Check for updates

Received: 21 March 2025 | Accepted: 31 July 2026

DOI: 10.1111/1365-2435.70443

Functional Ecology

RESEARCH ARTICLE

Invasive insects outperform their native counterparts

Hester Weaving[1] | Ingrid A. Minnaar[1] | Cang Hui[2,3] | Michael L. Logan[1,4] | Susana Clusella-Trullas[1]

[1]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

[2]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Stellenbosch, South Africa

[3]Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Cape Town, South Africa

[4]Department of Biology and Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Nevada, USA

Correspondence
Hester Weaving
Email: hesterweaving@gmail.com

Funding information
DSI-NRF Centre of Excellence for Invasion Biology; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: DBI-1402497; Natural Environment Research Council, Grant/Award Number: NE/V007548/1; National Research Foundation, Grant/Award Number: 89967; Innovation Doctoral Scholarship, NRF; National Research Foundation of South Africa (NRF)

Handling Editor: Julia Cooke

Abstract

1. Invasive alien species cause substantial ecological damage worldwide, driving biodiversity loss and negatively impacting human livelihoods. Although invasive insects have some of the most severe impacts, the traits associated with their invasiveness remain unclear.
2. We conducted a meta-analysis comparing phenotypic traits of matched, co-occurring invasive and native insect pairs (sympatric congeners or confamilials) in the invaded range. In total, we compared 922 invasive-native pairs using 1327 effect sizes from 182 studies. These pairs comprised 144 unique invasive insect species and 403 unique native species.
3. We found that invasive insects generally have greater fecundity, shorter development times, faster population growth rates and enhanced foraging and competitive capabilities compared with their native counterparts. However, some of these patterns changed after excluding the two most data-rich families (i.e. Coccinellidae and Formicidae), likely due to divergent evolutionary histories, life history strategies and selection pressures.
4. This study represents the most comprehensive systematic comparison of trait differences between co-occurring native and invasive insect species and highlights that a diverse array of traits can contribute to invasiveness. Moreover, our open-access database of insect trait data will facilitate further research into the causes and consequences of insect invasions.

KEYWORDS
alien insect, environmental change, exotic insect, functional traits, invasion pathways, life history, pests, risk assessment

1 | INTRODUCTION

Invasive alien species are among the top five drivers of biodiversity loss, disrupting ecosystem function and threatening human livelihoods through their impacts on agriculture and health (Jaureguiberry et al., 2022; Shackleton et al., 2019). Invasive insects are understudied relative to other taxonomic groups (Diniz-Filho et al., 2010), despite their extensive global diversity, including

Hester Weaving and Ingrid A. Minnaar are joint first authors.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2026 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

agricultural pests and disease vectors, the high and increasing number of invasions (Huang et al., 2011; Seebens et al., 2017), and the extensive ecological and economic damage they cause (Bradshaw et al., 2021; Cuthbert et al., 2022). Given the negative effects of alien invasive (hereafter, 'invasive') insect species, there is a strong impetus to predict future invasions, prevent the introduction of species likely to become invasive, and flag 'problematic' species among those already established for closer monitoring and management.

Several approaches have been developed to determine the invasiveness of plant and animal species and the likelihood of their establishment in new areas (Fournier et al., 2019; Gallien & Carboni, 2017). Many studies use climate niche modelling or environmental suitability models to predict potential range expansions (Fernandes et al., 2019; Liu et al., 2020), while other studies adopt trait-based approaches where phenotypic traits, such as life history, stress tolerance and niche breadth, are used as predictors of invasiveness (Divíšek et al., 2018; Mathakutha et al., 2019; Zhang et al., 2023). These characteristics can help invasive species overcome barriers during the invasion process, including transportation, introduction, establishment and spread (Blackburn et al., 2011; Renault et al., 2018; Theoharides & Dukes, 2007), and enhance their ability to outcompete native species that are ecologically equivalent (Minnaar et al., 2022; Raak-van den Berg et al., 2018). Examining these traits between closely related native–alien species pairs can provide insight into common factors that contribute to successful invasions (e.g. Aizen et al., 2011; Bednar et al., 2013; Hajek et al., 2017).

Many hypotheses have been proposed to explain the traits that increase the probability of successful invasions (Catford et al., 2009; Enders et al., 2020). For example, the 'Ideal Weed Hypothesis', originally developed in the context of plant invasion, suggests that invasive species possess life-history characteristics that facilitate invasion, such as greater fecundity and rapid growth (Baker, 1965; Chown & McGeoch, 2023; Rejmánek & Richardson, 1996; Sutherland, 2004). Invasion can also be facilitated by generalist or highly plastic phenotypes, which permit tolerance to a broad range of environmental conditions or the ability to feed upon diverse resources, promoting invasion across a variety of niches (Catford et al., 2009; Chown & McGeoch, 2023). Other hypotheses suggest that release from natural enemies in a new environment enables invasive species to shift resources from defence mechanisms to growth and reproduction, facilitating establishment and spread (Catford et al., 2009; Enders et al., 2020). Empirical studies support these ideas, showing that invasive insects often have enhanced population growth (e.g. intrinsic rate of increase, reproductive lifespan, voltinism and hatching success), dispersal and competitive ability (Hayes & Barry, 2008; Nahrung & Swain, 2015; Radville et al., 2014; Reitz & Trumble, 2002; Tscharntke et al., 2005; Ward & Masters, 2007).

Global syntheses and meta-analyses of trait comparisons between native and alien species have been undertaken primarily for plants (Divíšek et al., 2018; Mathakutha et al., 2019; Sutherland, 2004; van Kleunen et al., 2010), with less studies focused on animals (Boltovskoy et al., 2020). Syntheses on fish, amphibians and reptiles have found that invasiveness is associated with high fecundity, early maturity and greater longevity (Allen et al., 2017; Liu et al., 2017). Additionally, several syntheses have found greater thermal tolerance in invasive animals, including some insect species (e.g. Bates et al., 2013; Kelley & Cooke, 2014). Even fewer studies focus on insects exclusively, and although there are comparative analyses within some orders (e.g. Simões et al., 2023) and families (e.g. Wong et al., 2022), only two studies have undertaken global syntheses on insect species where invasive-native phenotypic trait differences are examined. Zhao et al. (2023) selected 100 of the 'worst' invasive insect species (defined as species with widespread invasive ranges and negative impacts on the environment, economy and human health) and found that invasive species had greater fecundity, faster development and shorter lifespans compared with taxonomically related non-invasive species, and that they occurred in more habitat types. Another study, Jarošík et al. (2015), examined differences in thermal tolerance for 100 insect species pairs and found that invasive insects had greater tolerance to cold and developed faster than taxonomically related non-invasive insects originating from the same continent. Although valuable, these studies fail to capture the extensive diversity of insects with both limited to only 100 species or species pairs.

Here, we expand on these analyses to include the rich life history and ecological diversity of insects, comparing a broad suite of phenotypic traits across a variety of insect taxa by undertaking a large-scale, comprehensive meta-analysis. Importantly, we target studies which directly compare traits of invasive insects and their native counterparts (i.e. co-occurring species related at least to the family level) in the introduced range. This methodology differs from previous systematic studies that compared related invasive-native species pairs from the global pool of available studies. By limiting studies to those that directly compare traits of invasive and native insects within the same study, we aim to reduce variation that stems from using different methodologies and, therefore, increase the robustness of our comparisons. We hypothesised that, relative to native insects, invasive species should have (1) fitness and life-history traits that indicate an increased capacity for rapid population growth, (2) performance behaviours and defence mechanisms that increase the likelihood of successfully establishing and spreading in the introduced range and (3) broader niches, reflected by greater stress tolerance. Moreover, we expected that differences between invasive and native insects would vary by taxonomic group and diet guild (e.g. predators compared with phytophagous insects) due to different life-history strategies and/or evolutionary histories (Holway et al., 2002; Liebhold et al., 2024; Mally et al., 2024). Systematic analyses such as this one can pinpoint key traits associated with insect invasiveness, and flag species for risk-assessment protocols and management policies.

2 | METHODS

2.1 | Data collection

We report our full dataset on Dryad: https://doi.org/10.5061/dryad.c59zw3rrk (Weaving et al., 2026) and on OSF under accession code: https://osf.io/qtgz7/. We performed each step according

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

to the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Page et al., 2021). Authors IAM and HW compiled studies published from 1970 and October 2023 using the Web of Science® (all databases) and Scopus. The following term combinations were used in a Boolean search: (insect* OR Dipter* OR Hymenopter* OR Homopter* OR Coleopter* OR Hemipter* OR Lepidopter* OR Isopter*) AND (inva* OR introduced OR exotic* OR alien* OR pest* OR biocontrol OR foreign OR non-indigenous OR nonindigenous OR non-native* OR nonnative* OR "biological control" OR "non indigenous" OR "non native") AND (native* OR indigenous). From this search, we obtained 13,550 studies which were evaluated for relevance using their title and abstract. The methodology and results of relevant papers (711 articles) were scanned in detail by one observer (IAM or HW).

2.2 | Eligibility criteria

We defined 'invasive' insect species as non-native species that have established and spread in the introduced range (Liebhold & Tobin, 2008). When invasion status was unclear, establishment and spread were verified using the published literature and the Centre for Agriculture and Bioscience International (CABI) database (2024). Most primary studies in our dataset used the term 'invasive' for non-native species with documented negative impacts. However, because evidence of impact is often unavailable or difficult to quantify and directly attribute to a particular species due to cascading effects (Clarke & McGeoch, 2023), our operational definition also includes some species whose impacts have not yet been documented.

Only studies that empirically measured phenotypic traits of terrestrial invasive and native insect pairs related at least at the family level were included. Study eligibility was further assessed using the following criteria: (i) the same experimental methods were used for both species, (ii) individuals from each species pair co-occurred in the introduced range of the invasive species or were sampled within 30 km of one another, and (iii) studies reported sample sizes, means and standard deviations (or standard errors), confidence intervals (CIs), proportional data (e.g. percentage mortality) or test statistic values (e.g. *F* for ANOVA and *t* for *t*-test). We provide a detailed list of exclusion criteria in Appendix S1. Briefly, we excluded studies in which insects were bred for biocontrol purposes, the collection area was unknown, experimental specimens were kept for more than three generations without replenishing the genetic pool (increasing the potential for inbreeding and laboratory adaptation), studies that reported only species abundance, diversity or richness and studies in which the identity of the invasive and/or native species was not provided.

2.3 | Data extraction

The criteria above resulted in the inclusion of 182 articles in our final analyses which are listed in the Data Sources section and Appendix S2. Data only available in study figures were extracted using Adobe© Photoshop© (version CS5.1) or using WebPlotDigitizer (Rohatgi, 2010).

We grouped traits into five broad categories: fitness and life history, ecological performance, stress tolerance, enemy defence and body size. We conducted a separate meta-analysis for each category. Some traits could be assigned to more than one category (e.g. the effect of temperature on survival). To avoid inflating sample sizes, each trait was included only once and assigned to the category that best reflected the primary hypotheses of the original study.

2.4 | Moderators

Within each category, we investigated phenotypic trait differences between invasive and native species. We grouped phenotypic traits within each category based on the response variable measured (Table 1 and Appendix S3). For example, within the fitness and life-history category, phenotypic traits included development time, egg size, fecundity (e.g. number of eggs produced), realised fecundity (e.g. number of eggs which reached adulthood), population growth and mating success.

We also investigated invasive diet guild as a moderator for both the immature and adult life stages. Immature diet guilds comprised brood-fed, detritivore, omnivore, parasitoid, phytophagous, predator, sap feeder and wood borer. Adult diet guilds comprised detritivore, hematophagous, nectar-feeding, non-feeding, omnivore, phytophagous, predator, sap feeder, scavenger and wood

TABLE 1 List of categories and phenotypic traits included in the meta-analyses.

Category	Phenotypic traits
Fitness and life history	Development time, egg size, egg clutch size, fecundity (e.g. number of eggs produced), realised fecundity (e.g. number of eggs reaching adulthood), population growth, mating success
Ecological performance	Foraging: consumption or collection rate, foraging: search or recruitment time, intraspecific aggression, interspecific aggression, aggression directed to humans, interspecific exploitative competition, interspecific interference competition
Stress tolerance	Desiccation resistance, cold tolerance, heat tolerance
Enemy defence	Level of pathogen or parasitoid infection, infection resistance strategies, antimicrobial activity, predator/host defence
Body size	Body mass, body length

Note: A separate meta-analysis was run for each category, with phenotypic trait as a moderator. Specific values extracted from the literature and assigned to each phenotypic trait are provided in Appendix S3.

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

borer. We also classified diet breadth of each life stage as either generalist or specialist based on whether the invasive species fed on organisms from more than one family. We used the Global Biodiversity Information Facility (GBIF) (2025) and CABI (2024) databases to classify diet guilds and, where this information was unavailable, consulted the primary literature. The majority of invasive adult insect species in our dataset were generalists ($n = 95$), with only five having specialist diets and the remaining unknown or non-feeding. As immature invasive species, the majority were also generalists ($n = 76$), with 15 species being specialists and the remaining unknown. Because invasive species were overwhelmingly generalists at both life stages, we did not examine diet breadth as a moderator.

We also investigated the type of metamorphosis (holometabolous or hemimetabolous) and sociality (social or non-social) as moderator variables. However, these variables were highly biased, with some levels dominated by a single family (e.g. most social species were ants), thereby confounding the family-level effects in the analysis. Sample sizes for these variables are presented in Figure S1.

2.5 | Effect size calculation

We used mean differences between invasive-native species pairs to derive effect sizes. Most studies provided mean trait values and a corresponding measure of variation, allowing the calculation of Hedges' g as follows:

$$g = \frac{\left(\overline{X}_{\text{invasive}} - \overline{X}_{\text{native}}\right)}{S} J$$

where $\overline{X}$ indicates the mean trait value. S is the unbiased least-squares estimate of the pooled standard deviation which is calculated from the sample sizes (n) and standard deviations (s) of the two groups (following van Kleunen et al., 2010):

$$S = \sqrt{\frac{\left(n_{\text{invasive}} - 1\right)s^2_{\text{invasive}} + \left(n_{\text{native}} - 1\right)s^2_{\text{native}}}{n_{\text{invasive}} + n_{\text{native}} - 2}}$$

Since Hedges' g overestimates the effect size, especially when sample sizes are small, we applied a correction factor J that accounts for sample size:

$$J = 1 - \frac{3}{4\left(n_{\text{invasive}} + n_{\text{native}} - 2\right) - 1}$$

The variance of Hedges' g was calculated as follows:

$$v_d = \frac{n_{\text{invasive}} + n_{\text{native}}}{n_{\text{invasive}} \cdot n_{\text{native}}} + \frac{g^2}{2\left(n_{\text{invasive}} + n_{\text{native}}\right)}$$

When studies did not provide trait means and associated measures of variation for pair comparisons, we calculated effect sizes and their variances from the reported pairwise statistical analyses (Lipsey & Wilson, 2001). Effect sizes for proportional data were calculated using the effect size index proposed by Cox (1970), as it has been shown to be the least biased estimator for this type of data (Sánchez-Meca et al., 2003). We first calculated the log odds ratio (L_{OR}) for comparisons using proportional outcomes (P):

$$L_{\text{OR}} = \log\left[\frac{P_{\text{invasive}}\left(1 - P_{\text{native}}\right)}{P_{\text{native}}\left(1 - P_{\text{invasive}}\right)}\right],$$

and subsequently divided by the constant 1.65 to obtain the effect size (Sánchez-Meca et al., 2003). The sampling variance was then calculated as follows:

$$S^2_{d_{\text{Cox}}} = 0.376\left[\frac{1}{P_{\text{invasive}}} + \frac{1}{\left(1 - P_{\text{invasive}}\right)} + \frac{1}{P_{\text{native}}} + \frac{1}{\left(1 - P_{\text{native}}\right)}\right]$$

For traits where higher values indicate better performance (e.g. fecundity), native species served as the control group and, thus, a positive effect size indicated that invasive species outperformed native species. For traits where lower values were hypothesised to confer an advantage (e.g. shorter developmental time), we reversed the sign of the effect size so that positive values consistently represented superior performance by invasive species (Appendix S3).

More than one effect size could be obtained for a particular invasive-native species pair when studies included multiple experimental treatments or multiple trait measurements (e.g. body mass in mg and body length in mm). To avoid pseudo-replication, single effect sizes were calculated for each species pair within each trait, within each study. In such cases, we calculated a 'summary effect' as follows: (1) the inverse of the variance (i.e. the weight) was determined for each effect size, (2) each effect size was then multiplied by its weight to obtain a weighted effect size and (3) all the weighted effect sizes for each invasive-native pair were then summed and divided by sum of the weights to obtain one weighted mean (Gleser & Olkin, 2007). The variance of the summary effect was calculated as the inverse of the sum of the weights (van Kleunen et al., 2010).

2.6 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Invasive-native species pairs	Invasive-native species pairs	1327 effect sizes from 182 studies

2.7 | Data analysis

We report all analysis code on OSF under accession code: https://osf.io/qtgz7/. Data were analysed in R (v. 4.2.3; R Core Team, 2023). The 'metafor' package (v. 4.4–0; Viechtbauer, 2010) was used to

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

perform multilevel random effects meta-analytic models. A separate meta-analysis was conducted for each trait category.

We considered non-independence from study effects, phylogenetic relationships, species identity, phylogenetic relatedness within the species pair (i.e. genus, sub-family and family), and within-study effects (effect size ID). We constructed phylogenetic trees using the Open Tree of Life and 'rotl' (v. 3.1.0; Michonneau et al., 2016), 'ape' (v. 5.7–1; Paradis & Schliep, 2019) and 'phytools' (v. 2.0–3; Revell, 2024). We then generated a family-level phylogenetic correlation matrix based on hypothetical relatedness of species pairs as family represented the highest level of comparison for all species pairs. Branch lengths were assigned following Grafen's method (Grafen, 1989). The final random effects structure for each model was selected based on the proportion of heterogeneity explained by each random effect, and therefore differed among trait categories (Appendix S4).

Statistical significance was inferred when 95% CIs excluded zero. Following Cohen's definition, effect sizes were classified as 'small', 'medium' and 'large' for values of 0.2, 0.5 and 0.8, respectively (Cohen, 1988).

Intercept models were fitted to assess the overall difference between invasive and native species for each trait category. We first fitted univariable moderator models for taxonomic order, phenotypic trait, adult diet guild and immature diet guild. For moderator levels represented by $k \leq 5$, effect sizes should be interpreted with caution, as such estimates are likely to be unreliable (Borenstein et al., 2011). For each trait category, we then fitted a multivariable model, including taxonomic order, phenotypic trait and the diet guild for whichever life stage (immature or adult) explained the greatest proportion of variation. We used the 'Dredge' function from the 'MuMIn' package (Version 1.47.5; Barton, 2020) to assess which combination of moderators had the best fit. We assessed residuals for homogeneity of variance visually and used the 'robust.rma.mv' function when residuals were heterogeneous ('metafor' package). For each trait category, we calculated I^2 total (the overal heterogeneity), and the proportion of heterogeneity explained by each random effect (Appendix S4).

2.8 | Publication bias and sensitivity analyses

Effect sizes were large according to typical standards, for which a large effect size is 0.8–1 (Cohen, 1988). Therefore, we conducted a series of sensitivity analyses to determine whether our conclusions were driven by extreme effect sizes or particular subsets of data. First, we performed the analysis on a subset where sample sizes for species pair/trait combinations below five were removed. We also performed two analyses after excluding studies outside the 95th and 99th percentiles. Additionally, some native species included in our dataset could be invasive elsewhere outside their native range. We therefore performed an analysis for each category after excluding these species. Species were classified as invasive outside their native range by searching three databases: the Global Invasive Species Database (GISD; Invasive Species Specialist Group ISSG, 2015), CABI (2024) and Global Register of Introduced and Invasive Species (GRIIS; Pagad et al., 2022). Species identified as invasive in at least two databases were classified accordingly. Using this criterion, 15 of the total 403 native species (3.7%) were identified as invasive outside their native range.

We also performed an analysis on a subset of data where only invasive species with documented negative impacts in the literature were included. Species were classified as impactful if they were included in the '100 worst invasive insect species' listed in Zhao et al. (2023) or had a mean negative impact score in the GIDIAS (Global Impacts Dataset of Invasive Alien Species) database (Bacher et al., 2025), based on impacts on nature or human activities. Using these criteria, 42 of the 144 invasive species were classified as impactful and retained in this sensitivity analysis.

Finally, we performed a leave-one-out analysis by iteratively removing one species pair, family or study to determine whether outliers affected model outcome. Where a single family dominated the dataset, we repeated the analyses with and without the family group, that is Formicidae (ants) and Coccinellidae (ladybird beetles), and report both sets of results.

To assess publication bias, we used funnel plots and Egger's regression test by fitting standard error (SE) as a moderator. If significant, we then fitted SE^2 as a moderator to calculate the corrected effect size (Nakagawa et al., 2022). Code was adapted from Macartney et al. (2019), Pottier et al. (2021) and Weaving et al. (2022). We made figures using the 'orchaRd' package (Nakagawa et al., 2023) and display both CIs and prediction intervals (i.e. the interval within which the effect size of a new study is likely to fall).

3 | RESULTS

We compiled data from 922 invasive-native species pairs belonging to 28 families, giving a total of 1327 effect sizes. Species pairs consisted of 403 native species and 144 invasive species. The largest trait category was body size ($k = 688$), followed by ecological performance ($k = 283$), fitness and life history ($k = 142$), enemy defence ($k = 131$), and, finally, stress tolerance ($k = 83$). Species pairs were compared at the family level ($k = 191$), sub-family level ($k = 357$) or genus level ($k = 781$). Invasive species outperformed natives in several ecological performance and fitness and life-history traits in the introduced range. While no clear differences were found in phenotypic traits related to stress tolerance, enemy defence or body size overall, there were differences in certain phenotypic traits and taxonomic orders. Diet guild was important in explaining variation in performance for fitness and enemy defence categories. Because data for some models were dominated by ladybird beetles or ants, we conducted additional subset analyses excluding these families. These analyses revealed that several phenotypic traits were influenced by the overrepresentation of these taxa (see below).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

3.1 | Fitness and life history

For fitness and life-history traits, we found that invasive species moderately outperformed native species in their introduced range, albeit CIs spanned zero ($k=142$; ES = 0.40; 95% CI = −0.12, 0.92). The heterogeneity in the model was very large ($I^2=98.4\%$), with 19.6% explained by differences between studies, 13.5% explained by phylogeny, and 65.3% explained by the residuals (effect size ID). Ladybird beetles dominated the dataset, with 47.9% of effect sizes (68 of 142) originating from Coccinellidae species pairs. When we excluded Coccinellidae from the dataset, invasive species significantly outperformed native species in traits related to fitness and life history ($k=74$; ES = 0.51; 95% CI = 0.20, 0.83). When investigated alone, ladybird beetles showed no significant difference in fitness and life-history traits between native and invasive species pairs overall ($k=68$; ES = −0.004; 95% CI = −0.28, 0.27). Overall, we found no evidence of publication bias for fitness and life-history traits ($k=142$; ES = 0.78; 95% CI = −0.45, 2.00).

We investigated how the moderators taxonomic order, phenotypic trait, immature diet and adult diet explained variation in fitness and life history between invasive and native species pairs. We found that order explained only 1.3% of the variation, with effect sizes for each order given in Appendix S7. In contrast, our model investigating phenotypic traits explained 15.8% of the variation, adult diet explained 5.6% and immature diet explained 10.0% of variation. Using the Dredge procedure, the best model included order and phenotypic trait but not immature diet. Adult diet was not included in the model due to its overlap with the immature diet guild.

Specifically, we found that invasive species had significantly greater fecundity than native species (Figure 1; $k=34$; ES = 0.94; 95% CI = 0.31, 1.56). There was a trend towards faster population growth rates ($k=29$; ES = 0.41; 95% CI = −0.28, 1.10) and shorter development times in invasive species ($k=26$; ES = 0.37; 95% CI = −0.29, 1.03), but CIs spanned zero for both traits. Egg size of native species was larger than that of invasive species, but sample sizes were small, and CIs spanned zero ($k=5$; ES = −0.86; 95% CI = −1.90, −0.05). Realised fecundity (e.g. offspring survival) did not differ between species pairs ($k=45$; ES = 0.03; 95% CI = −0.59, 0.66). There was no difference in mating propensity between invasive-native species pairs, however, sample sizes were too small for robust results ($k=3$; ES = 0.45; 95% CI = −0.82, 1.72).

When we removed ladybird beetles from the dataset, the same overall trends were found in phenotypic traits ($k=74$). Invasive species had significantly greater fecundity ($k=18$; ES = 1.09; 95% CI = 0.66, 1.52) and shorter development times ($k=11$; ES = 0.77; 95% CI = 0.24, 1.30). Population growth rates tended to be faster in invasive species, albeit CIs marginally crossed zero ($k=12$; ES = 0.51; 95% CI = −0.03, 1.04). We found no difference in egg size when ladybirds were excluded, however, sample sizes were too small to be interpreted with confidence ($k=2$; ES = −0.66; 95% CI = −1.74, 0.43). There were no differences between invasive and native species in realised fecundity ($k=28$; ES = 0.09; 95% CI = −0.28, 0.47). We found no difference in mating propensity, albeit sample sizes were too small for robust results ($k=3$; ES = 0.35; 95% CI = −0.93, 1.64).

When investigating trait as a moderator for ladybird beetles alone (Figure S2), we found greater fecundity in invasive species ($k=16$;

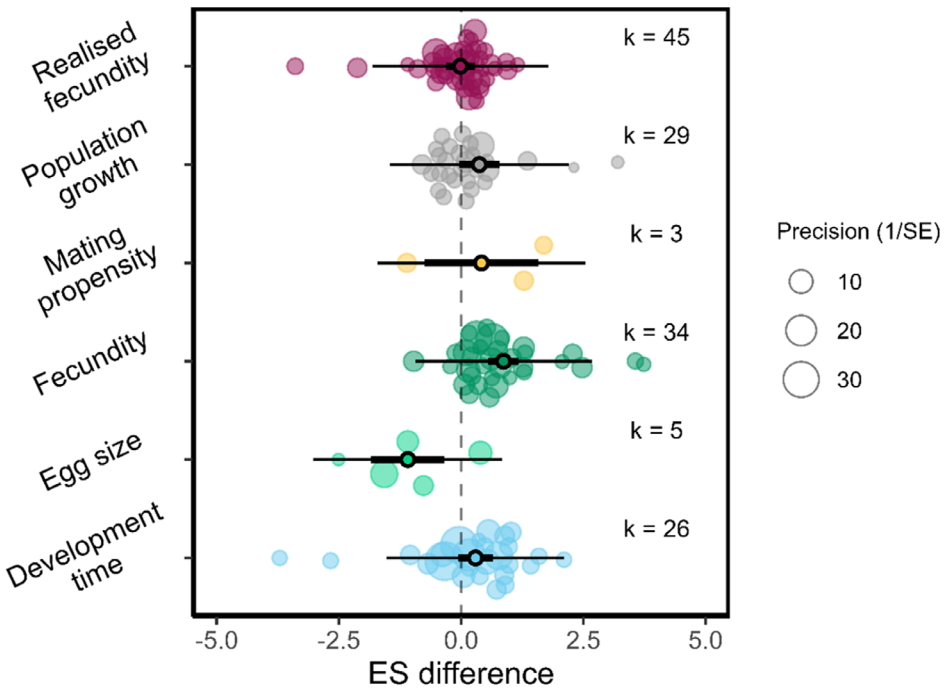

FIGURE 1 Co-occurring native and invasive insects differed in fitness and life-history traits. Effect sizes (ES) greater than 0 indicate that the invasive species outperformed the native species. Bold lines show 95% confidence intervals; non-bold lines show prediction intervals. k = the number of effect sizes. Data point size is proportional to study precision (1/SE, where SE is the standard error).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ES = 0.51; 95% CI = 0.08, 0.94). Egg size was significantly smaller in native species, but sample sizes were too small for robust interpretation ($k = 3$; ES = −1.47; 95% CI = −2.40, −0.43). We present additional results for phenotypic traits in ladybird beetles alone in Appendix S8.

Using diet guild as a moderator, there was a strong effect of invasive species outperforming native species in fitness and life-history traits when the invasive was brood-fed at the immature stage ($k = 12$; ES = 1.12; 95% CI = 0.47, 1.76). However, other diet guilds did not show significant differences between native and invasive species in fitness and life-history traits, although several were close to significance, such as detritivores and phytophagous insects (Appendices S9 and S10).

Sensitivity analyses excluding cases with the highest and lowest percentile of variance, sample sizes below 5 and native species that were invasive outside their native range produced similar results (Appendix S6). When the analysis was limited to invasive species with documented negative impacts in the literature, the estimated difference between native and invasive species in fitness and life-history traits was larger, but CIs were much wider ($k = 56$; ES = 0.79; 95% CI = −0.56, 2.16). The leave-one-out analysis showed that removing individual studies or species had little effect on the overall mean effect size or its CI, indicating robust results (Appendix S5). However, removing families led to a modest decrease in the mean effect size (from 0.40 to 0.29) and a marked widening of the CI (−0.68,1.26), suggesting that family-level differences contribute to variation in fitness and life-history responses.

3.2 | Ecological performance

We found that invasive species moderately outperformed native species in ecological performance traits ($k = 283$; ES = 0.38; 95% CI = 0.21, 0.54). Heterogeneity in the model was very large ($I^2 = 97.2\%$), with 16.6% explained by differences between studies, 3.0% explained by differences between species, and 77.8% explained by the residuals (effect size ID). Results were robust to the exclusion of ants ($k = 120$ of 283 (42%); ES = 0.33; 95% CI = 0.09, 0.57). However, there was evidence of publication bias ($k = 283$; ES = 0.95; 95% CI = 0.25, 1.66). Accounting for this bias resulted in a smaller, but still significant, difference in ecological performance traits between invasive and native insects ($k = 283$; ES = 0.25; 95% CI = 0.06, 0.43).

Order was not an important moderator, explaining only 1.3% of the variation. Effect sizes for each order are given in Appendix S11, with Coleoptera ($k = 68$; ES = 0.34; 95% CI = 0.01, 0.67) and Hymenoptera ($k = 191$; ES = 0.39; 95% CI = 0.16, 0.62) showing significant outperformance of invasive compared with native species in ecological performance traits. Phenotypic trait explained 4.1% of the variation, and adult and immature diet explained 2.7% and 6.0%, respectively. The best model using Dredge included order, trait and immature diet.

Investigation of phenotypic traits showed that invasive species had greater foraging performance, with significantly shorter search times (Figure 2; $k = 42$; ES = 0.59; 95% CI = 0.25, 0.94) and faster foraging rates ($k = 122$; ES = 0.43; 95% CI = 0.17, 0.70). When in direct

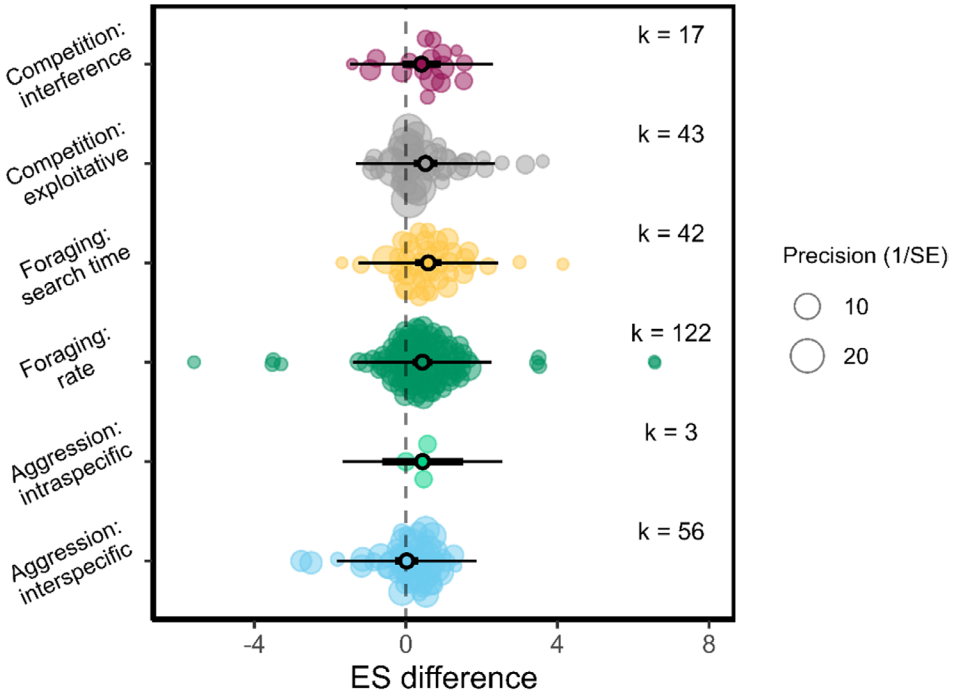

FIGURE 2 Co-occurring native and invasive insects differed in ecological performance traits. Search time refers to the length of time it takes to locate a resource, whereas foraging rate refers to how quickly a resource is collected once it is located. Effect sizes (ES) greater than zero indicate that invasive species outperformed native species. Bold lines show 95% confidence intervals, and non-bold lines show prediction intervals. k = the number of effect sizes. Data point size is proportional to study precision (1/SE, where SE is the standard error).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

exploitative competition with natives, invasive species significantly outcompeted native species ($k=43$; ES = 0.52; 95% CI = 0.21, 0.83). We also found a trend towards greater interference competition in invasive species, albeit CIs spanned zero ($k=17$; ES = 0.41; 95% CI = −0.10, 0.92). However, we did not find that invasive species were more aggressive than native species, either inter-specifically ($k=56$; ES = 0.02; 95% CI = −0.29, 0.33) or intra-specifically ($k=3$; ES = 0.44; 95% CI = −0.63, 1.50). When ants were excluded, differences remained in the same direction (Appendix S12), except that we found no difference between insect pairs in foraging search time, although the sample size was too small for this result to be reliable ($k=2$; ES = 0.06; 95% CI = −1.81, 1.69). Invasive ants outperformed native ants when investigated as a subset (Figure S3; $k=163$; ES = 0.32; 95% CI = 0.03, 0.61). Further results for ants are reported in Appendix S13.

When investigating the effect of adult diet guild on the difference in ecological performance between invasive-native species pairs, we found that omnivorous ($k=134$; ES = 0.41; 95% CI = 0.17, 0.65) and predatory insects ($k=94$; ES = 0.28; 95% CI = 0.01, 0.56) moderately outperformed their native counterparts. Adult phytophagous invasive species also outperformed native species, however, sample sizes were low ($k=5$; ES = 0.99; 95% CI = −0.01, 1.99). When diet guild was investigated for the immature stage, brood-fed ($k=176$; ES = 0.46; 95% CI = 0.21, 0.72) and predatory invasive insects ($k=45$; ES = 0.42; 95% CI = 0.07, 0.76) outperformed natives in ecological performance. Results comparable to adults were also found for immature phytophagous insects ($k=3$; ES = 1.18; 95% CI = 0.08, 2.27). Further results for the effect of adult and immature diet guild can be found in Appendices S14 and S15, respectively.

Sensitivity analyses excluding cases with the highest and lowest percentile of variance, sample sizes below 5 and native species that were invasive outside of their native range produced similar results (Appendix S6). When only invasive species with documented negative impacts were included, the difference between native and invasive species in ecological performance traits was larger ($k=192$; ES = 0.53; 95% CI = 0.29, 0.76). The leave-one-out analysis showed that removing individual studies, species or families had little effect on the overall mean effect size or its CI, indicating robust results (Appendix S5).

3.3 | Stress tolerance

Invasive species did not have greater stress tolerance than natives ($k=83$; ES = 0.04; 95% CI = −0.29, 0.36). Heterogeneity was very high ($I^2=98.7\%$), with 3.6% of the variation explained by differences between studies, 49.8% explained by differences between species, and 45.3% explained by residuals. When ants ($k=60$ of 83 (72%)) were removed from the analysis, invasive species were significantly more stress tolerant than native species, although the difference was small ($k=23$; ES = 0.23; 95% CI = 0.02, 0.44). When ants were analysed alone, there was no difference in stress tolerance between invasive-native species pairs ($k=60$; ES = −0.23; 95% CI = −0.73, 0.27). Additionally, Egger's regression test indicated potential publication bias ($k=83$; ES = 1.41; 95% CI = −0.01, 2.84), although the test was marginally insignificant.

Order explained only 1.7% of the variation, and the three orders included (Coleoptera, Diptera and Hymenoptera) did not show a significant difference between invasive and native species in stress tolerance traits (Appendix S16). Tolerance trait (heat tolerance, cold tolerance, desiccation resistance) also explained a limited amount of variation (3.5%), with no trait showing a significant difference between native and invasive species pairs, although some potential trends were evident (Figure 3). There was slightly greater heat tolerance in invasive species than native species, but CIs crossed zero and the difference was small ($k=59$; ES = 0.17; 95% CI = −0.16, 0.50). There was also a trend of invasive species being moderately less cold tolerant ($k=15$; ES = −0.33; 95% CI = −0.84, 0.18), although, again, CIs spanned zero. There was no difference in resistance to desiccation between species, although these data comprised only ants ($k=9$; ES = −0.12; 95% CI = −0.92, 0.68).

When ants were excluded, results should be interpreted in the context of the remaining species being only from orders Coleoptera and Diptera. Invasive species had marginally greater heat tolerance than native species ($k=13$; ES = 0.26; 95% CI = 0.01, 0.51). Invasive species were also slightly, but non-significantly, more cold tolerant when ants were excluded ($k=10$; ES = 0.19; 95% CI = −0.10, 0.48). When ants were investigated as a subset, invasive ants were less cold tolerant than their native counterparts; despite the large effect size, the sample size was too small for reliable interpretation ($k=5$; ES = −1.79; 95% CI = −2.51, −1.08). Further results for ants as a subset are reported in Appendix S17 and Figure S4.

When investigating the effect of invasive diet guild on differences between native and invasive species pairs, we found no effect of adult diet guild (Appendix S18), with only 1.4% of the variation explained (although the dataset was largely composed of omnivorous ants; $n=60$ of 83 effect sizes). Immature diet explained only 1.6% of the variation, also with no diet guild showing a significant effect, and the dataset was similarly dominated by brood-fed ants (Appendix S19). Using Dredge, the best model contained immature diet and trait.

The leave-one-out sensitivity analyses indicated that no families, species or studies had a large effect on the results, with all model averages still indicating no significant difference in thermal tolerant traits between native and invasive species overall (Appendix S5). Excluding the highest and lowest percentiles of variance and studies with the smallest sample sizes also did not appreciably affect the results. However, when the analysis was restricted to invasive species with documented negative impacts in the literature, native species appeared more tolerant than invasive species, albeit CIs spanned zero, which indicates a lack of robustness in these results ($k=44$; ES = −0.28; 95% CI = −0.59, 0.03).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

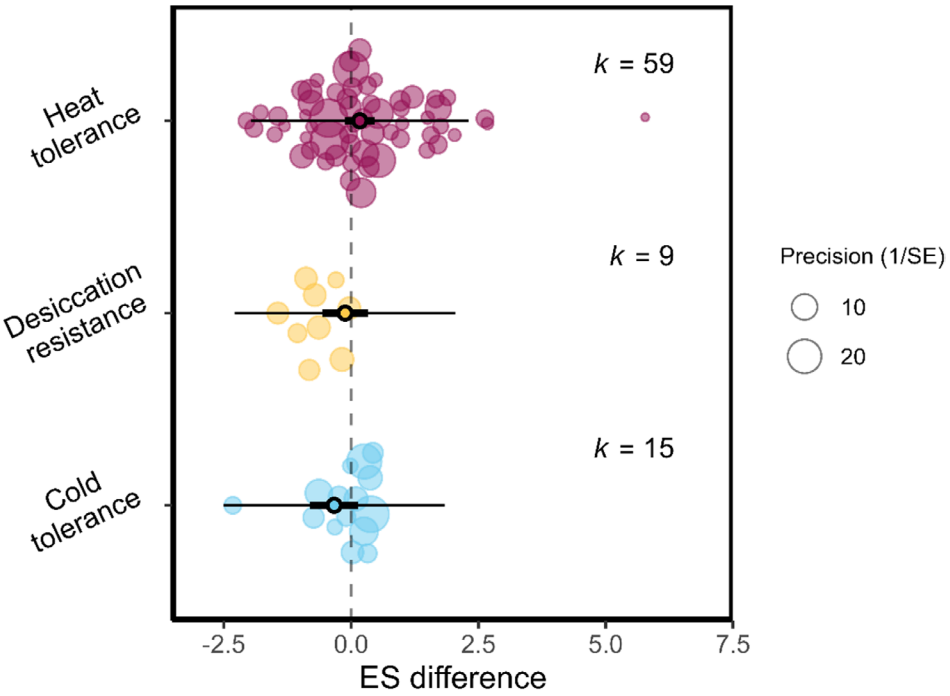

FIGURE 3 Co-occurring native and invasive insects did not differ significantly in stress tolerance. Effect sizes (ES) greater than zero indicate that invasive species outperformed native species. Bold lines show 95% confidence intervals, and non-bold lines show prediction intervals. *k* = the number of effect sizes. Data point size is proportional to study precision (1/SE, where SE is the standard error).

3.4 | Enemy defence

Overall, native and invasive insect species did not differ in enemy defence traits ($k = 131$; ES = 0.04; 95% CI = −0.68, 0.72). Heterogeneity was very high ($I^2 = 97.0\%$), with 53.9% of the variation explained by differences between studies, 2.0% explained by phylogeny, 5.1% explained by the level of phylogenetic comparison, and 35.9% explained by residuals. This remained the case whether ladybird beetles were excluded ($k = 64$; ES = −0.04; 95% CI = −0.75, 0.67) or were considered alone ($k = 67$; ES = 0.42; 95% CI = −0.63, 1.47). There was no evidence of publication bias for enemy defence traits ($k = 131$; ES = 0.04; 95% CI = −0.68, 0.77).

The results did not vary depending on which trait was measured (Figure 4), including antimicrobial activity ($k = 11$; ES = −0.27; 95% CI = −1.17, 0.63), level of pathogen/parasitoid infection ($k = 70$; ES = −0.08; 95% CI = −0.41, 0.24), and resistance to pathogen/parasitoid infection ($k = 5$; ES = −0.01; 95% CI = −0.65, 0.64). There was a trend towards better predator and plant host defence in invasive species ($k = 45$; ES = 0.31; 95% CI = −0.11, 0.73), but CIs spanned zero. Trait explained 7.0% of the variation in the model.

There were still no significant trait differences when ladybird beetles were excluded (Appendix S20), although there was a trend towards better defensive strategies against predators and hosts in invasive species ($k = 14$; ES = 0.46; 95% CI = −0.14, 1.07). However, CIs still spanned zero. When ladybird beetles were investigated alone, invasive species were significantly better at defence against predators than native species (Figure S5; $k = 31$; ES = 0.73; 95% CI = 0.02, 1.43). Further results for ladybird beetles are reported in Appendix S21.

Order explained 12.7% of the variation in the model. The model indicated that invasive Coleoptera were better able to defend themselves against enemies than their native counterparts ($k = 67$; ES = 0.34; 95% CI = −0.03, 0.72), albeit CIs marginally passed zero. Other enemy defence results by order are given in Appendix S22.

Adult and immature diet explained 11.6% and 10.6% of the variation in enemy defence responses between invasive and native species pairs, respectively. For both adult ($k = 68$; ES = 0.35; 95% CI = −0.01, 0.71) and immature diets ($k = 45$; ES = 0.38; 95% CI = 0.04, 0.72), invasive predators were either close to or significantly better at defending themselves against enemies than their native counterparts. All other diet guilds did not show any significant differences (Appendices S23 and S24). The best model using Dredge included trait and adult diet.

Leave-one-out sensitivity analyses showed that no studies, species or families had a significant effect on the overall results (Appendix S5). Additionally, excluding the highest and lowest percentiles of variance, studies with the smallest sample sizes and invasive species without documented negative impacts did not appreciably affect results (Appendix S6).

3.5 | Body size

Invasive and native insects were similar in size overall ($k = 688$; ES = 0.34; 95% CI = −5.25, 5.92), and when ants were excluded from the analysis (Figure 5; $k = 86$; ES = 0.86; 95% CI = −0.78, 2.50).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

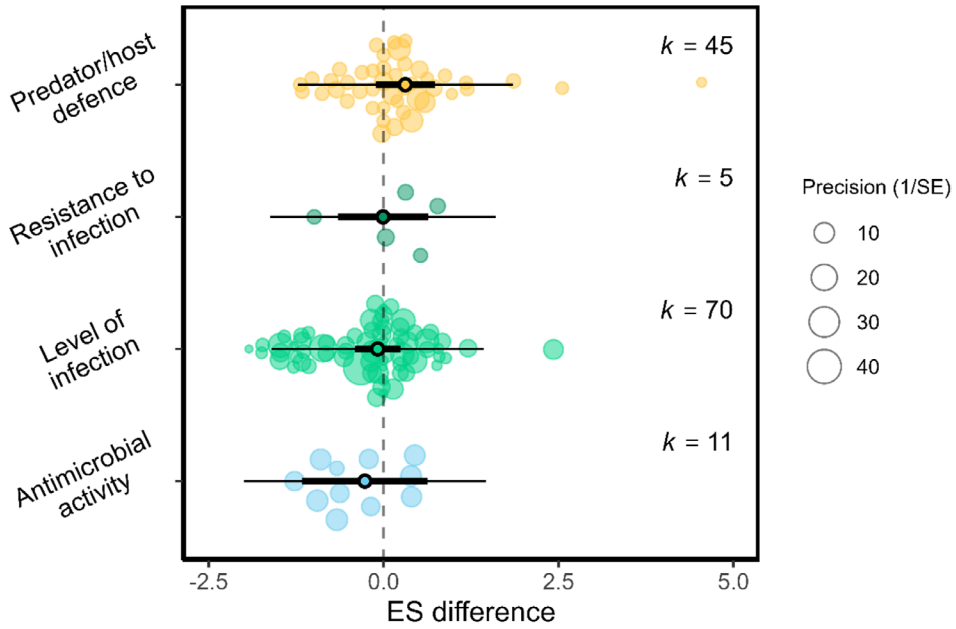

FIGURE 4 Co-occurring native and invasive insects did not differ in enemy defence. Effect sizes (ES) greater than zero indicate that invasive species outperformed native species. Bold lines show 95% confidence intervals, and non-bold lines show prediction intervals. *k* = the number of effect sizes. Data point size is proportional to study precision (1/SE, where SE is the standard error).

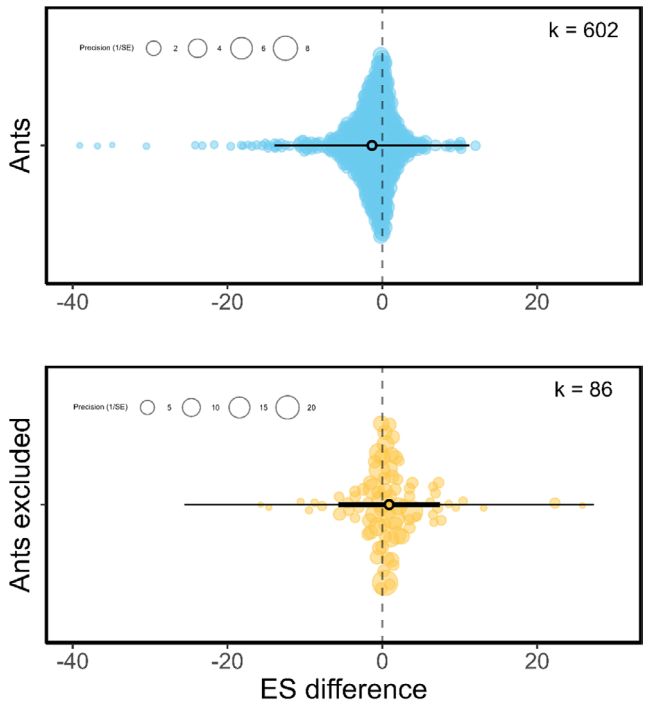

FIGURE 5 Co-occurring native and invasive insects did not differ in body size when ants were excluded from the analysis, but invasive ants were smaller when Formicidae were investigated separately. Effect sizes (ES) greater than zero indicate that invasive species were larger than native species. Bold lines show 95% confidence intervals, and non-bold lines show prediction intervals. *k* = the number of effect sizes. Data point size is proportional to study precision (1/SE, where SE is the standard error).

Heterogeneity was very high in the main model (I^2 = 99.4%), with 41.9% of the variation explained by differences between studies, 22.0% explained by species differences, 14.7% explained by the level of phylogenetic comparison between species pairs, and 20.9% explained by residuals. Overall, Egger's regression test revealed significant publication bias (*k* = 688; ES = −4.11; 95% CI = −4.53, −3.69). Once corrected, invasive and native insects remained similar in size (ES = 0.64; 95% CI = −17.25, 18.53). However, when ants were analysed alone (*k* = 602 of 688, 88% of comparisons), invasive ant species were much smaller than their native counterparts (Figure 5; ES = −1.34; 95% CI = −1.64, −1.04).

When investigating moderators, no insect order showed a significant difference in body size between invasive and native species (Appendix S25) and order explained only 0.04% of the variation. Adult and immature diet explained 3.9% and 1.5% of the variation, respectively, but no diet guild significantly explained differences in body size between invasive and native species, except for adult detritivores where invasive species were much larger than native species (*k* = 15; ES = 6.04; 95% CI = 1.22, 10.86). We report the results for adult and immature diet in Appendices S26 and S27, respectively.

Our sensitivity analysis revealed that no species, studies or families disproportionately affected the results (Appendix S5). However, results varied among the sensitivity analyses when considering only invasive species with documented negative impacts, excluding the highest and lowest percentiles of variance, and studies with small sample sizes. Nevertheless, all analyses consistently indicated that there was no significant body size difference between invasive-native species pairs (Appendix S6).

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

4 | DISCUSSION

Our study indicates that for invasive species that have established and spread, fitness and ecological performance traits, such as fecundity, foraging performance and competitive ability, are important across many families of insects. These findings are supported by theoretical expectations from invasion biology (Sakai et al., 2001) and by other plant and animal systems examined in previous meta-analyses (Boltovskoy et al., 2020; van Kleunen et al., 2010). In contrast, invasive species did not have larger body size or improved enemy defence compared with their native counterparts in the introduced range.

We expected that invasive species would outperform native species in traits closely related to fitness. Indeed, we found that invasive insect species typically have greater fecundity than native species. Many invasive insects also had faster population growth rates and shorter development times, and these differences became more robust when the most data-rich taxonomic family in the dataset (Coccinellidae) was excluded. These traits may increase the likelihood that invasive species can rapidly augment their population size (Baker, 1965; Rejmánek & Richardson, 1996; Sutherland, 2004). Additionally, we found that invasive species had smaller body size and egg size than native species when analysing invasive ants and ladybird beetles, respectively. Fast life histories are frequently linked to small body size and short development times (Lawton & Brown, 1986), and similar studies on insects highlight these traits as contributing to the establishment of non-native populations (Liebhold et al., 2024; Zhao et al., 2023). In agreement, Zhao et al. (2023) found in their selected 100 'worst' invasive insect species that invasive species showed higher fecundity, faster development and shorter generation times than native species. Consistent with these findings, we found that fitness differences were amplified when the analysis was restricted to invasive species with documented negative impacts. Other studies have also linked invasiveness to traits such as fecundity, growth rate and lifespan (McKnight et al., 2017; Ordonez et al., 2010; van Kleunen et al., 2010), although results are mixed and depend on context (Daehler, 2003; Hulme & Bernard-Verdier, 2018; Kueffer et al., 2013).

Invasive insects had enhanced foraging performance, including shorter search and handling times, as well as superior competitive ability. Enhanced foraging performance allows invasive species to exploit resources more quickly, which may contribute to enhanced fitness through greater allocation to growth and reproduction while reducing the fitness of native species when resources are shared. Indeed, our study showed that invasive species outperformed native species in direct competition, based on traits such as survival and population growth rates measured when invasive-native species pairs were reared together experimentally. A similar meta-analysis found that invasive phyllophagous insects had higher fecundity than native species when in direct competition but did not outperform natives in survival, growth or development time (Radville et al., 2014). We found enhanced ecological performance in omnivorous, predatory and phytophagous diet guilds. Moreover, differences in ecological performance between invasive and native species were greater when the analysis was restricted to invasive species with documented negative impacts.

We did not find a difference in enemy defence between invasive and native species. This could reflect adaptation of enemies (including parasites, viruses, bacteria and predators) to the host, since we focused on species that had established in the introduced range (Brian & Catford, 2023). However, we found that invasive ladybird beetles were better than their native counterparts at defending against other predators, and that invasive predators generally outperformed native species in enemy defence traits. These patterns can also be explained by selection acting on natural enemy populations in the introduced range (Brian & Catford, 2023; Catford et al., 2009). We also note that natural enemy densities were not accounted for in field studies included in our analysis (46% of effect sizes). Thus, although invasive and native individuals were collected from the same site in these studies, natural enemy densities were not standardised and may have influenced these results.

We predicted that invasive species would have greater stress tolerance (i.e. broader fundamental niches) than native species due to their successful colonisation of regions with potentially novel environmental conditions. Overall, we found no differences in heat, cold or desiccation tolerance between invasive and native species. A previous study (Jarošík et al., 2015) found that invasive insects were less cold tolerant than non-invasive species due to requiring warmer temperatures for successful development. Differences between studies are likely due to differences in methodology: insect pairs in Jarošík et al. (2015) could be located anywhere on the same continent. In contrast, our study only included studies where collections sites of species pairs overlapped or were within 30 km, meaning that species were likely to experience similar thermal environments. Similarities in tolerance between invasive and native species could have originated prior to invasion, allowing invasive species to fill niches with similar abiotic environments (Fridley, 2013; van Kleunen et al., 2015). Alternatively, similarities in stress tolerance may result from rapid evolution, plasticity or the evolution of plasticity (e.g. genetic assimilation) of the invasive species in its new environment, if these phenotypes confer the highest fitness in the introduced range (Colautti & Lau, 2015; Lau & Funk, 2023). We found that higher fecundity in invasive species did not translate to higher realised fecundity, which could indicate selection for phenotypes better adapted to the invaded abiotic environment. However, the stress tolerance dataset was limited to three orders. Future stress tolerance research should focus on comparative studies between related invasive and native species, particularly in orders beyond Coleoptera, Diptera and Hymenoptera, as thermal tolerance limits are important determinants of fundamental niche boundaries. Comparative studies of desiccation resistance would also be fruitful due to its potential importance during the transport phase of invasion.

Our study has some limitations. Phenotypic traits of the invasive-native species pairs were recorded after the invasive species had become established, preventing differentiation of phenotypic traits associated with the transport and establishment phases of invasion.

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Future studies could address this limitation by incorporating interception data (e.g. from ports of entry) as a proxy for the transport phase, thereby enabling identification of phenotypic traits associated with each phase of invasion.

We also did not compare invasive species between their native and invasive ranges, or between invasive and non-invasive alien species, because of the paucity of such studies for insects. Such data are more common for plants and have supported the role of particular traits in conferring invasiveness (Divíšek et al., 2018; Gallagher et al., 2015; van Kleunen et al., 2010). The lack of comparable insect data likely reflects the fact that non-native insects often remain undetected for long periods due to their accidental introduction and small size (Elton, 1958; Gippet et al., 2019; Kenis et al., 2007; Liebhold et al., 2016; Roderick & Navajas, 2015). By the time of detection, most invasive insects have increased in abundance and become established (MacLachlan et al., 2021). Consequently, studies reporting phenotypic traits of invasive insects are more likely to characterise species that have successfully established than species that were introduced but failed to establish (Zenni & Nuñez, 2013).

Additionally, we found some large effect sizes, especially for body size where the largest effect size was close to 50. Large effect sizes are typically defined as 0.8–1 (Cohen, 1988). Our large effect sizes likely derive from the small standard deviations associated with body size measurements, as well as from comparing species related at taxonomic levels above genus, which generally represent greater evolutionary divergence. Indeed, when we investigated only congeneric species pairs in the body size dataset, we found much less variation in effect size (genus only: $k = 632$; ES = −0.63; 95% CI = −2.72, 1.46; all data: $k = 688$; ES = 0.34; 95% CI = −5.23, 5.92), despite the subset including 91.9% of the dataset. To ensure that these effect sizes were not unduly influential, we excluded studies that had particularly small sample sizes (<5) and extreme variances, and performed leave-one-out sensitivity analyses in which each study, species or family was excluded in turn. These analyses did not substantially alter the results of our study (Appendices S5 and S6).

Furthermore, we observed substantial biases in the literature regarding which phylogenetic groups and diet guilds have been scored for each trait category. For example, Coleoptera and Hemiptera make up most non-native insect richness globally and are the most frequently intercepted at ports of entry (Liebhold et al., 2024; Turner et al., 2021), yet we have limited phenotypic trait data for these groups. Hemiptera accounted for only 23 of our 1327 effect sizes, and although Coleoptera accounted for 269 effect sizes, 246 of these came from ladybird beetles. Ants, likewise, dominated the dataset, contributing 850 of 1327 effect sizes. Herbivorous insects (insects feeding on living plants, including phytophagous, wood-boring and sap-feeding species) were highly underrepresented in the immature diet grouping (72 effect sizes; 5.4%). Data from Mally et al. (2024) indicate that this group makes up 52% of non-native species, with invasions of herbivores being dominant and increasing over the last 150 years. Similarly, insects that are detritivorous at the immature stage were underrepresented in our dataset (78 effect sizes; 5.9%), despite representing approximately 18% of non-native insect species globally (Mally et al., 2024). Further research is needed to better understand lesser studied groups especially given their association with biological invasions (Bonnamour et al., 2023). It is also surprising that stress tolerance was the least studied category considering its importance for predicting the spread of invasive vectors of disease and crop pests under climate change (Harvey et al., 2023; Logan et al., 2020).

To conclude, we present the most comprehensive systematic comparison of phenotypic traits between sympatric native and invasive insects to date. We highlight several traits associated with successful insect invaders, including greater fecundity, faster development and enhanced foraging performance and exploitative competition. Moreover, we found that invasive species outperformed native species in almost all traits examined, underscoring the role of the invasion process in selecting for traits that promote invasiveness and highlighting the importance of trait-based assessments in invasion biology. There is a need for further research on understudied groups, as well as comparisons between insect species in their invaded and native ranges. Although much remains to be understood about the drivers of insect invasiveness worldwide, our results identify key phenotypic traits associated with insect invasiveness, highlight important research gaps and demonstrate the value of comparative trait analyses. These findings provide a foundation for incorporating the suite of identified traits into post-introduction risk-assessment schemes and may help guide future invasive surveillance and control efforts (Chown & McGeoch, 2023; Lieurance et al., 2023).

AUTHOR CONTRIBUTIONS

Susana Clusella-Trullas, Ingrid A. Minnaar and Cang Hui conceived the ideas. Ingrid A. Minnaar and Susana Clusella-Trullas designed the methodology, Ingrid A. Minnaar and Hester Weaving collected the data and performed the meta-analysis, Hester Weaving statistically analysed the data, Ingrid A. Minnaar wrote the first draft, Hester Weaving led the writing of the manuscript. All authors (Hester Weaving, Ingrid A. Minnaar, Cang Hui, Michael L. Logan and Susana Clusella-Trullas) contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to Patrice Pottier for advice on the statistical analysis and to Jeff Garnas, Helen Roy and Julie Coetzee for comment on an earlier version of this manuscript. Ingrid A. Minnaar and Hester Weaving were supported by funding from the DSI-NRF Centre of Excellence for Invasion Biology and incentive funding from the National Research Foundation of South Africa (NRF) to Susana Clusella-Trullas, respectively. Ingrid A. Minnaar was supported by an Innovation Doctoral Scholarship from the NRF. Hester Weaving, Ingrid A. Minnaar and Cang Hui were also partially supported by the National Research Foundation (NRF grant 89967), for visiting fellowship, scholarship support and research, respectively. Cang Hui also acknowledges additional support from the

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Global Insect Threat-Response Synthesis (GLiTRS), funded by the UK Natural Environment Research Council (grant NE/V007548/1). Michael L. Logan was supported by the United States National Science Foundation Postdoctoral Fellowship in Biology (award no.: DBI-1402497).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.c59zw3rrk (Weaving et al., 2026). We report all analysis code on OSF under accession code: https://osf.io/qtgz7.

DATA SOURCES

Data were sourced from 182 articles which are given in the data sources section of the paper.

ORCID

Hester Weaving https://orcid.org/0000-0002-9093-0556
Ingrid A. Minnaar https://orcid.org/0000-0003-2833-622X
Michael L. Logan https://orcid.org/0000-0003-2242-1810
Susana Clusella-Trullas https://orcid.org/0000-0002-8891-3597

REFERENCES

Aizen, M. A., Lozada, M., & Morales, C. L. (2011). Comparative nectar-foraging behaviors and efficiencies of an alien and a native bumble bee. *Biological Invasions*, *13*, 2901–2909. https://doi.org/10.1007/s10530-011-9972-3

Allen, W. L., Street, S. E., & Capellini, I. (2017). Fast life history traits promote invasion success in amphibians and reptiles. *Ecology Letters*, *20*, 222–230. https://doi.org/10.1111/ELE.12728;WGROUP:STRING:PUBLICATION

Bacher, S., Ryan-Colton, E., Coiro, M., Cassey, P., Galil, B. S., Nuñez, M. A., Ansong, M., Dehnen-Schmutz, K., Fayvush, G., Fernandez, R. D., Hiremath, A. J., Ikegami, M., Martinou, A. F., McDermott, S. M., Preda, C., Vilà, M., Weyl, O. L. F., Aravind, N. A., Angelidou, I., … Zengeya, T. A. (2025). Global impacts dataset of invasive alien species (GIDIAS). *Scientific Data*, *12*, 832. https://doi.org/10.1038/S41597-025-05184-5

Baker, H. G. (1965). Characteristics and modes of origin of weeds. In *Genetics of colonizing species*. Academic Press.

Barton, K. (2020). MuMIn: Multi-model inference.

Bates, A. E., McKelvie, C. M., Sorte, C. J. B., Morley, S. A., Jones, N. A. R., Mondon, J. A., Bird, T. J., & Quinn, G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131958. https://doi.org/10.1098/RSPB.2013.1958;PAGE:STRING:ARTICLE/CHAPTER

Bednar, D. M., Shik, J. Z., & Silverman, J. (2013). Prey handling performance facilitates competitive dominance of an invasive over native keystone ant. *Behavioral Ecology*, *24*, 1312–1319. https://doi.org/10.1093/beheco/art069

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, *26*, 333–339. https://doi.org/10.1016/J.TREE.2011.03.023

Boltovskoy, D., Correa, N. M., Burlakova, L. E., Karatayev, A. Y., Thuesen, E. V., Sylvester, F., & Paolucci, E. M. (2020). Traits and impacts of introduced species: A quantitative review of meta-analyses. *Hydrobiologia*, *848*(9), 2225–2258. https://doi.org/10.1007/S10750-020-04378-9

Bonnamour, A., Blake, R. E., Liebhold, A. M., Nahrung, H. F., Roques, A., Turner, R. M., Yamanaka, T., & Bertelsmeier, C. (2023). Historical plant introductions predict current insect invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *120*, e2221826120. https://doi.org/10.1073/PNAS.2221826120/SUPPL_FILE/PNAS.2221826120.SAPP.PDF

Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2011). *Introduction to meta-analysis*. John Wiley & Sons.

Bradshaw, C. J. A., Hoskins, A. J., Haubrock, P. J., Cuthbert, R. N., Diagne, C., Leroy, B., Andrews, L., Page, B., Cassey, P., Sheppard, A. W., & Courchamp, F. (2021). Detailed assessment of the reported economic costs of invasive species in Australia. *NEOBIOTA*, *67*, 511–550. https://doi.org/10.3897/neobiota.67.58834

Brian, J. I., & Catford, J. A. (2023). A mechanistic framework of enemy release. *Ecology Letters*, *26*, 2147–2166. https://doi.org/10.1111/ELE.14329;PAGE:STRING:ARTICLE/CHAPTER

CABI. (2024). *CABI Compendium [WWW Document]*. CAB International. https://www.cabidigitallibrary.org/journal/cabicompendium

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*, 22–40. https://doi.org/10.1111/J.1472-4642.2008.00521.X

Chown, S. L., & McGeoch, M. A. (2023). Functional trait variation along animal invasion pathways. *Annual Review of Ecology, Evolution, and Systematics*, *54*, 151–170. https://doi.org/10.1146/ANNUREV-ECOLSYS-102220-013423/1

Clarke, D. A., & McGeoch, M. A. (2023). Invasive alien insects represent a clear but variable threat to biodiversity. https://doi.org/10.1016/j.cris.2023.100065

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*, *statistical power analysis for the behavioral sciences*. Lawrence Earlbaum Associates. https://doi.org/10.4324/9780203771587

Colautti, R. I., & Lau, J. A. (2015). Contemporary evolution during invasion: Evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology*, *24*, 1999–2017. https://doi.org/10.1111/MEC.13162

Cox, D. R. (1970). *Analysis of binary data*. Chapman & Hall/CRC.

Cuthbert, R. N., Diagne, C., Haubrock, P. J., Turbelin, A. J., & Courchamp, F. (2022). Are the "100 of the world's worst" invasive species also the costliest? *Biological Invasions*, *24*, 1895–1904. https://doi.org/10.1007/S10530-021-02568-7/FIGURES/4

Daehler, C. C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 183–211. https://doi.org/10.1146/ANNUREV.ECOLSYS.34.011802.132403/1

Diniz-Filho, J. A. F., de Marco, P., & Hawkins, B. A. (2010). Defying the curse of ignorance: Perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, *3*, 172–179. https://doi.org/10.1111/J.1752-4598.2010.00091.X

Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N. J., Lososová, Z., Pyšek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nature Communications*, *9*(1), 1–10. https://doi.org/10.1038/s41467-018-06995-4

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. The University of Chicago Press.

Enders, M., Havemann, F., Ruland, F., Bernard-Verdier, M., Catford, J. A., Gómez-Aparicio, L., Haider, S., Heger, T., Kueffer, C., Kühn, I., Meyerson, L. A., Musseau, C., Novoa, A., Ricciardi, A., Sagouis, A., Schittko, C., Strayer, D. L., Vilà, M., Essl, F., … Jeschke, J. M. (2020). A conceptual map of invasion biology: Integrating hypotheses into a consensus network. *Global Ecology and Biogeography*, *29*, 978–991. https://doi.org/10.1111/GEB.13082;WEBSITE:WEBSITE:PERIC

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

LES;JOURNAL:JOURNAL:14668238;WGROUP:STRING:PUBLICATION

Fernandes, R. F., Honrado, J. P., Guisan, A., Roxo, A., Alves, P., Martins, J., & Vicente, J. R. (2019). Species distribution models support the need of international cooperation towards successful management of plant invasions. *Journal for Nature Conservation*, *49*, 85–94. https://doi.org/10.1016/J.JNC.2019.04.001

Fournier, A., Penone, C., Pennino, M. G., & Courchamp, F. (2019). Predicting future invaders and future invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 7905–7910. https://doi.org/10.1073/PNAS.1803456116/SUPPL_FILE/PNAS.1803456116.SAPP.PDF

Fridley, J. D. (2013). Plant invasions across the northern hemisphere: A deep-time perspective. *Annals of the New York Academy of Sciences*, *1293*, 8–17. https://doi.org/10.1111/NYAS.12107

Gallagher, R. V., Randall, R. P., & Leishman, M. R. (2015). Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. *Conservation Biology*, *29*, 360–369. https://doi.org/10.1111/COBI.12399

Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, *40*, 335–352. https://doi.org/10.1111/ECOG.02446

GBIF. (2025). GBIF Home Page. https://www.gbif.org

Gippet, J. M., Liebhold, A. M., Fenn-Moltu, G., & Bertelsmeier, C. (2019). Human-mediated dispersal in insects. *Current Opinion in Insect Science*, *35*, 96–102. https://doi.org/10.1016/J.COIS.2019.07.005

Gleser, L. J., & Olkin, I. (2007). *Stochastically dependent effect sizes*. Deparment of Statistics, Stanford University.

Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *326*, 119–157. https://doi.org/10.1098/RSTB.1989.0106

Hajek, A. E., Henry, J. C., Standley, C. R., & Foelker, C. J. (2017). Comparing functional traits and abundance of invasive versus native woodwasps. *NeoBiota*, *36*, 39–55. https://doi.org/10.3897/neobiota.36.14953

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., de Boer, J. G., De Snoo, G. R., Deacon, C., Dell, J. E., Desneux, N., Dillon, M. E., Duffy, G. A., Dyer, L. A., … Chown, S. L. (2023). Scientists' warning on climate change and insects. *Ecological Monographs*, *93*, e1553. https://doi.org/10.1002/ECM.1553

Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success? *Biological Invasions*, *10*, 483–506. https://doi.org/10.1007/s10530-007-9146-5

Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., & Case, T. J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology, Evolution, and Systematics*, *33*, 181–233. https://doi.org/10.1146/ANNUREV.ECOLSYS.33.010802.150444/CITE/REFWORKS

Huang, D., Haack, R. A., & Zhang, R. (2011). Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. *PLoS One*, *6*, e24733. https://doi.org/10.1371/JOURNAL.PONE.0024733

Hulme, P. E., & Bernard-Verdier, M. (2018). Comparing traits of native and alien plants: Can we do better? *Functional Ecology*, *32*, 117–125. https://doi.org/10.1111/1365-2435.12982/SUPPINFO

Invasive Species Specialist Group ISSG. (2015). Global Invasive Species Database Version 2015.1. [WWW Document]. https://www.iucngisd.org/gisd

Jarošík, V., Kenis, M., Honek, A., Skuhrovec, J., & Pysek, P. (2015). Invasive insects differ from non-invasive in their thermal requirements. *PLoS One*, *10*, e0131072. https://doi.org/10.1371/journal.pone.0131072

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*, 9982. https://doi.org/10.1126/SCIADV.ABM9982/SUPPL_FILE/SCIADV.ABM9982_DATA_S1.ZIP

Kelley, A. L., & Cooke, S. (2014). The role thermal physiology plays in species invasion. *Conservation Physiology*, *2*, cou045. https://doi.org/10.1093/CONPHYS/COU045

Kenis, M., Rabitsch, W., Auger-Rozenberg, M.-A., & Roques, A. (2007). How can alien species inventories and interception data help us prevent insect invasions? *Bulletin of Entomological Research*, *97*, 489–502. https://doi.org/10.1017/S0007485307005184

Kueffer, C., Pyšek, P., & Richardson, D. M. (2013). Integrative invasion science: Model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, *200*, 615–633. https://doi.org/10.1111/NPH.12415

Lau, J. A., & Funk, J. L. (2023). How ecological and evolutionary theory expanded the 'ideal weed' concept. *Oecologia*, *203*(3), 251–266. https://doi.org/10.1007/S00442-023-05397-8

Lawton, J. H., & Brown, K. C. (1986). The population and community ecology of invading insects. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *314*, 607–617. https://doi.org/10.1098/RSTB.1986.0076

Liebhold, A. M., & Tobin, P. C. (2008). Population ecology of insect invasions and their management. *Annual Review of Entomology*, *53*, 387–408. https://doi.org/10.1146/ANNUREV.ENTO.52.110405.091401/CITE/REFWORKS

Liebhold, A. M., Turner, R. M., Bartlett, C. R., Bertelsmeier, C., Blake, R. E., Brockerhoff, E. G., Causton, C. E., Matsunaga, J. N., McKamey, S. H., Nahrung, H. F., Owen, C. L., Pureswaran, D. S., Roques, A., Schneider, S. A., Sanborn, A. F., & Yamanaka, T. (2024). Why so many Hemiptera invasions? *Diversity and Distributions*, *30*, e13911. https://doi.org/10.1111/DDI.13911

Liebhold, A. M., Yamanaka, T., Roques, A., Augustin, S., Chown, S. L., Brockerhoff, E. G., & Pyšek, P. (2016). Global compositional variation among native and non-native regional insect assemblages emphasizes the importance of pathways. *Biological Invasions*, *18*, 893–905. https://doi.org/10.1007/s10530-016-1079-4

Lieurance, D., Canavan, S., Behringer, D. C., Kendig, A. E., Minteer, C. R., Reisinger, L. S., Romagosa, C. M., Flory, S. L., Lockwood, J. L., Anderson, P. J., Baker, S. M., Bojko, J., Bowers, K. E., Canavan, K., Carruthers, K., Daniel, W. M., Gordon, D. R., Hill, J. E., Howeth, J. G., … Wanamaker, C. (2023). Identifying invasive species threats, pathways, and impacts to improve biosecurity. *Ecosphere*, *14*, e4711. https://doi.org/10.1002/ECS2.4711

Lipsey, M. W., & Wilson, D. B. (2001). *Practical meta-analysis*. Sage Publications, Inc.

Liu, C., Comte, L., & Olden, J. D. (2017). Heads you win, tails you lose: Life-history traits predict invasion and extinction risk of the world's freshwater fishes. *Aquatic Conservation*, *27*, 773–779. https://doi.org/10.1002/AQC.2740;WGROUP:STRING:PUBLICATION

Liu, C., Wolter, C., Xian, W., & Jeschke, J. M. (2020). Most invasive species largely conserve their climatic niche. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 23643–23651. https://doi.org/10.1073/PNAS.2004289117/SUPPL_FILE/PNAS.2004289117.SD01.XLSX

Logan, M. L., Minnaar, I. A., Keegan, K. M., & Clusella-Trullas, S. (2020). The evolutionary potential of an insect invader under climate change*. *Evolution*, *74*, 132–144. https://doi.org/10.1111/EVO.13862

Macartney, E. L., Crean, A. J., Nakagawa, S., & Bonduriansky, R. (2019). Effects of nutrient limitation on sperm and seminal fluid: A systematic review and meta-analysis. *Biological Reviews*, *94*, 1722–1739. https://doi.org/10.1111/brv.12524

MacLachlan, M. J., Liebhold, A. M., Yamanaka, T., & Springborn, M. R. (2021). Hidden patterns of insect establishment risk revealed from two centuries of alien species discoveries. *Science Advances*, *7*, eabj1012. https://doi.org/10.1126/SCIADV.ABJ1012/SUPPL_FILE/SCIADV.ABJ1012_SM.PDF

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Mally, R., Turner, R. M., Nahrung, H. F., Yamanaka, T., Fenn-Moltu, G., Bertelsmeier, C., & Liebhold, A. M. (2024). Historical invasion rates vary among insect trophic groups. *Current Biology*, *34*, 5374–5381. e3. https://doi.org/10.1016/J.CUB.2024.09.068

Mathakutha, R., Steyn, C., le Roux, P. C., Blom, I. J., Chown, S. L., Daru, B. H., Ripley, B. S., Louw, A., & Greve, M. (2019). Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science*, *30*, 994–1006. https://doi.org/10.1111/JVS.12772

McKnight, E., García-Berthou, E., Srean, P., & Rius, M. (2017). Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. *Global Change Biology*, *23*, 1861–1870. https://doi.org/10.1111/GCB.13524

Michonneau, F., Brown, J., & Winter, D. (2016). Rotl: An R package to interact with the open Tree of life data. *Methods in Ecology and Evolution*, *7*, 1476–1481.

Minnaar, I. A., Hui, C., & Clusella-Trullas, S. (2022). Jack, master or both? The invasive ladybird *Harmonia axyridis* performs better than a native coccinellid despite divergent trait plasticity. *NeoBiota*, *77*, 179–207. https://doi.org/10.3897/neobiota.77.91402

Nahrung, H. F., & Swain, A. J. (2015). Strangers in a strange land: Do life history traits differ for alien and native colonisers of novel environments? *Biological Invasions*, *17*, 699–709. https://doi.org/10.1007/s10530-014-0761-7

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, *13*, 4–21. https://doi.org/10.32942/OSF.IO/K7PMZ

Nakagawa, S., Lagisz, M., O'Dea, R. E., Pottier, P., Rutkowska, J., Senior, A. M., Yang, Y., & Noble, D. W. A. (2023). orchaRd 2.0: An R package for visualising meta-analyses with orchard plots. *Methods in Ecology and Evolution*, *14*, 2003–2010. https://doi.org/10.1111/2041-210X.14152

Ordonez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology*, *24*, 1353–1361. https://doi.org/10.1111/J.1365-2435.2010.01739.X

Pagad, S., Bisset, S., Genovesi, P., Groom, Q., Hirsch, T., Jetz, W., Ranipeta, A., Schigel, D., Sica, Y. V., & McGeoch, M. A. (2022). Country compendium of the global register of introduced and invasive species. *Scientific Data*, *9*(1), 1–13. https://doi.org/10.1038/s41597-022-01514-z

Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., … Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *BMJ*, *372*, n71. https://doi.org/10.1136/BMJ.N71

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pottier, P., Burke, S., Drobniak, S. M., Lagisz, M., & Nakagawa, S. (2021). Sexual (in)equality? A meta-analysis of sex differences in thermal acclimation capacity across ectotherms. *Functional Ecology*, *35*, 2663–2678. https://doi.org/10.1111/1365-2435.13899

R Core Team. (2023). R: A language and environment for statistical computing.

Raak-van den Berg, C. L., de Jong, P. W., Gort, G., Manly, B. F. J., & van Lenteren, J. C. (2018). Life histories of an invasive and native ladybird under field experimental conditions in a temperate climate. *Entomologia Experimentalis et Applicata*, *166*, 151–161. https://doi.org/10.1111/EEA.12658

Radville, L., Gonda-King, L., Gomez, S., Kaplan, I., & Preisser, E. L. (2014). Are exotic herbivores better competitors? A meta-analysis. *Ecology*, *95*, 30–36. https://doi.org/10.1890/13-0728.1

Reitz, S. R., & Trumble, J. T. (2002). Competitive displacement among insects and arachnids. *Annual Review of Entomology*, *47*, 435–465. https://doi.org/10.1146/annurev.ento.47.091201.145227

Rejmánek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, *77*, 1655–1661. https://doi.org/10.2307/2265768

Renault, D., Laparie, M., McCauley, S. J., & Bonte, D. (2018). Environmental adaptations, ecological filtering, and dispersal central to insect invasions. *Annual Review of Entomology*, *63*, 345–368. https://doi.org/10.1146/ANNUREV-ENTO-020117-043315/1

Revell, L. J. (2024). Phytools 2.0: An updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ*, *12*, e16505. https://doi.org/10.7717/PEERJ.16505

Roderick, G. K., & Navajas, M. (2015). Invasions of terrestrial arthropods: Mechanisms, pathways, and dynamics. In *Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions* (pp. 75–87). De Gruyter Open. https://doi.org/10.1515/9783110438666-008

Rohatgi, A. (2010). WebPlotDigitizer—extract data from plots, images, and maps. Arohatgi.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., & Weller, S. G. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, *32*, 305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Sánchez-Meca, J., Marín-Martínez, F., & Chacón-Moscoso, S. (2003). Effect-size indices for dichotomized outcomes in meta-analysis. *Psychological Methods*, *8*, 448–467.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*(1), 1–9. https://doi.org/10.1038/ncomms14435

Shackleton, R. T., Shackleton, C. M., & Kull, C. A. (2019). The role of invasive alien species in shaping local livelihoods and human well-being: A review. *Journal of Environmental Management*, *229*, 145–157. https://doi.org/10.1016/J.JENVMAN.2018.05.007

Simões, M. V. P., Nuñez-Penichet, C., Warren, D., Schmitt, T., & Krull, M. (2023). Regional anthropogenic disturbance and species-specific niche traits influence the invasiveness of European beetle species. *Frontiers in Ecology and Evolution*, *11*, 1160598. https://doi.org/10.3389/FEVO.2023.1160598/FULL

Sutherland, S. (2004). What makes a weed a weed: Life history traits of native and exotic plants in the USA. *Oecologia*, *141*, 24–39. https://doi.org/10.1007/S00442-004-1628-X

Theoharides, K. A., & Dukes, J. S. (2007). Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, *176*, 256–273. https://doi.org/10.1111/J.1469-8137.2007.02207.X

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, *8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Turner, R. M., Brockerhoff, E. G., Bertelsmeier, C., Blake, R. E., Caton, B., James, A., Macleod, A., Nahrung, H. F., Pawson, S. M., Plank, M. J., Pureswaran, D. S., Seebens, H., Yamanaka, T., Liebhold, A. M., Turner, R. M., Brockerhoff, E. G., Bertelsmeier, C., Blake, R. E., Caton, B., … Liebhold, A. M. (2021). Worldwide border interceptions provide a window into human-mediated global insect movement. *Ecological Applications*, *31*, e02412. https://doi.org/10.1002/EAP.2412

van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology*, *24*, 1954–1968. https://doi.org/10.1111/MEC.13013

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*, 235–245. https://doi.org/10.1111/J.1461-0248.2009.01418.X

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor. *Journal of Statistical Software*, *36*, 1–48.

Ward, N. L., & Masters, G. J. (2007). Linking climate change and species invasion: An illustration using insect herbivores. *Global Change Biology*, *13*, 1605–1615. https://doi.org/10.1111/j.1365-2486.2007.01399.x

Weaving, H., Minnaar, I. A., Hui, C., Logan, M. L., & Clusella-Trullas, S. C. (2026). Data from: Invasive insects outperform their native counterparts. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.c59zw3rrk

Weaving, H., Terblanche, J. S., Pottier, P., & English, S. (2022). Meta-analysis reveals weak but pervasive plasticity in insect thermal limits. *Nature Communications*, *13*, 5292. https://doi.org/10.1038/s41467-022-32953-2

Wong, M. K. L., Lee, R. H., Leong, C. M., Lewis, O. T., & Guénard, B. (2022). Trait-mediated competition drives an ant invasion and alters functional diversity. *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20220504. https://doi.org/10.1098/RSPB.2022.0504;CTYPE:STRING:JOURNAL

Zenni, R. D., & Nuñez, M. A. (2013). The elephant in the room: The role of failed invasions in understanding invasion biology. *Oikos*, *122*, 801–815. https://doi.org/10.1111/J.1600-0706.2012.00254.X

Zhang, B., Hastings, A., Grosholz, E. D., & Zhai, L. (2023). The comparison of dispersal rate between invasive and native species varied by plant life form and functional traits. *Movement Ecology*, *11*, 1–10. https://doi.org/10.1186/S40462-023-00424-Y/FIGURES/3

Zhao, Z., Hui, C., Peng, S., Yi, S., Li, Z., Reddy, G. V. P., & van Kleunen, M. (2023). The world's 100 worst invasive alien insect species differ in their characteristics from related non-invasive species. *Journal of Applied Biology*, *60*, 1929-1938. https://doi.org/10.1111/1365-2664.14485

DATA SOURCES

Abril, S., & Gómez, C. (2009). Ascertaining key factors behind the coexistence of the native ant species *Plagiolepis pygmaea* with the invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae). *Sociobiology*, *53*, 559–568.

Aizen, M. A., Lozada, M., & Morales, C. L. (2011). Comparative nectar-foraging behaviors and efficiencies of an alien and a native bumble bee. *Biological Invasions*, *13*(12), 2901–2909.

Alba-Lynn, C., & Henk, S. (2010). Potential for ants and vertebrate predators to shape seed-dispersal dynamics of the invasive thistles *Cirsium arvense* and *Carduus nutans* in their introduced range (North America). *Plant Ecology*, *210*(2), 291–301.

Alto, B. W., Malicoate, J., Elliott, S. M., & Taylor, J. (2012). Demographic consequences of predators on prey: Trait and density mediated effects on mosquito larvae in containers. *PLoS One*, *7*(11), e45785.

Aluja, M., Lopez, M., & Sivinski, J. (1998). Ecological evidence for diapause in four native and one exotic species of larval-pupal fruit fly (Diptera: Tephritidae) parasitoids in tropical environments. *Annals of the Entomological Society of America*, *91*(6), 821–833.

Alvarez-Blanco, P., Caut, S., Cerdá, X., & Angulo, E. (2017). Native predators living in invaded areas: Responses of terrestrial amphibian species to an Argentine ant invasion. *Oecologia*, *185*(1), 95–106.

Al-wahaibi, A. K., & Morse, J. G. (2009). Egg stage of *Homalodisca vitripennis* and *Homalodisca liturata* (Hemiptera: Cicadellidae): Ovometrics, embryonic development, and nonparasitic mortality. *Annals of the Entomological Society of America*, *102*, 249–260.

Al-Wahaibi, A. K., & Morse, J. G. (2010). Temporal patterns in homalodisca spp. (Hemiptera: Cicadellidae) oviposition on Southern California citrus and jojoba. *Environmental Entomology*, *39*(1), 15–30.

Arismendi, N., Riveros, G., Zapata, N., Smagghe, G., González, C., & Vargas, M. (2021). Occurrence of bee viruses and pathogens associated with emerging infectious diseases in native and non-native bumble bees in southern Chile. *Biological Invasions*, *23*(4), 1175–1189.

Armstrong, T. R., & Stamp, N. E. (2003). Colony productivity and foundress behaviour of a native wasp versus an invasive social wasp. *Ecological Entomology*, *28*(6), 635–644.

Asfiya, W., Yeeles, P., Lach, L., Majer, J. D., Heterick, B., & Didham, R. K. (2016). Abiotic factors affecting the foraging activity and potential displacement of native ants by the invasive African big-headed ant Pheidole megacephala (FABRICIUS, 1793) (Hymenoptera: Formicidae). *Myrmecological News*, *22*, 43–54.

Barahona-Segovia, R. M., Grez, A. A., & Bozinovic, F. (2016). Testing the hypothesis of greater eurythermality in invasive than in native ladybird species: From physiological performance to life-history strategies. *Ecological Entomology*, *41*(2), 182–191.

Barbosa, L. S., Couri, M. S., Coelho, V. M. A., & Avelino-Capistrano, F. (2016). The classic episode of biological invasion: *Cochliomyia macellaria* (Fabricius, 1775) versus *Chrysomya megacephala* (Fabricius, 1794) (Diptera: Calliphoridae)—evaluation of the biotic potential. *Anais Da Academia Brasileira de Ciencias*, *88*(3), 1401–1406.

Bednar, D. M., Shik, J. Z., & Silverman, J. (2013). Prey handling performance facilitates competitive dominance of an invasive over native keystone ant. *Behavioral Ecology*, *24*(6), 1312–1319.

Benadé, P. C., Veldtman, R., Samways, M. J., & Roets, F. (2014). Rapid range expansion of the invasive wasp *Polistes dominula* (Hymenoptera: Vespidae: Polistinae) and first record of parasitoids on this species and the native *Polistes marginalis* in the Western Cape Province of South Africa. *African Entomology*, *22*, 220–225.

Berthiaume, R., Bert, C. H., & Cloutier, C. (2007). Comparative use of *Mindarus abietinus* (Homoptera: Aphididae) by two Coccinellids (Coleoptera: Coccinellidae), the native Anatis Mali and the exotic *Harmonia axyridis*, in a Christmas tree plantation. *Environmental Entomology*, *36*(2), 319–328.

Bertleff, D., Diekmann, J., Brand, S., Ünlü, A. G., & Bucher, R. (2021). Predation and avoidance behaviour in aphid-ladybird interactions of native and invasive ladybirds in Europe. *Ecological Entomology*, *46*(1), 41–47.

Berville, L., & Darrouzet, E. (2019). Wood excavation, construction, and architecture in two Reticulitermes subterranean termites. *Insectes Sociaux*, *66*(3), 403–411.

Bhuyain, M. M. H., & Lim, U. T. (2019). Interference and exploitation competition between *Frankliniella occidentalis* and *F. intonsa* (Thysanoptera: Thripidae) in laboratory assays. *Florida Entomologist*, *102*(2), 322–328.

Blight, O., Provost, E., Renucci, M., Tirard, A., & Orgeas, J. (2010). A native ant armed to limit the spread of the Argentine ant. *Biological Invasions*, *12*(11), 3785–3793.

Boher, F., Jaksic, F. M., Martel, S. I., Orellana, M. J., & Bozinovic, F. (2018). Does thermal physiology explain the ecological and evolutionary success of invasive species? Lessons from ladybird beetles. *Evolutionary Ecology Research*, *19*, 243–255.

Boivin, T., Rouault, G., Chalon, A., & Candau, J. N. (2008). Differences in life history strategies between an invasive and a competing resident seed predator. *Biological Invasions*, *10*(7), 1013–1025.

Brossette, L., Bagnères, A. G., Millot, A., Blanchard, S., Dupont, S., & Lucas, C. (2017). Termite's royal cradle: Does colony foundation success differ between two subterranean species? *Insectes Sociaux*, *64*(4), 515–523.

Brossette, L., Meunier, J., Dupont, S., Bagnères, A. G., & Lucas, C. (2019). Unbalanced biparental care during colony foundation in two subterranean termites. *Ecology and Evolution*, *9*(1), 192–200.

Brundage, A., Benbow, M. E., & Tomberlin, J. K. (2014). Priority effects on the life-history traits of two carrion blow fly (Diptera, Calliphoridae) species. *Ecological Entomology*, *39*(5), 539–547.

Bugila, A. A. A., Branco, M., da Silva, E. B., & Franco, J. C. (2014). Host selection behaviour and specificity of the solitary parasitoid of mealybugs *Anagyrus* sp. nr. Pseudococci (Girault) (Hymenoptera, Encyrtidae). *Biocontrol Science and Technology*, *24*(1), 22–38.

Bujan, J., Roeder, K. A., Yanoviak, S. P., & Kaspari, M. (2020). Seasonal plasticity of thermal tolerance in ants. *Ecology*, *101*(6), e03051.

Buonocore Biancheri, M. J., Suárez, L., Kirschbaum, D. S., Garcia, F. R. M., Funes, C. F., & Ovruski, S. M. (2022). Natural parasitism influences biological control strategies against both global invasive pests *Ceratitis capitata* (Diptera: Tephritidae) and *Drosophila suzukii* (Diptera: Drosophilidae), and the Neotropical-Native Pest *Anastrepha fraterculus* (Diptera: Tephritidae). *Environmental Entomology*, *51*(6), 1120–1135.

Bürgi, L. P., & Mills, N. J. (2014). Lack of enemy release for an invasive leafroller in California: Temporal patterns and influence of host plant origin. *Biological Invasions*, *16*(5), 1021–1034.

Buxton, M., Nyamukondiwa, C., Dalu, T., Cuthbert, R. N., & Wasserman, R. J. (2020). Implications of increasing temperature stress for predatory biocontrol of vector mosquitoes. *Parasites and Vectors*, *13*(1), 604.

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Camacho-Cervantes, M., Mendoza-Arroyo, W., Arellano-Sánchez, D., & del-Val, E. (2021). Exotic predators are not better biocontrol agents: The harlequin ladybird is not the most voracious in Mexico. *PeerJ*, *9*, e12503.

Cao, Y., Yang, H., Li, J., Zhang, G., Wang, Y., Li, C., & Gao, Y. (2019). Population development of *Frankliniella occidentalis* and *Thrips hawaiiensis* in constant and fluctuating temperatures. *Journal of Applied Entomology*, *143*(1–2), 49–57.

Carmo, R. F. R., Astúa, D., & Vasconcelos, S. D. (2022). Environmental conditions differently affect the wing size and shape of two blow fly species (Calliphoridae) of forensic importance in the Brazilian tropical ecosystems. *International Journal of Tropical Insect Science*, *42*(2), 1903–1911.

Carmo, R. F. R., Vasconcelos, S. D., Brundage, A. L., & Tomberlin, J. K. (2018). How do invasive species affect native species? Experimental evidence from a carrion blowfly (Diptera: Calliphoridae) system. *Ecological Entomology*, *43*(4), 483–493.

Carpintero, S., Retana, J., Cerda´, X., Cerda´, C., Reyes-Lo'pez, J., Lo'pez, L., Arias, A. L., & Reyna, D. E. (2007). Exploitative strategies of the invasive Argentine ant (*Linepithema humile*) and native ant species in a southern Spanish pine Forest. *Environmental Entomology*, *36*(5), 1100–1111.

Carpintero, S., & Reyes-López, J. (2008). The role of competitive dominance in the invasive ability of the Argentine ant (*Linepithema humile*). *Biological Invasions*, *10*(1), 25–35.

Cilia, G., Flaminio, S., Ranalli, R., Zavatta, L., Nanetti, A., Bortolotti, L., & Bogo, G. (2023). Presence of Apis mellifera pathogens in different developmental stages of wild Hymenoptera species. *Bulletin of Insectology*, *76*(1), 147–154.

Comont, R. F., Purse, B. v., Phillips, W., Kunin, W. E., Hanson, M., Lewis, O. T., Harrington, R., Shortall, C. R., Rondoni, G., & Roy, H. E. (2014). Escape from parasitism by the invasive alien ladybird, *Harmonia axyridis*. *Insect Conservation and Diversity*, *7*(4), 334–342.

Cornelius, M. L., Herlihy, M. v., Vinyard, B. T., Weber, D. C., & Greenstone, M. H. (2021). Parasitism and predation on sentinel egg masses of three stink bug species (Hemiptera: Pentatomidae) in native and exotic ornamental landscapes. *Journal of Economic Entomology*, *114*(2), 590–596.

Cottrell, T., & Shapiro-Ilan, D. (2008). Susceptibility of endemic and exotic north American ladybirds (Coleoptera: Coccinellidae) to endemic fungal entomopathogens. *European Journal of Entomology*, *105*, 455–460.

Cottrell, T. E. (2005). Predation and cannibalism of lady beetle eggs by adult lady beetles. *Biological Control*, *34*(2), 159–164.

Cottrell, T. E. (2007). Predation by adult and larval lady beetles (Coleoptera: Coccinellidae) on initial contact with lady beetle eggs. *Environmental Entomology*, *36*, 390–401.

Cottrell, T. E., & Yeargan, K. V. (1998). Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of the Kansas Entomological Society*, *71*(2), 159–163.

Cremer, S., Ugelvig, L. v., te Lommen, S., Petersen, K. S., & Pedersen, J. S. (2006). Attack of the invasive garden ant: Aggression behaviour of *Lasius neglectus* (Hymenoptera: Formicidae) against native Lasius species in Spain. *Myrmecologische Nachrichten*, *9*, 13–19.

Curtis, T., & Stamp, N. (2006). Effects of human presence on two social wasp species. *Ecological Entomology*, *31*, 13–19.

Curtis, T. R., Aponte, Y., & Stamp, N. E. (2005). Nest paper absorbency, toughness, and protein concentration of a native vs. an invasive social wasp. *Journal of Chemical Ecology*, *31*(5), 1089–1100.

Daane, K. M., da Silva, P. G., Stahl, J. M., Scaccini, D., & Wang, X. (2022). Comparative life history parameters of three stink bug pest species. *Environmental Entomology*, *51*(2), 430–439.

Day, W. H. (1999). Host preferences of introduced and native parasites (Hymenoptera: Braconidae) of phytophagous plant bugs (Hemiptera: Miridae) in alfalfa-grass fields in the northeastern USA. *BioControl*, *44*, 249–261.

Dejean, A., Kenne, M., & Moreau, C. S. (2007). Predatory abilities favour the success of the invasive ant *Pheidole megacephala* in an introduced area. *Journal of Applied Entomology*, *131*(9–10), 625–629.

Divya, J., Kalleshwaraswamy, C. M., Mallikarjuna, H. B., & Deshmukh, S. (2021). Does recently invaded fall armyworm, *Spodoptera frugiperda* displace native lepidopteran pests of maize in India? *Current Science*, *120*(8), 1358–1367.

Drescher, J., Feldhaar, H., & Blüthgen, N. (2011). Interspecific aggression and resource monopolization of the invasive ant *Anoplolepis gracilipes* in Malaysian Borneo. *Biotropica*, *43*(1), 93–99.

Duan, J. J., & Messing, R. H. (2000a). Effect of *Diachasmimorpha tryoni* on two nontarget flowerhead-feeding tephritids. *BioControl*, *45*, 113–125.

Duan, J. J., & Messing, R. H. (2000b). Host specificity tests of *Dichasmimorpha kraussii* (Hymenoptera: Braconidae), a newly introduced opiine fruit fly parasitoid with four nontarget tephritids in Hawaii. *Biological Control*, *19*(1), 28–34.

Dufek, M. I., Battán-Horenstein, M., & Mulieri, P. R. (2021). Blow flies, synanthropy and sex ratio: Are the deviations in the sex proportion linked to human transformation of landscapes? *Acta Tropica*, *222*, 106052.

Duyck, P. F., & Quilici, S. (2002). Survival and development of different life stages of three *Ceratitis* spp. (Diptera: Tephritidae) reared at five constant temperatures. *Bulletin of Entomological Research*, *92*(6), 461–469.

Fabre, J.-P., Auger-Rozenberg, M.-A., Chalon, A., Boivin, S., & Roques, A. (2004). Competition between exotic and native insects for seed resources in trees of a Mediterranean forest ecosystem. *Biological Invasions*, *6*, 11–22.

Fincham, W. N. W., Dunn, A. M., Brown, L. E., Hesketh, H., & Roy, H. E. (2019). Invasion success of a widespread invasive predator may be explained by a high predatory efficacy but may be influenced by pathogen infection. *Biological Invasions*, *21*(12), 3545–3560.

Finlayson, C. J., Alyokhin, A. v., & Porter, E. W. (2009). Interactions of native and non-native lady beetle species (Coleoptera: Coccinellidae) with aphid-tending ants in laboratory arenas. *Environmental Entomology*, *38*, 846–855.

Gabín-García, L. B., Bartolomé, C., Guerra-Tort, C., Rojas-Nossa, S. v., Llovo, J., & Maside, X. (2021). Identification of pathogens in the invasive hornet *Vespa velutina* and in native Hymenoptera (Apidae, Vespidae) from SW-Europe. *Scientific Reports*, *11*, 11233.

Gamboa, G., Greig, E., & Thom, M. (2002). The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera,Vespidae). *Insectes Sociaux*, *49*, 45–49.

Gammans, N., Drummond, F., & Groden, E. (2018). Impacts of the invasive European red ant (*Myrmica rubra* (L.): Hymenoptera; Formicidae) on a Myrmecochorous system in the northeastern United States. *Environmental Entomology*, *47*(4), 908–917.

Garnas, J., Groden, E., & Drummond, F. A. (2014). Mechanisms of competitive displacement of native ant fauna by invading *Myrmica rubra* (Hymenoptera: Formicidae) populations. *Environmental Entomology*, *43*(6), 1496–1506.

Gegner, T., Otti, O., Tragust, S., & Feldhaar, H. (2015). Do microsporidia function as "biological weapon" for *Harmonia axyridis* under natural conditions? *Insect Science*, *22*(3), 353–359.

Gippet, J. M. W., Colin, T., Grangier, J., Winkler, F., Haond, M., Dumet, A., Tragust, S., Mondy, N., & Kaufmann, B. (2021). Land-cover and climate factors contribute to the prevalence of the ectoparasitic fungus *Laboulbenia formicarum* in its invasive ant host *Lasius neglectus*. *Fungal Ecology*, *51*, 101045.

Greenberg, L., Kabashima, J. N., Allison, C. J., Rust, M. K., Klotz, J. H., Hurvois, J.-P., & Paine, T. D. (2008). Lethality of red imported fire ant venom to Argentine ants and other ant species. *Annals of the Entomological Society of America*, *101*(6), 1162–1168.

Haavik, L. J., Allison, J. D., MacQuarrie, C. J. K., Nott, R. W., Ryan, K., de Groot, P., & Turgeon, J. J. (2016). Nonlethal effects of nematode infection on *Sirex noctilio* and *Sirex nigricornis* (Hymenoptera: Siricidae). *Environmental Entomology*, *45*(2), 320–327.

Haavik, L. J., Yu, Q., Turgeon, J. J., & Allison, J. D. (2016). Horizontal transmission of a parasitic nematode from a non-native to a native woodwasp? *Biological Invasions*, *18*(2), 355–358.

Haelewaters, D., Hiller, T., Kemp, E. A., van Wielink, P. S., Shapiro-Ilan, D. I., Catherine Aime, M., Nedvěd, O., Pfister, D. H., & Cottrell, T. E. (2020). Mortality of native and invasive ladybirds co-infected by ectoparasitic and entomopathogenic fungi. *PeerJ*, *8*, e10110.

Haelewaters, D., Minnaar, I. A., & Clusella-Trullas, S. (2016). First finding of the parasitic fungus *Hesperomyces virescens* (Laboulbeniales) on native and invasive ladybirds (Coleoptera, Coccinellidae) in South Africa. *Parasite*, *23*, 5.

Hajek, A. E., Henry, J. C., Standley, C. R., & Foelker, C. J. (2017). Comparing functional traits and abundance of invasive versus native woodwasps. *NeoBiota*, *36*, 39–55.

Harwood, J., Ricci, C., Romani, R., Pitz, K., Weir, A., & Obrycki, J. (2006). Prevalence and association of the laboulbenialean fungus *Hesperomyces virescens* (Laboulbeniales: Laboulbeniaceae) on coccinellid hosts (Coleoptera: Coccinellidae) in Kentucky, USA. *European Journal of Entomology*, *103*, 799–804.

Hentley, W. T., Vanbergen, A. J., Beckerman, A. P., Brien, M. N., Hails, R. S., Jones, T. H., & Johnson, S. N. (2016). Antagonistic interactions between an invasive alien and a native coccinellid species may promote coexistence. *Journal of Animal Ecology*, *85*(4), 1087–1097.

Holway, D. A. (1999). Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology*, *80*(1), 238–251.

Holway, D. A., Suarez, A. v., & Case, T. J. (2002). Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. *Ecology*, *83*(6), 1610–1619.

Honek, A., Martinkova, Z., & Ceryngier, P. (2019). Different parasitization parameters of pupae of native (*Coccinella septempunctata*) and invasive (*Harmonia axyridis*) coccinellid species. *Bulletin of Insectology*, *72*(1), 77–83.

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hoogendoorn, M., & Heimpel, G. E. (2002). Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biological Control*, *25*, 224–230.

Inoue, M. N., Yokoyama, J., & Washitani, I. (2008). Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Journal of Insect Conservation*, *12*(2), 135–146.

Jackson, K. A., McCord, J. S., & White, J. A. (2017). A window of opportunity: Subdominant predators can use suboptimal prey. *Ecology and Evolution*, *7*(14), 5269–5275.

Jones, C., & DiRienzo, N. (2018). Behavioral variation post-invasion: Resemblance in some, but not all, behavioral patterns among invasive and native praying mantids. *Behavioural Processes*, *153*, 92–99.

Jones, C. M., & Brown, M. J. F. (2014). Parasites and genetic diversity in an invasive bumblebee. *Journal of Animal Ecology*, *83*(6), 1428–1440.

Juliano, S. A., Westby, K. M., & Ower, G. D. (2019). Know your enemy: Effects of a predator on native and invasive container mosquitoes. *Journal of Medical Entomology*, *56*(2), 320–328.

Kajita, Y., & Evans, E. W. (2009). Ovarian dynamics and oosorption in two species of predatory lady beetles (Coleoptera: Coccinellidae). *Physiological Entomology*, *34*(2), 185–194.

Kajita, Y., & Evans, E. W. (2010a). Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle. *Biological Invasions*, *12*(7), 2293–2302.

Kajita, Y., & Evans, E. W. (2010b). Relationships of body size, fecundity, and invasion success among predatory lady beetles (Coleoptera: Coccinellidae) inhabiting alfalfa fields. *Annals of the Entomological Society of America*, *103*(5), 750–756.

Kajita, Y., Evans, E. W., & Yasuda, A. H. (2009). Reproductive responses of invasive and native predatory lady beetles (Coleoptera: Coccinellidae) to varying prey availability. *Environmental Entomology*, *38*(4), 1283–1292.

Kambura, C., Tanga, C. M., Kilalo, D., Muthomi, J., Salifu, D., Rwomushana, I., Mohamed, S. A., & Ekesi, S. (2018). Composition, host range and host suitability of vegetable-infesting Tephritids on cucurbits cultivated in Kenya. *African Entomology*, *26*(2), 398–406.

Kaufman, L. V., & Wright, M. G. (2010). Parasitism of a Hawaiian endemic moth by invasive and purposely introduced hymenoptera species. *Environmental Entomology*, *39*(2), 430–439.

Kerr, N. Z., Crone, E. E., & Chew, F. S. (2020). Life history trade-offs are more pronounced for a noninvasive, native butterfly compared to its invasive, exotic congener. *Population Ecology*, *62*(1), 119–133.

Koyama, S., & Majerus, M. E. N. (2008). Interactions between the parasitoid wasp *Dinocampus coccinellae* and two species of coccinellid from Japan and Britain. *BioControl*, *53*(1), 253–264.

Kwon, O., & Choi, M. B. (2020). Interspecific hierarchies from aggressiveness and body size among the invasive alien hornet, *Vespa velutina nigrithorax*, and five native hornets in South Korea. *PLoS One*, *15*, e0226934.

Labrie, G., Coderre, D., & Lucas, E. ´. (2008). Overwintering strategy of multicolored Asian lady beetle (Coleoptera: Coccinellidae): Cold-free space As a factor of invasive success. *Annals of the Entomological Society of America*, *101*, 860–866.

LeCroy, K. A., Krichilsky, E., Grab, H. L., Roulston, T. H., & Danforth, B. N. (2023). Spillover of chalkbrood fungi to native solitary bee species from non-native congeners. *Journal of Applied Ecology*, *60*(6), 1067–1076.

Lefort, M. C., Brown, S., Boyer, S., Worner, S., & Armstrong, K. (2014). The PGI enzyme system and fitness response to temperature as a measure of environmental tolerance in an invasive species. *PeerJ*, *2*(2), e676.

Leonetti, D., Centorame, M., & Fanfani, A. (2019). Differences in exploitation and interference ability between two dominant ants: The invasive Argentine ant (*Linepithema humile*) and Tapinoma magnum. *Ethology Ecology & Evolution*, *31*(4), 369–385.

Liebert, A. E., Gamboa, G. J., Stamp, N. E., Curtis, T. R., Monnet, K. M., Turillazzi, S., & Starks, P. T. (2006). Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. *Annales Zoologici Fennici*, *43*(5), 595–624.

Lin, Z. H., Wu, C. H., & Ho, C. K. (2018). Warming neutralizes host-specific competitive advantages between a native and invasive herbivore. *Scientific Reports*, *8*(1), 11130.

Long, A. K., Knapp, D. D., Mccullough, L., Smith, L. L., Conner, L. M., & Mccleery, R. A. (2015). Southern toads alter their behavior in response to red-imported fire ants. *Biological Invasions*, *17*(7), 2179–2186.

Losey, J., Perlman, J., Kopco, J., Ramsey, S., Hesler, L., Evans, E., Allee, L., & Smyth, R. (2012). Potential causes and consequences of decreased body size in field populations of *Coccinella novemnotata*. *Biological Control*, *61*, 98–103.

Lounibos, L. P., O'meara, G. F., Escher, R. L., Nishimura, N., Cutwa, M., Nelson, T., Campos, R. E., & Juliano, S. A. (2001). Testing predictions of displacement of native Aedes by the invasive Asian tiger mosquito *Aedes albopictus* in Florida, USA. *Biological Invasions*, *3*, 151–166.

Lu, P., Hao, E., Bao, M., Liu, R., Gao, C., & Qiao, H. (2022). Mating behavior and identification of male-produced pheromone components in two Woodwasps, *Sirex noctilio* and *Sirex nitobei*, in China. *Insects*, *13*(10), 966.

Luan, J. B., de Barro, P. J., Ruan, Y. M., & Liu, S. S. (2013). Distinct behavioural strategies underlying asymmetric mating interactions between invasive and indigenous whiteflies. *Entomologia Experimentalis et Applicata*, *146*(1), 186–194.

Lymbery, S. J., Webber, B. L., & Didham, R. K. (2023). Complex battlefields favor strong soldiers over large armies in social animal warfare. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(37), e2217973120.

Lytle, A. J., Costa, J. T., & Warren, R. J. (2020). Invasion and high-elevation acclimation of the red imported fire ant, *Solenopsis invicta*, in the southern Blue Ridge Escarpment region of North America. *PLoS One*, *15*(5), e0232264.

Mamantov, M. A., & Sheldon, K. S. (2021). Behavioural responses to warming differentially impact survival in introduced and native dung beetles. *Journal of Animal Ecology*, *90*(1), 273–281.

McGlynn, T. P. (1999). Non-native ants are smaller than related native ants. *American Naturalist*, *154*(6), 690–699.

Mcgrannachan, C. M., & Lester, P. J. (2013). Temperature and starvation effects on food exploitation by Argentine ants and native ants in New Zealand. *Journal of Applied Entomology*, *137*(7), 550–559.

Migani, V., Ekesi, S., & Hoffmeister, T. S. (2014). Physiology vs. environment: What drives oviposition decisions in mango fruit flies (*Bactrocera invadens* and *Ceratitis cosyra*)? *Journal of Applied Entomology*, *138*(6), 395–402.

Mignault, M. P., Roy, M., & Brodeur, J. (2006). Soybean aphid predators in Québec and the suitability of Aphis glycines as prey for three Coccinellidae. *BioControl*, *51*(1), 89–106.

Miller, G. L., Donnelly, C. R., & Gamboa, G. J. (2013). A ten-year comparative study of the population dynamics and parasitoidism in the native paper wasp *Polistes fuscatus* and the invasive *P. dominulus*. *Insectes Sociaux*, *60*(1), 49–56.

Minnaar, I. A., Hui, C., & Clusella-Trullas, S. (2022). Jack, master or both? The invasive ladybird *Harmonia axyridis* performs better than a native coccinellid despite divergent trait plasticity. *NeoBiota*, *77*, 179–207.

Mirande, L., Desneux, N., Haramboure, M., & Schneider, M. I. (2015). Intraguild predation between an exotic and a native coccinellid in Argentina: The role of prey density. *Journal of Pest Science*, *88*(1), 155–162.

Moser, S. E., & Obrycki, J. J. (2009). Competition and Intraguild predation among three species of Coccinellids (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America*, *102*, 419–425.

Muturi, E. J., Gardner, A. M., & Bara, J. J. (2015). Impact of an alien invasive shrub on ecology of native and alien invasive mosquito species (Diptera: Culicidae). *Environmental Entomology*, *44*(5), 1308–1315.

Nagamitsu, T., Kenta, T., Inari, N., Horita, H., Goka, K., & Hiura, T. (2007). Foraging interactions between native and exotic bumblebees: Enclosure experiments using native flowering plants. *Journal of Insect Conservation*, *11*(2), 123–130.

Nelson, R. A., MacArthur-Waltz, D. J., & Gordon, D. M. (2023). Critical thermal limits and temperature-dependent walking speed may mediate coexistence between the native winter ant (*Prenolepis imparis*) and the invasive Argentine ant (*Linepithema humile*). *Journal of Thermal Biology*, *111*, 103392.

Nie, L., Bamisile, B. S., Li, Y., Ran, H., Wang, S., Wang, L., & Xu, Y. (2023). Interspecific competition predicts the potential impact of little fire ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) invasion on resident ants in southern China. *Insect Science*, *30*(5), 1518–1530.

Nyamukondiwa, C., Kleynhans, E., & Terblanche, J. S. (2010). Phenotypic plasticity of thermal tolerance contributes to the invasion potential of Mediterranean fruit flies (*Ceratitis capitata*). *Ecological Entomology*, *35*(5), 565–575.

Nyamukondiwa, C., & Terblanche, J. S. (2009). Thermal tolerance in adult Mediterranean and Natal fruit flies (*Ceratitis capitata* and *Ceratitis rosa*): Effects of age, gender and feeding status. *Journal of Thermal Biology*, *34*(8), 406–414.

Nyamukondiwa, C., & Terblanche, J. S. (2010). Within-generation variation of critical thermal limits in adult Mediterranean and Natal fruit flies *Ceratitis capitata* and *Ceratitis rosa*: Thermal history affects short-term responses to temperature. *Physiological Entomology*, *35*(3), 255–264.

Nyamukondiwa, C., Weldon, C. W., Chown, S. L., le Roux, P. C., & Terblanche, J. S. (2013). Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests. *Journal of Insect Physiology*, *59*(12), 1199–1211.

Obrycki, J. J., Giles, K. L., & Ormord, A. M. (1998). Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia*, *117*, 279–285.

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Obrycki, J. J., Ormord, A. M., & Giles, K. L. (1997). Partial life table analysis for larval *Coleomegilla maculata* (Degeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in Alfalfa. *Journal of the Kansas Entomological Society*, *70*(4), 339–346.

Oliver, T., Pettitt, T., Leather, S., & Cook, J. (2008). Numerical abundance of invasive ants and monopolisation of exudate-producing resources—A chicken and egg situation. *Insect Conservation and Diversity*, *1*(4), 208–214.

Paris, C. I., & Espadaler, X. (2009). Honeydew collection by the invasive garden ant *Lasius neglectus* versus the native ant *L. grandis*. *Arthropod-Plant Interactions*, *3*(2), 75–85.

Paula, D. P., Togni, P. H. B., Costa, V. A., Souza, L. M., Sousa, A. A. T. C., Tostes, G. M., Pires, C. S. S., & Andow, D. A. (2021). Scrutinizing the enemy release hypothesis: Population effects of parasitoids on *Harmonia axyridis* and local host coccinellids in Brazil. *BioControl*, *66*(1), 71–82.

Perdereau, E., Dedeine, F., Christidès, J. P., Dupont, S., & Bagnères, A. G. (2011). Competition between invasive and indigenous species: An insular case study of subterranean termites. *Biological Invasions*, *13*(6), 1457–1470.

Phoofolo, M. W., & Obrycki, J. J. (1998). Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomologia Experimentalis et Applicata*, *89*(1), 47–55.

Pilowsky, J. A., & Starks, P. T. (2018). Displacement and replacement in real time: *Polistes dominula*'s impact on *P. fuscatus* in the northeastern U.S. *Biological Invasions*, *20*(5), 1161–1169.

Pinkus-Rendon, M. A., Parra-Tabla, V., & Meléndez-Ramírez, V. (2005). Floral resource use and interactions between *Apis mellifera* and native bees in cucurbit crops in Yucatán, México. *Canadian Entomologist*, *137*(4), 441–449.

Poidatz, J., Bressac, C., Bonnard, O., & Thiéry, D. (2018). Comparison of reproductive traits of foundresses in a native and an invasive hornet in Europe. *Journal of Insect Physiology*, *109*, 93–99.

Polidori, C., & Luis Nieves-Aldrey, J. (2015). Comparative flight morphology in queens of invasive and native Patagonian bumblebees (Hymenoptera: Bombus). *Comptes Rendus. Biologies*, *338*(2), 126–133.

Reiskind, M. H., & Wilson, M. L. (2008). Interspecific competition between larval *Culex restuans* Theobald and *Culex pipiens* L. (Diptera: Culicidae) in Michigan. *Journal of Medical Entomology*, *45*(1), 20–27.

Rhainds, M., Heard, S. B., Sweeney, J. D., Silk, P., & Flaherty, L. (2010). Phenology and spatial distribution of native and exotic tetropium longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, *39*(6), 1794–1800.

Riddick, E. W., & Cottrell, T. E. (2010). Is the prevalence and intensity of the ectoparasitic fungus *Hesperomyces virescens* related to the abundance of entomophagous coccinellids? *Bulletin of Insectology*, *63*(1), 71–78.

Roets, F., Benadé, P. C., Samways, M. J., & Veldtman, R. (2019). Better colony performance, not natural enemy release, explains numerical dominance of the exotic *Polistes dominula* wasp over a native congener in South Africa. *Biological Invasions*, *21*(3), 925–933.

Romanov, D. A., & Matveikina, E. A. (2022). *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) in the cities of Moscow and Yalta: Its competition with native species of Coccinellids and the influence of parasitoids on its number. *Russian Journal of Biological Invasions*, *13*(1), 87–104.

Rondoni, G., Ielo, F., Ricci, C., & Conti, E. (2017). Behavioural and physiological responses to prey-related cues reflect higher competitiveness of invasive vs. native ladybirds. *Scientific Reports*, *7*(1), 3716.

Rosa, G. S., de Carvalho, L. R., & Godoy, W. A. C. (2004). Survival rate, body size and food abundance in pure and mixed blowfly cultures. *African Entomology*, *12*, 97–105.

Saito, T., & Bjørnson, S. (2008). Effects of a microsporidium from the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae), on three non-target coccinellids. *Journal of Invertebrate Pathology*, *99*(3), 294–301.

Sarty, M., Abbott, K. L., & Lester, P. J. (2006). Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia*, *149*(3), 465–473.

Sato, S., Yasuda, H., & Evans, E. W. (2005). Dropping behaviour of larvae of aphidophagous ladybirds and its effects on incidence of intraguild predation: Interactions between the intraguild prey, *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecological Entomology*, *30*(2), 220–224.

Sato, S., Yasuda, H., Evans, E. W., & Dixon, A. F. G. (2009). Vulnerability of larvae of two species of aphidophagous ladybirds, *Adalia bipunctata* Linnaeus and *Harmonia axyridis* Pallas, to cannibalism and intraguild predation. *Entomological Science*, *12*(2), 111–115.

Schilman, P. E., Lighton, J. R. B., & Holway, D. A. (2005). Respiratory and cuticular water loss in insects with continuous gas exchange: Comparison across five ant species. *Journal of Insect Physiology*, *51*(12), 1295–1305.

Schilman, P. E., Lighton, J. R. B., & Holway, D. A. (2007). Water balance in the Argentine ant (*Linepithema humile*) compared with five common native ant species from southern California. *Physiological Entomology*, *32*(1), 1–7.

Serra, C. A., Ferreira, M., García, S., Santana, L., Castillo, M., Nolasco, C., Morales, P., Holler, T., Roda, A., Aluja, M., & Sivinski, J. (2011). Establishment of the west Indian fruit Fly (Diptera: Tephritidae) parasitoid Doryctobracon areolatus (Hymenoptera: Braconidae) in The Dominican Republic. *Florida Entomologist*, *94*(4), 809–816.

Shimizu, K., & Fujisaki, K. (2006). Geographic variation in diapause induction under constant and changing conditions in *Helicoverpa armigera*. *Entomologia Experimentalis et Applicata*, *121*, 253–260.

Silagi, S. A., Gamboa, G. J., Klein, C. R., & Noble, M. A. (2003). Behavioral differences between two recently sympatric paper wasps, the native Polistes Fuscatus and the invasive Polistes Dominulus. *The Great Lakes Entomologist*, *36*, 99–104.

Smith, C. D., Freed, T. Z., & Leisnham, P. T. (2015). Prior hydrologic disturbance affects competition between aedes mosquitoes via changes in leaf litter. *PLoS One*, *10*(6), e0128956.

Snyder, W. E., & Clevenger, G. M. (2004). Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles. *Biological Control*, *31*(3), 353–361.

Song, Y., Yang, X., Zhang, H., Zhang, D., He, W., Wyckhuys, K. A. G., & Wu, K. (2021). Interference competition and predation between invasive and native herbivores in maize. *Journal of Pest Science*, *94*(4), 1053–1063.

Stephens, F. A., Woodard, A. M., & Marsico, T. D. (2012). Comparison between eggsticks of two cactophagous moths, *Cactoblastis cactorum* and *Melitara prodenialis* (Lepidoptera: Pyralidae). *Florida Entomologist*, *95*(4), 939–943.

Sunamura, E., Tamura, S., Mukai, H., Tokoro, M., & Shoda-Kagaya, E. (2022). Mating behavior between alien Asian longhorned beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) and a native related species *Anoplophora chinensis* in Japan. *Applied Entomology and Zoology*, *57*(3), 275–281.

Takizawa, T., & Snyder, W. E. (2012). Alien vs. predator: Could biotic resistance by native generalist predators slow lady beetle invasions? *Biological Control*, *63*(2), 79–86.

Thomas, M. L., & Holway, D. A. (2005). Condition-specific competition between invasive Argentine ants and Australian Iridomyrmex. *Journal of Animal Ecology*, *74*(3), 532–542.

Tillman, P. G., Grabarczyk, E. E., Kesheimer, K. A., & Balusu, R. (2023). Seasonal density and natural mortality of *Halyomorpha halys* (Stål) and indigenous stink bugs (Hemiptera: Pentatomidae) in a field crop agroecosystem. *Journal of Economic Entomology*, *116*(5), 1636–1648.

Tsagkarakis, A. E., Perdikis, D. C., & Lykouressis, D. P. (2013). Introduced and native parasitoids of *Phyllocnistis citrella* Stainton in Greece: Short term post-release evaluation. *Phytoparasitica*, *41*(4), 417–428.

Tsujii, M., Endo, T., Matsui, Y., & Sugiura, S. (2022). Indirect interactions between a native and a supposedly non-native wasp species (Hymenoptera: Vespidae: Eumeninae: Anterhynchium). *European Journal of Entomology*, *119*, 122–132.

Tumminello, G., Ugine, T. A., & Losey, J. E. (2015). Intraguild interactions of native and introduced coccinellids: The decline of a flagship species. *Environmental Entomology*, *44*(1), 64–72.

Tyndale-Biscoe, M. (1994). Dung burial by native and introduced dung beetles (Scarabaeidae). *Australian Journal of Agricultural Research*, *45*, 1799–1808.

Ünlü, A. G., Obrycki, J. J., & Bucher, R. (2020). Comparison of native and non-native predator consumption rates and prey avoidance behavior in North America and Europe. *Ecology and Evolution*, *10*(23), 13334–13344.

Villada-Bedoya, S., Córdoba-Aguilar, A., Escobar, F., Martínez-Morales, I., & González-Tokman, D. (2019). Dung beetle body condition: A tool for disturbance evaluation in contaminated pastures. *Environmental Toxicology and Chemistry*, *38*(11), 2392–2404.

Vindstad, O. P. L., Schott, T., Hagen, S. B., Jepsen, J. U., Kapari, L., & Ims, R. A. (2013). How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid. *Biological Invasions*, *15*(7), 1573–1589.

Walters, A. C., & Mackay, D. A. (2003). An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): Comparisons with a native Iridomyrmex species in South Australia. *Insectes Sociaux*, *50*(4), 355–360.

Walters, A. C., & Mackay, D. A. (2004). Comparisons of upper thermal tolerances between the invasive Argentine ant (hymenoptera: Formicidae) and two

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

native Australian ant species. *Annals of the Entomological Society of America*, *97*, 971–975.
Walters, A. C., & Mackay, D. A. (2005). Importance of large colony size for successful invasion by Argentine ants (Hymenoptera: Formicidae): Evidence for biotic resistance by native ants. *Austral Ecology*, *30*, 395–406.
Wang, M., Wang, L., Fu, N., Gao, C., Ao, T., Ren, L., & Luo, Y. (2020). Comparison of wing, ovipositor, and cornus morphologies between *Sirex noctilio* and *Sirex nitobei* using geometric morphometrics. *Insects*, *11*(2), 84.
Warren, R. J., Candeias, M., Lafferty, A., & Chick, L. D. (2020). Regional-scale environmental resistance to non-native ant invasion. *Biological Invasions*, *22*(2), 813–825.
Warren, R. J., Reed, K., Mathew, A., Krupp, K., Goodman, M., Archibald, K., & Spiering, D. J. (2019). Release from intraspecific competition promotes dominance of a non-native invader. *Biological Invasions*, *21*(3), 895–909.
Weiner, S. A., Noble, K., Upton, C. T., Woods, W. A., & Starks, P. T. (2011). A role for thermoregulation in the *Polistes dominulus* invasion: A comparison of the thermoregulatory abilities of the invasive wasp *P. dominulus* and the native wasp *P. fuscatus*. *Insectes Sociaux*, *58*(2), 185–190.
Wilson-Rich, N., & Starks, P. T. (2010). The Polistes war: Weak immune function in the invasive *P. dominulus* relative to the native *P. fuscatus*. *Insectes Sociaux*, *57*(1), 47–52.
With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K., & Fisher, J. L. (2002). Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications*, *12*, 52–65.
Wong, L., Grainger, T. N., Start, D., & Gilbert, B. (2017). An invasive herbivore structures plant competitive dynamics. *Biology Letters*, *13*(11), 20170374. https://doi.org/10.1098/rsbl.2017.0374
Woodard, A. M., Ervin, G. N., & Marsico, T. D. (2012). Host plant defense signaling in response to a coevolved herbivore combats introduced herbivore attack. *Ecology and Evolution*, *2*(5), 1056–1064.
Yang, C. H., Qiao, F. J., Lu, Z., Li, C. Y., Liu, T. X., Gao, Y. L., & Zhang, B. (2023). Interspecific competitions between *Frankliniella intonsa* and *Frankliniella occidentalis* on fresh lentil bean pods and pepper plants. *Insects*, *14*(1), 1.
Yasuda, H., Evans, E. W., Kajita, Y., Urakawa, K., & Takizawa, T. (2004). Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia*, *141*(4), 722–731.
Yee, D. A., Kaufman, M. G., & Juliano, S. A. (2007). The significance of ratios of detritus types and micro-organism productivity to competitive interactions between aquatic insect detritivores. *Journal of Animal Ecology*, *76*(6), 1105–1115.
Yee, W. L., Goughnour, R. B., & Feder, J. L. (2021). Distinct adult Eclosion traits of sibling species *Rhagoletis pomonella* and *Rhagoletis zephyria* (Diptera: Tephritidae) under laboratory conditions. *Environmental Entomology*, *50*(1), 173–182.
Yong-Yue, L., Bi-Qiu, W., Ling, Z., & Yi-Juan, X. (2012). Comparison of foraging ability between *Solenopsis invicta* and *Tapinoma melanocephalum* (Hymenoptera: Formicidae). *Sociobiology*, *59*, 1015–1024.
Zapponi, L., Bon, M. C., Fouani, J. M., Anfora, G., Schmidt, S., & Falagiarda, M. (2020). Assemblage of the egg parasitoids of the invasive stink bug *Halyomorpha halys*: Insights on plant host associations. *Insects*, *11*(9), 1–17.
Zaviezo, T., Soares, A. O., & Grez, A. A. (2019). Interspecific exploitative competition between *Harmonia axyridis* and other coccinellids is stronger than intraspecific competition. *Biological Control*, *131*, 62–68.
Zee, J., & Holway, D. (2006). Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*. *Insectes Sociaux*, *53*(2), 161–167.
Zhou, A., Lu, Y., Zeng, L., Xu, Y., & Liang, G. (2012). Does mutualism drive the invasion of two alien species? The case of *Solenopsis invicta* and *Phenacoccus solenopsis*. *PLoS One*, *7*(7), e41856.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Additional exclusion criteria of published studies for meta-analysis.

Appendix S2. Studies from which data were extracted for the meta-analysis ($n = 182$).

Appendix S3. List of detailed traits compiled from the literature that were included in each trait class within trait categories: fitness and life history, ecological performance, stress tolerance, enemy defence and body size. For specific traits in which a lower value would indicate greater performance (e.g. cold temperature tolerance), the effect size sign was changed to positive to reflect that the invasive alien outperformed the native and is indicated by '(−)' in the table.

Appendix S4. Random effect structure for each meta-analysis. Total heterogeneity and heterogeneity explained by each random effect is given.

Appendix S5. Leave-one-out sensitivity analysis for each meta-analysis category.

Appendix S6. Sensitivity analysis results for subset data where: species had evidence of negative impact, the native species is invasive outside its native range, sample sizes for either of the species pair were below 5 for pooled data, data were excluded outside the 95th and 99th percentile of variance.

Appendix S7. Investigation of fitness and life history traits by order.

Appendix S8. Investigation of fitness and life history traits with ladybird beetles (Coccinellidae) only.

Appendix S9. Investigation of fitness and life history traits by adult diet guild.

Appendix S10. Investigation of fitness and life history traits by immature diet guild.

Appendix S11. Investigation of ecological performance by order.

Appendix S12. Investigation of ecological performance traits with ants (Formicidae) excluded.

Appendix S13. Investigation of ecological performance traits with ants (Formicidae) only.

Appendix S14. Investigation of ecological performance traits by adult diet.

Appendix S15. Investigation of ecological performance traits by immature diet.

Appendix S16. Investigation of stress tolerance traits by order.

Appendix S17. Investigation of stress tolerance traits with ants (Formicidae) as a subset.

Appendix S18. Investigation of stress tolerance traits by adult diet guild.

Appendix S19. Investigation of stress tolerance traits by immature diet guild.

Appendix S20. Investigation of enemy defence traits with ladybirds (Coccinellidae) excluded.

Appendix S21. Investigation of enemy defence traits with ladybirds (Coccinellidae) only.

Appendix S22. Investigation of enemy defence traits by order.

Appendix S23. Investigation of enemy defence traits by adult diet.

Appendix S24. Investigation of enemy defence traits by immature diet.

Appendix S25. Investigation of body size by order.

Appendix S26. Investigation of body size by adult diet.

Appendix S27. Investigation of body size by immature diet.

Figure S1. Barplots representing counts of effect sizes from species pairs (invasive–native) per trait variable (fitness, ecological performance, stress tolerance, enemy defence and body size) and potential additional moderators (metamorphosis type; sociality), colour coded by family. Sociality includes social species (e.g. species that form social colonies) and non-social species (all other insect

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

species). Metamorphosis type includes hemimetabolous (Hemi) and holometabolous (Holo) species.

Figure S2. Data subset for ladybird beetles (Coccinellidae) only. Co-occurring native and invasive ladybird beetles differed in fitness and life history traits. Effect sizes (ES) greater than 0 correspond with the invasive species significantly outperforming the native species. 95% confidence intervals are depicted in heavy black lines (and partially hidden by the mean data points), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). *k* = number of effect sizes per phenotypic trait.

Figure S3. Data subset for ants (Formicidae) only. Co-occurring native and invasive ants differed in some ecological performance traits. Effect sizes (ES) greater than 0 indicate that the invasive species outperformed the native species. 95% confidence intervals are depicted in heavy black lines (and partially hidden by the mean data points), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). *k* = number of effect sizes per phenotypic trait.

Figure S4. Data subset for ants (Formicidae) only. Co-occurring native and invasive ants differed in some stress tolerance traits. Effect sizes (ES) greater than 0 indicate that the invasive species outperformed the native species. 95% confidence intervals are depicted in heavy black lines (and partially hidden by the mean data points), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). *k* = number of effect sizes per phenotypic trait.

Figure S5. Data subset for ladybird beetles (Coccinellidae) only. Co-occurring native and invasive ladybird beetles differed in one enemy defence trait. Effect sizes (ES) greater than 0 indicate that the invasive species outperformed the native species. 95% confidence intervals are depicted in heavy black lines (and partially hidden by the mean data points), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). *k* = number of effect sizes per phenotypic trait.

How to cite this article: Weaving, H., Minnaar, I. A., Hui, C., Logan, M. L., & Clusella-Trullas, S. (2026). Invasive insects outperform their native counterparts. *Functional Ecology*, *00*, 1–21. https://doi.org/10.1111/1365-2435.70443

13652435, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.70443 by University Of Nevada Reno, Wiley Online Library on [03/11/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License