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Biocontrol insects have stronger effects than non-biocontrol insects on plants

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Abstract We used meta-analyses to compare the effects of 44 single insect species used as biocontrol agents against invasive weeds with the effects of 51 species of non-biocontrol insects on native plants. The effects of biocontrol insects on plant morphometrics were stronger than those of non-biocontrol insects. Overall effects of both groups together were significantly different across plant growth forms with grasses, shrubs, and trees impacted more than vines and herbs. The effect of plant organ was also significant, with roots and fruits suffering the greatest impacts. Insect order had a significant effect: Hemiptera and Coleoptera showed strong effects and Diptera weak effects. Insect feeding guild had significant effects with leaf chewers, sap suckers, stem borers, and stem gallers having the strongest effects. There were no significant effects of study duration or latitude of location. For most categories of plant growth form, plant organ attacked, insect order and feeding guild, biocontrol insects had significantly stronger effects than their non-biocontrol counterparts. The effects of non-biocontrol insects grouped alone against native plants were not always a reliable guideline for how biocontrol insects grouped alone affected their target plants.

Keywords Classical biocontrol · Introduced insect herbivores · Invasive plants · Meta-analysis · Native insect herbivores · Native plants

Introduction

In biocontrol, one of the most frequently posed questions concerns biocontrol agent efficacy. Why do some biocontrol agents effectively control their hosts while others fail to establish (Hall et al. 1980; Stiling 1993; Kimberling 2004)? Success in biocontrol has often been attributed to the right series of ecological traits being possessed by the target, the enemy or both (Harris 1973; Crawley 1989a; Blossey 1995). Selecting agents based on their potential impact has been argued to be the holy grail of biocontrol (McFadyen 1998). In the biocontrol of invasive plants, characteristics of insect herbivores, such as insect order, plant organ attacked and mode of feeding, and characteristics of plants, such as size, nutrient quality and level of defenses are thought to impact the degree of plant damage and mortality (Myers and Sarfraz 2017). But do biocontrol agents actually cause more damage than similar native insects? Are plant growth forms or organs damaged

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the most by biocontrol agents, the same as plant growth forms and organs most damaged by non-biocontrol insects? If not, then are we releasing the best insects for biocontrol?

Several meta-analyses, or similar large-scale analyses, have compared the success of biocontrol programs against invasive alien plants in an attempt to answer the question “what factors impact natural enemy efficacy”? Stiling and Cornelissen (2005) synthesized experimental outcomes from 26 studies, involving 71 independent comparisons of 21 target weed species and 24 biocontrol agents and showed significant effects of these agents on plant height, biomass, leaf number, and flower and seed production. Clewley et al. (2012) carried out meta-analyses of 61 studies, from 2000 to 2011, involving 173 comparisons of 28 target species and 49 different biocontrol agents, and found significant reductions in plant size, biomass and flower and seed production.

Paynter et al. (2012) collated biocontrol data from 80 weed species against which 232 biocontrol agents had been released. Because this data set contained similar species, in congeneric plants that shared traits, for example *Opuntia* species and *Centaurea* species, the impacts were averaged for congeneric species with identical traits, which reduced the database to 69 species. Generalized Regression Analysis and Spatial Prediction (GRASP, Lehmann et al. 2002) was used to model the efficacy of biocontrol against plant factors. Schwarzländer et al. (2018) and Panta et al. (2024) used the fifth edition of “Biological control of weeds: a worldwide catalog of agents and their target weeds” (Winston et al. 2014) to examine data on intentional releases of biocontrol agents against species of target weeds. In the absence of formal meta-analyses, their data was couched in terms of percent of releases established, successful or with heavy impact.

Meta-analyses of the effects of native insects against native plants are not as common as those concerning the effects of biocontrol insects and few have attempted cross taxa comparisons. More common are studies that examine the effect of single feeding guilds such as sap-feeding insects (Zvereva et al. 2010) or temperate herbivorous communities (Coupe and Cahill 2003). As far as we are aware, no studies have performed extensive comparisons of the effect strength of biocontrol and non-biocontrol insects, or have compared their efficacy across multiple plant and insect groups.

Here we report phylogenetic meta-analyses (Lajeunesse 2009) comparing the effects of individual biocontrol insect species against 44 weedy plant species, involving 153 independent comparisons, *versus* non-biocontrol insects feeding on 51 native plant species involving 187 independent comparisons. Our use of a mixed-effect meta-analysis also models phylogenetic non-independence among all insects and plants synthesized.

Materials and methods

We performed a Web of Science search (all databases), using the inclusive search string “insect AND herbivory” up to and including June 2021. This search returned 20,158 candidate studies. An additional 316 candidate studies were retrieved from the references of four earlier reviews on insect herbivory (Bigger and Marvier 1998; Stiling and Cornelissen 2005; Zvereva et al. 2010; Clewley et al. 2012). After combining and deduplicating the bibliographic information of these two sources, the titles and abstracts were then screened and assessed for inclusion using the abstract screener interface offered by the package metagear (v. 0.7; Lajeunesse 2016) in R (R Core Team 2024). Any study that did not report information on the effects of herbivory on plant morphometrics (e.g., leaves, stems, roots) were excluded during screening. This screening resulted in 1282 candidates.

For these 1282 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 herbivory by one insect species, as opposed to simulated herbivory/damage via clipping, and a control where plants were not exposed to that species of herbivore. Studies containing multiple species of herbivore lumped into one insect herbivory treatment were excluded since we were interested in the effects of individual known species of herbivores and partitioning the effects of multiple species in an exclusion treatment would be difficult. Furthermore, our method avoids comparisons where greater numbers of herbivore species may be excluded in some studies and compared to the effects of exclusion of fewer herbivore species in others. Herbivore exclusion was usually achieved by field cages, insecticides, or by the use of greenhouse experiments.

While comparisons of insect-infested plants to insect-free plants sometimes used a range of herbivore densities on the infested plants, our comparisons used densities closest to field densities (as indicated within studies) and studies providing no comparisons with natural field densities were excluded. Only those studies lasting for a generation of herbivores, or at least four weeks exposure, were included and those examining herbivore effects on plants for a few days or a week in the laboratory were also not included. End of growing season data was used if possible and sometimes this occurred weeks after herbivores died or were removed. Studies had to provide simultaneous data on treatments and controls, and this precluded the use of some data for biological control of weeds which was gathered without controls over longer time periods. In total, 44 published studies involving biocontrol agents and 51 involving non-biocontrol insects met these criteria for synthesis (see Supplementary Tables S1 and S2). Biocontrol studies were further divided into pre-release studies performed in quarantine or in cages in the agent's native range, or post-release studies following the release of biocontrol agents in their native range.

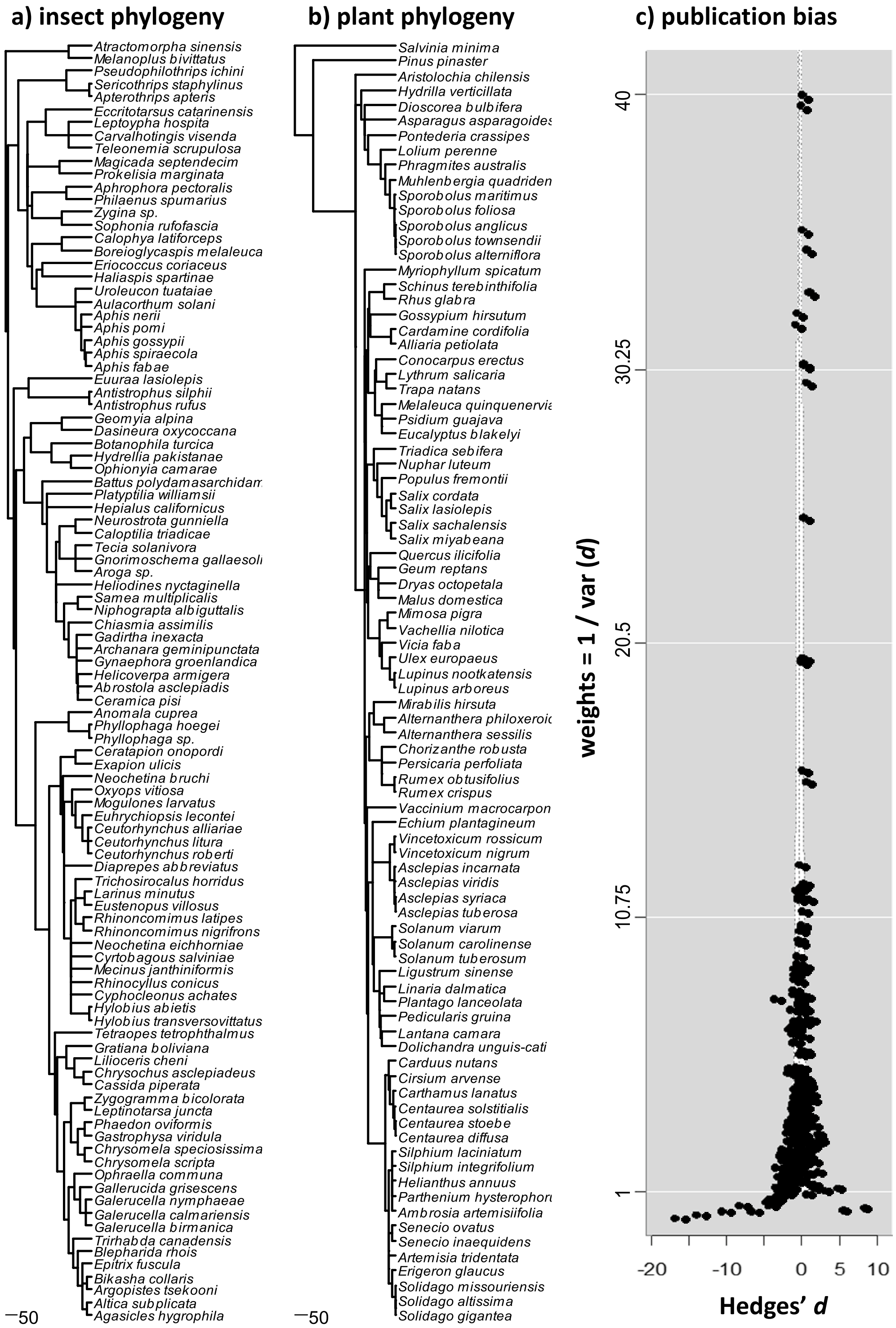
We primarily quantified study outcomes as herbivory (treatment, T) *versus* no-herbivory (control, C) effects on various plant morphometrics including whole individuals, flowers, fruits, seeds, stems (stem/shoot/branch), leaves (leaf/rosette), or roots (root/tiller/tuber). Measured variables on plants included absolute biomass, number, length (length/height/diameter), area or percent change of herbivory on plant morphometrics. Plant life form was categorized as either herb, shrub, tree, vine, and grass (all perennial), and studies were also classified as either aquatic or terrestrial ecosystems. Insects were subdivided into taxonomic orders (Coleoptera, Hemiptera, Lepidoptera, Orthoptera, Diptera, Hymenoptera, and Thysanoptera), feeding guilds (leaf or root chewer, flower or seed feeder, stem or root borer, leaf galler, leaf miner, and sap sucker), insect feeding location (above or below ground) and plant ecosystem (terrestrial or aquatic). Finally, experimental duration and latitude of experimental location was also extracted from each study.

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. These criteria excluded some early studies which only reported means (e.g., McEvoy et al. 1993). When these study measures were only available in figures, the juicr package in R was used to extract numerical values (v. 0.1; Lajeunesse 2021). These study parameters were used to compute the standardized mean difference between (T) treatment and (C) control groups, also known as the Hedges' d effect size metric (Hedges 1981; Lajeunesse 2013). Additional information about how effect sizes were calculated is found in the Supplementary Information S3.

Some weeds were often the subject of multiple studies using different herbivore species, or the same species of herbivores in different continents or different parts of the same country. When multiple studies used the same species of herbivore attacking the same species of plant in the same location, we used only the most comprehensive study to compute effect sizes. However, if authors used the same species, but measured different things in different studies such as leaf area, leaf weight, and root weight in one study and seed production, seed weight, and seed germination in another, then these studies both had effect sizes computed.

Biocontrol and non-biocontrol studies grouped together

In total, we had 153 effect sizes across 44 studies for biocontrol studies and 187 effect sizes across 51 studies for non-biocontrol insects (Supplementary Tables S1-S3). We conducted a phylogenetic mixed-effect meta-analysis using the metafor package in R (v. 4.0-0; Viechtbauer 2010) for the complete data set grouped together and for biocontrol and non-biocontrol insects grouped separately. We also noted whether biocontrol studies were conducted pre-release or post-release. For the complete data set all meta-analyses included the following four random-effects components: the between-study variance (τ^2; as typical for meta-analysis), the variance modelling overrepresentation of multiple effect sizes within studies (γ^2; 94 levels), the unstructured covariance of (I)nsect phylogeny (ρ_{I}^2; 100 levels/species), and the


a) insect phylogeny
Atractomorpha sinensis
Melanoplus bivittatus
Pseudophilothrips ichini
Sericothrips staphylinus
Apterothrips apteris
Eccritotarsus catarinensis
Leptoypha hospita
Carvalhotingis visenda
Teleonemia scrupulosa
Magicada septendecim
Prokelisia marginata
Aphrophora pectoralis
Philaenus spumarius
Zygina sp.
Sophonia rufofascia
Calophya latiforceps
Boreioglycaspis melaleuca
Eriococcus coriaceus
Haliaspis spartinae
Uroleucon tuataiae
Aulacorthum solani
Aphis nerii
Aphis pomi
Aphis gossypii
Aphis spiraecola
Aphis fabae
Euuraa lasiolepis
Antistrophus silphii
Antistrophus rufus
Geomyia alpina
Dasineura oxycoccana
Botanophila turcica
Hydrellia pakistanae
Ophionyia camarae
Battus polydamasarchidam
Platyptilia williamsii
Hepialus californicus
Neurostrota gunniella
Caloptilia triadicae
Tecia solanivora
Gnorimoschema gallaesoli
Aroga sp.
Heliodines nyctaginella
Samea multiplicalis
Niphograpta albiguttalis
Chiasmia assimilis
Gadirtha inexacta
Archanara geminipunctata
Gynaephora groenlandica
Helicoverpa armigera
Abrostola asclepiadis
Ceramica pisi
Anomala cuprea
Phyllophaga hoegei
Phyllophaga sp.
Ceratapion onopordi
Exapion ulicis
Neochetina bruchi
Oxyops vitiosa
Mogulones larvatus
Euhrychiopsis lecontei
Ceutorhynchus alliariae
Ceutorhynchus litura
Ceutorhynchus roberti
Diaprepes abbreviatus
Trichosirocalus horridus
Larinus minutus
Eustenopus villosus
Rhinoncomimus latipes
Rhinoncomimus nigrifrons
Neochetina eichhorniae
Cyrtobagous salviniae
Mecinus janthiniformis
Rhinocyllus conicus
Cyphocleonus achates
Hylobius abietis
Hylobius transversovittatus
Tetraopes tetrophthalmus
Gratiana boliviana
Lilioceris cheni
Chrysochus asclepiadeus
Cassida piperata
Zygogramma bicolorata
Leptinotarsa juncta
Phaedon oviformis
Gastrophysa viridula
Chrysomela speciosissima
Chrysomela scripta
Ophraella communa
Gallerucida grisescens
Galerucella nymphaeae
Galerucella calmariensis
Galerucella birmanica
Trirhabda canadensis
Blepharida rhois
Epitrix fuscula
Bikasha collaris
Argopistes tsekooni
Altica subplicata
Agasicles hygrophila
50
b) plant phylogeny
Salvinia minima
Pinus pinaster
Aristolochia chilensis
Hydrilla verticillata
Dioscorea bulbifera
Asparagus asparagoide
Pontederia crassipes
Lolium perenne
Phragmites australis
Muhlenbergia quadriden
Sporobolus maritimus
Sporobolus foliosa
Sporobolus anglicus
Sporobolus townsendii
Sporobolus alterniflora
Myriophyllum spicatum
Schinus terebinthifolia
Rhus glabra
Gossypium hirsutum
Cardamine cordifolia
Alliaria petiolata
Conocarpus erectus
Lythrum salicaria
Trapa natans
Melaleuca quinquenervi
Psidium guajava
Eucalyptus blakelyi
Triadica sebifera
Nuphar luteum
Populus fremontii
Salix cordata
Salix lasiolepis
Salix sachalensis
Salix miyabeana
Quercus ilicifolia
Geum reptans
Dryas octopetala
Malus domestica
Mimosa pigra
Vachellia nilotica
Vicia faba
Ulex europaeus
Lupinus nootkatensis
Lupinus arboreus
Mirabilis hirsuta
Alternanthera philoxeroi
Alternanthera sessilis
Chorizanthe robusta
Persicaria perfoliata
Rumex obtusifolius
Rumex crispus
Vaccinium macrocarpon
Echium plantagineum
Vincetoxicum rossicum
Vincetoxicum nigrum
Asclepias incarnata
Asclepias viridis
Asclepias syriaca
Asclepias tuberosa
Solanum viarum
Solanum carolinense
Solanum tuberosum
Ligustrum sinense
Linaria dalmatica
Plantago lanceolata
Pedicularis gruina
Lantana camara
Dolichandra unguis-cati
Carduus nutans
Cirsium arvense
Carthamus lanatus
Centaurea solstitialis
Centaurea stoebe
Centaurea diffusa
Silphium laciniatum
Silphium integrifolium
Helianthus annuus
Parthenium hysterophor
Ambrosia artemisiifolia
Senecio ovatus
Senecio inaequidens
Artemisia tridentata
Erigeron glaucus
Solidago missouriensis
Solidago altissima
Solidago gigantea
50
c) publication bias
weights = 1 / var (d)
40
30.25
20.5
10.75
1
-20
-10
0
5
10
Hedges' d

◂**Fig. 1** The effect sizes and phylogenies of insects and plants used in mixed-effect meta-analyses. **a** Hypothesized ultrametric phylogenetic tree of 100 insect species used in a phylogenetic meta-analysis to model unexplained phylogenetic heterogeneity among study outcomes (ρ_{I}^2). **b** The phylogenetic tree for 86 plant species (ρ_{P}^2). Topology and branch-length distances of phylogenetic trees are primarily based on TimeTree (Hedges and Kumar 2009; also see the Materials and Methods section), and branch-length distances here are in millions of years. **c** Visualization of potential publication bias using a funnel plot of Hedges' *d* effect sizes ($k = 340$) and their inverse variances (meta-analysis weights). Funnel symmetry, with similar tails on funnel shape, would indicate little systematic heterogeneity due to publication bias (e.g., positive, null, and negative study outcomes are equally represented in the data)

unstructured covariance of (P)lant phylogeny (ρ_{P}^2; 86 levels/species). In matrix notation, this model is:

$$\boldsymbol{d} = \mathbf{W}\boldsymbol{\beta} + \boldsymbol{\varepsilon} + \rho_{\mathrm{I}}^2\mathbf{C}_{\mathrm{I}}\mathbf{J}_{\mathrm{I}} + \rho_{\mathrm{P}}^2\mathbf{C}_{\mathrm{P}}\mathbf{J}_{\mathrm{P}} + \gamma^2 + \tau^2,$$

where $\boldsymbol{d}$ is a column vector of Hedges' d effect sizes ($k = 340$), **W** is the regression design matrix of $f + 1$ (f is the number of moderators + intercept) size, and **β** is the column vector of $f + 1$ regression coefficients. The weighting of each effect sizes via *var*(*d*) is defined by the diagonal variance–covariance matrix **ε**, and finally **C** is the phylogenetic correlation matrix expanded by **J**, the indicator matrix linking multiple effect sizes to single species in **C**. The ultrametric composite insect phylogeny of 47 biocontrol species and 55 non-biocontrol species (Fig. 1a) used to define $\mathbf{C}_{\mathrm{I}}$ was constructed using Timetree (visited June 10, 2023; Hedges and Kumar 2009; see NEWICK phylogeny in Supplementary Information S1). Pairwise relationships among Lepidoptera were further resolved using Kawahara & Breinholt (2014), thrips with Buckman et al. (2013), and beetles with Zhang et al. (2022). The ultrametric composite plant phylogeny of 86 species (Fig. 1b) used to define $\mathbf{C}_{\mathrm{P}}$ was constructed using Timetree (visited June 10, 2023; Hedges and Kumar 2009; Supplementary Information S2). The phylogenetic relationships among the *Sporobolus* were resolved using Peterson et al. (2014) and *Asclepias* with Fishbein et al. (2018). The branch-length distances used to define **C** assumed a Brownian motion model of phenotypic evolution (Rohlf 2001) and was constructed using the vcv() function of the ape package in R (v. 5.6-2; Paradis et al. 2004). The four random-effect components (τ^2, γ^2, ρ_{I}^2, ρ_{P}^2) were estimated via residual maximum likelihood (REML) using the nlminb optimizer. Pooled effects were considered non-zero if 95% confidence intervals did not overlap zero, fixed-effect within-group homogeneity (H) tests were assessed using Q_{df}^{H} with a df of k–1, differences (B) between m number of groups within categorical moderators were tested using Q_{df}^{B} omnibus tests with df = m–1 (both Q_{df}^{H} and Q_{df}^{B} are ANOVA-style χ^2 tests following Hedges and Olkin 1985), and the significance of regression coefficients (i.e., non-zero tests) as well as contrasts between two groups were evaluated using z-tests. Likelihood ratio tests based on Wald-type χ^2 were used to test the significance of multiple (fixed-effect) moderators and their interaction. Finally, the metafor's regtest() function was used to implement Egger's test for publication bias (Egger et al. 1997). Figure 1c is called a funnel plot and is a way to visualize potential issues with publication bias among the effect sizes used in our synthesis. If the funnel is unbalanced (e.g., effect sizes are not symmetrically distributed on both sides of the funnel), then this may indicate issues with publication trends that may impact our overall synthesis. Along with Egger's test, the funnel plot is useful to diagnose the extent of potential publication bias. Here, the funnel plot does not show strong asymmetry. Further, although Egger's test found bias in terms of few positive effects of herbivory on plants ($z = -17.25$, $p < 0.001$, slope = 0.277, 95% CI [0.194, 0.360]; see funnel plot symmetry in Fig. 1c), the composition of the effect sizes violated one of the four assumptions of the test (i.e., significant between-study heterogeneity: $Q^{\mathrm{H}} = 1461.75$, df = 339, $p < 0.001$; see Ioannidis and Trikalinos 2007). Further, a heavy composition of negative study outcomes is also expected given that biocontrol experiments aim to maximally manipulate effects of herbivory on target plants by selecting insects with the greatest potential to achieve this goal.

Biocontrol and non-biocontrol studies grouped separately

We used similar analyses to examine both biocontrol and non-biocontrol insect groups separately. These analyses were again phylogenetic mixed-effect meta-analysis but here used only the between study-variance (τ^2), the variance modelling overrepresentation

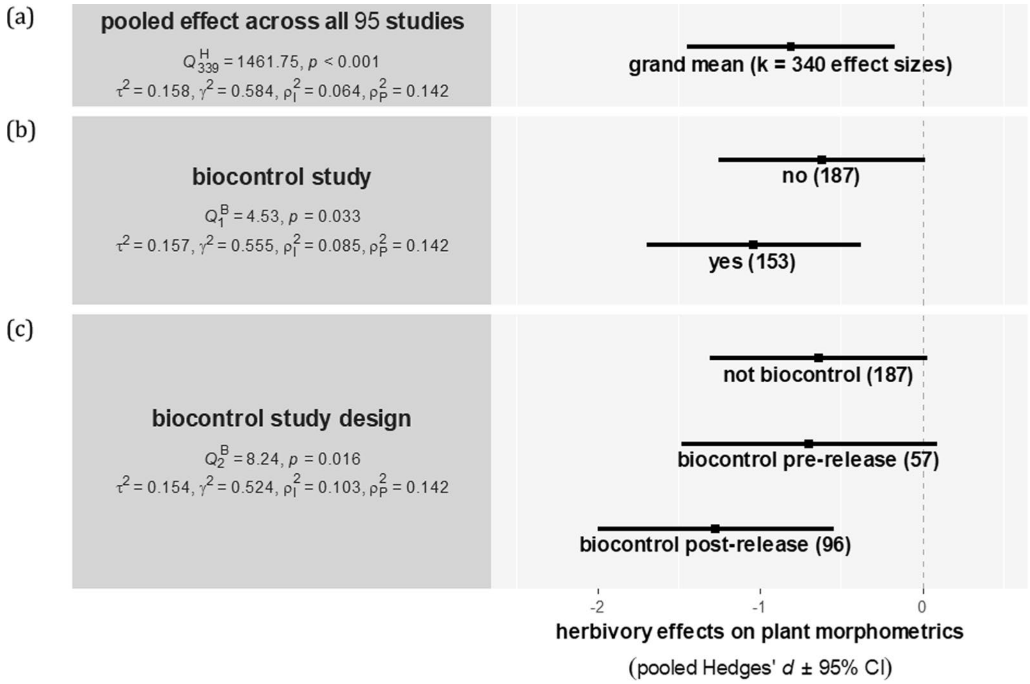


Fig. 2 Forest plots of effects of insect herbivores on plant morphometrics using three separate phylogenetic mixed-effect meta-analyses across 95 published studies (Supplementary Tables S1 and S2). Pooled effects (squares), their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group in brackets (*k*) are parsed among three effect groups: **a** the grand mean effect across all 95 published studies, **b** the pooled effects among biocontrol studies versus studies of native insects on native plants (non-biocontrol), and **c** the pooled effects of non-biocontrol studies *versus* biocontrol studies parsed as either biocontrol pre-release or post-release. Random effects included in this meta-analysis included the between study-variance (τ^2), the variance modelling overrepresentation of multiple effect sizes per study (γ^2 with 94 levels), insect phylogeny (ρ^2_{I} with 100 levels; see Fig. 1a), and plant phylogeny (ρ^2_{P} with 86 levels; see Fig. 1b). Finally, $Q^{\mathrm{H}}_{\mathrm{df}}$ is the fixed-effect (H)omogeneity test across all effect sizes, $Q^{\mathrm{B}}_{\mathrm{df}}$ are the omnibus tests for differences (B)etween groups of pooled effects, and df is the degrees of freedom of these Q^B tests. When 95% CI overlap with zero, this indicates no evidence for an effect of herbivory on plant morphometrics, while pooled effects less than zero indicates negative effects on plants (e.g., more leaf damage than compared to the control group without herbivory). Non-zero values for τ^2, γ^2, ρ^2_{I}, and ρ^2_{P} indicate the amount of variability associated with each random-effects across the pooled Hedges' *d* effect sizes

of multiple effect sizes within studies (γ^2), and the unstructured covariance of (I)nsect phylogeny (ρ^2_{I}), because in analyzing these data sets separately we were aware that biocontrol practitioners can only select their target insects and not their target plants. In matrix notation, this model is:

$$\boldsymbol{d} = \mathbf{W}\boldsymbol{\beta} + \boldsymbol{\varepsilon} + \rho^2_{\mathrm{I}}\mathbf{C}_{\mathrm{I}}\mathbf{J}_{\mathrm{I}} + \gamma^2 + \tau^2.$$

This model was implemented again using the metafor package in R with all the same parameterization and significance testing as the complete model described earlier.

Results

Pooling outcomes across all 95 studies, and using phylogenetic meta-analysis, there was a significant effect of insect herbivores on plant morphometrics (non-zero *z*-test = –2.5, $p = 0.0124$, $k = 340$; Fig. 2a). When parsing studies among those with biocontrol insects and non-biocontrol insects there was significant effects on plant morphometrics among biocontrol studies (non-zero *z*-test = –3.1, $p = 0.0019$, $k = 153$; Fig. 2b), but not among non-biocontrol insects (non-zero *z*-test = –1.92, $p = 0.0549$, $k = 187$; Fig. 2b).

Insect herbivores used in biocontrol studies showed significantly greater effect on plant morphometrics than insects in non-biocontrol studies (pairwise contrast z-test = –2.13, $p = 0.0333$; Fig. 2b). However, while biocontrol post-release studies also showed a significantly greater effect of herbivores than native studies (non-zero z-test = –3.44, $p = 0.0006$, $k = 96$; Fig. 2b), pre-release studies did not show a difference compared to native studies (non-zero z-test = –1.74, $p = 0.0816$, $k = 57$; Fig. 2c). There were also no differences between pre- and post-release studies (pairwise contrast z-test = –1.887, $p = 0.0591$; Fig. 2c).

Biocontrol and non-biocontrol studies grouped together

Plant traits

Plant growth form significantly moderated the strength of effects of insect herbivores ($\chi^2 = 8.29$, df = 1, $p = 0.004$; Fig. 3b), with grasses, shrubs and trees being impacted more than vines and herbs. Biocontrol status was also significant ($\chi^2 = 16.93$, df = 1, $p = 0.002$) with biocontrol insects exhibiting significantly greater effects across most plant growth forms when compared to the non-biocontrol counterparts (Fig. 3b). However, there was an interaction of plant growth form and biocontrol status since non-biocontrol studies involving grasses and shrubs also showed strong effects of insect herbivores ($\chi^2 = 13.81$, df = 1, $p = 0.0079$).

There was a significant effect of plant organ on herbivory ($\chi^2 = 6.99$, df = 1, $p = 0.0082$; Fig. 3c), with roots and fruits suffering the greatest amounts of herbivory. Biocontrol status was also important here since seven of the eight strongest effects among our 14 categories (plant organ by biocontrol status) were exhibited by biocontrol agents ($\chi^2 = 25.91$, df = 1, $p = 0.0002$; Fig. 3c). There was a significant interaction of plant organ and biocontrol status since the effects of non-biocontrol agents on roots were also quite strong ($\chi^2 = 12.75$, df = 1, $p = 0.0471$; Fig. 3c).

Above ground herbivory had significantly stronger effects than below ground herbivory ($\chi^2 = 9.04$, df = 1, $p = 0.0026$; Fig. 4b), presumably because the strong effects of root feeders did not translate into strong above ground effects. Biocontrol status was also significant ($\chi^2 = 42.46$, df = 1, $p < 0.001$; Fig. 4b) with most biocontrol insects having strong effects. There was also a significant interaction between insect feeding location and biocontrol status since below ground biocontrol agents did not have as strong effects as non-biocontrol insects ($\chi^2 = 23.08$, df = 1, $p = 0.0008$; Fig. 4b).

There was a significant effect of plant ecosystem on strength of herbivory since herbivory in terrestrial systems was significantly greater than in aquatic systems ($\chi^2 = 8.54$, df = 1, $p = 0.0065$; Fig. 4c). Once again, biocontrol status was important with biocontrol insects having significantly stronger effects than non-biocontrol insects ($\chi^2 = 6.41$, df = 1, $p = 0.0113$; Fig. 4c). There was no significant interaction between plant ecosystem and biocontrol status ($\chi^2 = 3.64$, df = 1, $p = 0.0564$; Fig. 4c).

The duration of the study had no effect for either biocontrol or non-biocontrol insects (biocontrol agents,slope = –0.1112, slope z-test = –0.811, $p = 0.4174$, $k = 153$; non-biocontrol agents, slope = –0.1701, slope z-test = –1.28, $p = 0.1997$, $k = 187$; Fig. 5a and b). Likewise, latitude of study location had no effect on strength of herbivory for either biocontrol insects or non-biocontrol insects (biocontrol agents, slope = –0.0207, slope z-test = –1.658, $p = 0.0973$, $k = 153$; non-biocontrol agents, slope = –0.0047, slope z-test = -0.2993, $p = 0.7647$, $k = 187$; Fig. 5c and d).

Insect traits

There were significant differences among insect orders in strength of herbivory ($\chi^2 = 7.7$, df = 1, $p = 0.0055$; Fig. 6b) with Hemiptera and Coleoptera showing strong effects and Diptera weak effects. The low numbers of studies involving Thysanoptera ($k = 4$), Hymenoptera ($k = 5$) and Orthoptera ($k = 4$) means that results for these orders should be viewed with caution. Biocontrol status was also significant ($\chi^2 = 23.2$, df = 1, $p = 0.0007$; Fig. 6b) with biocontrol insects having stronger effects than their non-biocontrol counterparts for all of Lepidoptera, Hemiptera, Coleoptera, and Diptera. Once more there was a significant interaction effect ($\chi^2 = 19.39$, df = 1, $p = 0.0007$; Fig. 6b) with lepidopteran biocontrol agents having much stronger effects than non-biocontrol lepidopterans, while the differences between biocontrol and non-biocontrol insects for other orders was smaller.

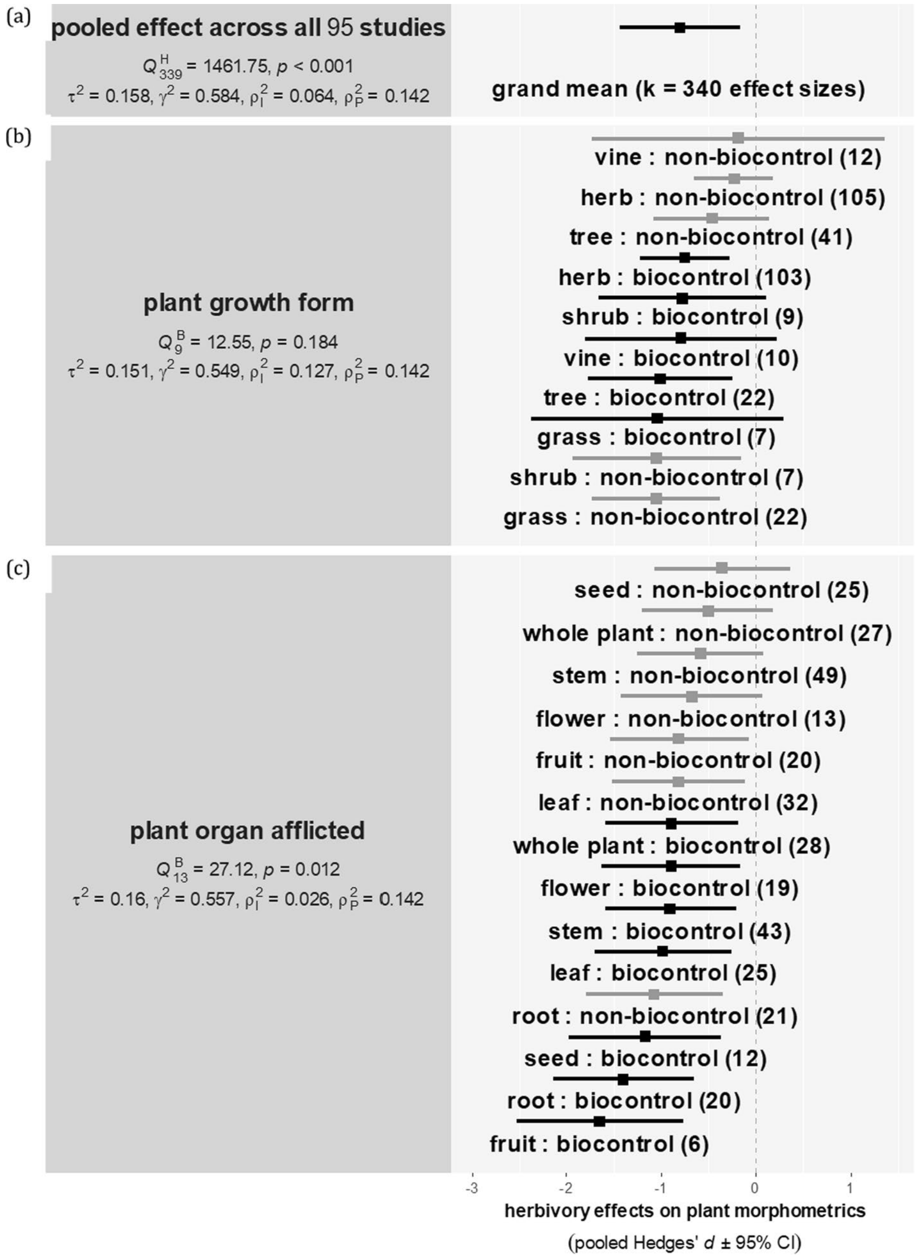


Fig. 3 Forest plots of effects of insect herbivores on plant morphometrics using three separate phylogenetic mixed-effect meta-analyses across 95 published studies (Supplementary Tables S1 and S2). Pooled effects (squares), their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group in brackets (*k*) are parsed among three effect groups: **a** the grand mean effect across all 95 published studies, **b** the pooled effects among biocontrol studies *versus* studies of native insects on native plants (non-biocontrol) passed among plant growth forms, and **c** the pooled effects of non-biocontrol studies *versus* biocontrol studies parsed among plant organs afflicted. Random effects included in this meta-analysis included the between study-variance (τ^2), the variance modelling overrepresentation of multiple effect sizes per study (γ^2 with 94 levels), insect phylogeny (ρ^2_I with 100 levels; see Fig. 1a), and plant phylogeny (ρ^2_P with 86 levels; see Fig. 1b). Finally, Q^{H}_{df} is the fixed-effect (H)omogeneity test across all effect sizes, Q^{B}_{df} are the omnibus tests for differences (B)etween groups of pooled effects, and df is the degrees of freedom of these Q^B tests. When 95% CI overlap with zero, this indicates no evidence for an effect of herbivory on plant morphometrics, while pooled effects less than zero indicates negative effects on plants (e.g., more leaf damage than compared to the control group without herbivory). Non-zero values for τ^2, γ^2, ρ^2_I, and ρ^2_P indicate the amount of variability associated with each random-effects across the pooled Hedges' *d* effect sizes

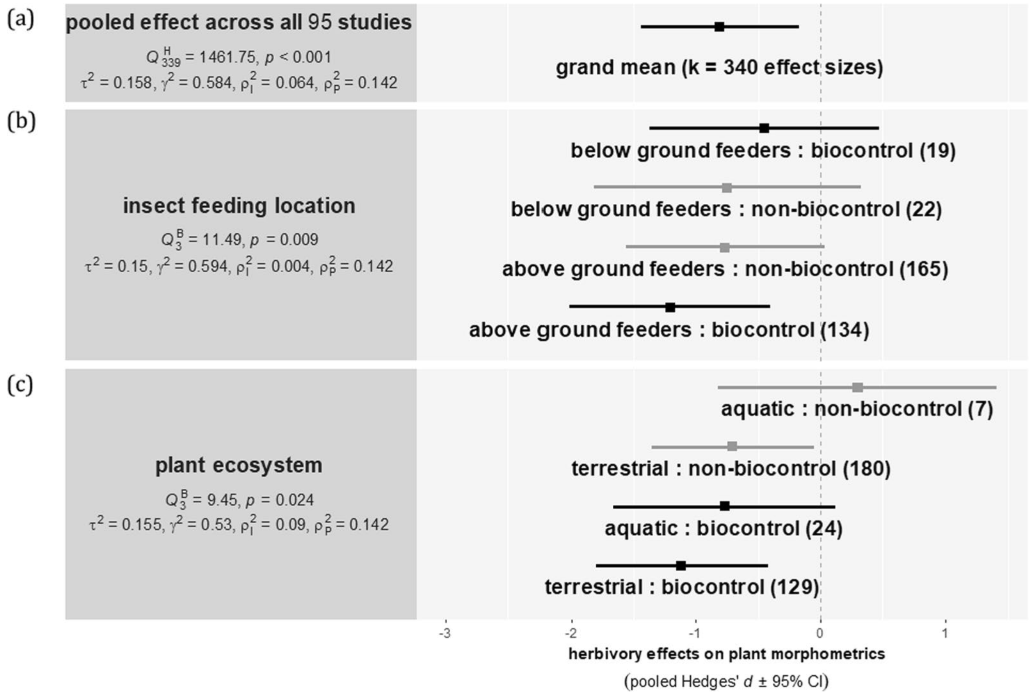
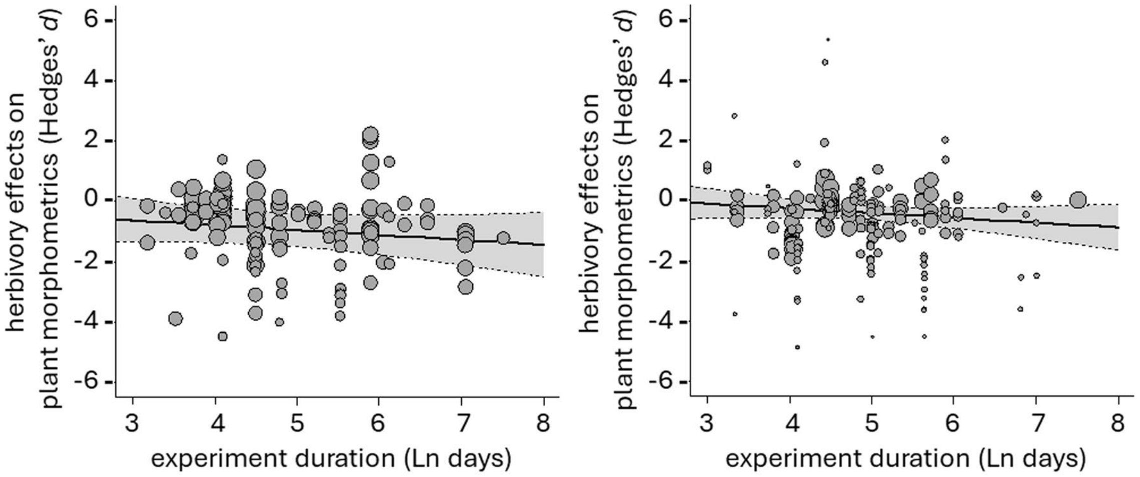


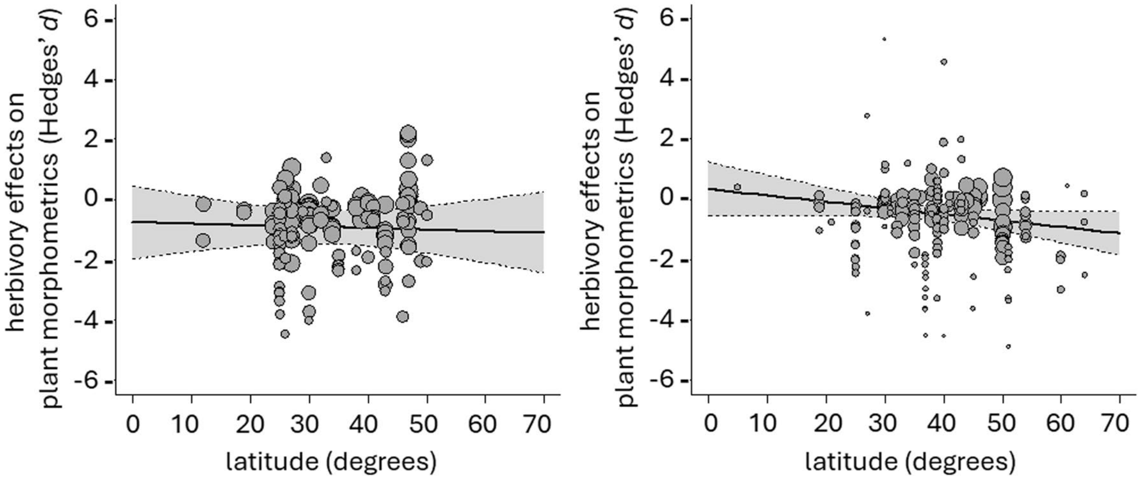
Fig. 4 Forest plots of effects of insect herbivores on plant morphometrics using three separate phylogenetic mixed-effect meta-analyses across 95 published studies (Supplementary Tables S1 and S2). Pooled effects (squares), their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group in brackets (k) are parsed among three effect groups: **a** the grand mean effect across all 95 published studies, **b** the pooled effects among biocontrol studies *versus* studies of native insects on native plants (non-biocontrol) parsed among insect feeding locations, and **c** the pooled effects of non-biocontrol studies *versus* biocontrol studies parsed among plant ecosystems. Random effects included in this meta-analysis included the between study-variance (τ^2), the variance modelling overrepresentation of multiple effect sizes per study (γ^2 with 94 levels), insect phylogeny (ρ_{I}^2 with 100 levels; see Fig. 1a), and plant phylogeny (ρ_{P}^2 with 86 levels; see Fig. 1b). Finally, $Q_{\mathrm{df}}^{\mathrm{H}}$ is the fixed-effect (H)omogeneity test across all effect sizes, $Q_{\mathrm{df}}^{\mathrm{B}}$ are the omnibus tests for differences (B)etween groups of pooled effects, and df is the degrees of freedom of these Q^B tests. When 95% CI overlap with zero, this indicates no evidence for an effect of herbivory on plant morphometrics, while pooled effects less than zero indicates negative effects on plants (e.g., more leaf damage than compared to the control group without herbivory). Non-zero values for τ^2, γ^2, ρ_{I}^2, and ρ_{P}^2 indicate the amount of variability associated with each random-effects across the pooled Hedges' *d* effect sizes

The effects of insect feeding guild were also significant (χ^2 = 9.05, df = 1, p = 0.0026; Fig. 6c) with leaf chewers, sap suckers, stem borers, and stem gallers having relatively strong effects and seed feeders and flower feeders relatively weak effects. Biocontrol status was again significant (χ^2 = 42.46, df = 1, p < 0.0001; Fig. 6c) with the effects of biocontrol agents *versus* non-biocontrol agents stronger for leaf chewers, sap suckers, stem borers, root chewers, root borers, flower feeders, and seed feeders. For some feeding guilds such as stem gallers, leaf miners, leaf gallers and stem chewers, there was insufficient data to compare biocontrol *versus* non-control insects. There was also a significant interaction between feeding guilds and biocontrol status (χ^2 = 23.08, df = 1, p = 0.0008; Fig. 6c) with the differences in herbivory between biocontrol *versus* non-biocontrol insects being greater for some guilds such as root chewers and root borers, and much less for other guilds such as sap suckers, flower feeders, and seed feeders.



(a) biocontrol studies

(b) non-biocontrol studies



(c) biocontrol studies

(d) non-biocontrol studies

Fig. 5 Bubble plot of effects of insect herbivores on plant morphometrics using two separate phylogenetic mixed-effect meta-analyses: **a** and **b** meta-regression of herbivores effects predicted by study duration (ln days), and **c** and **d** predicted by latitude (degrees), both presented separately for biocontrol and non-biocontrol studies. Presented is the phylogenetic mixed-effect meta-regression slope (full line) with 95% confidence intervals (dashed lines) and bubbles sizes are based on the relative model weights (inverse variance) of each Hedges' *d* effect size to emphasize that effect sizes are not weighted equally in each meta-regression (see the "Materials and methods" section)

Biocontrol and non-biocontrol studies grouped separately

Non-biocontrol studies

Across all non-biocontrol studies ($k=187$) there was no significant effect of plant growth form on effects of herbivores ($Q^B = 9.17$, df = 4, $p=0.057$) but there was a significant effect of plant organ ($Q^B = 13.83$, df = 6, $p=0.032$) with roots, leaves and fruit more affected than seeds or stems. There were no significant effects of experimental duration (slope z-test = –0.5814, $p=0.561$) or latitude (slope z-test = –1.8492, $p=0.0644$) on strength of herbivory by non-biocontrol agents. There were no significant effects of insect order or effects of insect feeding guild on strength of herbivory (order: $Q^B = 7.42$, df = 6, $p=0.284$; feeding guild: $Q^B = 5.51$, df = 8, $p=0.702$). There was no effect of insect feeding location (Q^B = 0.032, df = 1, p = 0.858), but there was a significant effect of terrestrial versus aquatic ecosystem on herbivory (Q^B = 4.98, df = 1, p = 0.0256) with terrestrial plants damaged more than aquatic plants, thought the sample size for aquatic plants was low and this result should be treated with caution.

Biocontrol studies

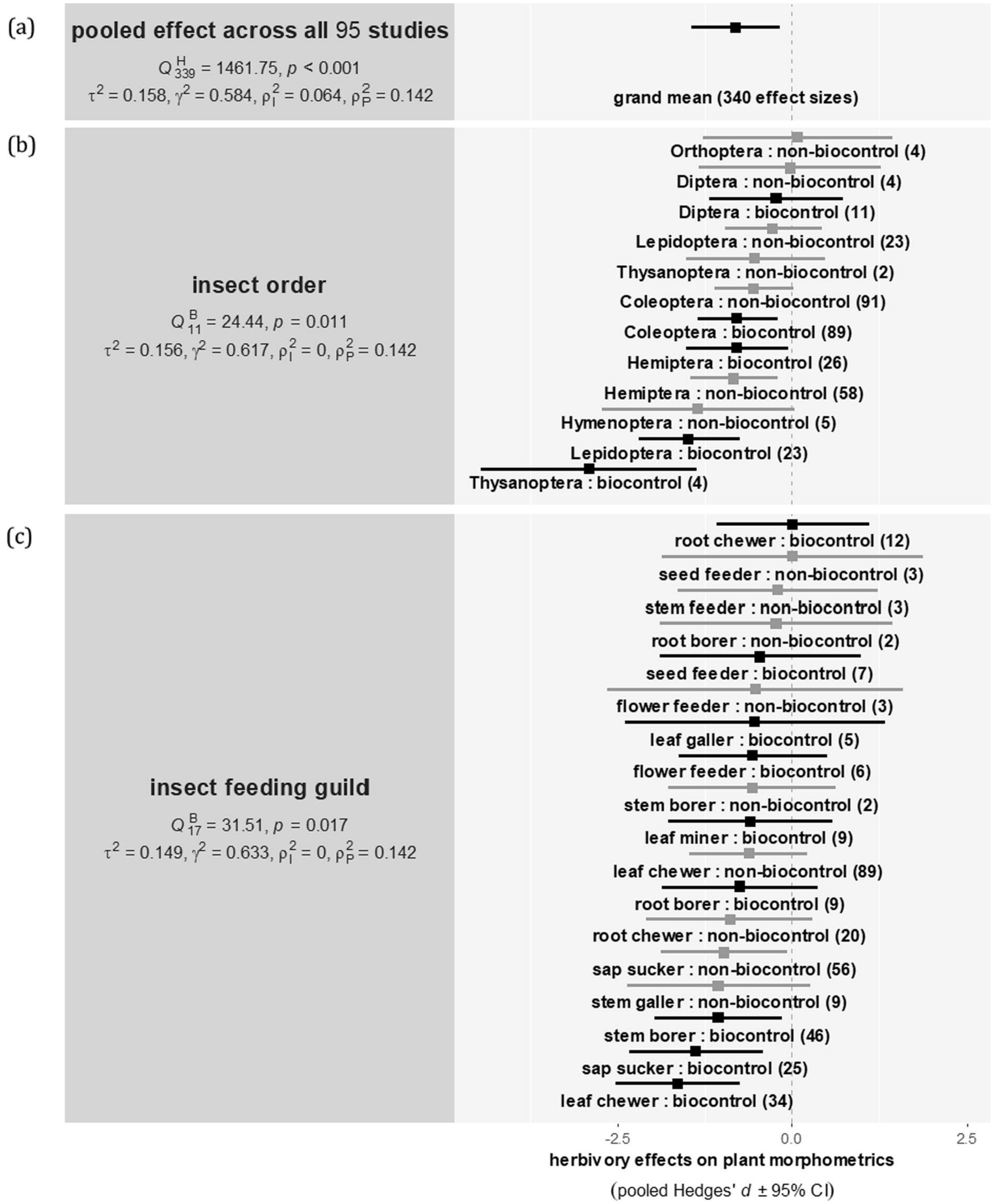
Across all biocontrol studies (k = 153) there were no significant effects of plant growth form (Q^B = 0.12, df = 4, p = 0.998) or plant organ (Q^B = 7.81, df = 6, p = 0.252) on the strength of effects of biocontrol agents. There were also no significant effects of experimental duration (slope z-test = –1.12, p = 0.2623) or latitude (slope z-test = –0.21, p = 0.8394) on strength of herbivory by biocontrol agents. Although there was no significant effect of insect order on strength of herbivory (Q^B = 7.24, df = 4, p = 0.123), there was a significant effect of insect feeding guild (Q^B = 18.86, df = 9, p = 0.0156) with leaf chewers, sap suckers and stem borers having stronger effects and root chewers having weaker effects. There was no significant effect of insect feeding location (Q^B = 3.487, df = 1, p = 0.0619) with above ground feeders having similar effects to below ground feeders. Finally, there was no significant effect of terrestrial versus aquatic ecosystem on herbivory (Q^B = 0.53, df = 1, p = 0.4665).

Discussion

Our synthesis revealed that insect herbivores had a significant effect on plant morphometrics (Fig. 2). This reinforces results from other meta-analyses, which also found significant effects of insect herbivores on their host plants (Bigger and Marvier 1998; Hawkes and Sullivan 2001; Morris et al. 2007; Zvereva et al. 2010; Katz 2016; Jia et al. 2018) including those that have examined the effectiveness of classical biocontrol on invasive plants (Stiling and Cornelissen 2005; Clewley et al. 2012).

Biocontrol insects had significantly stronger effects than non-biocontrol insects on plants. This supports the idea that biocontrol is not a natural phenomenon since released weed control agents have stronger effects than the average native insect herbivore on its native plant (Hawkins et al. 1999). Marone and Crone (2006) also documented stronger effects of biocontrol insects than native invertebrate consumers on native plants, as measured by their impacts on plant abundance. However, pre-release studies of biocontrol agents have no stronger effects on plants than non-biocontrol studies. Presumably, pre-release studies help promote the release of “better than average” biocontrol agents. This supports the idea that biocontrol is not a given process but, where it succeeds, is more likely due to hard work in pre-release studies and candidate selection before biocontrol is even attempted. An alternative is that biocontrol agents may no longer be constrained by their own natural enemies, which are present only in their native range. Studies of the same plant-herbivore combinations in their native and introduced ranges could shed light on this possibility, but our database contains no such studies. However, pre-release biocontrol agents also suffer no attack from their co-evolved enemies yet had similar effects to native herbivores on native plants, which does not support lack of natural enemies as a mechanism for stronger effects of biocontrol agents. Also, biocontrol agents in their introduced ranges may suffer attack from generalist natural enemies with which they did not co-evolve.

There is at least one caveat to address. Studies of native insects on native plants can sometimes show compensatory herbivory, whereas for biocontrol insects this is less likely. However, we found only three instances of compensatory herbivory for non-biocontrol studies (Nowaza and Ohgushi 2002; Poveda et al. 2010; Long and Porturas 2014). Furthermore, surprisingly, some biocontrol studies showed greater plant growth with than without herbivores (e.g., Wheeler et al. 2017). There was no support for the idea that the magnitude of herbivore effect sizes for either biocontrol or non-biocontrol insects changed with latitude, supporting the conclusions of Jia et al. (2018) who found no effect of latitude, biome type, net productivity, mean annual temperature or rainfall on the strength of herbivores on plants using a meta-analysis of animal exclusions. We also found no evidence that studies of longer duration were more likely to show increased effect sizes of herbivores. The success of weed biocontrol has been linked to both plant and enemy traits (Stiling and Cornelissen 2005; Clewley et al. 2012; Paynter et al. 2012; Schwarzländer et al. 2018; Panta et al. 2024) and the effects of both traits are discussed below.


(a)
pooled effect across all 95 studies
$Q^{H}_{339} = 1461.75$, $p < 0.001$
$\tau^2 = 0.158$, $\gamma^2 = 0.584$, $\rho^2_I = 0.064$, $\rho^2_P = 0.142$
grand mean (340 effect sizes)
(b)
insect order
$Q^{B}_{11} = 24.44$, $p = 0.011$
$\tau^2 = 0.156$, $\gamma^2 = 0.617$, $\rho^2_I = 0$, $\rho^2_P = 0.142$
Orthoptera : non-biocontrol (4)
Diptera : non-biocontrol (4)
Diptera : biocontrol (11)
Lepidoptera : non-biocontrol (23)
Thysanoptera : non-biocontrol (2)
Coleoptera : non-biocontrol (91)
Coleoptera : biocontrol (89)
Hemiptera : biocontrol (26)
Hemiptera : non-biocontrol (58)
Hymenoptera : non-biocontrol (5)
Lepidoptera : biocontrol (23)
Thysanoptera : biocontrol (4)
(c)
insect feeding guild
$Q^{B}_{17} = 31.51$, $p = 0.017$
$\tau^2 = 0.149$, $\gamma^2 = 0.633$, $\rho^2_I = 0$, $\rho^2_P = 0.142$
root chewer : biocontrol (12)
seed feeder : non-biocontrol (3)
stem feeder : non-biocontrol (3)
root borer : non-biocontrol (2)
seed feeder : biocontrol (7)
flower feeder : non-biocontrol (3)
leaf galler : biocontrol (5)
flower feeder : biocontrol (6)
stem borer : non-biocontrol (2)
leaf miner : biocontrol (9)
leaf chewer : non-biocontrol (89)
root borer : biocontrol (9)
root chewer : non-biocontrol (20)
sap sucker : non-biocontrol (56)
stem galler : non-biocontrol (9)
stem borer : biocontrol (46)
sap sucker : biocontrol (25)
leaf chewer : biocontrol (34)
-2.5
0.0
2.5
herbivory effects on plant morphometrics
(pooled Hedges' d ± 95% CI)

◂**Fig. 6** Forest plots of effects of insect herbivores on plant morphometrics using three separate phylogenetic mixed-effect meta-analyses across 95 published studies (Supplementary Tables S1 and S2). Pooled effects (squares), their 95% confidence intervals (CI), and number of Hedges' *d* effect sizes pooled per group in brackets (*k*) are parsed among three effect groups: **a** the grand mean effect across all 95 published studies, **b** the pooled effects among biocontrol studies *versus* studies of native insects on native plants (non-biocontrol) parsed among insect orders, and **c** the pooled effects of non-biocontrol studies *versus* biocontrol studies parsed among insect feeding guilds. Random effects included in this meta-analysis included the between-study variance (τ^2), the variance modelling overrepresentation of multiple effect sizes per study (γ^2 with 94 levels), insect phylogeny (ρ_I^2 with 100 levels; see Fig. 1a), and plant phylogeny (ρ_P^2 with 86 levels; see Fig. 1b). Finally, Q_df^H is the fixed-effect (H)omogeneity test across all effect sizes, Q_df^B are the omnibus tests for differences (B)etween groups of pooled effects, and df is the degrees of freedom of these Q^B tests. When 95% CI overlap with zero, this indicates no evidence for an effect of herbivory on plant morphometrics, while pooled effects less than zero indicates negative effects on plants (e.g., more leaf damage than compared to the control group without herbivory). Non-zero values for τ^2, γ^2, ρ_I^2, and ρ_P^2 indicate the amount of variability associated with each random-effects across the pooled Hedges' *d* effect sizes

Plant traits

There was support for the idea that the effects of insect herbivores changed with plant growth form. Bigger and Marvier (1998) suggested that long-lived plants with large growth forms, such as trees, shrubs and vines could draw on large resources to resist the effects of herbivores. Our data suggests that while relatively short-lived species and small species, such as grasses, are subject to the strongest effects of herbivores, herbs, which also have short life spans, did not appear to be impacted as much. Trees were also strongly impacted. When non-biocontrol insects were analyzed separately, there was no significant effect of plant growth form on effect strength. For biocontrol agents analyzed alone, there was also no significant effect of plant growth form showing that biocontrol can be successful against any plant growth form.

The effects of insect herbivores varied with plant organ attacked, with roots and fruits subject to some of the strongest effects and seeds and flowers suffering weaker effects. However, these strong effects on roots did not translate into strong effects on the rest of the plant, since below-ground herbivores had weaker effects than above-ground herbivores. When non-biocontrol agents were analyzed alone, there was a significant effect of plant organ with roots, leaves and fruits suffering stronger effects from herbivores than seeds and stems. Once again, this suggests targeting certain areas of the plant for attack by biocontrol agents might yield more effective results than targeting other areas. However, when biocontrol agents were analyzed alone, there was no effect of plant organ suggesting that, in practice, biocontrol can be effective when targeting any part of the plant. Stiling and Cornelissen (2005) also showed significant effects of biocontrol agents on flower production, seed production, leaf number, plant height, plant biomass and root weight. Clewley et al. (2012) showed significant effects of biocontrol agents on plant size, plant mass, seed production, flower production and target diversity. Panta et al. (2024) suggested that agents feeding on vegetative plant tissues had the strongest impacts. However, a recent review on plant biocontrol in New Zealand suggested that the use of agents that attack plant reproductive parts are unlikely to be solely successful (Paynter 2024). Separate analyses on non-biocontrol insects suggested stronger effects in terrestrial ecosystems than in aquatic ones but for biocontrol agents there were no significant differences, again showing biocontrol can be effective in terrestrial and aquatic systems.

Enemy traits

Separate analyses for biocontrol insects and non-biocontrol insects had suggested no significant effect of insect order on strength of herbivory. However, in our combined analyses there was a significant effect of insect order on strength of herbivory. Schwarzländer et al. (2018) concluded from their analysis that "Coleoptera and Hemiptera appear to be the biological control agent taxa with the highest likelihood of success, in terms of establishment rate and in causing heavy impact." Clewley et al. (2012) found that, among beetles, weevils (Curculionidae) and leaf-beetles (Chrysomelidae) had strong effects, perhaps because they suffer less parasitism than other insect herbivore families (Goeden and Louda 1976; McFadyen and Spafford 2004) and/or because of the level of damage they inflict on their host plants (Crawley 1989b; Clewley et al. 2012). In addition, such external feeders maybe chosen for biocontrol since they are easier to rear than internal feeders. In our study, Hemiptera and Lepidoptera both had strong effects on their host plants as did Thysanoptera and Hymenoptera, but for the latter two orders, low sample size means caution is needed when quantifying their effects. Ignoring these taxa with small sample sizes, for biocontrol insects, lepidopterans and hemipterans had strong effects while for non-biocontrol insects, Hemiptera had the strongest effects.

Our analyses showed a significant effect of insect feeding guild on strength of herbivory on host plants, with leaf chewers, sap suckers, and stem borers having the strongest effects. Stiling and Cornelissen (2005) also showed strong effects of biocontrol folivores and sap feeders on leaf and stem numbers, plant biomass and flower production. In our study, for non-biocontrol insects, analyzed separately, insect feeding guild did not significantly effect degree of damage but, for biocontrol insects, damage levels were affected by insect feeding guild with leaf chewers, sap suckers and stem borers having strong effects and other guilds having weak effects. Panta et al. (2024) suggested that agents feeding externally have the greatest effects. In conclusion, we found that the effects of biocontrol and non-biocontrol insects on plants are strong and hold for most plant growth forms and against many different plant parts but the effects of biocontrol insects are significantly stronger than for non-biocontrol insects. The reasons for these effects are not entirely clear but apply for most plant growth forms or organs attacked, and for most insect orders or feeding guilds. In addition, non-biocontrol systems are not always an accurate signpost for biocontrol systems since results from non-biocontrol can suggest certain plant growth forms or plant organs are subject to more damage than others, or that certain insect orders or feeding guilds maybe the most successful. In actuality, biocontrol can be successful against most types of plants using most insect orders or feeding guilds.

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Author contributions PS: Conceptualization, methodology, data creation, data curation, analysis interpretation, writing-original draft, review, and editing. ML: Data creation, formal analysis, visualizations, analysis interpretation, writing-review, and editing.

Declarations

Competing 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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