower strips to provide nectar and pollen for parasitoids (Wackers and van Rijn 2012; Tschumi et al. 2016) and maintaining natural areas in agricultural landscapes for birds (Diaz-Siefer et al. 2022). This contrasts with classical biocontrol where a natural enemy of an invasive pest is imported and established to provide long-term control (Heimpel and Mills 2017). The biocontrol agent is typically collected from the pest species itself, usually in its country of origin. To date, there have been no systematic comparisons of these two biocontrol techniques. Here, we compare the strength of conservation biocontrol and classical biocontrol on insects and also ask how strongly these different techniques affect insect host plants via trophic cascades.

Schmitz et al. (2000) found that vertebrate carnivores generally had stronger effects than invertebrate carnivores on trophic cascades. This suggests that the use of invertebrate biocontrol agents against crop pests would not cause as big of a reduction in pest density or increase in plant production as the effects of natural vertebrate enemies on naturally occurring insects and their host plants, though this has not been explicitly tested. Interestingly, Stiling and Lajeunesse (2025) have recently shown that the effects of insect biocontrol agents on weeds have stronger effects than native insect herbivores on native plants. Here we also test the two contrasting ideas that biocontrol insects have weaker or stronger effects than naturally occurring enemies, such as birds, bats, spiders, ants, and other native insects, on host plants.

Materials and methods

We performed a Web of Science search (all databases, University of South Florida subscription), using the broad and inclusive search string "insect AND natural enemies" up to and including March 2023. This search returned 9291 candidate studies. The titles and abstracts of these studies were then screened using the package *metagear* (v. 0.7; Lajeunesse 2016) in R (v. 4.3.2; R Core Team 2023). Any study that did not report information on the effects of natural enemies on insect density, insect survivorship, insect biomass or insect growth, hereafter collectively known as density, since this was the most commonly reported measure, were excluded during screening. This screening resulted in 175 candidates.

For these 175 candidate studies to be included in our meta-analysis, they further needed to meet the following inclusion/exclusion criteria. First, the study had to contain numerical information on a treatment that included 'true' insect predation or parasitism by one or more species of natural enemy, as opposed to enemy attack on dummy targets such as plasticine caterpillars or simulated attacks by wasps, and a control where insects were not exposed to natural enemies. More specifically, studies often targeted multiple species of insect prey grouped together as "insects" (number of studies: $k = 134$) but sometimes targets were individual insect species ($k = 89$), particularly where these were subject to biocontrol. Both types of studies were included in our meta-analysis. Enemy exclusion was usually achieved by field cages/exclosures or sticky traps for ants or ground insects, and more rarely manual removal.

Effects of enemies on insect prey

While comparisons of insect prey densities on enemy-infested plants to insect prey densities on enemy-free plants sometimes used a range of enemy densities on the infested plants, our comparisons used enemy

densities closest to field densities (as indicated within studies). While some exclusion experiments were maintained for a year, only those studies lasting for a generation or more of herbivores, or at least two weeks exposure, were included. In total, 72 published studies involving 223 comparisons met these criteria for synthesis (Supplementary Table S1).

Enemies were classified into enemies used in biocontrol agents against invasive pest insects or native natural enemies against native insects (two comparisons involved predation on introduced weed biocontrol insects). Enemies were also classified broadly as invertebrates or vertebrates. Enemy types were further subdivided into ground insect predators (other than ants), flying insect predators, parasitoids, ants, spiders, birds, frogs and bats. One study classified enemies only as insect predators. Studies that excluded many different taxa of natural enemies simultaneously were excluded since we wanted to compare the effects across different taxa, where possible. For ants, we were interested only in the effects of free-ranging species, as were all other enemies, and not those which enter into mutualistic relationships with plants, which can offer shelter and food rewards. Indirect ant-plant interactions can also be mediated by honeydew-producing hemipterans where ants deter or prey upon other insects, increasing plant fitness, and these were also excluded. The effects of ants in both these types of mutualisms have been well reviewed elsewhere (Rosumek et al. 2009; Zhang et al. 2012). Enemy origin was classified as native, introduced, or invasive.

Insect prey was subdivided into feeding guilds: detritivores, predators, leaf chewers, sapsuckers, concealed feeders (such as leaf miners, leaf rollers and leaf gallers) and seed feeders. Many studies simply classified prey as "insects" (k = 33) or leaf feeders (k = 43) and these were not included in this part of the analysis. Plant origin of the herbivore insect was categorized as either native, introduced (crops) or invasive, and plant growth form as either herb, shrub, tree, vine, grass, or sedge.

Effects of enemies on plants: tri-trophic effects

In addition to the different effects of insect predators on herbivores, we also extracted tri-trophic outcomes of natural enemies on host plants when reported. Outcomes include various host plant morphometrics such as whole individuals, flowers, fruits, seeds, stems (stem/shoot/branch), leaves (leaf/rosette), or roots (root/tiller/tuber; k = 69). Measured variables on plants included absolute biomass, number, length (length/height/diameter), or area. We did not extract percent change of herbivory since some plants are tolerant to herbivory and an increase or decrease in herbivory is not always a good indicator of effects of herbivores on plant fitness (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Foroni 2011).

In tri-trophic analyses, studies were grouped according to biocontrol (yes or no), enemy as vertebrate or invertebrate, enemy type, origin of the target insect (native, invasive or introduced), origin of the insect host plant [native, introduced (e.g., crops), or invasive], and plant growth form. Three extra studies, not used in our enemies' analyses, were included in our tri-trophic analyses since they only examined the effects of enemies on host plants, not on the insect prey themselves.

In total, among the 72 studies reporting effects of enemies on prey (k = 223 effect sizes), 30 also reported trophic effects on plant morphometrics (k = 69). One of the 73 studies reported effects from the same experiment across two publications (van Veen et al. 2009; van Veen and Sanders 2013). Two additional studies which met our inclusion criteria, and which we still included in our meta-analysis, reported an incomplete experimental design that did not report enemy effects on prey but only enemy effects on plants (Schmitz et al. 2000; Visakorpi et al. 2015).

Effect sizes and synthesis approach

We primarily quantified study outcomes as with enemies (treatment, *T*) versus no-enemies (control, *C*) effects on insect prey density or for trophic effects on plant morphometrics Studies included in our analyses had to report means ($\bar{x}$), standard deviations (*SD*, or some measure of dispersion like SE or confidence intervals), and sample sizes (*N*) to compute effect sizes of study outcomes. When these study measures were only available in figures, the juicr package for R was used to extract numerical values (v. 0.1; Lajeunesse 2021). These study parameters were used to compute the standardized mean difference between the (*T*)treatment and (*C*)ontrol group, also known

as the Hedges' d effect size metric (Hedges 1981) defined as:

$$d = \frac{\bar{x}_T - \bar{x}_C}{\sqrt{\frac{(N_T-1)SD_T^2+(N_C-1)SD_C^2}{N_T+N_C-2}}} \times \left(1 - \frac{3}{4[N_T+N_C]-9}\right).$$

The variance (var) for meta-analysis weighting of effect sizes was calculated as: $var(d) = 1/N_T + 1/N_C + 0.5d^2/(N_T+N_C)$. Finally, when studies reported only SE or confidence intervals (CI), these needed to be converted to SD for computing effect sizes. Here we back calculated using $SD = SE\sqrt{N}$ and $SD = \sqrt{N}(upper95\%CI - \bar{x})/1.96$. Further, one study reported effects as a t-test only, and we converted this t to a d with:

$$d = t\sqrt{\frac{N_T+N_C}{N_T N_C}}\left(1 - \frac{3}{4[N_T+N_C]-9}\right).$$

These conversions are found in Lajeunesse (2013), and all the study parameters extracted from each study (e.g., $\bar{x}$, SD, and N) are found in the Supplementary Table S2.

We conducted mixed-effect meta-analyses using the metafor package for R (v. 4.0-0; Viechtbauer 2010). All meta-analyses included both the between study-variance (τ^2; as required for meta-analysis) and an additional random-effects component modelling overrepresentation of multiple effect sizes within studies (γ^2; 71 levels). In matrix notation, this model is:

$$\boldsymbol{d} = \mathbf{W}\boldsymbol{\beta} + \boldsymbol{\varepsilon} + \gamma^2 + \tau^2,$$

where $\boldsymbol{d}$ is a column vector of Hedges' d effect sizes, $\mathbf{W}$ is the regression design matrix of $f+1$ size (f is the number of moderators + intercept), and $\boldsymbol{\beta}$ is the column vector of $f+1$ regression coefficients. The weighting of each effect size via $var(d)$ is defined by the diagonal variance-covariance matrix $\boldsymbol{\varepsilon}$. The two random-effect components (τ^2, γ^2) were estimated via restricted maximum likelihood (REML) using the nlminb optimizer. Pooled effects were considered non-zero if 95% confidence intervals (CI) did not overlap zero, fixed-effect within-group homogeneity (H) tests were assessed using Q^{H}_{df} with degrees of freedom (df) of k – 1, and differences (B) between m number of groups within categorical moderators were tested using Q^{B}_{df} tests with df = m – 1 (following Hedges and Olkin 1985). Wald-type z-tests were also applied to evaluate if pooled effects differed from zero, and whether two groups of pooled effects differed from one another. Finally, metafor's regtest() function was used to implement Egger's test for publication bias while assuming a fixed-effects model (Egger et al. 1997).

We also performed a bivariate meta-analysis to quantify the correlation between enemy effects on prey densities and enemy effects on plant morphometrics. This bivariate meta-analysis model, which has the same parameters as the mixed-effects model presented earlier, has an additional random-effects components estimated from the two main underlying effect groups of effects of enemies on prey (d^{prey}; k = 223), effects on plants (d^{plants}; k = 69), and their pairwise covariance (*sensu* van Houwelingen et al. 1993). This unstructured bivariate model has a multivariate Normal ($MV\mathcal{N}$) between-study random-effects ($\boldsymbol{u}$) defined with means of zero with variances (ρ^2) and covariances (cov) defined as:

$$\begin{bmatrix} u_{prey} \\ u_{plants} \end{bmatrix} \sim MV\mathcal{N}$$
$$\left(0 = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \boldsymbol{u} = \begin{bmatrix} \rho^2_{prey} & cov(\rho_{prey}, \rho_{plants}) \\ cov(\rho_{prey}, \rho_{plants}) & \rho^2_{plants} \end{bmatrix}\right).$$

Results

Biocontrol *versus* non-biocontrol studies

Pooling outcomes across 72 studies there was a significant negative effect of enemies on insect prey density (random-effects meta-analysis: non-zero $z = -8.32$, $p < 0.001$, k = 223; Fig. 1a) and no evidence for publication bias among these effects ($z = -1.79$, $p = 0.0719$, slope = −0.52, 95% CI = [−0.659, −0.373]; Fig. 2a). However, enemies used in biocontrol studies showed significantly greater effects on insect prey than enemies in non-biocontrol studies ($z = -2.44$, $p = 0.015$; Fig. 1b).

Effects of enemies on insect prey

Non-vertebrate enemies had no stronger effects than vertebrate enemies (effect group contrast: $z = 1.71$, $p = 0.088$; Fig. 3b). However, when enemy type was

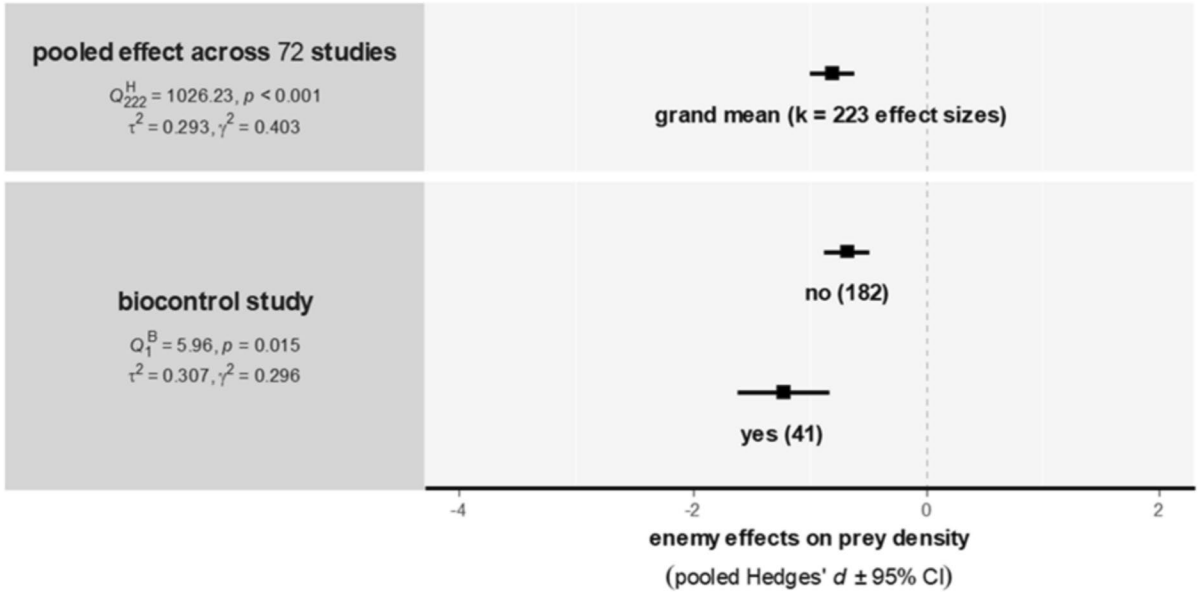

Fig. 1 Forest plots of effects of natural enemies on insect prey across 72 published studies (found in Supplementary Tables S1 and S2). Pooled effects (squares), their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled in brackets (k) for the grand mean effect across all 72 studies (top panel), and the pooled effects parsed among biocontrol studies *versus* studies of natural enemies on native insects (non-biocontrol; bottom panel). Random-effects included in this meta-analysis included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 72 levels). Finally, Q^{H}_{df} is the fixed-effect (H)omogeneity test across all effect sizes, Q^{B}_{df} is the omnibus tests for differences (B)etween groups of pooled effects, and *df* is the degrees of freedom of these Q^{B} tests (i.e., number of groups – 1). When 95% CI overlap with zero, this indicates no evidence for enemy effects on insect prey density, while pooled effects less than zero indicates negative enemy effects on insect prey density (e.g., fewer prey individuals than compared to the control group without enemies)

subdivided further, the differences among taxa were significant with invertebrates such as parasitoids, flying insect predators, ground insect predators and spiders having stronger effects than ants or vertebrate taxa such as bats, birds and frogs ($Q^{B} = 22.62$, df = 8, $p = 0.004$; Fig. 3b). There were no significant effects of insect target origin, where the prey was native, invasive or introduced ($Q^{B} = 1.60$, df = 2, $p = 0.448$; Fig. 4b), nor were there differences among prey insects when grouped among feeding guilds ($Q^{B} = 6.53$, df = 5, $p = 0.258$; Fig. 4c). Finally, there was no significant effect of host plant origin, native, introduced (crops) or invasive, on enemy effects ($Q^{B} = 0.23$, df = 2, $p = 0.891$; Fig. 5b), but there was a significant effect of insect host plant growth form, with insects living on shrubs and herbs suffering stronger effects than those on trees ($Q^{B} = 19.08$, df = 5, $p = 0.0019$; Fig. 5c).

Effects of enemies on plants: trophic interactions

Pooling outcomes across 32 studies, there was no significant effect of natural enemies on host plant morphometrics ($z = 1.62$, $p = 0.106$, k = 69; Fig. 6a) or evidence of publication bias among these effects ($z = 1.03$, $p = 0.3035$, slope = 0.028, 95% CI = [−0.224, 0.280]; Fig. 6b).

Effects of enemies used in biocontrol studies were not larger than those in non-biocontrol studies ($z = -0.983$, $p = 0.3263$; Fig. 6b). There were no significant differences between the effects of vertebrate and non-vertebrate enemies on plants ($Q^{B} = 2.57$, df = 1, $p = 0.109$), nor were there significant

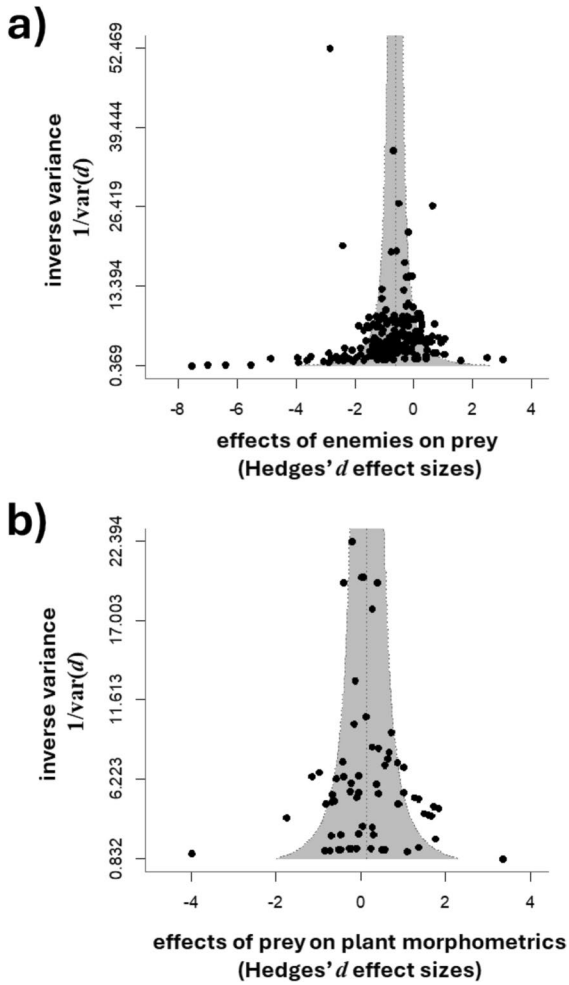

Fig. 2 Visualization of publication bias using a funnel plot of Hedges' *d* effect sizes: **a** for effects of enemies on insect prey ($k = 223$) and their inverse variances (meta-analysis weights), and **b** for effects of enemies on host plant morphometrics (k = 69). Dashed vertical line is the pooled effect using a fixed-effect meta-analysis (weighting but no random effects) and the curved funnel region shaded in grey is the pseudo-confidence region (± 1.96 SE) of this pooled effect

differences between different taxa of natural enemies on plants ($Q^B = 6.65$, df = 7, $p = 0.466$). There were no significant effects of insect target origin, native, introduced or invasive on enemy effects ($Q^B = 0.76$, df = 2, $p = 0.683$), nor were there significant effects of plant origin ($Q^B = 1.07$, df = 2, $p = 0.585$). Plant growth form had no significant effect on trophic effects ($Q^B = 8.35$, df = 4, $p = 0.08$).

When negative effects of enemies on insect prey were combined with positive effects on host plants across all of our 74 studies, the grand pooled effect was negative and significant (random-effects meta-analysis: pooled Hedges' $d = -0.92$, 95% CI [−0.618, −0.366], k = 292, $\tau^2 = 0.604$, $\gamma^2 = 0.054$). This shows that the direct effects of enemies on insect prey were stronger than the tri-trophic effects of enemies on host plants.

Bivariate effects of enemies on both prey and plants

Our final model simultaneously synthesizes the effects of enemies on both prey and plants using a single unified bivariate mixed-effects meta-analysis. This synthesis was necessary given that effects of prey will likely have a correlated effect on plants, and was possible to test because 30 studies reported enemy effect on both prey and plants.

With this bivariate meta-analysis, we found that effect of enemies on prey density was significantly negatively correlated with effects on plant morphometrics ($r = -0.719$, 95% CI [−1.0, −0.129], 30 paired effect size levels). These results indicate that the more enemies negatively impact prey densities, the more this will increase their impacts on the prey host plants. Given this joint model, the pooled effect of enemies on prey remained significant and negative (bivariate meta-analysis: pooled Hedges' $d = -0.801$, 95% CI [−0.991, −0.612], k = 223), while there was a marginal positive effect on plant morphometrics (bivariate meta-analysis: pooled Hedges' $d = 0.213$, 95% CI [−0.023, 0.448], k = 69). Finally, pooled effects on prey and pooled effect on plant morphometrics differed (effect group contrast: $z = 5.809$, $p < 0.001$; $\tau^2 = 0.262$ [292 levels], $\gamma^2 = 0.048$ [73 levels]). However, in terms of variability among these two groups, effects of enemies on prey were less variable and more consistent (bivariate random-effects among prey: $\rho^2_{prey} = 0.446$, 95% CI = [0.1785, 0.9694]) than enemy effects on plant morphometrics (bivariate random-effects among plants: $\rho^2_{plants} = 0.9249$, 95% CI = [0.3677, 2.1121]).

Discussion

The effects of natural enemies on insect prey were large and significant. However, the effects of introduced biocontrol agents on their insect prey were

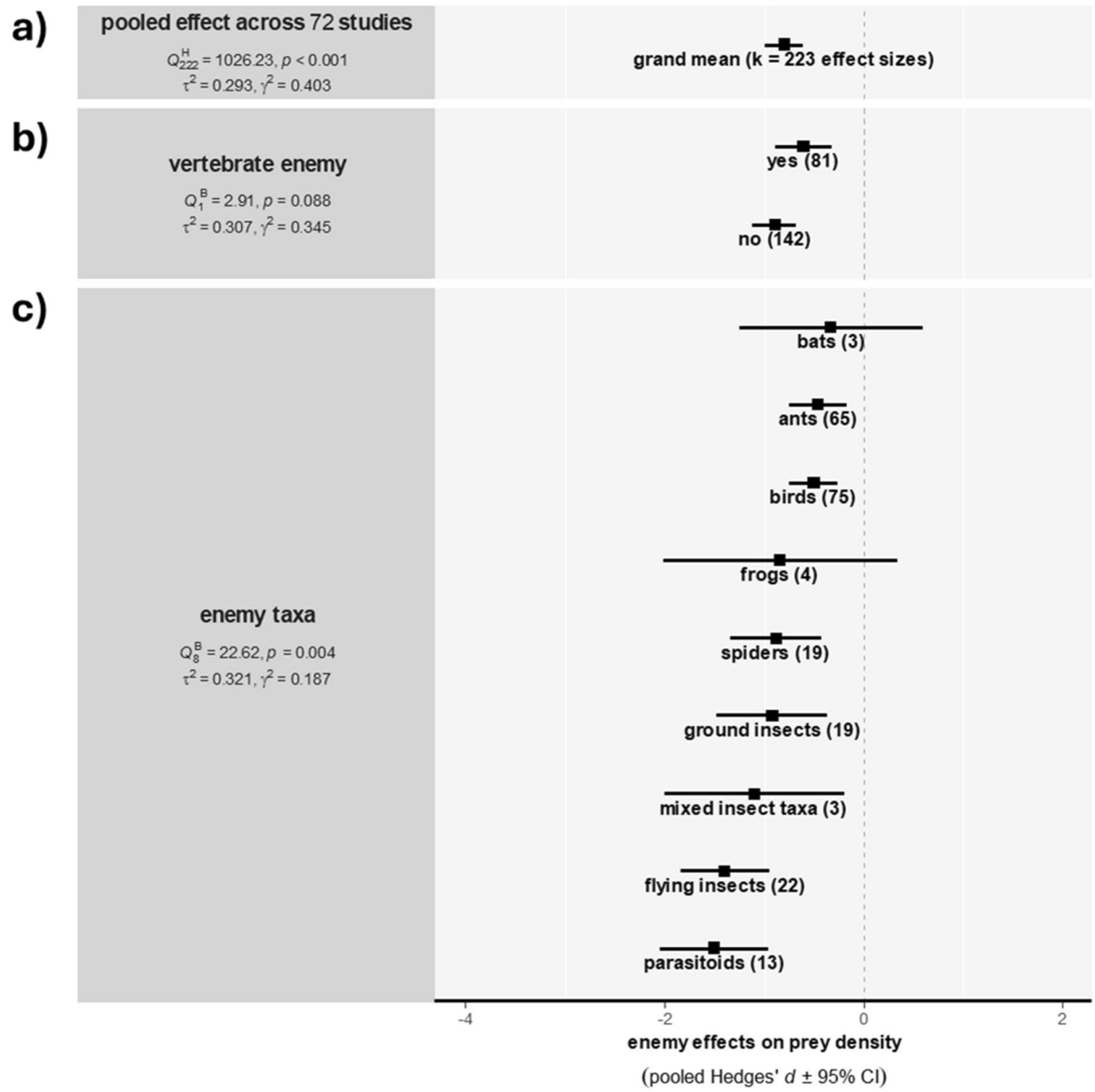

Fig. 3 Forest plots of the effects of natural enemies on insect prey density using three separate meta-analyses across 72 studies, first across all studies (**a**) then grouped among effects of vertebrates and invertebrates (**b**) and finally effects of enemy type (**c**). Pooled effects, their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group (k) are shown as the grand mean effect across all 72 published studies. Random-effects included in this meta-analysis included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 72 levels). Finally, Q^{H}_{df} is the fixed-effect (H)omogeneity test across all effect sizes, Q^{B}_{df} is the omnibus tests for differences (B)etween groups of pooled effects, and *df* is the degrees of freedom of these Q^{B} tests (i.e., number of groups – 1). When 95% CI overlap with zero, this indicates no evidence for enemy effects on insect prey density, while pooled effects less than zero indicates negative enemy effects on insect prey density (e.g., fewer prey individuals than compared to the control group without enemies)

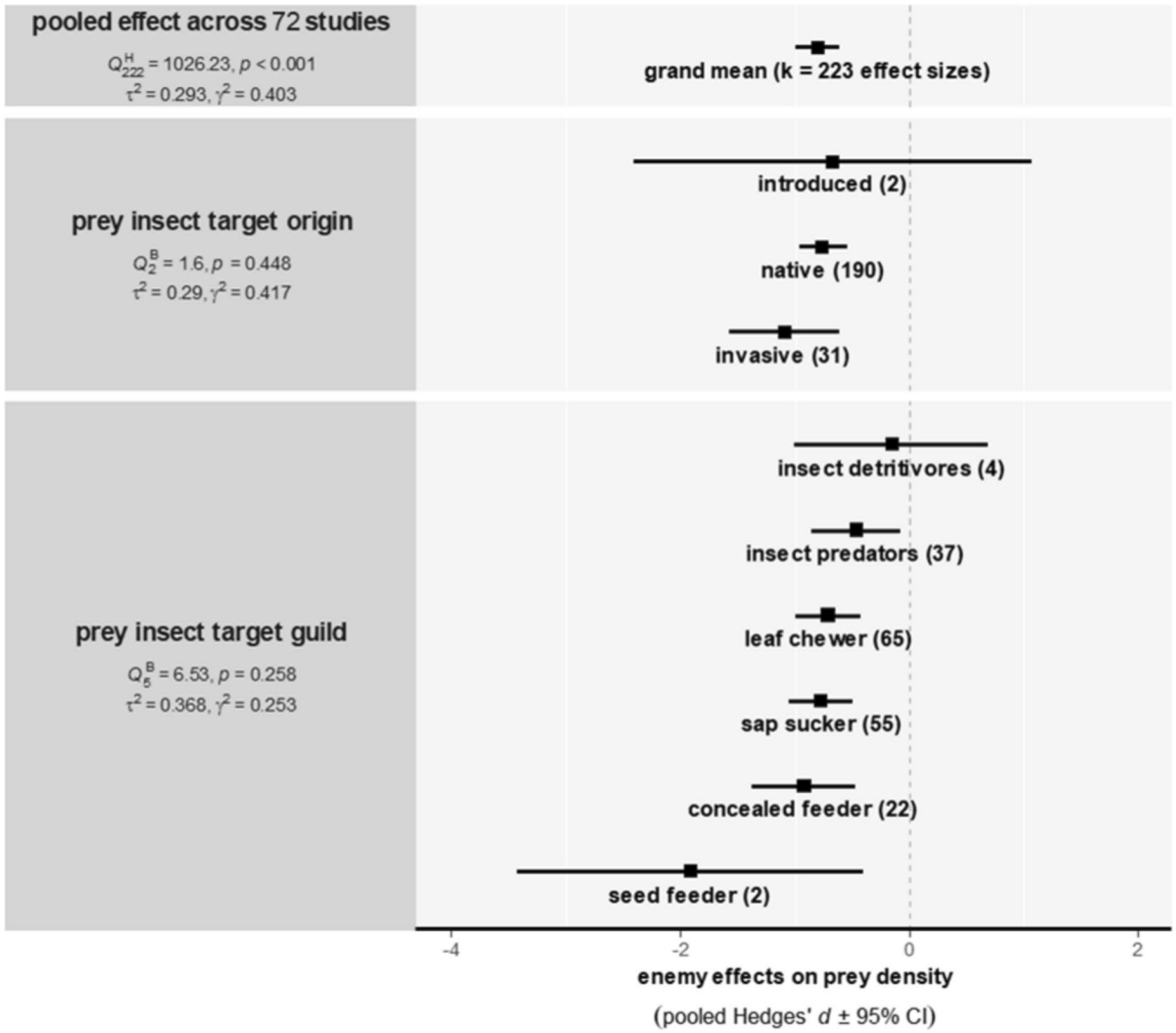

Fig. 4 Forest plots of the effects of natural enemies on insect prey using three separate mixed-effect meta-analyses across 72 studies, first across all studies (**a**), then grouped among effects of insect target origin (invasive, native or introduced) (**b**), and finally effects of insect target guild (**c**). Random-effects included in this meta-analysis included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 72 levels). Finally, Q^H_{df} is the fixed-effect (H)omogeneity test across all effect sizes, Q^B_{df} is the omnibus tests for differences (B)etween groups of pooled effects, and *df* is the degrees of freedom of these Q^B tests (i.e., number of groups – 1). When 95% CI overlap with zero, this indicates no evidence for enemy effects on insect prey density, while pooled effects less than zero indicates negative enemy effects on insect prey density (e.g., fewer prey individuals than compared to the control group without enemies)

stronger than the effects of naturally occurring enemies, such as birds, spiders, ants and other predatory insects, suggesting insect pest control can be improved by the addition of biocontrol agents. Other reviews on the effectiveness of natural enemies on insect prey have not compared the effects of biocontrol agents *versus* natural biocontrol. Stiling and Lajeunesse (2025) showed that the effects of introduced biocontrol insects on weeds were stronger than the effects of natural insect herbivores on native plants, and the same phenomenon appears to be true for insect enemies on insect prey.

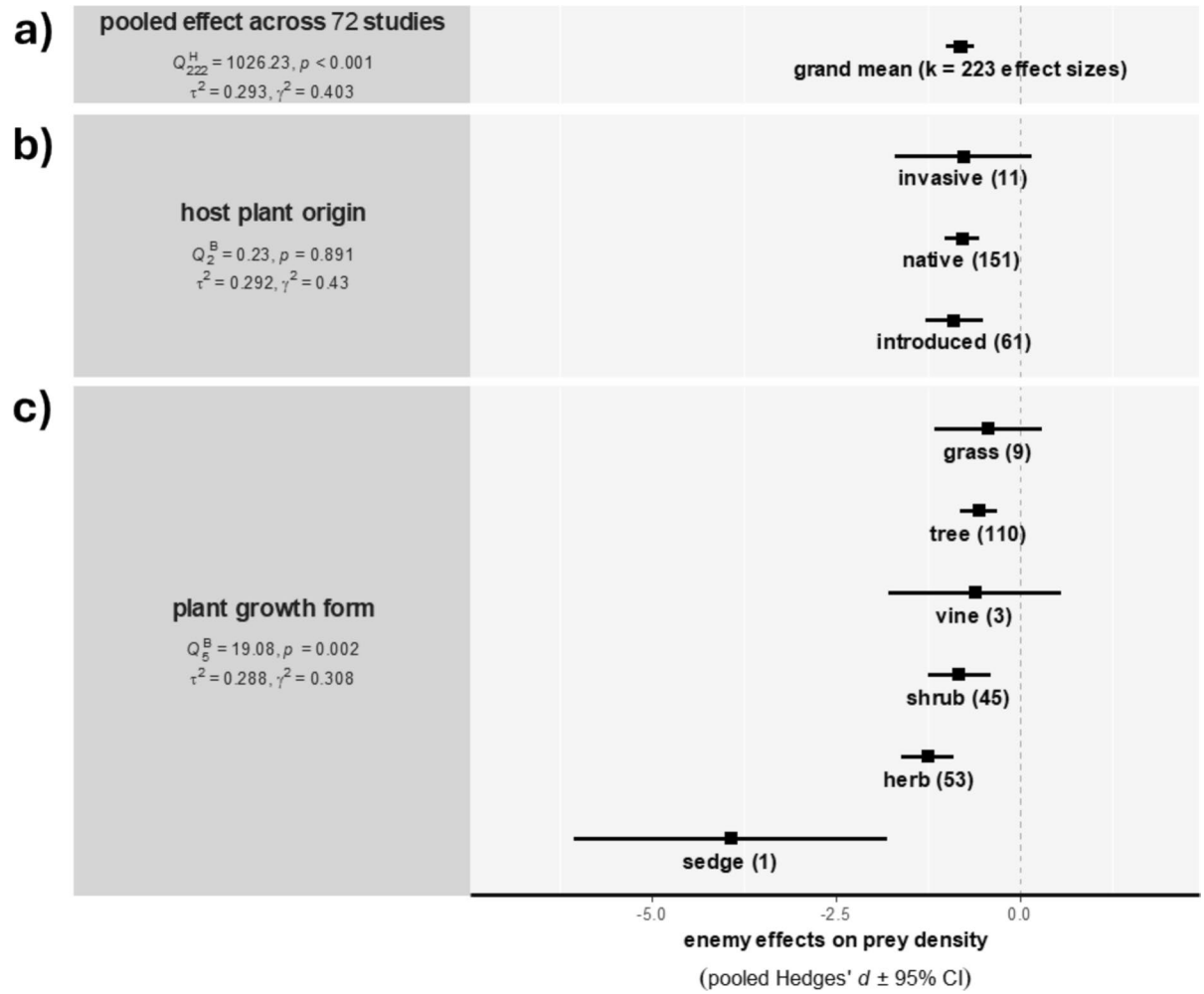

Fig. 5 Forest plots of the effects of natural enemies on insect prey using three separate mixed-effect meta-analyses across 72 studies, first across all studies (**a**), then grouped among effects host plant origin (invasive, native, or introduced) (**b**), and finally plant growth form (**c**). Pooled effects, their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group (k) are shown as the grand mean effect across all 72 published studies. Random-effects included in this meta-analysis included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 72 levels). Finally, Q^{H}_{df} is the fixed-effect (H)omogeneity test across all effect sizes, Q^{B}_{df} is the omnibus tests for differences (B)etween groups of pooled effects, and *df* is the degrees of freedom of these Q^{B} tests (i.e., number of groups – 1). When 95% CI overlap with zero, this indicates no evidence for enemy effects on insect prey density, while pooled effects less than zero indicates negative enemy effects on insect prey density (e.g., fewer prey individuals than compared to the control group without enemies)

Effects of enemies on insect prey

When parsed by enemy taxa, parasitoids, flying insect predators and ground insect predators had greater effects than vertebrate predators, spiders and non-mutualistic ants though all had significant effects on insect prey. A recent review by Boldorini et al. (2024) on the effects of natural enemies on crop pests found similar results to ours with significant effects of birds, beetles, spiders, and other invertebrates (including ants) on insect prey, but no significant effects of bats or true bugs. Strong effects of birds on insect densities have also been found in tropical agroforestry and across many other crops, such as coffee, cereals,

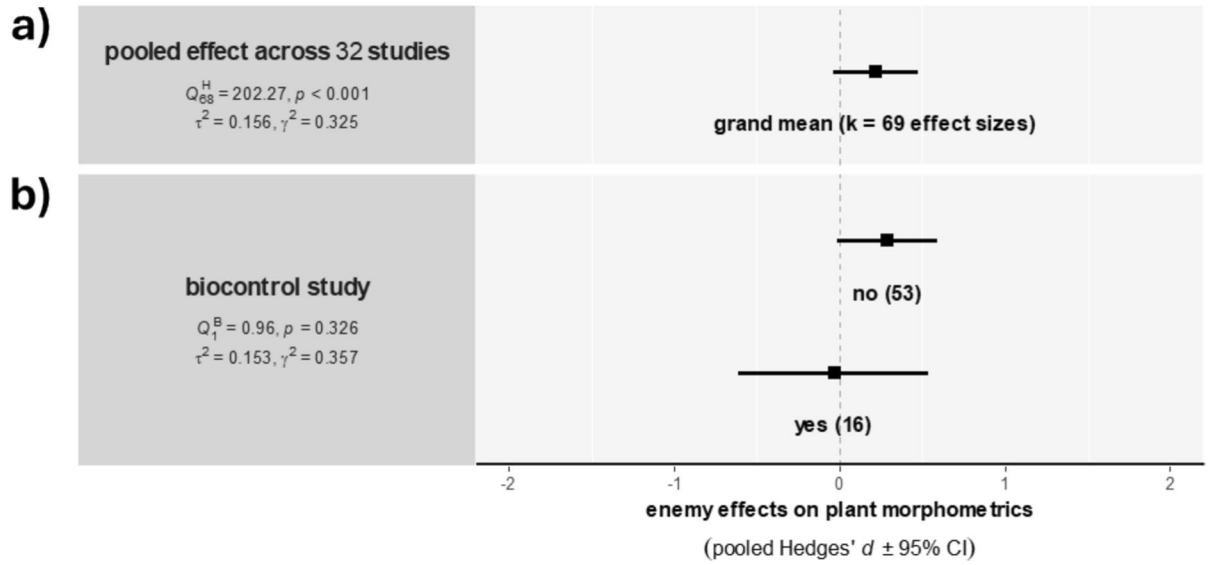

Fig. 6 Forest plots of the effects of natural enemies on insect target host plant morphometrics using two separate mixed-effect meta-analyses grouped among effects of **a** all studies and **b** biocontrol studies. Pooled effects, their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group (k) are shown as the grand mean effect across all 32 published studies. Random-effects included in these meta-analyses included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 32 levels). Random-effects included in this meta-analysis included the between study-variance (τ^2) and the variance modelling over-representation of multiple effect sizes per study (γ^2 with 72 levels). Finally, Q_{df}^{H} is the fixed-effect (H)omogeneity test across all effect sizes, Q_{df}^{B} is the omnibus tests for differences (B)etween groups of pooled effects, and *df* is the degrees of freedom of these Q^{B} tests (i.e., number of groups – 1). When 95% CI overlap with zero, this indicates no evidence for enemy effects on plant morphometrics, while pooled effects greater than zero indicates positive enemy effects on plant morphometrics (e.g., less plant damage due to prey herbivory)

apples, *Brassica*, vineyards and others (van Bael et al. 2008, Diaz-Siefer et al. 2022). A separate meta-analysis of 113 experiments showed strong effects of insectivorous birds, bats, and lizards on both predacious and herbivorous insects (Mooney et al. 2010). Finally, a separate meta-analysis on the effects of spiders on agricultural insect pests showed significant effects on pest densities (Michalko et al. 2018). Our results are similar to other meta-analyses in that they show strong effects of many different taxa of enemies.

The origin of both insect prey or insect host plant did not affect the success of natural enemies in our synthesis since effects of enemies on native and invasive insect prey or on native or introduced plants (crops) were both similar. Many of the studies targeting invasive insect prey used introduced biocontrol agents from the same country as the pest insects, which would constitute an evolutionarily similar relationship to native insect predators attacking native insect prey. However, enemy effects were stronger for insects feeding on herbs and shrubs, compared to those feeding on trees and grasses. The reasons for this difference are not clear, but part of this effect can be driven by the increased impacts of biocontrol enemies which reduce pest populations in herbaceous crop systems. Crop systems tend to be simpler environments than natural or semi-natural habitats, including trees, which could lead to stronger species interactions (Boldorini et al. 2024).

Feeding guild of prey was not significant even though the effects of enemies on detritivores and insect predators appeared slightly weaker than those on leaf chewers, sap suckers, and concealed feeders, suggesting that the hidden nature of concealed feeders such as leaf miners, leaf rollers, and leaf rollers does not give them added protection from predators. In a separate study of spiders, main effect sizes were similar across prey taxa, such as Auchenorrhyncha, Coleoptera, Diptera, and Lepidoptera (Michalko et al. 2018), though the variety of feeding guilds for these external feeders was not as great as in our meta-analysis.

Effects of enemies on plants: tri-trophic effects

In our synthesis, although there were positive indirect effects of enemies on host plants, these were not as strong as the direct impact of enemies on insect herbivores. This could be because in studies examining effects of enemies on many plant species collectively, some plants containing anti-herbivore defenses grow better when non-defended plants are preferentially eaten. Similarly, herbivore species diversity on plant collectives may weaken tri-trophic effects since removal of some herbivore species may allow competitive release of others. Finally, relaxation of intraguild predation by removal of top predators may allow lower-level predators to proliferate. The effects of biocontrol enemies on crops were not significantly different from the effects of natural enemies on native host plants, suggesting similar attenuations of effects as they ripple through both crop and natural food webs.

Other studies have shown mixed effects of enemies on crop performance and crop yield and on the production of non-crop host plants. Boldorini et al. (2024) showed significant effects of enemies on crop yields. However, many of the crop species included in that study were closely related and the authors failed to find an impact of different predators on crop yield when crop phylogeny was considered. In a separate study, excluding wild birds alone significantly reduced crop yields, but more so on conventional farms, using traditional chemical controls rather than on organic farms (Diáz-Siefer et al. 2022). Other studies have shown strong tri-trophic effects of birds on both agricultural and natural plants (Mooney et al. 2010; Mäntylä et al. 2011).

As with the effects of natural enemies on insects, the origin of insect target, native, invasive, or introduced, or the origin of the host plant, native, introduced (crops) or invasive, did not affect the strength of tri-trophic effects. Boldorini et al. (2024) also found no significant differences of natural enemies on different crop types such as cereals, vegetables or other crops. Similarly, the effects of vertebrate and invertebrate enemies on plants were not significantly different, nor were the effects of different enemy taxa, plant growth form.

In conclusion, we show that both conservation biocontrol and classical biocontrol have strong effects on pests in both natural and agricultural communities. However, the effects of biocontrol agents on insect prey are stronger than the effects of naturally occurring predators on insect prey. This is important as it highlights how the addition of biocontrol agents to crop systems may be beneficial even where naturally occurring enemies of pest insects are conserved.

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Declarations

Conflict of interest The authors declare that they have no competing interests that are directly or indirectly related to the work submitted for publication.

Ethical Approval This research involved no human or animal participants.

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