

# 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 tradeoff in which exotic species in non-native ranges become larger and more competitive, but invest less in consumer defenses, relative to populations in native ranges. This tradeoff is exceptionally complex because detecting concomitant biogeographical shifts in competitive ability and consumer defense depend upon which traits are targeted, how competition is measured, the defense chemicals quantified, whether defense 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 tradeoff 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 defense 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 tradeoffs, we do not know if the biogeographical differences we found were caused by tradeoffs *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 tradeoffs fundamental to EICA.

## 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 vs. defense tradeoffs, initiated by Blossey & Notzold's (1995) proposal that escape from natural, specialist enemies in non-native ranges leads to relaxed selection for defense. In turn, such relaxed selection might lead to the reallocation of resources, no longer needed for defense, 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 & Notzold's (1995) Evolution of Increased Competitive Ability (EICA) hypothesis, many of which have been synthesized 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 tradeoff at the heart of EICA does not – i.e., there is little evidence for decreased allocation to defense concomitant with higher growth (Bossdorf *et al.*, 2005; Colautti *et al.*, 2009; Atwood & Meyerson 2011; 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* defense, only seven showed range-based differences that were consistent with an EICA-like tradeoff. 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 tradeoff-based predictions of the EICA hypothesis. More specifically, they did not find significant reductions in physical and chemical defenses, 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 & Holeski (2018) meta-analyzed only studies that measured *both* growth and defense 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 vs. the responses of herbivores, and these might differ between generalists vs. 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) vs. 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 sterilized 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 tradeoffs that occur during exotic invasion. For instance, Blossey & 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 toward herbivore communities dominated by generalists. They suggested that in non-native ranges, qualitative toxin-based defenses 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 defenses such as structural tissue toughness, lignins, tannins, and perhaps some phenolics, should decrease in non-native ranges. This perspective is articulated as the Shifting Defense Hypothesis (SDH; see Doorduyn & 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, Wikström *et al.* 2006, Pearson *et al.* 2011; Schaffner *et al.* 2011; Tallamy *et al.* 2011; Lucero & Callaway 2018; Lucero *et al.* 2019). 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 toward 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 tradeoffs hypothesized by EICA in a new light. These nuances are illustrated as the general hypothesis, general predictions and specific predictions, organized generally following van Kluenen *et al.* (2010) and Heger & Jeshcke (2014) in Box 1. We also present the hypothesis and predictions for the Shifting Defense Hypothesis in Box 2. These hypotheses emphasize that trade-offs, *per se*, are exceptionally difficult to test. For example, increased growth and decreased chemical defense 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 tradeoffs 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 vs. specialist herbivores (see Felker-Quinn *et al.* 2013). Third, we parsed whether any biogeographical differences in competition were driven by competitive effects (suppression of neighbors) vs. competitive responses (tolerance to neighbors). Fourth, and based on a second literature search and meta-analysis, we tested whether biogeographical differences in defense levels were significantly influenced by qualitative (chemical) or quantitative (structural) defenses. Our first test represented a traditional, conjoined approach for examining tradeoffs 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 naturalized and invasive exotics (McKinney & La Sorte 2007; Pearson *et al.* 2016). The majority of the exotic species considered here were nonetheless highly invasive (Supplementary Information, Table S1, Table S2).

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 (species presented in Table S1). 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 (species presented in Table S2). 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 (Fig. S1).

Our searches yielded ten classes of measurements that we extracted for meta-analysis: competitive effects of exotics on neighbors (“competitive effect”), competitive effects of neighbors 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 defenses against herbivores (“chemical defense”), and quantitative defenses against herbivores



(“structural defense”) (Table 1). 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 defense included chemicals in leaves thought to be related to herbivore defense, 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 defense chemicals were odoratin, phenylpropanoid glycosides, pyrrolizidine alkaloids, glycosides, flavonoids, sinigrin, phytol, alliarinoside, hypericin, and hypericides (Table 1). We emphasize that many of these chemicals are poorly understood and might also affect specialists (Ali & Agrawal 2012; Massad *et al.* 2011). Structural, quantitative, defenses 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 vs. specialist defense are based on the literature described above, but see Ali & Agrawal (2012) for how disturbingly little is known about the function of these defense 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 vs. non-native ranges, we conducted meta-analyses in R version 4.2.0 (R-Development-Core-Team, 2022) using the package metafor version 3.0-2 (Viechtbauer 2017). In total, five random mixed-effects 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 specialization 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 modeling experimental range as a moderator. The fourth parsed competitive effects (competitive suppression) from competitive responses (competitive tolerance) and examined effect sizes by modeling the metric of competition (competitive suppression vs. competitive tolerance) as a moderator. The fifth and last partitioned quantitative defenses 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 defense (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-analyzed 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 were tested in all models, and findings in all instances were robust (i.e., modeling 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).

## Results

At the first level of analysis, only size reflected biogeographical patterns consistent with EICA (Fig. 1a;  $X^2 = 43.06$ ,  $p = 0.0001$ ,  $n = 217$ , 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, Fig. 1a; 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 (Fig. 1a; Box 1; Box 2).

Damage done to plants by insects and the responses of insects to plants (growth or survival) depended upon herbivore specialization (specialist vs. generalist) and biogeographic context, though not as predicted by EICA (see Felker-Quinn 2013; Fig. 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 were conducted (Fig. 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 (Fig. 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 neighbors similarly. Thus, parsing competitive suppression (plant effects on neighbors) from competitive tolerance (plant responses to neighbors; see Miller & Werner 1987, Goldberg 1990; Atwater *et al.* 2021) is important or examining the predictions of EICA.

Levels of *in situ* quantitative defenses at the leaf level varied with the type of quantitative defense (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 1a, which included all chemistry measurements across all of the publications we analyzed, the majority of which were qualitative (see Methods for list of chemicals). Consistent with predictions of EICA, levels of physical quantitative defenses were higher in plants from native ranges than non-native ranges (Fig. 2, model  $X^2 = 11.3$ ,  $p = 0.003$ ; Box 1). However, chemistry-based quantitative defenses 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 defenses. 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 ( $X^2 = 42.7$ ,  $p = 0.0001$ ,  $n = 317$ , 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 defenses (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 defenses in non-native ranges are based on modest sample sizes, but combining these measurements of quantitative defenses with size and competition differences provides new circumstantial support for the classic tradeoff originally proposed in the EICA (Blossey & Notzold 1995). That said, we emphasize that this pattern is consistent with an EICA-like tradeoff, but does not necessarily demonstrate an evolutionary tradeoff relationship between enemy release and subsequent decreases in defensive traits.

Blossey & 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 tradeoffs within taxa, but our results for quantitative defense 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 defenses, 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 & Holeski (2018) reported structural leaf differences as evidence for the loss of defenses 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 defense? In an in-depth review of plant physical defenses, 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 defense 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 defenses, but expressed concern that it 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 emphasize that LSM is a “soft trait” that affects many plant functions and therefore cannot be interpreted as a “smoking gun” for actual tradeoffs. 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 toward 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 tradeoffs (e.g., growth vs. qualitative defense chemicals) are subject to the same limitations in tradeoffs 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 specialized 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 defenses” were opposite to those reported by Rotter & 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 & Holeski (2018) included few. In addition, they restricted their analyses to studies that

measured both fitness and defense traits, limiting their sample size to six publications with physical defense measurements. Regardless, Rotter & Holeski's (2018) report of *increased* physical defenses in non-native range populations provides an important caution - accurately understanding what actually represents physical defenses is complex, and our emphasis here on LSM as an indicator of quantitative defense is likely to be only part of the story.

Our results are also consistent with the Shifting Defense Hypothesis (SDH; Müller-Schärer *et al.* 2004; Doorduyn & Vrieling 2011; Lin *et al.* 2015; 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 defenses 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 defense chemicals, indicating that the latter had experienced selection for greater defense against generalists. Our synthesis highlights the complexity of evolutionary responses by exotics, but given appropriate experimental designs, tradeoffs 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 defenses, 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 neighbors 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 & 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*

387 *biomass than individuals taken from the species native range*". Similar results for competition  
388 have been reported by Callaway *et al.* (2011), Inderjit *et al.* (2011), and Aschehoug *et al.* (2012).  
389 Specialist insects did not damage plants from non-native ranges more, nor did they grow better  
390 on these plants, again consistent with all other reviews. This is inconsistent with the originally  
391 phrased idea of EICA (Blossey & Notzold 1995) that "*specialized herbivores (i.e., those with*  
392 *potential for introduction as biological control agents) will show improved performance on plant*  
393 *individuals originating from an area where plants have been introduced*". In sum, precise  
394 definitions of the metric used (i.e., structural vs. chemical defenses rather than combining the  
395 two) appear to be very important in the exploration of EICA, and EICA-like evolution. Thus,  
396 EICA continues to provide both a challenging set of ideas, and also complex opportunities to  
397 better test evolution resulting from the invasion process.

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

407         As noted, a focus on leaf structure, primarily LSM, provides direct but not fully  
408 independent experimental evidence that links to drivers of both growth and defense against  
409 specialists (Feng *et al.* 2009; Huang *et al.* 2020), and thus to a strong mechanistic relationship

410 between growth, competition, and defense against specialists. Why might biogeographical  
411 patterns in the physical structure of leaves provide better evidence for the EICA tradeoff than  
412 measurements of specialist performance or damage done to plants? First, as pointed out by  
413 Orians & Ward (2010), evolutionary responses in defenses depends on variation in the cost of  
414 particular defenses, chemical novelty, the relative abundance of generalist and specialist  
415 herbivores, and available resources. The effect of these and other factors on the often very  
416 diverse specialist communities in native ranges make evolutionary response hard to detect  
417 without sampling far more insect species than have been tested to date. Structural qualities of  
418 the plants may integrate these factors. Importantly, our trend for specialist performance was  
419 based on only seven studies, the same number as in the search by Felker-Quinn (2013), and of  
420 these, two grew the herbivores on leaf discs rather than on living plants. Even more concerning,  
421 our trend across the seven studies was based on only four plant species. Of the seven specialist  
422 insect species identified in our search, six of them are biological control agents, meaning that the  
423 target exotic invaders had not completely escaped these specialists. Lastly, all tests of specialist  
424 performance were conducted in greenhouses where shade, low temperatures, and plentiful water  
425 can substantially reduce LSM and the production of secondary metabolites, including those  
426 involved in defense (Lavola *et al.* 1998; Einhellig & Eckrich 1984; Lobón *et al.* 2002; Chen *et*  
427 *al.* 2013). There were six measurements in the literature search of damage by specialist insects,  
428 compiled from six different studies and involving six different insect species. Again, five of  
429 these were done in greenhouses. These issues cast serious doubt on whether the performance of  
430 specialists, or damage done by them, has been adequately measured, and thus provide modest  
431 evidence for supporting or not supporting EICA in meta-analyses. It may be that the lack for  
432 evidence for specialist defense-competitive ability tradeoffs, 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 Golivets & 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 neighbors (Callaway *et al.* 2011; Aschehoug *et al.* 2012), 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 of 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 defenses (primarily LSM) helps fill the gap in knowledge described above for evolutionary responses to release from specialists. Support for predictions derived from EICA-like tradeoffs involving specialists are likely to depend to a large degree on the presumed high costs of quantitative defenses, such as leaf structure, because they inherently and consistently constrain plant growth (see Poorter & de Jong 1999; Müller-Schärer *et al.* 2004). 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 defenses, whereas slow growing species were associated with quantitative defenses (also see Herms & Mattson 1992).

Hints of such tradeoffs can also be found in leaf trait comparisons of native and exotic species. A recent “mini-review” by Montesinos (2021) described exotic invasive species as being “faster” than natives, i.e., 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 defenses against specialists.

One of the most thorough studies of evolution in specialist defenses across ranges was not identified in our searches. Agrawal *et al.* (2015) found that concentrations of inducible latex defenses 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 defenses after introduction, but without the commonly found increase in size. A second pivotal study, Uesugi & Kessler (2013), was identified in our first search, but was excluded from the meta-analysis because they did not use

the native vs. non-native experimental contrasts in a common garden. Nevertheless, this study provided strong support for the EICA tradeoff. 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 *et al.* (2013) for a conceptual integration of this study, and Inderjit *et al.* (2011), Qin *et al.* (2012) and Zheng *et al.* (2014) for comparisons of native and non-native range populations in which tradeoffs in defense 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 (Einhellig & Eckrich 1984; Lobón *et al.* 2002; Barraza *et al.* 2004). 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* (Fig. 1d), suggesting that non-native plants had evolved greater defenses against



generalists, consistent with our measurements of generalist-related chemistry (Fig. 1a) and damage done by generalists (Fig. 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 utilizing the literature on leaf traits, primarily Leaf Specific Mass, we report that populations of species from non-native ranges have substantially lower quantitative defenses than conspecifics in native ranges (also see detailed experiments by Feng *et al.* 2009, 2011). These quantitative defenses 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 defenses 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) defenses in plants from non-native ranges (see Doorduyn & Vrieling 2011), indicating selection for increased defense against generalists in non-native ranges, the SDH. Even so, our results are

consistent with predictions derived from the initial proposal for EICA - a tradeoff between reduced specialist defenses and increased competitive ability.

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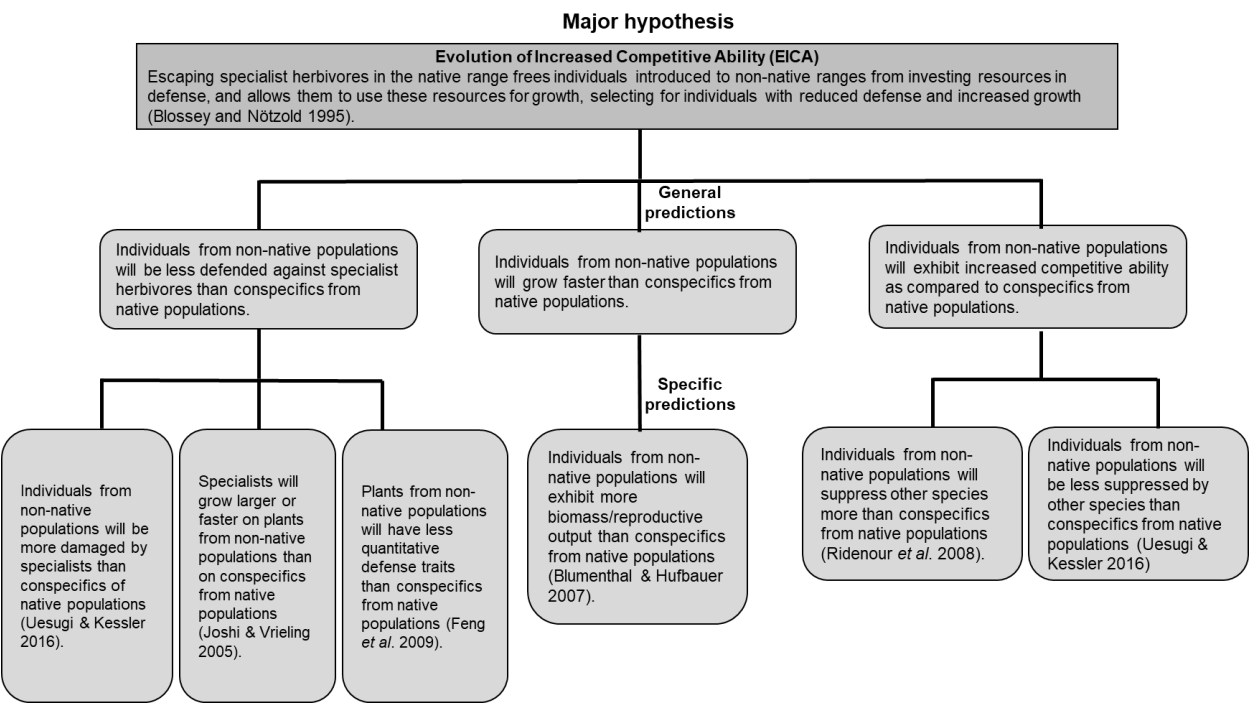
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Table 1. Variables and metrics used in meta-analyses.

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

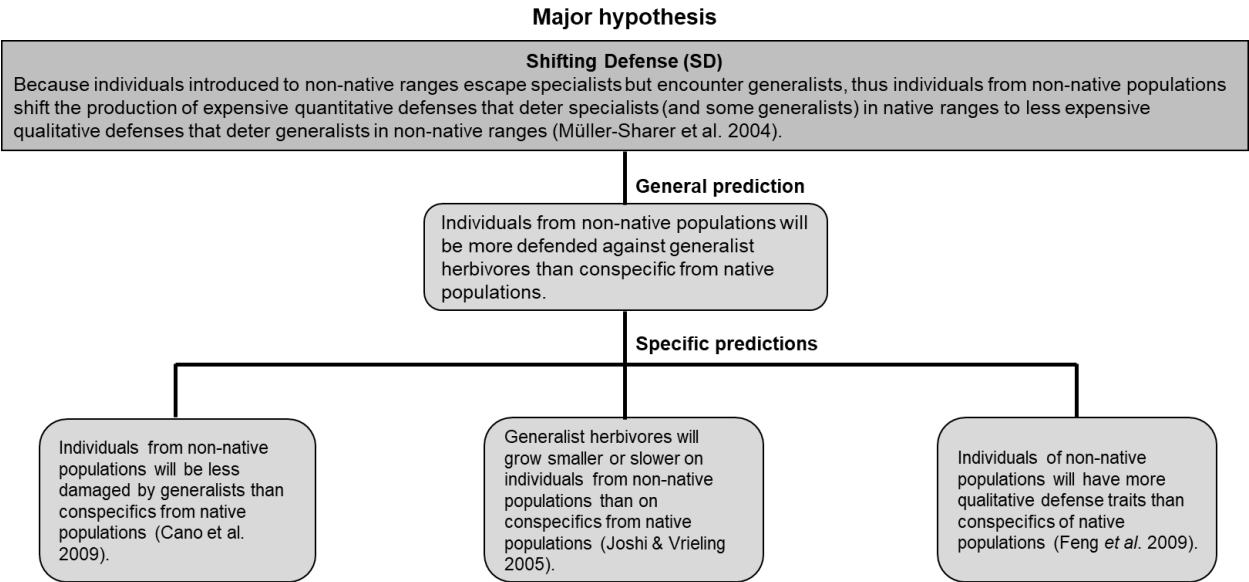
840    Box 1. Organization of general and specific predictions for the Evolution of Increased  
 841    Competitive Ability Hypothesis. Not all possible predictions are included.



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844    Box 2. Organization of general and specific predictions for the Shifting Defense Hypothesis.



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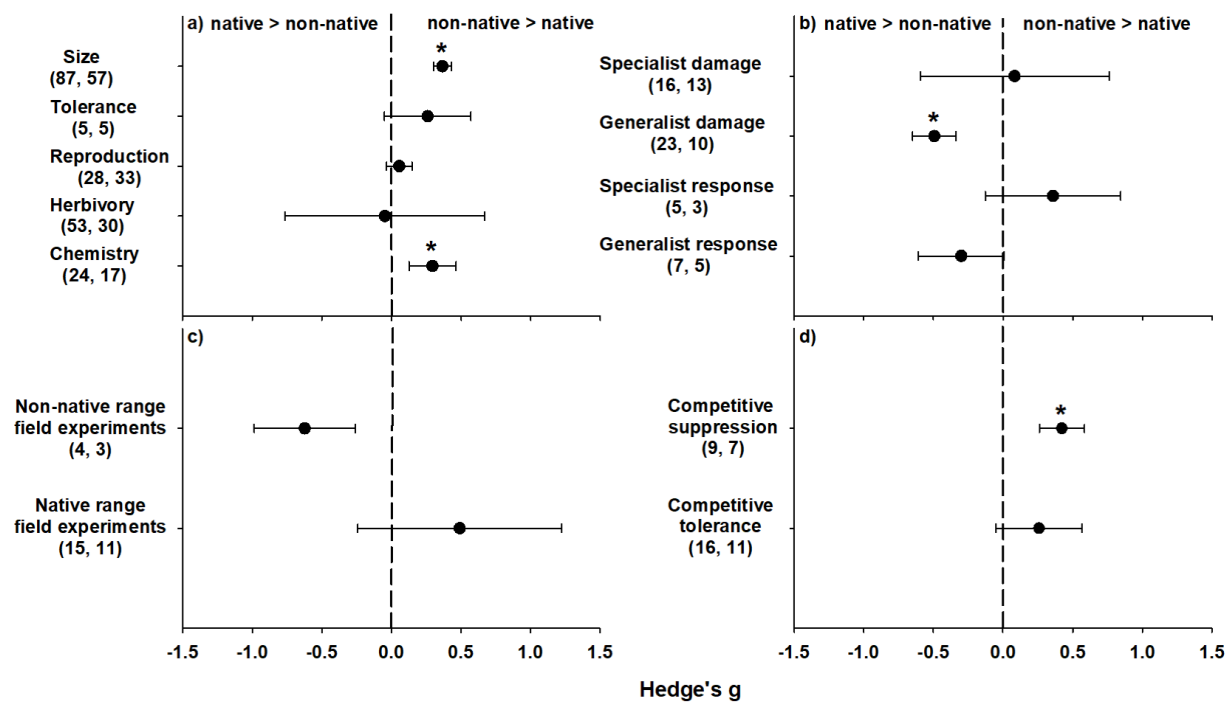
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## Figure Legends

Figure 1a. 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 defenses 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 neighbors) and competitive response (ability to tolerate suppression by neighbors) 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; i.e., 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.

Figure 2. Mean Hedge's  $g$  for quantitative defenses, including leaf chemical traits most related to quantitative defense (e.g., lignin, tannins) and the physical structure of leaves related to quantitative defense (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; i.e., 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.





**Figure 1**

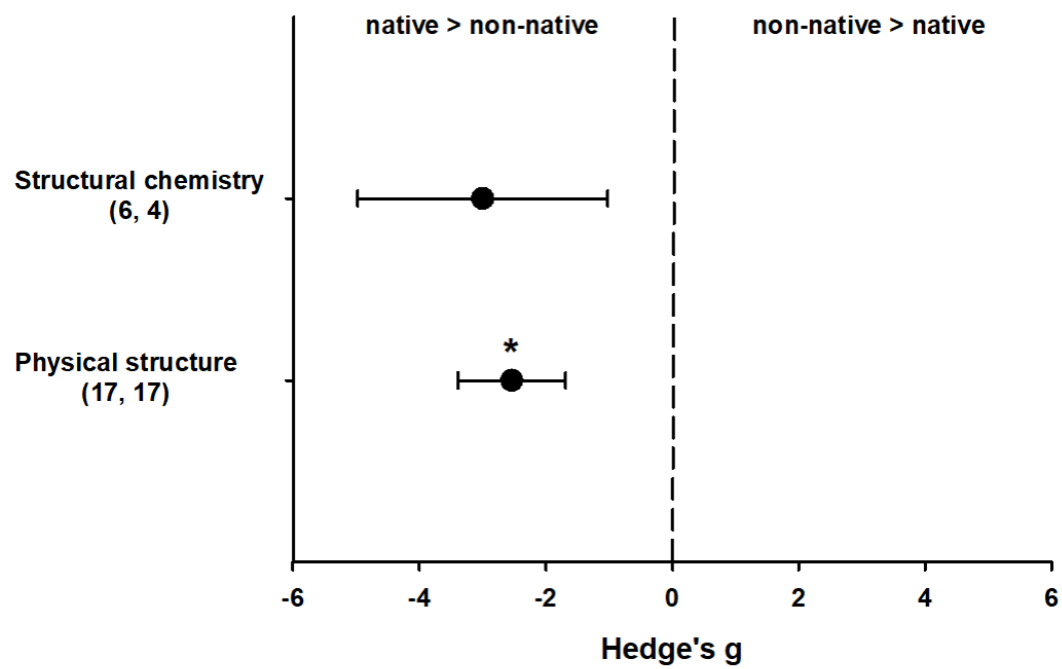


Figure 2