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SYNTHESIS

The EICA is dead? Long live the EICA!

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Abstract

An important hypothesis for how plants respond to introduction to new ranges is the evolution of increased competitive ability (EICA). EICA predicts that biogeographical release from natural enemies initiates a trade-off in which exotic species in non-native ranges become larger and more competitive, but invest less in consumer defences, relative to populations in native ranges. This trade-off is exceptionally complex because detecting concomitant biogeographical shifts in competitive ability and consumer defence depends upon which traits are targeted, how competition is measured, the defence chemicals quantified, whether defence chemicals do more than defend, whether 'herbivory' is artificial or natural, and where consumers fall on the generalist-specialist spectrum. Previous meta-analyses have successfully identified patterns but have yet to fully disentangle this complexity. We used meta-analysis to reevaluate traditional metrics used to test EICA theory and then expanded on these metrics by partitioning competitive effect and competitive tolerance measures and testing Leaf-Specific Mass in detail as a response trait. Unlike previous syntheses, our meta-analyses detected evidence consistent with the classic trade-off inherent to EICA. Plants from non-native ranges imposed greater competitive effects than plants from native ranges and were less quantitatively defended than plants from native ranges. Our results for defence were not based on complex leaf chemistry, but instead were estimated from tannins, toughness traits and primarily Leaf-Specific Mass. Species specificity occurred but did not influence the general patterns. As for all evidence for EICA-like trade-offs, we do not know if the biogeographical differences we found were caused by trade-offs per se, but they are consistent with predictions derived from the overarching hypothesis. Underestimating physical leaf structure may have contributed to two decades of tepid perspectives on the trade-offs fundamental to EICA.

KEYWORDS
competition, evolution, evolution of increased competitive ability, exotic, generalist, herbivory, invasion, meta-analysis, shifting defence hypothesis, specialist

INTRODUCTION

A large body of evidence for rapid evolution by exotic plant species demonstrates how plants can adapt to new ecological conditions. Much of this evidence is in the context of growth versus defence trade-offs, initiated by Blossey and Notzold's (1995) proposal that escape from natural, specialist enemies in non-native ranges leads to relaxed selection for defence. In turn, such relaxed selection might lead to the reallocation of resources, no longer needed for defence, to traits that increase competitive ability or reproduction, which are ostensibly in demand in both native and non-native ranges. Since their proposal, there have been hundreds of studies tackling some aspect of Blossey and Notzold's (1995) Evolution of Increased Competitive Ability (EICA) hypothesis, many of which have been synthesised in a series of thorough and robust reviews and meta-analyses. Generally, syntheses of EICA conclude that the pattern of larger conspecifics in non-native ranges has strong empirical support, but the competitive ability-defensive trait trade-off at the heart of EICA does not—that is there is little evidence for decreased allocation to defence concomitant with higher growth (Atwood & Meyerson, 2011; Bossdorf et al., 2005; Colautti et al., 2009; Felker-Quinn et al., 2013).

Bossdorf et al. (2005) found empirical support for rapid 'evolutionary change' in studies that had accumulated for 10 years after the EICA hypothesis was published, but of the 17 studies that tested some aspect of both growth *and* defence, only seven showed range-based differences that were consistent with an EICA-like trade-off. Colautti et al. (2009) assessed the literature quantitatively and found differences for reproduction between ranges and strong significant interaction effects showing that range effects were highly contingent on latitudinal clines (also see Atwater et al., 2018; Rosche et al., 2019). A meta-analysis by Felker-Quinn et al. (2013) found much evidence for rapid evolution by plant species in their non-native ranges, but not for the trade-off-based predictions of the EICA hypothesis. More specifically, they did not find significant reductions in physical and chemical defences, increased herbivore growth, or greater herbivore damage for plants from the non-native range than conspecifics from the native range. However, Felker-Quinn et al. (2013) found that plants from non-native ranges were larger or grew faster, but only in the absence of competition. Finally, Rotter and Holeski (2018) meta-analysed only studies that measured *both* growth and defence traits in common conditions ($n = 30$), and found evidence for trade-offs between plant fitness traits and herbivore growth, but in contrast to other syntheses found that generalist growth *improved* on plants from non-native ranges. This was opposite to the trend in Felker-Quinn et al.'s (2013) results.

The devil may be in the details for some of the metrics used to test for EICA, and slight differences in the choice and parsing of some metrics might lead to contradictory syntheses (see explanations in Rotter & Holeski, 2018). For example, there might be striking differences in the effects versus the responses of herbivores, and these might differ between generalists versus specialists (as noted by Felker-Quinn et al., 2013 and Müller-Schärer et al., 2004). And, perhaps size and growth rates are not consistently indicative of actual competitive ability (Pearse et al., 2019). Selection pressure might be different for competitive effect (suppression) versus competitive response (tolerance; i.e. Atwater et al., 2021). If so, the way competitive interactions are measured might also be crucial for finding, or not, support for EICA. For instance, common garden experiments performed in the field, where plants are exposed to live soil biota, might yield different results than in common greenhouse conditions with sterilised or commercial substrate. If in the field, common gardens in the native range, where soil biota are typically more inhibitory, might yield different results than common gardens in non-native ranges, where exotic plants often escape the negative effects of soil biota (Callaway et al., 2004; Kulmatiski et al., 2008).

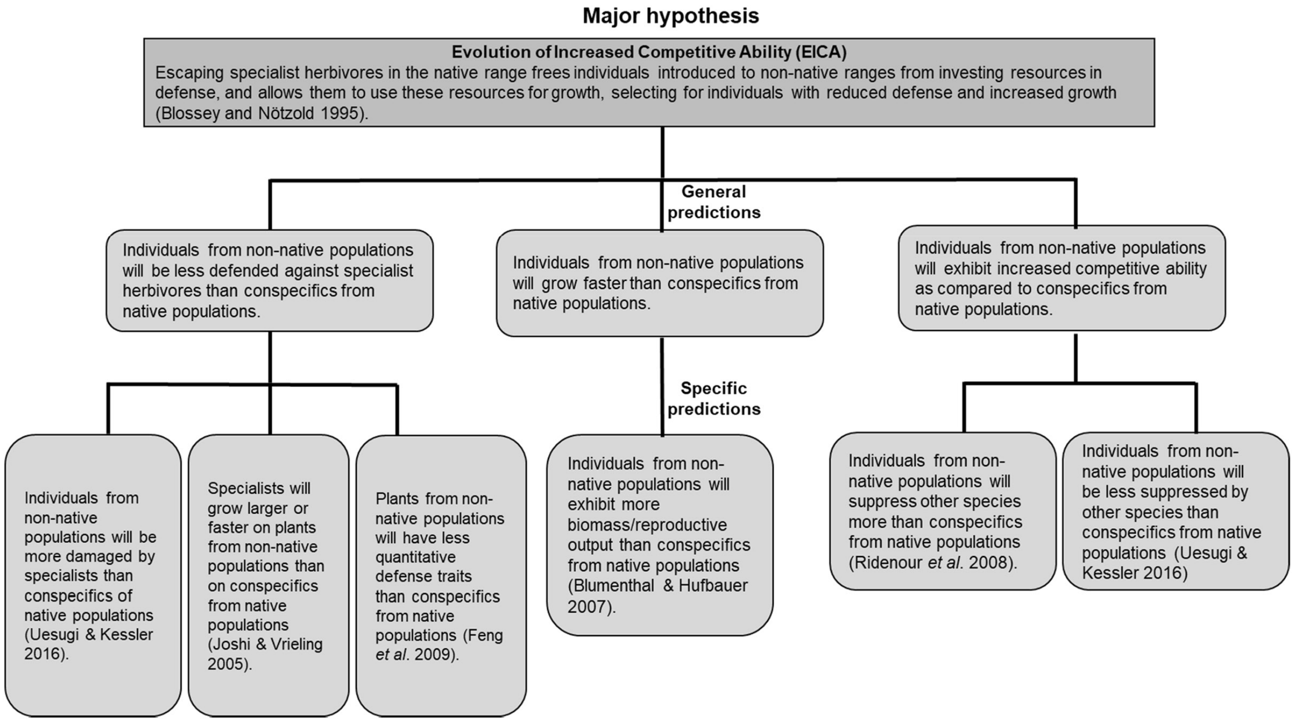
Teasing apart some of the complex nuances in the many measurements used to explore EICA may increase our understanding of the scope, extent and mechanisms of any evolutionary trade-offs that occur during exotic invasion. For instance, Blossey and Notzold (1995) focused exclusively on specialists. They reasoned that exotics escape only specialists in their non-native ranges, unless specialists are co-introduced or introduced later as biological controls (see Müller-Schärer et al., 2004). Thus, Müller-Schärer et al. (2004) pointed out that a key aspect of 'escape from enemies' in new ranges is a biogeographical shift towards herbivore communities dominated by generalists. They suggested that in non-native ranges, qualitative toxin-based defences might actually increase in concentration (especially those that actually attract specialists in native ranges) instead of decreasing, as predicted by extrapolating Blossey and Notzold's (1995) focus on specialist performance. Correspondingly, Müller-Schärer et al. (2004) argued that quantitative defences such as structural tissue toughness, lignins, tannins and perhaps some phenolics, should decrease in non-native ranges. This perspective is articulated as the Shifting Defence Hypothesis (SDH; see Doorduin & Vrieling, 2011; Zhang et al., 2018).

There is evidence that exotic invaders in non-native ranges can also 'escape' the effects of generalists relative to populations in native ranges (Cappuccino & Carpenter, 2005; Lucero & Callaway, 2018; Lucero et al., 2019; Pearson et al., 2011; Schaffner et al., 2011; Tallamy et al., 2010; Wikström et al., 2006). Thus, separating the effects and responses of generalists and specialists in meta-analyses might yield different insights than when they are grouped. Felker-Quinn et al. (2013) separated the performance (growth and survival) of generalists and specialists in their meta-analysis and found trends towards decreased performance of generalists and increased performance of specialists on plants collected in non-native ranges compared to plants from their native ranges. Again, this is consistent with the SDH. Zhang et al. (2018) reported that the biogeographic origin, or provenance, of generalist herbivores affected the relative damage done to native and non-native conspecifics. Plants from non-native ranges showed increased resistance to generalists native to either range, but generalists from the non-native ranges of plants imposed larger proportional damage than generalists from the native ranges of plants.

If the biogeographical patterns described above are indicative of evolution, then further disentangling of the complexity embedded within the original elegance of the EICA hypothesis might shed more light on the evolution of exotic species in their non-native ranges. In this context, our objective was to parse some of the nuances that are often conjoined in syntheses of EICA and thereby explore trade-offs hypothesised by EICA in a new light. These nuances are illustrated as the general hypothesis, general predictions and specific predictions, organised generally following Van Kleunen et al. (2010) and Heger and Jeschke (2014) in Box 1. We also present the hypothesis and predictions for the Shifting Defence Hypothesis in Box 2. These hypotheses emphasise that trade-offs, per se, are exceptionally difficult to test. For example, increased growth and decreased chemical defence might occur simultaneously via direct selection on both traits independently without any trade-off required. In this context, all tests of EICA to date have examined predictions and evaluated patterns that are *consistent* with trade-offs inherent to the hypotheses, and the syntheses here are no different. Furthermore, scientific syntheses of existing evidence compile and test (provided they include a meta-analysis) the extent that a body of work generally supports the framework of a hypothesis (Lortie, 2014).

Our objectives were to examine classic metrics traditionally used to detect evidence for EICA-like trade-offs and then expand upon traditional metrics by parsing out previously overlooked factors inherent to plant–herbivore and plant–plant interactions. First, we tested the fundamental assertions of EICA that plant species collected in non-native ranges are (a) more competitive, (b) larger, (c) more fecund, (d) less affected by herbivores and (e) less defended against herbivores than conspecifics in native ranges. Second, we parsed whether any biogeographic differences in herbivory are driven by the effects or responses of generalist versus specialist herbivores (see Felker-Quinn et al., 2013). Third, we parsed whether any biogeographical differences in competition were driven by competitive effects (suppression of neighbours) versus competitive responses (tolerance to neighbours). Fourth, and based on a second literature search and meta-analysis, we tested whether biogeographical differences in defence levels were significantly influenced by qualitative (chemical) or quantitative (structural) defences. Our first test represented a traditional, conjoined approach

BOX 1 Organization of general and specific predictions for the evolution of increased competitive ability hypothesis. Not all possible predictions are included



Evolution of Increased Competitive Ability (EICA)
Escaping specialist herbivores in the native range frees individuals introduced to non-native ranges from investing resources in defense, and allows them to use these resources for growth, selecting for individuals with reduced defense and increased growth (Blossey and Nötzold 1995).

Individuals from non-native populations will be less defended against specialist herbivores than conspecifics from native populations.

Individuals from non-native populations will grow faster than conspecifics from native populations.

Individuals from non-native populations will exhibit increased competitive ability as compared to conspecifics from native populations.

Individuals from non-native populations will be more damaged by specialists than conspecifics of native populations (Uesugi & Kessler 2016).

Specialists will grow larger or faster on plants from non-native populations than on conspecifics from native populations (Joshi & Vrieling 2005).

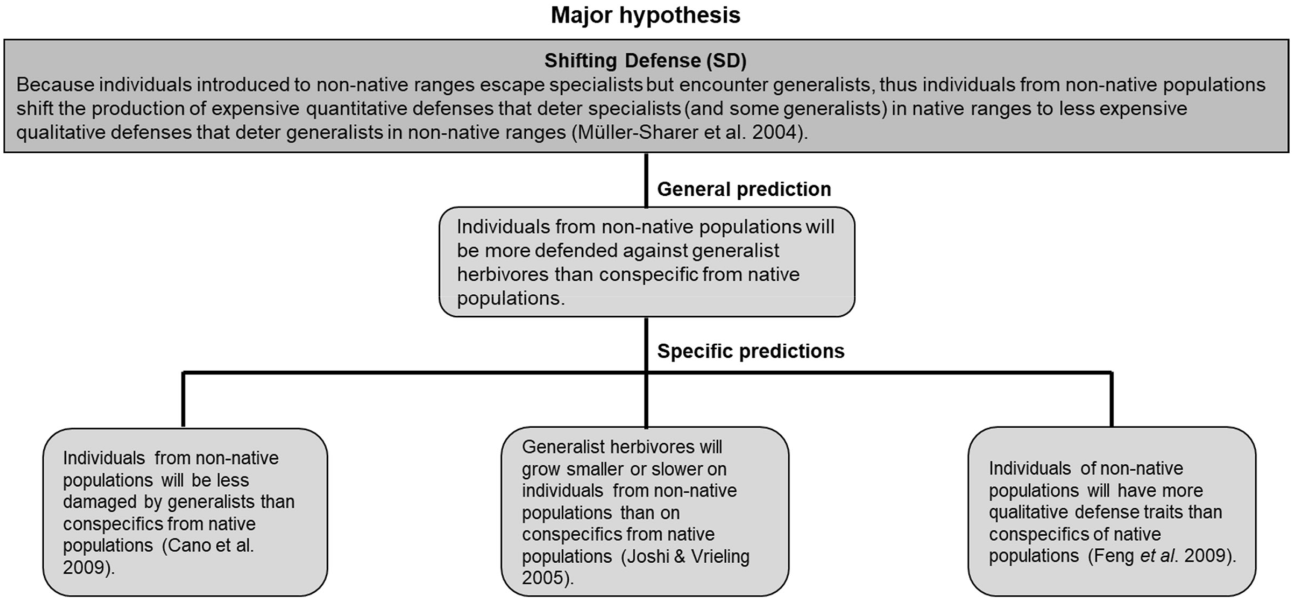
Plants from non-native populations will have less quantitative defense traits than conspecifics from native populations (Feng *et al.* 2009).

Individuals from non-native populations will exhibit more biomass/reproductive output than conspecifics from native populations (Blumenthal & Hufbauer 2007).

Individuals from non-native populations will suppress other species more than conspecifics from native populations (Ridenour *et al.* 2008).

Individuals from non-native populations will be less suppressed by other species than conspecifics from native populations (Uesugi & Kessler 2016)

BOX 2 Organization of general and specific predictions for the shifting Defence hypothesis



Major hypothesis

Shifting Defense (SD)

Because individuals introduced to non-native ranges escape specialists but encounter generalists, thus individuals from non-native populations shift the production of expensive quantitative defenses that deter specialists (and some generalists) in native ranges to less expensive qualitative defenses that deter generalists in non-native ranges (Müller-Sharer et al. 2004).

General prediction

Individuals from non-native populations will be more defended against generalist herbivores than conspecific from native populations.

Specific predictions

Individuals from non-native populations will be less damaged by generalists than conspecifics from native populations (Cano et al. 2009).

Generalist herbivores will grow smaller or slower on individuals from non-native populations than on conspecifics from native populations (Joshi & Vrieling 2005).

Individuals of non-native populations will have more qualitative defense traits than conspecifics of native populations (Feng *et al.* 2009).

for examining trade-offs predicted by EICA. The remaining tests examined the relative importance of plant–plant and plant–herbivore interactions that are often overlooked but that can be critical for better examinations of EICA.

METHODS

Search procedures

We defined exotic plant species as those introduced by humans to a biogeographically different part of the world than where they originated, usually to a different continent, though we also included islands (see Manea et al., 2019). Europe and Asia were grouped as Eurasia (see Engelkes et al., 2008; van Grunsven et al., 2010). We did not attempt to classify the 'invasiveness' of exotic species, either via abundance or impact, despite the practical importance of distinguishing between naturalised and invasive exotics (McKinney & La Sorte, 2007; Pearson et al., 2016). The majority of the exotic species considered here were nonetheless highly invasive (All data and code are publicly available; Callaway et al., 2022).

We identified primary studies for our synthesis with two independent searches of the Web of Science bibliometric resource. Our first search used the terms '(EICA OR "evolution of increased competitive ability"), plants' in June of 2020. This first search returned 179 peer-reviewed publications on competition, size, fecundity and herbivores. To identify additional studies on leaf traits, which were not well represented in our first search, we conducted a second search in May 2021 using the terms 'evolution AND increased AND competitive AND ability AND leaf traits'. This second search returned 28 peer-reviewed publications. Studies from both searches were screened to meet the following criteria: (1) primary studies (i.e. reviews, syntheses, or commentaries were not included), (2) common growth conditions (i.e. common gardens) and (3) primary data (sample mean, sample size, estimate of variance) could be extracted. Our screening process yielded 93 relevant studies for a total of 304 unique and independent observations. Additional details of the screening process are shown in a PRISMA figure (Figure S1).

Our searches yielded 10 classes of measurements that we extracted for meta-analysis: competitive effects of exotics on neighbours ('competitive effect'), competitive effects of neighbours on exotics ('competitive response'), size, reproduction, growth response to simulated damage, or artificial herbivory ('damage tolerance'), performance (growth and survival) of herbivores ('herbivore performance'), actual damage done by herbivores ('herbivore damage'), plant response to actual herbivore damage ('response to herbivore damage'), qualitative defences against herbivores ('chemical defence') and quantitative defences against herbivores ('structural defence'). Competitive effects included experiments with allelopathy. Size estimates included aboveground biomass, total biomass and height. Reproduction estimates included flower number, seed number and inflorescence mass. Some studies used clipping as artificial herbivory and then subsequently measured plant growth responses. However, clipping does not always mimic herbivory

(Baldwin, 1990), thus we considered plant growth responses to clipping and artificial herbivory as damage tolerance. Herbivore performance included the mass, egg count, or survival of specialist or generalist insect herbivores. Herbivore damage, as opposed to artificial damage, included holes in leaves or removal of leaf area. Response to herbivore damage included measures of plant growth responses to damage done by specialist or generalist insect herbivores. Measurements of herbivore damage were taken in both greenhouse and field common gardens, with the latter exposing plants to a milieu of both specialist and generalist herbivores. Therefore, we classified field measurements of herbivore damage and response to herbivore damage by whether they were conducted in native or non-native ranges, because these ranges should differ in the relative abundance of generalists and specialists. Measurements of chemical defence included chemicals in leaves thought to be related to herbivore defence, but we only included chemicals that were mostly likely to target generalists (see Discussion). The roles of other putative defensive chemicals, such as tannins and general phenolics, are surprisingly unclear (see review by Massad et al., 2011). Specifically, our qualitative defence chemicals were odoratin, phenylpropanoid glycosides, pyrrolizidine alkaloids, glycosides, flavonoids, sinigrin, phytol, alliarinoside, hypericin and hypericides (Table 1). We emphasise that many of these chemicals are poorly understood and might also affect specialists (Ali & Agrawal, 2012; Massad et al., 2011). Structural, quantitative, defences included measurements of leaf-specific mass; leaf-specific area; leaf toughness; and density of leaf prickles, trichomes and tannins and phenolics based on Müller-Schärer et al. (2004) and citations therein. Our assignments of chemicals to generalist versus specialist defence are based on the literature described above, but see Ali and Agrawal (2012) for how disturbingly little is known about the function of these defence chemicals.

For each observation taken in the native or non-native ranges of species, we calculated the Hedge's *g* effect size metric using the metafor R package (Viechtbauer, 2017). We selected Hedge's *g* because this effect size pools and weights the estimates of relative variance for measurement pairs ideal for small sample size meta-analyses (i.e. $n<20$) (Borenstein et al., 2010; Hedges & Olkin, 1985). In our calculations, Hedge's $g>0$ indicated larger effect sizes in the non-native range relative to the native range, Hedge's $g<0$ indicated larger effect sizes in the native range relative to the non-native range and Hedge's $g = 0$ indicated equal effect sizes in the native and non-native ranges.

Data analyses

To contrast measurements of performance or biotic interactions between populations of species in native versus non-native ranges, we conducted meta-analyses in R version 4.2.0 (R-Development-Core-Team, 2021) using the package metafor version 3.0-2 (Viechtbauer, 2017). In total, five random mixed-effects

TABLE 1 Variables and metrics used in meta-analyses

Variable	Metrics
Size	Plant total biomass, aboveground biomass, growth rate
Damage tolerance	Response to artificial damage/herbivory—plant total biomass, aboveground biomass, growth rate
Reproduction	Flower, fruit or seed number, seed size
Herbivory	
Specialist damage	Proportion of leaf or stem missing, chewed, discoloured
Specialist response	Insect biomass, growth rate
Generalist damage	Proportion of leaf or stem missing, chewed, discoloured
Generalist response	Insect biomass, growth rate
Chemistry	Concentration of odoratin, phenylpropanoid glycosides, pyrrolizidine alkaloids, glycosides, flavonoids, sinigrin, phytol, alliarinoside, hypericin, hypericides, tannins, phenolics
Field experiments	Damage done by all herbivores present naturally in field—proportion of leaf or stem missing, chewed, or discoloured
Competitive suppression	Biomass of *other* plants when grown with target exotic species vs. biomass of plants grown without the target exotic species
Competitive tolerance	Biomass of target species when grown with *other* plants vs. biomass of target species with grown without other plants
Structural chemistry	Concentration of tannins, phenolics
Physical structure	Leaf-specific mass, leaf-specific area, leaf toughness, density of leaves, prickles/trichomes

models (without intercepts for categorical moderators) were used to test for biogeographical differences among the effect sizes (Hedge's *g*) of specific moderators using the function 'rma' (Supplementary materials for trait and leaf-structure meta-analyses). The first tested effect sizes related to exotic plant size, damage tolerance, reproduction, herbivory and leaf chemistry—response measures that have been used traditionally to examine EICA theory. This model fit plant response measure as a moderator. The second further partitioned herbivory and tested effect sizes for specialist damage, generalist damage, specialist response and generalist response. This model fit herbivore specialisation as a moderator. The third tested the influence of experimental range (i.e. whether the experiment was conducted in the native or non-native range) on effect size by modelling experimental range as a moderator. The fourth parsed competitive effects (competitive suppression) from competitive responses (competitive tolerance) and examined effect sizes by modelling the metric of competition (competitive suppression vs. competitive tolerance) as a moderator. The fifth and last partitioned quantitative defences at the leaf level and tested effect sizes related to in situ levels of structural chemistry and physical structure. This model fit the type of leaf-level quantitative defence (structural chemistry vs. physical structure) as a moderator (Gurevitch et al., 2018). As primary studies included for formal synthesis reported and measured different variables, each of these random mixed-effects models examined the subsets of the compiled data relevant to the specific prediction of EICA tested here (sensitivity analyses and global models confirmed this was valid; see below). Simple post hoc *t*-tests for each mean effect size then were used and reported in figures to test for statistically significant differences from 0 (or no net effect of a specific moderator) at 95% confidence levels. Heterogeneity was examined using *Q*-statistics reported in the random-effects models (Koricheva & Gurevitch, 2014; Langan et al., 2019), and publication bias was explored using the 'regtest' function in metafor that reports Egger's regression test for funnel plot asymmetry (Egger et al., 1997; Jennions et al., 2013; Lin & Chu, 2018). The estimated 95% confidence intervals and estimated marginal means from the meta-analysis models were used in the forest plots (Lortie et al., 2013).

To explore the robustness of our analyses and to ensure that the random mixed-effects models described above were parsimonious and statistically justified, we re-analysed our data with global models (Halpern et al., 2020) fit to all data with response measure fit as a moderator. All global meta-analyses detected significant effects of response measure, indicating that the specific models described above were justified. Sensitivity analyses for the global model and subsequent individual response set analyses were also included, examining the relative importance of species-specificity. Classification of species as a fixed or random effect moderator was tested in all models, and findings in all instances were robust (i.e. modelling species as a fixed or random effect moderator did not influence our results). Data from the literature did not allow a complete integration of species into analyses simply because few studies used the same species. This problem is inherent to a synthetic approach that integrates disparate findings from many primary studies that do not share identical protocols but still nonetheless provides robust testing provided the same response variables were reported (as they were here in each of the 4 tests). All data and code are publicly available (Callaway et al., 2022).

RESULTS

At the first level of analysis, only size reflected biogeographical patterns consistent with EICA (Figure 1; $X^2 = 43.06$, $p = 0.0001$, $n = 217$, heterogeneity $Q = 288$, $p = 0.0001$, Supplement B for mean and error estimates). Consistent with predictions derived from EICA, we found that plants from non-native ranges were larger than conspecifics from native ranges (i.e. effect size estimates were different from 0, Figure 1; Box 1). In contrast, effect sizes for reproduction, tolerant and herbivory were not different from 0, suggesting no significant difference among conspecifics from native and non-native ranges. Interestingly, generalist-related secondary metabolite chemical concentrations were greater in populations from non-native ranges than native ranges. This finding is inconsistent with EICA-derived predictions but consistent with the SDH (Figure 1; Box 1; Box 2).

Damage done to plants by insects and the responses of insects to plants (growth or survival) depended upon herbivore specialisation (specialist vs. generalist) and biogeographic context, though not as predicted by EICA (see Felker-Quinn et al., 2013; Figure 1b, mean moderator net differences $X^2 = 10.85$, $p = 0.04$, $n = 76$; Box 1). Variance in the damage done to plants by specialist herbivores was very high, and we detected no difference between populations from native and non-native ranges. In contrast, damage done by generalist herbivores was greater on populations from native ranges than non-native ranges, inconsistent with EICA, although heterogeneity between groups was significant ($Q = 180$, $p = 0.0001$). However, there were no publication biases (Funnel-plot regression test, *Z*-score = 1.2, $p = 0.2$). The growth responses of specialist and generalist herbivores to plants from native and non-native ranges showed trends that were similar to the damage measurements, with specialists tending to perform better on plants from non-native ranges and generalists tending to perform better on conspecific plants from native ranges, though these trends were not statistically significant.

The outcome of common garden experiments depended upon the biogeographical range in which they

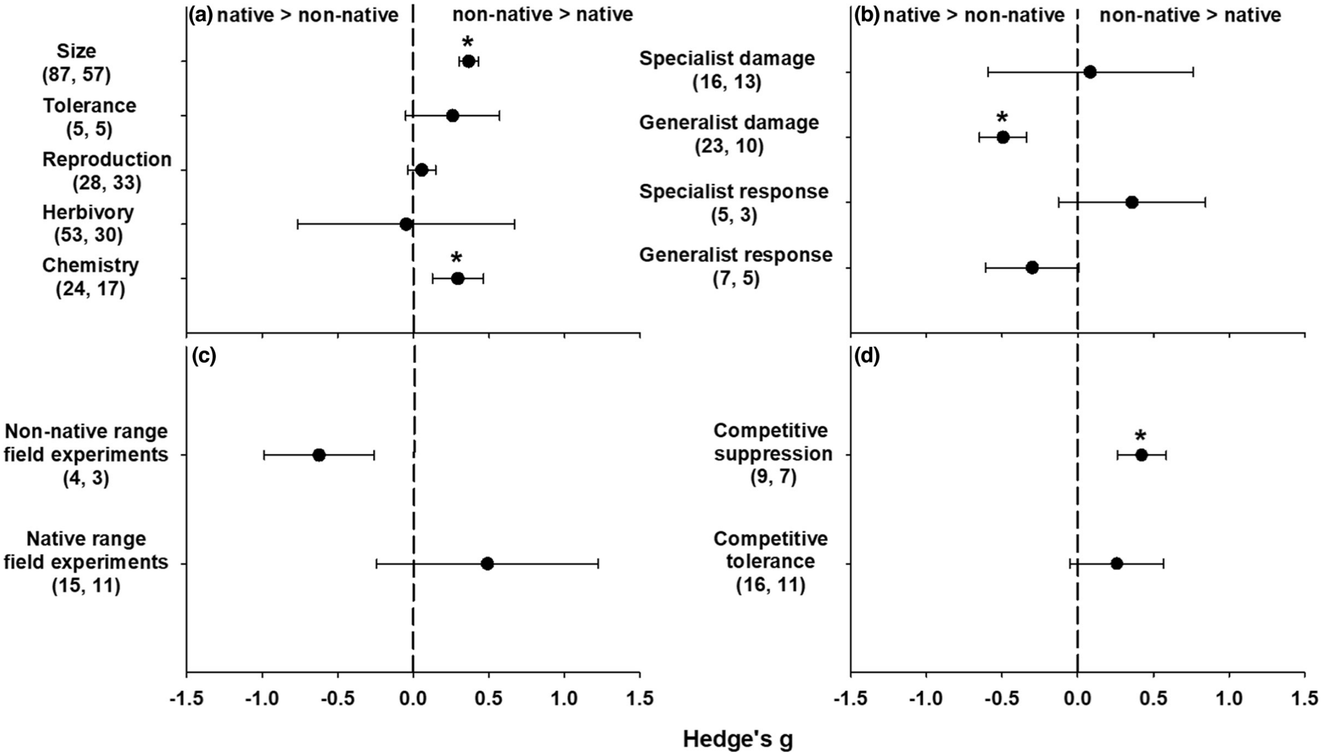


FIGURE 1 (a) Mean Hedge's *g* for plant size, damage tolerance (artificial herbivory), reproduction, herbivory (herbivore performance and herbivore damage combined) and chemistry most likely to contribute to qualitative defences for conspecific plants from native and non-native ranges, (b) mean Hedge's *g* for damage done by specialist and generalist herbivores to plants and the performance of specialist and generalist herbivores for conspecific plants from native and non-native ranges, (c) mean Hedge's *g* for damage done by all herbivores present naturally in field common gardens in non-native and native ranges of plants for conspecifics from native and non-native ranges, (d) mean Hedge's *g* for competitive effect (ability to suppress neighbours) and competitive response (ability to tolerate suppression by neighbours) for conspecifics from native and non-native ranges. Bars show 1 SE and asterisks are presented for Hedge's *g* values that are significantly different than zero; that is when plants from one range show different responses than plants from the other range. Numbers in parentheses indicate the number of studies used and species used.

were conducted (Figure 1c, model X^2 = 6.6, p = 0.03, n = 16; heterogeneity, Q = 80.9, p = 0.0008, post hoc t-test p<0.05; Box 1). When common gardens were constructed in non-native ranges, where generalist consumer effects on exotic species should disproportionately predominate (Keane & Crawley, 2002), plants from populations in non-native ranges suffered less damage than plants from native ranges. This is inconsistent with EICA but consistent with the SDH again suggesting increased tolerance to attack by generalists.

Effect sizes of plant–plant competition varied with how competition was measured (competitive suppression vs. competitive tolerance; measured experimentally rather than inferred from size in the absence of another species) and biogeographical range (Figure 1d, model X^2 = 7.8, p = 0.02, n = 16). Plants from non-native ranges suppressed other species more than plants from native ranges, which is consistent with EICA. However, plants from native and non-native ranges tolerated neighbours similarly. Thus, parsing competitive suppression (plant effects on neighbours) from competitive tolerance (plant responses to neighbours; see Atwater et al., 2021; Goldberg, 1990; Miller & Werner, 1987) is important or examining the predictions of EICA.

Levels of in situ quantitative defences at the leaf level varied with the type of quantitative defence (chemical [e.g. lignin, tannins, phenols] vs. physical [e.g. Leaf-Specific Mass toughness]; Hanley et al., 2007). This contrasts with the results for 'chemistry' in Figure 1, which included all chemistry measurements across all of the publications we analysed, the majority of which were qualitative (see Methods for list of chemicals). Consistent with predictions of EICA, levels of physical quantitative defences were higher in plants from native ranges than non-native ranges (Figure 2, model X^2 = 11.3, p = 0.003; Box 1). However, chemistry-based quantitative defences did not significantly differ from a mean net response of 0 (post hoc t-test, p>0.05), and there was significant heterogeneity in these studies (Q = 272, p = 0.0001). This heterogeneity suggests that there are other moderators needed in primary studies that test chemical defences. In addition, we found evidence for publication bias in these studies towards relatively small effect sizes (Z = −3.8, p = 0.0001).

The global meta-analytical model, with all data, detected significant differences between moderators supporting deeper, targeted analyses of specific subsets of these data using relevant data for each assumption

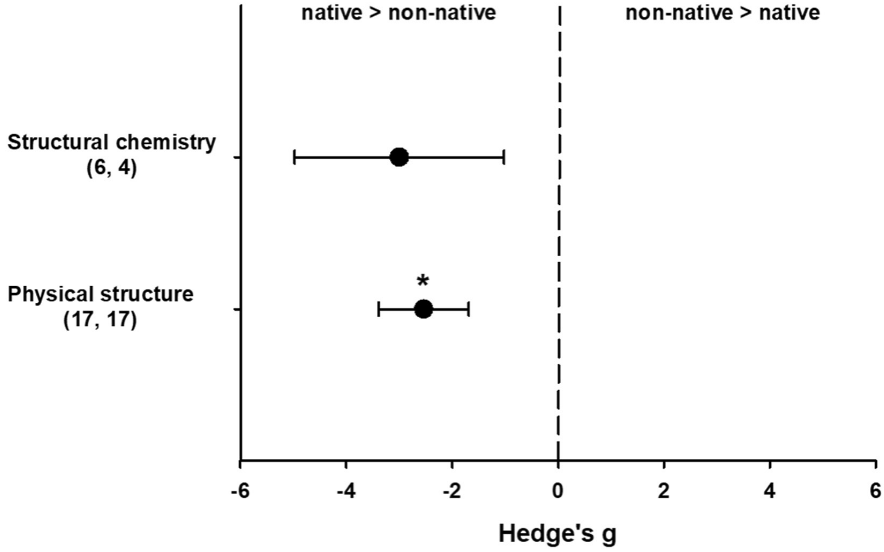


FIGURE 2 Mean Hedge's *g* for quantitative defences, including leaf chemical traits most related to quantitative defence (e.g. lignin, tannins) and the physical structure of leaves related to quantitative defence (primarily leaf-specific mass; Hanley et al., 2007) for conspecifics from native and non-native ranges. Bars show 1 SE and the asterisk is for the Hedge's *g* value that is significantly different than zero; that is when plants from one range show different responses than plants from the other range. Numbers in parentheses indicate the number of studies used and species used.

(X^2 = 42.7, p = 0.0001, n = 317 and heterogeneity was significant Q = 597, p = 0.0001). The sensitivity of all models was re-tested by a global screening model, and each of the five reported meta-analyses were also tested with species identity as an additional moderator. All effects reported were robust and consistent in the global models. Species included as a moderator did not change the outcome of the main moderators reported in in any of the results reported above. The general findings were thus not sensitive to variation that species identity potentially introduced to the larger patterns.

DISCUSSION

Our most important new contribution to understanding EICA was finding that the leaves of exotic invaders were less *quantitatively* defended, at least as estimated by physical structural defences (primarily LSM), in non-native ranges relative to native ranges. Adding LSM to databases is discussed below. So far, the results for lower quantitative structural defences in non-native ranges are based on modest sample sizes, but combining these measurements of quantitative defences with size and competition differences provides new circumstantial support for the classic trade-off originally proposed in the EICA (Blossey & Notzold, 1995). That said, we emphasise that this pattern is consistent with an EICA-like trade-off, but does not necessarily demonstrate an evolutionary trade-off relationship between enemy release and subsequent decreases in defensive traits.

Blossey and Notzold's (1995) initial articulation of the EICA hypothesis proposed how trait values *within a particular taxon* might evolve over time in response to translocation. Due to a lack of replication of species across studies, our meta-analyses could not explicitly test for apparent trade-offs within taxa, but our results for quantitative defence differences are highly consistent with detailed single-species studies by Feng et al. (2009, 2011). Feng et al. (2009) found that populations of a tropical invader, *Ageratina adenophora*, from the non-native range showed reduced allocation to cell walls, resulting in poorer structural defences, and increased nitrogen allocation to photosynthesis, related to growth. Perhaps most importantly, LSM was 15–20% higher for plants from the native range of Mexico than for plants from the non-native ranges of China and India. Following this, Feng et al. (2011) reported that *A. adenophora* plants from non-native ranges showed similar leaf construction costs to plants from the native range, but a much faster 'payback time' providing more detail to mechanistic explanations of the evolution of increased growth.

Rotter and Holeski (2018) reported structural leaf differences as evidence for the loss of defences against specialists, but multi-study data for Leaf-Specific Mass (LSM or the inverse, Specific Leaf Area, SLA) has not been fully marshalled in previous meta-analyses or reviews. But, is there evidence that LSM is a good indicator of greater herbivore defence? In an in-depth review of plant physical defences, Hanley et al. (2007) concluded that leaf-mass–area (LSM) is a 'robust index of sclerophylly as a surrogate for more rigorous mechanical properties used in herbivory studies'. Furthermore, Caldwell et al. (2016) reported that a suite of structural defence traits were strongly negatively correlated with SLA (i.e. positively correlated with LSM). In a study of many tropical species, one of these structural traits, toughness measured with a punch, was found by Coley (1983) to resist herbivory more than chemical traits. Peeters (2002) measured herbivorous insect assemblages on 18 plant species and found that densities of all herbivores were negatively correlated with LSM, along with other leaf traits. For *Microstegium vimineum*, a species detected in our second search (Flory et al., 2011), Dickinson (2012) found that lower LSM in non-native populations corresponded with lower leaf toughness and higher leaf herbivore damage. Sanson et al. (2001) argued that LSM provides a good 'coarse estimation' of structural leaf defences, but expressed concern that is might be inaccurate for comparisons among species. However, they noted that LSM could be used as an estimator of mechanical properties within species, as is the case for each of our individual comparisons of conspecifics from native and non-native ranges.

Regardless, we emphasise that LSM is a 'soft trait' that affects many plant functions and therefore cannot be interpreted as a 'smoking gun' for actual trade-offs. Most importantly, LSM is strongly negatively correlated with leaf nitrogen concentration per mass (Mooney & Gulmon, 1982), as increases in LSM inevitably reduces concentrations of nutrients, water and chemistry based on dry mass, and all of these may have significant effects on both herbivory and photosynthesis. In other words, decreased LSM could be directly selected on based on its effect on growth rates. However, such a decrease in LSM, the trend towards better specialist responses to non-native conspecifics, and concomitant increases in size and competitive ability are consistent with the predictions of EICA. It is important to note that all studies of such trade-offs (e.g. growth vs. qualitative defence chemicals) are subject to the same limitations in trade-offs that cannot be experimentally separated from independent selection.

Different specialist insect herbivores attack many plant parts, so do exotic invaders actually escape *leaf* specialists? It is hard to say, but of the ten species identified in our second search with measurements of LSM, we could find evidence for the presence of leaf specialists in native ranges for seven of them. Somewhat specialised leaf pathogens also appeared to be common in the native ranges of our species, but we do not know how LSM affects these consumers.

Our results for 'physical defences' were opposite to those reported by Rotter and Holeski (2018). This may have been for several reasons, but we included a large number of studies that compared LSM (or converted LSA) between native range and non-native populations, whereas Rotter and Holeski (2018) included few. In addition, they restricted their analyses to studies that measured both fitness and defence traits, limiting their sample size to six publications with physical defence measurements. Regardless, Rotter and Holeski's (2018) report of *increased* physical defences in non-native range populations provides an important caution—accurately understanding what actually represents physical defences is complex, and our emphasis here on LSM as an indicator of quantitative defence is likely to be only part of the story.

Our results are also consistent with the Shifting Defence Hypothesis (SDH; Doorduin & Vrieling, 2011; Lin et al., 2015; Müller-Schärer et al., 2004; Box 2). The SDH is that plant species in non-native ranges evolve reduced resistance to specialists and increased resistance to generalists due to escape from specialist, but not generalist, herbivores in the non-native range (Müller-Schärer et al., 2004). Müller-Schärer et al. (2004) predicted that quantitative defences should decrease in non-native ranges. In support of this, we found that plants from native ranges were damaged less by generalists than plants from non-native ranges, and that plants from non-native ranges had more generalist-related defence chemicals, indicating that the latter had experienced selection for greater defence against generalists. Our synthesis highlights the complexity of evolutionary responses by exotics, but given appropriate experimental designs, trade-offs in the evolution of exotic invasive species when they are released from specialist herbivory appear to be predictable and detectable (see Lin et al., 2015). In addition to reduced quantitative defences, we found, as did all other reviews, that plants from non-native ranges were larger; however, we also found that they were able to competitively suppress their neighbours more than plants from native ranges. This finding represents an important advance as it supports a more direct prediction of the EICA hypothesis. Such suppression was not part of Blossey and Notzold's (1995) original phrasing, which stated that '*…under identical growing conditions, individuals of a species taken from an area where they have been introduced will produce more biomass than individuals taken from the species native range*'. Similar results for competition have been reported by Callaway et al. (2011), Inderjit et al. (2011) and Aschehoug et al. (2012). Specialist insects did not damage plants from non-native ranges more, nor did they grow better on these plants, again consistent with all other reviews. This is inconsistent with the originally phrased idea of EICA (Blossey & Notzold, 1995) that '*specialised herbivores (i.e. those with potential for introduction as biological control agents) will show improved performance on plant individuals originating from an area where plants have been introduced*'. In sum, precise definitions of the metric used (i.e. structural vs. chemical defences rather than combining the two) appear to be very important in the exploration of EICA, and EICA-like evolution. Thus, EICA continues to provide both a challenging set of ideas, and also complex opportunities to better test evolution resulting from the invasion process.

Why might our results contrast in some ways with those of other syntheses? First, we had more than 20 new studies published since 2018, the date of the last review similar to ours (Rotter & Holeski, 2018). Second, we summarised and treated the number of response variables used from a single study conservatively, using no more than one observation per study, if available, per each of our variables. Third, we followed the general approach of parsing variables into more specific components taken by Felker-Quinn et al. (2013) and Rotter and Holeski (2018), but we parsed further. For example, we separated competitive effect and response, native ranges from non-native ranges for herbivore damage, and most importantly included more results for LSM-based structural defences (see Feng et al., 2009, 2011).

As noted, a focus on leaf structure, primarily LSM, provides direct but not fully independent experimental evidence that links to drivers of both growth and defence against specialists (Feng et al., 2009; Huang et al., 2020), and thus to a strong mechanistic relationship between growth, competition and defence against specialists. Why might biogeographical patterns in the physical structure of leaves provide better evidence for the EICA tradeoff than measurements of specialist performance or damage done to plants? First, as pointed out by Orians and Ward (2010), evolutionary responses in defences depend on variation in the cost of particular defences, chemical novelty, the relative abundance of generalist and specialist herbivores, and available resources. The effect of these and other factors on the often very diverse specialist communities in native ranges make evolutionary response hard to detect without sampling far more insect species than have been tested to date. Structural qualities of the plants may integrate these factors. Importantly, our trend for specialist performance was based on only seven studies, the same number as in the search by Felker-Quinn et al. (2013), and of these, two grew the herbivores on leaf discs rather than on living plants. Even more concerning, our trend across the seven studies was based on only four plant species. Of the seven specialist insect species identified in our search, six of them are biological control agents, meaning that the target exotic invaders had not completely escaped these specialists. Lastly, all tests of specialist performance were conducted in greenhouses where shade, low temperatures, and plentiful water can substantially reduce LSM and the production of secondary metabolites, including those involved in defence (Chen et al., 2013; Einhellig & Eckrich, 1984; Lavola et al., 1998; Lobón et al., 2002). There were six measurements in the literature search of damage by specialist insects, compiled from six different studies and involving six different insect species. Again, five of these were done in greenhouses. These issues cast serious doubt on whether the performance of specialists, or damage done by them, has been adequately measured, and thus provide modest evidence for supporting or not supporting EICA in meta-analyses. It may be that the lack for evidence for specialist defence-competitive ability trade-offs, on which EICA is based, is due to the paucity and nature of studies, rather than sufficient studies that report no evidence. This surprising lack of data for specialists may make our investigation of LSM an even more important opportunity for future studies. There was also a publication bias towards low effect size measure suggesting that more studies and more extensive testing is needed.

We found that plants from non-native ranges were superior at suppressing other species, competitively or through allelopathy, but the tolerance of competition from other species did not differ between ranges. While consistent with EICA, this is inconsistent with recent theory and evidence for the evolution of competition when exotics and natives encounter each other. Atwater et al. (2021) used experiments and simulations to show that when multiple native genotypes of the native *Pseudoroegneria spicata* competed together against the invasive *Centaurea stoebe*, the ability of the native to tolerate competition was far more important than the ability to suppress the invader. They attributed this to the 'demolition derby' nature of competition in natural communities, where strong suppressor genotypes have to share the benefits of eliminating competitors with other weak genotypes, diluting the selective advantage. Thus, in multi-genotype scenarios, those in which exotics must evolve, the tolerance of competitors should be more beneficial than suppression because it is not shared with other genotypes (also see Fletcher et al., 2016; MacDougall & Turkington, 2004). Our results also do not reconcile with a meta-analysis by Gollivets and Wallin (2018) who found that exotic plants outcompeted native species through a high ability to tolerate competition, rather than through stronger suppressive ability. Our results may have differed from these due to markedly different search terms and screening criteria, but it did not appear to be due to differences in sample size. However, competition is a highly conditional interaction, depending on who your competitor is, whether conspecifics or heterospecifics are matched (Joshi et al., 2014), the biogeographic origin of neighbours (Aschehoug et al., 2012; Callaway et al., 2011), the biota in the substrate used (Lekberg et al., 2018) and the abiotic conditions in which competition occurs (Brooker et al., 2005). Competitive effects and responses can also depend on different traits of the exotics (Puritty et al., 2018). All these factors might make it hard to detect consistent competitive outcomes. Our results, and similar and contrasting results of others, illustrate a fundamental weakness in the literature on competition in the context of EICA. Short-term growth experiments do not necessarily yield insight into long-term competitive outcomes, and long-term field studies exposing genotypes of different origin to a range of native competitors are important elements of EICA that has not substantially advanced.

Our exploration of the literature on leaf traits relevant to quantitative defences (primarily LSM) helps fill the gap in knowledge described above for evolutionary responses to release from specialists. Support for predictions derived from EICA-like trade-offs involving specialists is likely to depend to a large degree on the presumed high costs of quantitative defences, such as leaf structure, because they inherently and consistently constrain plant growth (see Müller-Schärer et al., 2004; Poorter & de Jong, 1999). In contrast, secondary metabolite-based toxins appear to be relatively cheap, constrain growth less and even attract co-evolved specialist herbivores (Orians & Ward, 2010). Coley et al. (1985) reported that species with the ability to grow fast were associated with qualitative defences, whereas slow-growing species were associated with quantitative defences (also see Herms & Mattson, 1992).

Hints of such trade-offs can also be found in leaf trait comparisons of native and exotic species. A recent 'mini-review' by Montesinos (2022) described exotic invasive species as being 'faster' than natives, that is faster nutrient acquisition, growth and reproduction in the context of the trait economics spectrum (Reich, 2014). Leishman et al. (2007) compiled leaf trait data for 75 native and 90 exotic invasive species, and exotic invasive species had significantly higher N and P per unit leaf mass, assimilation rates and leaf area per unit mass (in other words, lower LSM) than natives. Similarly, Huang et al. (2020) conducted a phylogenetically controlled meta-analysis of 47 pairs of exotic invasive species versus non-invasive exotics and natives combined that occurred in China. They found that the non-invasive exotic and native species groups had higher leaf density, cellulose, hemicellulose and lignin concentrations, and high nitrogen per leaf mass than invasive exotics. These, and other (Grotkopp & Rejmánek, 2007; Osunkoya et al., 2010; Sandel & Low, 2019; but see Leffler et al., 2014) trait comparisons of native and exotic invasive species suggest another route for exploring the assumptions that escaping specialists allows reallocation of resources to growth, perhaps a route that is easier to measure accurately and at large scales. Clearly, more common garden experiments are needed that investigate in more detail whether plants in their non-native ranges show evolutionary trait shifts that are consistent with the loss of quantitative, physical defences against specialists.

One of the most thorough studies of evolution in specialist defences across ranges was not identified in our searches. Agrawal et al. (2015) found that concentrations of inducible latex defences of *Asclepias syriaca* triggered by monarch butterflies, a specialist, were much lower in non-native populations, consistent with our general findings and the predictions of EICA. LSM was also lower in the non-native range, and specialist caterpillars grew far slower on plants from the native range than those from the non-native range, but this did not correspond with greater plant size in the non-native range. Considered together, these results provide some of the strongest evidence we know of for adaptive evolution in defences after introduction, but without the commonly found increase in size. A second pivotal study, Uesugi and Kessler (2013), was identified in our first search, but was excluded from the meta-analysis because they did not use the native versus non-native experimental contrasts in a common garden. Nevertheless, this study provided strong support for the EICA trade-off. They grew *Solidago altissima*, a North American native, but invasive in Eurasia, under artificial selection in the field in the native range and exposed them to herbivores or not. They found increased interspecific competitive ability when herbivores were excluded, but not in control plots with herbivores. This increase in competitive ability appeared to be due to increased production of allelopathic polyacetylenes. See Bossdorf (2013) for a conceptual integration of this study, and Inderjit et al. (2011), Qin et al. (2013) and Zheng et al. (2015) for comparisons of native and non-native range populations in which trade-offs in defence and allelopathic effects were identified.

We included both field and greenhouse common gardens, but greenhouse-grown plants provide limited tests of generalist and specialist performance and damage. As noted above, eliminating physical stress inherent to field conditions, and shade, can decrease production of secondary metabolites and their function (Barraza et al., 2004; Einhellig & Eckrich, 1984; Lobón et al., 2002). Second, shade leaves consistently have lower LSM than leaves grown in the sun. Such responses to greenhouse conditions might mask differences between native and non-native ranges. As noted above, almost all tests explicitly targeting either generalist or specialist insect growth responses, or the damage they did to plants, were in greenhouses. Field tests were almost completely limited to tests of damage done to plants, and included all herbivores present at the time of the experiment, both specialists and generalists. This is why the range in which damage was measured is so important—native ranges should have both groups of consumers, whereas generalists should dominate in non-native ranges. We found that plants from native populations were damaged more than plants from non-native populations *in non-native range field experiments* (Figure 1d), suggesting that non-native plants had evolved greater defences against generalists, consistent with our measurements of generalist-related chemistry (Figure 1) and damage done by generalists (Figure 1b), and consistent with the SDH.

The evolution of superior competitive ability has been, to a large degree, evaluated on the basis of increased size of plants from non-native ranges, the most common effect recorded in EICA experiments and syntheses, including ours. This may not always be a good assumption (but see Goldberg & Fleetwood, 1987). Puritty et al. (2018) found that the size of various native species was not a good predictor of competitive effect on or response to the invasive *Bromus madritensis*. Getman-Pickering et al. (2018) reported that apparent evolutionary increases in size of an invader did not correspond with its competitive effects on natives. In experiments, Besaw et al. (2011) found that nutrient addition altered competitive outcomes among exotics invaders and natives in ways that could not be predicted by the growth of the species when they were grown alone (also see Joshi et al., 2014; Shelby et al., 2016).

In sum, by utilising the literature on leaf traits, primarily Leaf-Specific Mass, we report that populations of species from non-native ranges have substantially lower quantitative defences than conspecifics in native ranges (also see detailed experiments by Feng et al., 2009, 2011). These quantitative defences are thought to target specialist herbivores primarily, but certainly affect many types of consumers, an important caveat for our general conclusions. The reduction in quantitative defences corresponded with large increases in plant size, and also with a stronger competitive ability to suppress other species, including through allelopathic effects. Muddying these evolutionary waters was a concomitant increase in qualitative (secondary metabolites) defences in plants from non-native ranges (see Doorduin & Vrieling, 2011), indicating selection for increased defence against generalists in non-native ranges, the SDH. Even so, our results are consistent with predictions derived from the initial proposal for EICA—a trade-off between reduced specialist defences and increased competitive ability.

AUTHORSHIP

RMC cultivated the idea, RMC, CJL, JEL and JLH designed the study, all authors performed the research. RMC 'visualised' the analyses but CJL and JEL performed the analyses, and RMC wrote the first draft of the manuscript. All authors contributed extensively to writing the final manuscript.

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DATA AVAILABILITY STATEMENT

No new data were used, but should the manuscript be accepted, the data will be archived in an appropriate public repository, and the data DOI will be included in the article.

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SUPPORTING INFORMATION

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

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