

# 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.

# The EICA is dead? Long live the EICA!

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1 **Abstract**

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3 increased competitive ability (EICA). EICA predicts that biogeographical release from natural  
4 enemies initiates a tradeoff in which exotic species in non-native ranges become larger and more  
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6 tradeoff is exceptionally complex because detecting concomitant biogeographical shifts in  
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9 than defend, whether “herbivory” is artificial or natural, and where consumers fall on the  
10 generalist-specialist spectrum. Previous meta-analyses have successfully identified patterns but  
11 have yet to fully disentangle this complexity. We used meta-analysis to reevaluate traditional  
12 metrics used to test EICA theory and then expanded on these metrics by partitioning competitive  
13 effect and competitive tolerance measures and testing Leaf Specific Mass in detail as a response  
14 trait. Unlike previous syntheses, our meta-analyses detected evidence consistent with the classic  
15 tradeoff inherent to EICA. Plants from non-native ranges imposed greater competitive effects  
16 than plants from native ranges and were less quantitatively defended than plants from native  
17 ranges. Our results for defense were not based on complex leaf chemistry, but instead were  
18 estimated from tannins, toughness traits, and primarily Leaf Specific Mass. Species specificity  
19 occurred but did not influence the general patterns. As for all evidence for EICA-like tradeoffs,  
20 we do not know if the biogeographical differences we found were caused by tradeoffs *per se*, but  
21 they are consistent with predictions derived from the overarching hypothesis. Underestimating  
22 physical leaf structure may have contributed to two decades of tepid perspectives on the tradeoffs  
23 fundamental to EICA.

## 24 **Introduction**

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

39 Bossdorf *et al.* (2005) found empirical support for rapid “evolutionary change” in studies  
40 that had accumulated for 10 years after the EICA hypothesis was published, but of the 17 studies  
41 that tested some aspect of both growth *and* defense, only seven showed range-based differences  
42 that were consistent with an EICA-like tradeoff. Colautti *et al.* (2009) assessed the literature  
43 quantitatively and found differences for reproduction between ranges and strong significant  
44 interaction effects showing that range effects were highly contingent on latitudinal clines (also  
45 see Atwater *et al.* 2018; Rosche *et al.* 2019). A meta-analysis by Felker-Quinn *et al.* (2013)  
46 found much evidence for rapid evolution by plant species in their non-native ranges, but not for

47 the tradeoff-based predictions of the EICA hypothesis. More specifically, they did not find  
48 significant reductions in physical and chemical defenses, increased herbivore growth, or greater  
49 herbivore damage for plants from the non-native range than conspecifics from the native range.  
50 However, Felker-Quinn *et al.* (2013) found that plants from non-native ranges were larger or  
51 grew faster, but only in the absence of competition. Finally, Rotter & Holeski (2018) meta-  
52 analyzed only studies that measured *both* growth and defense traits in common conditions  
53 (n=30), and found evidence for trade-offs between plant fitness traits and herbivore growth, but  
54 in contrast to other syntheses found that generalist growth *improved* on plants from non-native  
55 ranges. This was opposite to the trend in Felker-Quinn *et al.*'s (2013) results.

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

69 plants often escape the negative effects of soil biota (Callaway *et al.* 2004; Kulmatiski *et al.*  
70 2008).

71         Teasing apart some of the complex nuances in the many measurements used to explore  
72 EICA may increase our understanding of the scope, extent, and mechanisms of any evolutionary  
73 tradeoffs that occur during exotic invasion. For instance, Blossey & Notzold (1995) focused  
74 exclusively on specialists. They reasoned that exotics escape only specialists in their non-native  
75 ranges, unless specialists are co-introduced or introduced later as biological controls (see Müller-  
76 Schärer *et al.* 2004). Thus, Müller-Schärer *et al.* (2004) pointed out that a key aspect of “escape  
77 from enemies” in new ranges is a biogeographical shift toward herbivore communities  
78 dominated by generalists. They suggested that in non-native ranges, qualitative toxin-based  
79 defenses might actually increase in concentration (especially those that actually attract specialists  
80 in native ranges) instead of decreasing, as predicted by extrapolating Blossey and Notzold’s  
81 (1995) focus on specialist performance. Correspondingly, Müller-Schärer *et al.* (2004) argued  
82 that quantitative defenses such as structural tissue toughness, lignins, tannins, and perhaps some  
83 phenolics, should decrease in non-native ranges. This perspective is articulated as the Shifting  
84 Defense Hypothesis (SDH; see Doorduyn & Vrieling 2011; Zhang *et al.* 2018).

85         There is evidence that exotic invaders in non-native ranges can also “escape” the effects  
86 of generalists relative to populations in native ranges (Cappuccino & Carpenter 2005, Wikström  
87 *et al.* 2006, Pearson *et al.* 2011; Schaffner *et al.* 2011; Tallamy *et al.* 2011; Lucero & Callaway  
88 2018; Lucero *et al.* 2019). Thus, separating the effects and responses of generalists and  
89 specialists in meta-analyses might yield different insights than when they are grouped. Felker-  
90 Quinn *et al.* (2013) separated the performance (growth and survival) of generalists and  
91 specialists in their meta-analysis and found trends toward decreased performance of generalists

92 and increased performance of specialists on plants collected in non-native ranges compared to  
93 plants from their native ranges. Again, this is consistent with the SDH. Zhang *et al.* (2018)  
94 reported that the biogeographic origin, or provenance, of generalist herbivores affected the  
95 relative damage done to native and non-native conspecifics. Plants from non-native ranges  
96 showed increased resistance to generalists native to either range, but generalists from the non-  
97 native ranges of plants imposed larger proportional damage than generalists from the native  
98 ranges of plants.

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

114 Our objectives were to examine classic metrics traditionally used to detect evidence for  
115 EICA-like tradeoffs and then expand upon traditional metrics by parsing out previously  
116 overlooked factors inherent to plant-herbivore and plant-plant interactions. First, we tested the  
117 fundamental assertions of EICA that plant species collected in non-native ranges are a) more  
118 competitive, b) larger, c) more fecund, d) less affected by herbivores, and e) less defended  
119 against herbivores than conspecifics in native ranges. Second, we parsed whether any  
120 biogeographic differences in herbivory are driven by the effects or responses of generalist vs.  
121 specialist herbivores (see Felker-Quinn *et al.* 2013). Third, we parsed whether any  
122 biogeographical differences in competition were driven by competitive effects (suppression of  
123 neighbors) vs. competitive responses (tolerance to neighbors). Fourth, and based on a second  
124 literature search and meta-analysis, we tested whether biogeographical differences in defense  
125 levels were significantly influenced by qualitative (chemical) or quantitative (structural)  
126 defenses. Our first test represented a traditional, conjoined approach for examining tradeoffs  
127 predicted by EICA. The remaining tests examined the relative importance of plant-plant and  
128 plant-herbivore interactions that are often overlooked but that can be critical for better  
129 examinations of EICA.

## 130 **Methods**

### 131 Search procedures

132 We defined exotic plant species as those introduced by humans to a biogeographically  
133 different part of the world than where they originated, usually to a different continent, though we  
134 also included islands (see Manea *et al.* 2019). Europe and Asia were grouped as Eurasia (see  
135 Engelkes *et al.* 2008; van Grunsven *et al.* 2010). We did not attempt to classify the  
136 “invasiveness” of exotic species, either via abundance or impact, despite the practical importance

137 of distinguishing between naturalized and invasive exotics (McKinney & La Sorte 2007; Pearson  
138 *et al.* 2016). The majority of the exotic species considered here were nonetheless highly invasive  
139 (Supplementary Information, Table S1, Table S2).

140 We identified primary studies for our synthesis with two independent searches of the  
141 Web of Science bibliometric resource. Our first search used the terms ‘(EICA OR “evolution of  
142 increased competitive ability”), plants’ in June of 2020. This first search returned 179 peer-  
143 reviewed publications on competition, size, fecundity, and herbivores (species presented in Table  
144 S1). To identify additional studies on leaf traits, which were not well represented in our first  
145 search, we conducted a second search in May 2021 using the terms ‘evolution AND increased  
146 AND competitive AND ability AND leaf traits.’ This second search returned 28 peer-reviewed  
147 publications (species presented in Table S2). Studies from both searches were screened to meet  
148 the following criteria: 1) primary studies (i.e., reviews, syntheses, or commentaries were not  
149 included), 2) common growth conditions (i.e., common gardens), and 3) primary data (sample  
150 mean, sample size, estimate of variance) could be extracted. Our screening process yielded 93  
151 relevant studies for a total of 304 unique and independent observations. Additional details of the  
152 screening process are shown in a PRISMA figure (Fig. S1).

153 Our searches yielded ten classes of measurements that we extracted for meta-analysis:  
154 competitive effects of exotics on neighbors (“competitive effect”), competitive effects of  
155 neighbors on exotics (“competitive response”), size, reproduction, growth response to simulated  
156 damage, or artificial herbivory (“damage tolerance”), performance (growth and survival) of  
157 herbivores (“herbivore performance”), actual damage done by herbivores (“herbivore damage”),  
158 plant response to actual herbivore damage (“response to herbivore damage”), qualitative  
159 defenses against herbivores (“chemical defense”), and quantitative defenses against herbivores

160 (“structural defense”) (Table 1). Competitive effects included experiments with allelopathy.  
161 Size estimates included aboveground biomass, total biomass, and height. Reproduction  
162 estimates included flower number, seed number, and inflorescence mass. Some studies used  
163 clipping as artificial herbivory and then subsequently measured plant growth responses.  
164 However, clipping does not always mimic herbivory (Baldwin 1990), thus we considered plant  
165 growth responses to clipping and artificial herbivory as damage tolerance. Herbivore  
166 performance included the mass, egg count, or survival of specialist or generalist insect  
167 herbivores. Herbivore damage, as opposed to artificial damage, included holes in leaves or  
168 removal of leaf area. Response to herbivore damage included measures of plant growth  
169 responses to damage done by specialist or generalist insect herbivores. Measurements of  
170 herbivore damage were taken in both greenhouse and field common gardens, with the latter  
171 exposing plants to a milieu of both specialist and generalist herbivores. Therefore, we classified  
172 field measurements of herbivore damage and response to herbivore damage by whether they  
173 were conducted in native or non-native ranges, because these ranges should differ in the relative  
174 abundance of generalists and specialists. Measurements of chemical defense included chemicals  
175 in leaves thought to be related to herbivore defense, but we only included chemicals that were  
176 mostly likely to target generalists (see Discussion). The roles of other putative defensive  
177 chemicals, such as tannins and general phenolics, are surprisingly unclear (see review by Massad  
178 *et al.* 2011). Specifically, our qualitative defense chemicals were odoratin, phenylpropanoid  
179 glycosides, pyrrolizidine alkaloids, glycosides, flavonoids, sinigrin, phytol, alliarinoside,  
180 hypericin, and hypericides (Table 1). We emphasize that many of these chemicals are poorly  
181 understood and might also affect specialists (Ali & Agrawal 2012; Massad *et al.* 2011).  
182 Structural, quantitative, defenses included measurements of leaf specific mass; leaf specific area;

183 leaf toughness; and density of leaf prickles, trichomes, and tannins and phenolics based on  
184 Müller-Schärer *et al.* (2004) and citations therein. Our assignments of chemicals to generalist vs.  
185 specialist defense are based on the literature described above, but see Ali & Agrawal (2012) for  
186 how disturbingly little is known about the function of these defense chemicals.

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

#### 195 Data analyses

196         To contrast measurements of performance or biotic interactions between populations of  
197 species in native vs. non-native ranges, we conducted meta-analyses in R version 4.2.0 (R-  
198 Development-Core-Team, 2022) using the package metafor version 3.0-2 (Viechtbauer 2017).  
199 In total, five random mixed-effects models (without intercepts for categorical moderators) were  
200 used to test for biogeographical differences among the effect sizes (Hedge's  $g$ ) of specific  
201 moderators using the function 'rma' (Supplementary materials for trait and leaf-structure meta-  
202 analyses). The first tested effect sizes related to exotic plant size, damage tolerance,  
203 reproduction, herbivory, and leaf chemistry – response measures that have been used  
204 traditionally to examine EICA theory. This model fit plant response measure as a moderator.  
205 The second further partitioned herbivory and tested effect sizes for specialist damage, generalist

206 damage, specialist response, and generalist response. This model fit herbivore specialization as a  
207 moderator. The third tested the influence of experimental range (i.e., whether the experiment  
208 was conducted in the native or non-native range) on effect size by modeling experimental range  
209 as a moderator. The fourth parsed competitive effects (competitive suppression) from  
210 competitive responses (competitive tolerance) and examined effect sizes by modeling the metric  
211 of competition (competitive suppression vs. competitive tolerance) as a moderator. The fifth and  
212 last partitioned quantitative defenses at the leaf level and tested effect sizes related to *in situ*  
213 levels of structural chemistry and physical structure. This model fit the type of leaf-level  
214 quantitative defense (structural chemistry vs. physical structure) as a moderator (Gurevitch et al.  
215 2018). As primary studies included for formal synthesis reported and measured different  
216 variables, each of these random mixed-effects models examined the subsets of the compiled data  
217 relevant to the specific prediction of EICA tested here (sensitivity analyses and global models  
218 confirmed this was valid; see below). Simple post hoc *t*-tests for each mean effect size then were  
219 used and reported in figures to test for statistically significant differences from 0 (or no net effect  
220 of a specific moderator) at 95% confidence levels. Heterogeneity was examined using *Q*-  
221 statistics reported in the random-effects models ( Koricheva & Gurevitch 2014, Langan *et al.*,  
222 2019), and publication bias was explored using the ‘regtest’ function in metafor that reports  
223 Egger's regression test for funnel plot asymmetry (Egger *et al.* 1997; Jennions *et al.* 2013; Lin &  
224 Chu 2018). The estimated 95% confidence intervals and estimated marginal means from the  
225 meta-analysis models were used in the forest plots (Lortie *et al.* 2013).

226 To explore the robustness of our analyses and to ensure that the random mixed-effects  
227 models described above were parsimonious and statistically justified, we re-analyzed our data  
228 with global models (Halpern *et al.* 2020) fit to all data with response measure fit as a moderator.

229 All global meta-analyses detected significant effects of response measure, indicating that the  
230 specific models described above were justified. Sensitivity analyses for the global model and  
231 subsequent individual response set analyses were also included, examining the relative  
232 importance of species-specificity. Classification of species as a fixed or random effect  
233 moderator were tested in all models, and findings in all instances were robust (i.e., modeling  
234 species as a fixed or random effect moderator did not influence our results). Data from the  
235 literature did not allow a complete integration of species into analyses simply because few  
236 studies used the same species. This problem is inherent to a synthetic approach that integrates  
237 disparate findings from many primary studies that do not share identical protocols but still  
238 nonetheless provides robust testing provided the same response variables were reported (as they  
239 were here in each of the 4 tests).

## 240 **Results**

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

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

264           The outcome of common garden experiments depended upon the biogeographical range in  
265 which they were conducted (Fig. 1c, model  $X^2 = 6.6$ ,  $p = 0.03$ ,  $n = 16$ ; heterogeneity,  $Q = 80.9$ ,  $p$   
266  $= 0.0008$ , post hoc t-test  $p < 0.05$ ; Box 1). When common gardens were constructed in non-  
267 native ranges, where generalist consumer effects on exotic species should disproportionately  
268 predominate (Keane & Crawley 2002), plants from populations in non-native ranges suffered  
269 less damage than plants from native ranges. This is inconsistent with EICA but consistent with  
270 the SDH again suggesting increased tolerance to attack by generalists.

271           Effect sizes of plant-plant competition varied with how competition was measured  
272 (competitive suppression vs. competitive tolerance; measured experimentally rather than inferred  
273 from size in the absence of another species) and biogeographical range (Fig. 1d, model  $X^2 = 7.8$ ,

274  $p=0.02$ ,  $n = 16$ ). Plants from non-native ranges suppressed other species more than plants from  
275 native ranges, which is consistent with EICA. However, plants from native and non-native  
276 ranges tolerated neighbors similarly. Thus, parsing competitive suppression (plant effects on  
277 neighbors) from competitive tolerance (plant responses to neighbors; see Miller & Werner 1987,  
278 Goldberg 1990; Atwater *et al.* 2021) is important or examining the predictions of EICA.

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

291 The global meta-analytical model, with all data, detected significant differences between  
292 moderators supporting deeper, targeted analyses of specific subsets of these data using relevant  
293 data for each assumption ( $X^2 = 42.7$ ,  $p = 0.0001$ ,  $n = 317$ , and heterogeneity was significant  $Q =$   
294  $597$ ,  $p = 0.0001$ ). The sensitivity of all models was re-tested by a global screening model, and  
295 each of the five reported meta-analyses were also tested with species identity as an additional  
296 moderator. All effects reported were robust and consistent in the global models. Species

297 included as a moderator did not change the outcome of the main moderators reported in in any of  
298 the results reported above. The general findings were thus not sensitive to variation that species  
299 identity potentially introduced to the larger patterns.

## 300 **Discussion**

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

311         Blossey & Notzold's (1995) initial articulation of the EICA hypothesis proposed how  
312 trait values *within a particular taxon* might evolve over time in response to translocation. Due to  
313 a lack of replication of species across studies, our meta-analyses could not explicitly test for  
314 apparent tradeoffs within taxa, but our results for quantitative defense differences are highly  
315 consistent with detailed single-species studies by Feng *et al.* (2009, 2011). Feng *et al.* (2009)  
316 found that populations of a tropical invader, *Ageratina adenophora*, from the non-native range  
317 showed reduced allocation to cell walls, resulting in poorer structural defenses, and increased  
318 nitrogen allocation to photosynthesis, related to growth. Perhaps most importantly, LSM was

319 15-20% higher for plants from the native range of Mexico than for plants from the non-native  
320 ranges of China and India. Following this, Feng *et al.* (2011) reported that *A. adenophora* plants  
321 from non-native ranges showed similar leaf construction costs to plants from the native range,  
322 but a much faster “payback time” providing more detail to mechanistic explanations of the  
323 evolution of increased growth.

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

341 mechanical properties within species, as is the case for each of our individual comparisons of  
342 conspecifics from native and non-native ranges.

343         Regardless, we emphasize that LSM is a “soft trait” that affects many plant functions and  
344 therefore cannot be interpreted as a “smoking gun” for actual tradeoffs. Most importantly, LSM  
345 is strongly negatively correlated with leaf nitrogen concentration per mass (Mooney & Gulmon  
346 1982), as increases in LSM inevitably reduces concentrations of nutrients, water, and chemistry  
347 based on dry mass, and all of these may have significant effects on both herbivory and  
348 photosynthesis. In other words, decreased LSM could be directly selected on based on its effect  
349 on growth rates. However, such a decrease in LSM, the trend toward better specialist responses  
350 to non-native conspecifics, and concomitant increases in size and competitive ability are  
351 consistent with the predictions of EICA. It is important to note that all studies of such tradeoffs  
352 (e.g., growth vs. qualitative defense chemicals) are subject to the same limitations in tradeoffs  
353 that cannot be experimentally separated from independent selection.

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

360         Our results for “physical defenses” were opposite to those reported by Rotter & Holeski  
361 (2018). This may have been for several reasons, but we included a large number of studies that  
362 compared LSM (or converted LSA) between native range and non-native populations, whereas  
363 Rotter & Holeski (2018) included few. In addition, they restricted their analyses to studies that

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

369 Our results are also consistent with the Shifting Defense Hypothesis (SDH; Müller-  
370 Schärer *et al.* 2004; Doorduyn & Vrieling 2011; Lin *et al.* 2015; Box 2). The SDH is that plant  
371 species in non-native ranges evolve reduced resistance to specialists and increased resistance to  
372 generalists due to escape from specialist, but not generalist, herbivores in the non-native range  
373 (Müller-Schärer *et al.* 2004). Müller-Schärer *et al.* (2004) predicted that quantitative defenses  
374 should decrease in non-native ranges. In support of this, we found that plants from native ranges  
375 were damaged less by generalists than plants from non-native ranges, and that plants from non-  
376 native ranges had more generalist-related defense chemicals, indicating that the latter had  
377 experienced selection for greater defense against generalists. Our synthesis highlights the  
378 complexity of evolutionary responses by exotics, but given appropriate experimental designs,  
379 tradeoffs in the evolution of exotic invasive species when they are released from specialist  
380 herbivory appear to be predictable and detectable (see Lin *et al.* 2015). In addition to reduced  
381 quantitative defenses, we found, as did all other reviews, that plants from non-native ranges were  
382 larger; however, we also found that they were able to competitively suppress their neighbors  
383 more than plants from native ranges. This finding represents an important advance as it supports  
384 a more direct prediction of the EICA hypothesis. Such suppression was not part of Blossey &  
385 Notzold's (1995) original phrasing, which stated that "...under identical growing conditions,  
386 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

433 the paucity and nature of studies, rather than sufficient studies that report no evidence. This  
434 surprising lack of data for specialists may make our investigation of LSM an even more  
435 important opportunity for future studies. There was also a publication bias towards low effect  
436 size measure suggesting that more studies and more extensive testing is needed.

437 We found that plants from non-native ranges were superior at suppressing other species,  
438 competitively or through allelopathy, but the tolerance of competition from other species did not  
439 differ between ranges. While consistent with EICA, this is inconsistent with recent theory and  
440 evidence for the evolution of competition when exotics and natives encounter each other.  
441 Atwater *et al.* (2021) used experiments and simulations to show that when multiple native  
442 genotypes of the native *Pseudoroegneria spicata* competed together against the invasive  
443 *Centaurea stoebe*, the ability of the native to tolerate competition was far more important than  
444 the ability to suppress the invader. They attributed this to the ‘demolition derby’ nature of  
445 competition in natural communities, where strong suppressor genotypes have to share the  
446 benefits of eliminating competitors with other weak genotypes, diluting the selective advantage.  
447 Thus, in multi-genotype scenarios, those in which exotics must evolve, the tolerance of  
448 competitors should be more beneficial than suppression because it is not shared with other  
449 genotypes (also see Fletcher *et al.* 2016; MacDougall & Turkington 2004). Our results also do  
450 not reconcile with a meta-analysis by Golivets & Wallin (2018) who found that exotic plants  
451 outcompeted native species through a high ability to tolerate competition, rather than through  
452 stronger suppressive ability. Our results may have differed from these due to markedly different  
453 search terms and screening criteria, but it did not appear to be due to differences in sample size.  
454 However, competition is a highly conditional interaction, depending on who your competitor is,  
455 whether conspecifics or heterospecifics are matched (Joshi *et al.* 2014), the biogeographic origin

456 of neighbors (Callaway *et al.* 2011; Aschehoug *et al.* 2012), the biota in the substrate used  
457 (Lekberg *et al.* 2018), and the abiotic conditions in which competition occurs (Brooker *et al.*  
458 2005). Competitive effects and responses can also depend on different traits of the exotics  
459 (Puritty *et al.* 2018). All of these factors might make it hard to detect consistent competitive  
460 outcomes. Our results, and similar and contrasting results of others, illustrate a fundamental  
461 weakness in the literature on competition in the context of EICA. Short-term growth  
462 experiments do not necessarily yield insight into long-term competitive outcomes, and long-term  
463 field studies exposing genotypes of different origin to a range of native competitors are important  
464 elements of EICA that has not substantially advanced.

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

475         Hints of such tradeoffs can also be found in leaf trait comparisons of native and exotic  
476 species. A recent “mini-review” by Montesinos (2021) described exotic invasive species as  
477 being “faster” than natives, i.e., faster nutrient acquisition, growth and reproduction in the  
478 context of the trait economics spectrum (Reich 2014). Leishman *et al.* (2007) compiled leaf trait

479 data for 75 native and 90 exotic invasive species, and exotic invasive species had significantly  
480 higher N and P per unit leaf mass, assimilation rates and leaf area per unit mass (in other words,  
481 lower LSM) than natives. Similarly, Huang *et al.* (2020) conducted a phylogenetically  
482 controlled meta-analysis of 47 pairs of exotic invasive species versus non-invasive exotics and  
483 natives combined that occurred in China. They found that the non-invasive exotic and native  
484 species groups had higher leaf density, cellulose, hemicellulose and lignin concentrations, and  
485 high nitrogen per leaf mass than invasive exotics. These, and other (Grotkopp & Rejmánek  
486 2007; Osunkoya *et al.* 2010; Sandel & Low 2019; but see Leffler *et al.* 2014) trait comparisons  
487 of native and exotic invasive species suggest another route for exploring the assumptions that  
488 escaping specialists allows reallocation of resources to growth, perhaps a route that is easier to  
489 measure accurately and at large scales. Clearly, more common garden experiments are needed  
490 that investigate in more detail whether plants in their non-native ranges show evolutionary trait  
491 shifts that are consistent with the loss of quantitative, physical defenses against specialists.

492         One of the most thorough studies of evolution in specialist defenses across ranges was  
493 not identified in our searches. Agrawal *et al.* (2015) found that concentrations of inducible latex  
494 defenses of *Asclepias syriaca* triggered by monarch butterflies, a specialist, were much lower in  
495 non-native populations, consistent with our general findings and the predictions of EICA. LSM  
496 was also lower in the non-native range, and specialist caterpillars grew far slower on plants from  
497 the native range than those from the non-native range, but this did not correspond with greater  
498 plant size in the non-native range. Considered together, these results provide some of the  
499 strongest evidence we know of for adaptive evolution in defenses after introduction, but without  
500 the commonly found increase in size. A second pivotal study, Uesugi & Kessler (2013), was  
501 identified in our first search, but was excluded from the meta-analysis because they did not use

502 the native vs. non-native experimental contrasts in a common garden. Nevertheless, this study  
503 provided strong support for the EICA tradeoff. They grew *Solidago altissima*, a North American  
504 native, but invasive in Eurasia, under artificial selection in the field in the native range and  
505 exposed them to herbivores or not. They found increased interspecific competitive ability when  
506 herbivores were excluded, but not in control plots with herbivores. This increase in competitive  
507 ability appeared to be due to increased production of allelopathic polyacetylenes. See Bossdorf  
508 *et al.* (2013) for a conceptual integration of this study, and Inderjit *et al.* (2011), Qin *et al.* (2012)  
509 and Zheng *et al.* (2014) for comparisons of native and non-native range populations in which  
510 tradeoffs in defense and allelopathic effects were identified.

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

525 generalists, consistent with our measurements of generalist-related chemistry (Fig. 1a) and  
526 damage done by generalists (Fig. 1b), and consistent with the SDH.

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

537         In sum, by utilizing the literature on leaf traits, primarily Leaf Specific Mass, we report  
538 that populations of species from non-native ranges have substantially lower quantitative defenses  
539 than conspecifics in native ranges (also see detailed experiments by Feng *et al.* 2009, 2011).  
540 These quantitative defenses are thought to target specialist herbivores primarily, but certainly  
541 affect many types of consumers, an important caveat for our general conclusions. The reduction  
542 in quantitative defenses corresponded with large increases in plant size, and also with a stronger  
543 competitive ability to suppress other species, including through allelopathic effects. Muddying  
544 these evolutionary waters was a concomitant increase in qualitative (secondary metabolites)  
545 defenses in plants from non-native ranges (see Doorduyn & Vrieling 2011), indicating selection  
546 for increased defense against generalists in non-native ranges, the SDH. Even so, our results are

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

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

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798 **Variable** **Metrics**

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800 **Size** Plant total biomass, aboveground biomass, growth rate

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802 **Damage tolerance** Response to artificial damage/herbivory – plant total biomass,

803 aboveground biomass, growth rate

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805 **Reproduction** Flower, fruit or seed number, seed size

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807 **Herbivory**

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809 **Specialist damage** Proportion of leaf or stem missing, chewed, discolored

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811 **Specialist response** Insect biomass, growth rate

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813 **Generalist damage** Proportion of leaf or stem missing, chewed, discolored

814

815 **Generalist response** Insect biomass, growth rate

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817 **Chemistry** Concentration of odoratin, phenylpropanoid glycosides,

818 pyrrolizidine alkaloids, glycosides, flavonoids, sinigrin, phytol,

819 alliarinoside, hypericin, hypericides, tannins, phenolics

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821 **Field experiments** Damage done by all herbivores present naturally in field –

822 proportion of leaf or stem missing, chewed, or discolored

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824 **Competitive suppression** Biomass of *other* plants when grown with target exotic species vs.

825 biomass of plants grown without the target exotic species

826

827 **Competitive tolerance** Biomass of target species when grown with *other* plants vs.

828 biomass of target species with grown without other plants

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830 **Structural chemistry** Concentration of tannins, phenolics

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832 **Physical structure** Leaf specific mass, leaf specific area, leaf toughness, density of

833 leaves, prickles/trichomes

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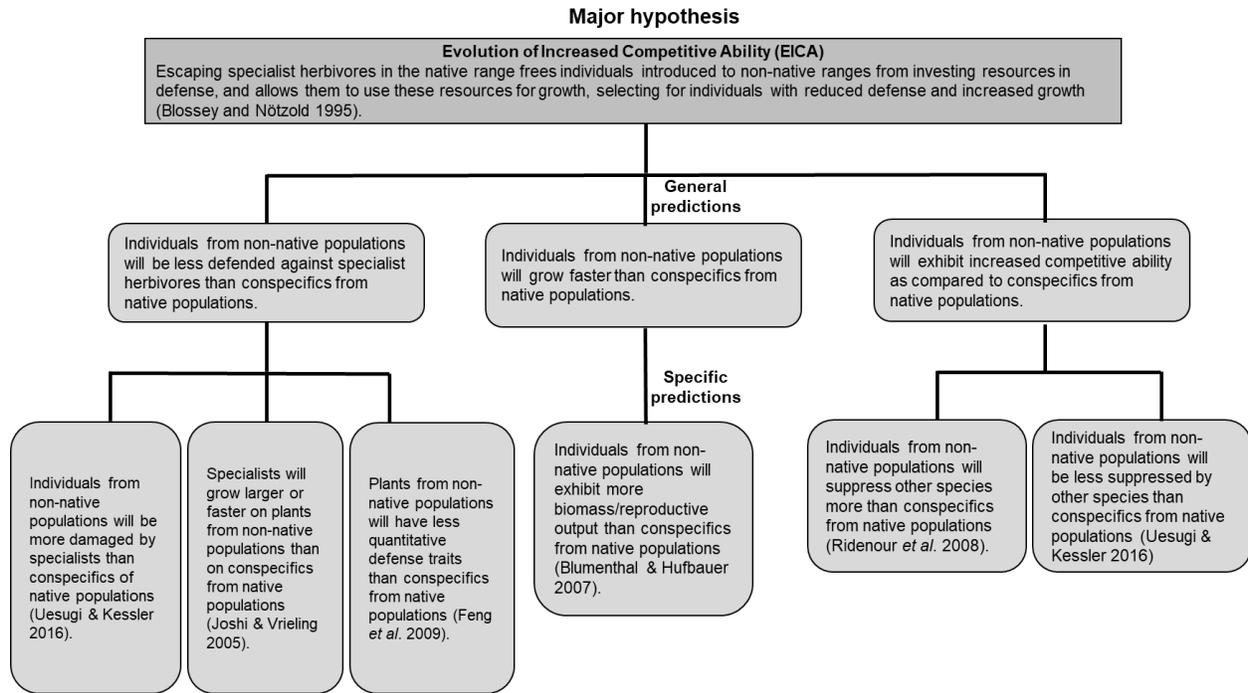
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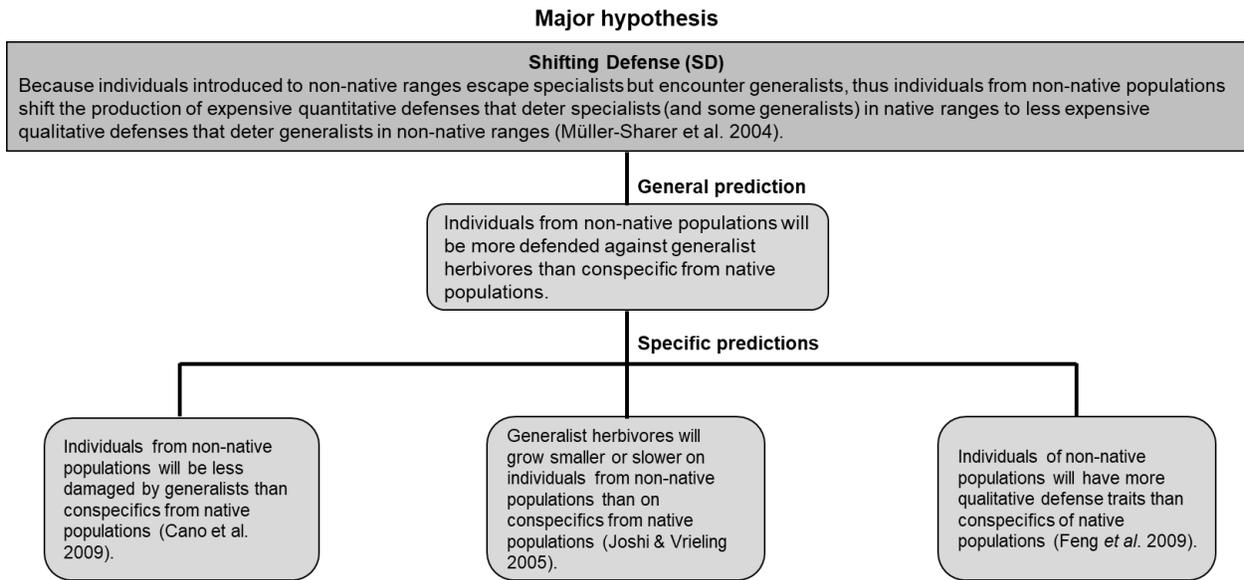
840 Box 1. Organization of general and specific predictions for the Evolution of Increased  
 841 Competitive Ability Hypothesis. Not all possible predictions are included.



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



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859 **Figure Legends**

860 Figure 1a. Mean Hedge's  $g$  for plant size, damage tolerance (artificial herbivory), reproduction,  
861 herbivory (herbivore performance and herbivore damage combined), and chemistry most likely  
862 to contribute to qualitative defenses for conspecific plants from native and non-native ranges, b)  
863 mean Hedge's  $g$  for damage done by specialist and generalist herbivores to plants and the  
864 performance of specialist and generalist herbivores for conspecific plants from native and non-  
865 native ranges, c) mean Hedge's  $g$  for damage done by all herbivores present naturally in field  
866 common gardens in non-native and native ranges of plants for conspecifics from native and non-  
867 native ranges, d) mean Hedge's  $g$  for competitive effect (ability to suppress neighbors) and  
868 competitive response (ability to tolerate suppression by neighbors) for conspecifics from native  
869 and non-native ranges. Bars show 1 SE and asterisks are presented for Hedge's  $g$  values that are  
870 significantly different than zero; i.e., when plants from one range show different responses than  
871 plants from the other range. Numbers in parentheses indicate the number of studies used and  
872 species used.

873 Figure 2. Mean Hedge's  $g$  for quantitative defenses, including leaf chemical traits most related to  
874 quantitative defense (e.g., lignin, tannins) and the physical structure of leaves related to  
875 quantitative defense (primarily Leaf Specific Mass; Hanley et al. 2007) for conspecifics from  
876 native and non-native ranges. Bars show 1 SE and the asterisk is for the Hedge's  $g$  value that is  
877 significantly different than zero; i.e., when plants from one range show different responses than  
878 plants from the other range. Numbers in parentheses indicate the number of studies used and  
879 species used.

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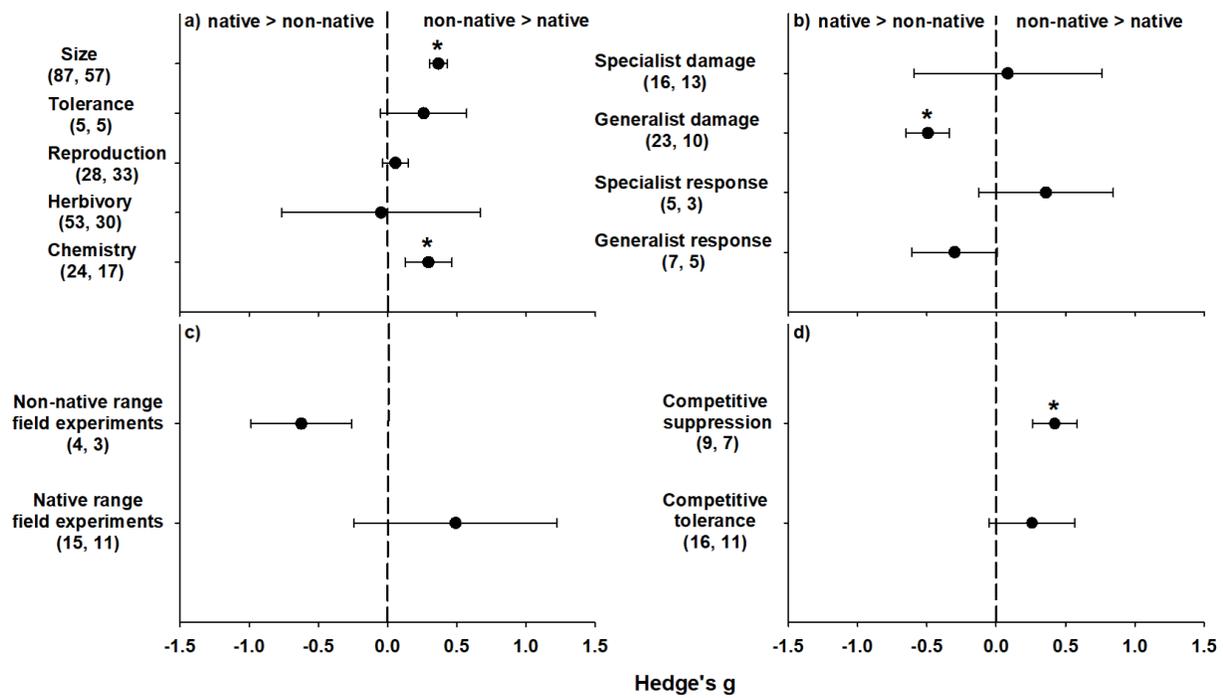


Figure 1

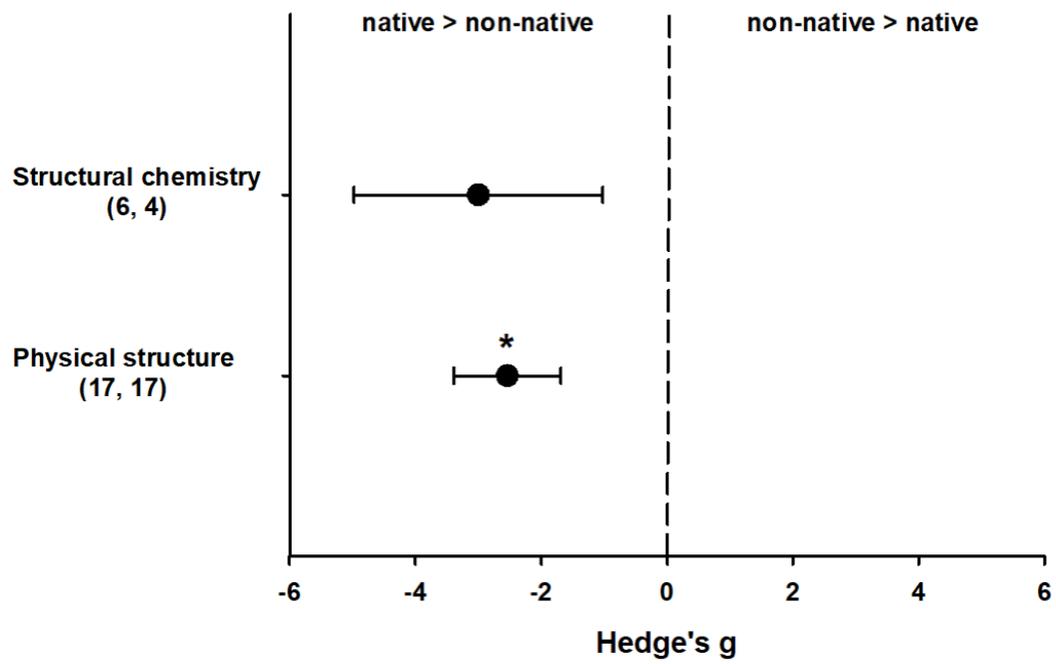


Figure 2