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ORIGINAL PAPER

A meta-analysis of the evolution of increased competitive ability hypothesis: genetic-based trait variation and herbivory resistance trade-offs

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Abstract Non-native organisms are an abundant component of almost all global ecosystems. A prominent framework to explain the success of non-native plants is the evolution of increased competitive ability (EICA) hypothesis. EICA predicts that plants escape from co-evolved herbivores after introduction into a non-native habitat. Assuming limited resources, a relaxation in selection pressures for resistance traits against the co-evolved specialist herbivores allows plants to allocate increased resources to traits related to fitness and/or competitive ability. Despite the prominence of the EICA hypothesis in the literature, empirical evidence has been mixed. We conducted a meta-analysis on 30 studies that focused on genetic-based trait variation and the trade-off between resistance traits and fitness to assess support for the EICA hypothesis. We found general support for EICA across studies. Performance of herbivores was higher on non-native plant populations than on native populations of the same species. Fitness trait values were higher in non-native populations, relative to native, and we found evidence for trade-offs between herbivore performance and plant fitness traits. Support for EICA was strongest when we focused on direct measurements of herbivore performance, and weakest when we assessed resistance traits, highlighting the complex and often unknown relationship between resistance traits and particular herbivores in many plant–herbivore systems.

Keywords Evolution of increased competitive ability · EICA · Herbivory · Non-native plants · Meta-analysis

Introduction

Due to the often drastic impacts of non-native plants on their communities and ecosystems, many researchers have sought to identify the factors that drive non-native plant success and/or invasiveness (Rejmánek and Richardson 1996). Understanding the evolutionary mechanisms underlying the long-term ecological success of non-native plants has been a long-standing goal of non-native organism research (Duncan and Williams 2002). The responses of non-native plant species to both biotic and abiotic selection pressures in the non-native region have been of particular interest, as these pressures often dictate the success of the community members (Sax et al. 2005).

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One framework to explain the success of non-native plants is the evolution of increased competitive ability (EICA) hypothesis (Blossey and Notzold 1995). The hypothesis was first formulated in an investigation of the success of purple loosestrife (*Lythrum salicaria*) in eastern North America after its introduction from Europe. Plants in non-native populations of purple loosestrife had significantly more reproductive output as well as greater biomass than those in native, European populations (Blossey and Notzold 1995). Increases in these trait values were also correlated with a decline in defenses against two specialist herbivores that, at the time, were not present in eastern North America. From this, the authors inferred that, given a finite amount of resources, plants that no longer have to defend themselves against specialist herbivores are able to shift allocation of resources from defense to biomass production and/or reproduction, allowing individuals to become more "competitive" against native plants by giving them a reproductive fitness advantage (Blossey and Notzold 1995). These changes are expected to be genetic changes rather than purely plastic responses. Since its advent, the EICA hypothesis has been more formally described as a series of testable ecological predictions within an evolutionary framework (Catford et al. 2009).

As originally formulated, the first EICA prediction is that when a plant species is introduced into a non-indigenous environment, 1(a) the species "escapes from" co-evolved specialist herbivores in its native range (Maron and Vilà 2001; Wolfe 2002). This escape should 1(b) reduce selection pressures on defense traits, as many specialists exert unique selection pressures upon specific resistance traits in their host plants (Doorduin and Vrieling 2011; van der Meijden 1996; Cornell and Hawkins 2003; Lankau 2007; Mithöfer and Boland 2008). The absence of specialist herbivores can result in reductions in levels of these resistance traits (Agrawal et al. 2012). Conversely, generalist herbivores respond, at least to some extent, to different resistance traits than do specialists. Generalist herbivores will routinely feed on non-native plants and may even prefer these non-native plants over native plants (Memmott et al. 2000; Parker and Hay 2005; Morrison and Hay 2011). Tests of EICA prediction 1(a) involve comparisons of the herbivore community in the native and non-native range of the focal plant species. Tests of EICA prediction 1(b) should involve field-based assessment of selection on particular resistance traits, and/or comparisons of genetic variation in levels of resistance traits, between native and non-native populations of the plant species of interest (Uesugi and Kessler 2013).

The second EICA prediction is that there will be a trade-off between allocation of resources for resistance against specialist herbivores and allocation to traits related to competitive ability (Pyšek and Richardson 2008; Van Kleunen et al. 2010). Plants invest considerable resources into reproduction, growth, and defense traits (Bazzaz et al. 1987). Given finite levels of resources, a decrease in investment in specialist-related resistance traits should allow increased resource allocation to traits related to growth, reproduction and/or competitive ability (Herms and Mattson 1992; Huang et al. 2010). Traits most important for competitive ability are likely to vary depending on plant life history and the ecological context. For example, non-native annual plants with increased seed production have higher competitive ability against native annual plants (Brooks 2000), while vegetative growth enhances competitive ability in native Californian perennial grasses against exotic grass species (Seabloom et al. 2003). Winter root growth, rather than seed production or aboveground biomass, gives non-native *Bromus tectorum* a competitive advantage over native *Agropyrum spicatum* within cold winter deserts of the Great Basin (Harris 1977). Because a trade-off between allocation of resources to resistance and competitive ability is inherent to the second EICA prediction, tests of this prediction should necessarily examine traits related to both factors. This might include investigation of genetic and/or phenotypic correlations between herbivory resistance and competitive ability traits, and/or tests of herbivore preference or performance and plant survivorship, growth, or reproductive fitness (Torchin et al. 2001).

Numerous studies have tested the predictions of EICA, yielding mixed empirical support and contradictory results even in studies of closely related plant species (Orians and Ward 2010). For example, in *Lepidium draba* (Brassicacea), specialist herbivores had no preference for non-native populations over native populations, and native and non-native populations had comparable levels of vigor (Cripps et al. 2009). In contrast, in a study with the closely related *Brassica nigra* (Brassicacea), when both native and non-native populations were released from herbivores, non-native populations had increased survivorship and seed production relative to native populations (Oduor et al. 2011). More than a decade ago, a narrative review of empirical tests of the EICA hypothesis assessed studies based in common gardens, as well as in field environments, to assess both genetic and phenotypic trait variation (Bossdorf et al. 2005). Fewer than half of the studies included in this review supported the predictions of EICA. Here, we update Bossdorf et al.'s (2005) study using a meta-analysis to evaluate evidence for the evolutionary herbivore resistance/competitive ability trade-offs inherent to the EICA hypothesis. We also compare and contrast our results to those of a meta-analysis testing several predictions of EICA that included publications from 2010 and prior (Felker-Quinn et al. 2013).

In contrast to Felker-Quinn et al. (2013), we focus on evidence for the evolutionary trade-offs inherent to EICA as originally formulated by Blossey and Notzold (1995), including only studies that assess genetic-based differences for some aspect of both herbivory resistance and fitness/competitive ability. Almost half of the publications included in our analysis (14/30) were too recent to be included in the Felker-Quinn et al. meta-analysis. Specifically, we test whether the literature shows (a) a decline in levels of herbivory resistance within non-native plant populations relative to those in native populations of the same species, and (b) a relative increase in fitness-related traits within the non-native populations. Finally, we examine (c) the strength and direction of the relationship between plant resistance to herbivores and fitness.

Methods

In this study, we defined non-native plants as those that had been introduced to a continent to which they are not considered endemic, and its co-evolved herbivores were absent at the time of introduction. We excluded studies reporting range-expanding plants within a continent, as these plants are likely to move with their co-evolved herbivore(s).

To evaluate support for EICA in the peer-reviewed literature, we searched Web of Science and Google Scholar with the search terms *plant–herbivore–defenses non-native plants* OR "*Evolution of Increased Competitive Ability*" in December of 2016. We did a second search using the same terms but spelling "defenses" as "defences," which returned identical results to the first search. From these studies, we also searched the literature cited sections, as well as the literature cited of two EICA reviews (Bossdorf et al. 2005; Felker-Quinn et al. 2013) as well as one about common gardens in non-native plant research (Moloney et al. 2009). This approach returned 135 papers that we screened by titles and abstracts to eliminate obviously irrelevant studies (e.g., papers discussing EICA in animal or algal systems). We performed an additional search in July 2017 in Web of Science to ensure that our original search terms were broad enough. This search included our original search terms, and added the terms "OR invas* OR exotic* OR nonnat* OR non-nat* OR alien* OR weed* OR nonindig* OR non-indig*". This expanded the results in Web of Science to 596,641. Narrowing the results to include only peer-reviewed articles from the "plant sciences" category on Web of Science left a total of 21,949 papers. We sorted these in Web of Science by relevance and then searched the first 4500 papers (> 20% of the results) for our inclusion criteria. None of these papers met our inclusion criteria. Our overall inclusion cut-off was July 2017.

To control for non-genetic based phenotypic variation (e.g. trait plasticity or environmental contributions) we included only studies that used a common "garden" to compare native and non-native populations of the same species, as comparisons in a common environment are necessary to assess genetic rather than environment-based changes between non-native and native populations. We further narrowed our search results to papers that included both a measure of plant resistance to herbivores and a measure of plant fitness and/or competitive ability in both native and non-native populations of the same species. These included feeding trials with generalist and/or a specialist herbivores, or direct measurements of resistance traits (e.g., trichome density, phytochemical concentrations, or leaf toughness). This was done to test the trade-off inherent to EICA prediction 2, that resistance against specialist herbivores should be reduced in non-native populations with concomitant increase in reproductive/competitive ability traits. In total 30 papers met our criteria and were included for analysis (Table 1).

Within each of the selected studies, we collected means, standard errors (which were back-calculated to standard deviations) and sample size of resistance

Table 1 Information for the plant species and traits measured for each studies included in the meta-analysis

Paper number	Reference	Species	Non-native continent	Fitness traits	Defense traits	Feeding trials
16	Cipollini et al. (2005)	*Alliaria petiolata*	N. America	T, D	C, C	None
9	Fukano and Yahara (2012)	*Ambrosia artemisiifolia*	Asia	D	None	S
26	Genton et al. (2005)	*Ambrosia artemisiifolia*	Europe	T	None	A, A, A
5	Agrawal et al. (2015)	*Asclepias syriaca*	Europe	T, A, B	C, P, T	S
27	Buschmann et al. (2005)	*Barbarea vulgaris, Bunias orientalis, Cardaria draba, Rorippa austriaca*	N. America	D, R, A	None	G, G, G, G
2	Oduor et al. (2011)	*Brassica nigra*	N. America	T, D, R, A	C, T	None
3	Ridenour et al. (2008)	*Centaurea maculosa*	N. America	T, R	C, P, T	G, S, S, S
20	Liao et al. (2014)	*Chromolaena odorata*	Asia	A	P, T	G, G, G
19	Zheng et al. (2015)	*Chromolaena odorata*	Asia	T	C	A, A,
11	Abhilasha and Joshi (2009)	*Conyza canadensis*	Europe	T, R	None	G, S
17	Reddy et al. (2015)	*Genista monspessulana*	N. America	A	None	S, S
8	Müller and Martens (2005)	*Lepidium draba*	N. America	T	C	None
1	Cripps et al. (2009)	*Lepidium draba*	N. America	T, A, B	None	A, S
7	Nötzold et al. (1997)	*Lythrum salicaria*	N. America	T, A, B	None	S, S
29	Willis et al. (1999)	*Lythrum salicaria*	N. America	A, B	None	G, S, S
21	Joshi and Tielbörger (2012)	*Lythrum salicaria*	N. America	A, B	None	A, A
24	Guo et al. (2011)	*Persicaria perfoliata*	N. America	T, D, A	C, P, P, P	G, G, G, G, G, S, S, S, S
15	Yang et al. (2014)	*Peuraria montana*	N. America	T, D, A, B	None	A
18	Huang and Ding (2015)	*Phytolacca americana*	Asia	T,R,A,B	None	A, A
25	Zou et al. (2008)	*Sapium sebiferum*	N. America	A	None	S
28	Siemann and Rogers (2001)	Sapium sebiferum	N. America	R, A	C	None
12	Joshi and Vrieling (2005)	*Senecio jacobaea*	N. America	R, A	C	G, G, S
4	Stastny et al. (2005)	*Senecio jacobaea*	N. America	T, R	C	S
10	Blair and Wolfe (2004)	*Silene latifolia*	N. America	D, R, A	P, T	None
30	Wolfe et al. (2004)	*Silene latifolia*	N. America	D, R	None	S, S

Table 1 continued

Paper number	Reference	Species	Non-native continent	Fitness traits	Defense traits	Feeding trials
13	Meyer et al. (2005)	*Solidago gigantea*	Europe	R, A, B	None	A
14	Huang et al. (2010)	*Triadica sebifera*	N. America	D, A, B	C	G, G, G, G, S, S, S, S
22	Hornoy et al. (2011)	*Ulex europus*	N. America	D, R, A	None	S
23	Alba et al. (2011)	*Verbascum thapsus*	N. America	T, D, A	C, C, P, T	None
6	Kumschick et al. (2013)	*Verbascum thapsus*	N. America	T, A, B	None	G

For fitness/competitive ability traits: *R* reproductive trait, *D* developmental rate, *B* belowground growth, *A* aboveground growth, *T* total biomass. For resistance traits: *T* trichomes, *P* physical resistance, *C* phytochemical resistance. For feeding trials: *G* generalist herbivore, *S* specialist herbivore, *A* ambient herbivores

traits, preference/performance results from feeding trials, and fitness trait measurements. When there were multiple measurements for a trait (e.g. biomass) along a time series we chose the final (total) measurement. We converted means into Hedges' *d* (Hedges and Olkin 1985) using Metawin Ver. 2.1 (Rosenberg et al. 2000). This calculation of effect size accounts for low sample sizes and unequal sampling variances and provides a lower rate of Type I error compared to other measures of effect size (Lajeunesse and Forbes 2003; Koricheva et al. 2013). We tested for effect size differences between non-native plant populations and native plant populations of the same species. Positive scores indicate an increase of resistance traits, insect performance, or plant fitness traits in the non-native populations relative to the native, while negative scores represent a decrease in trait value in the non-native populations relative to native populations.

Resistance traits and feeding trial results were assessed by overall trends, as well as in categories. Resistance traits were grouped according to whether they were trichome measurements, other physical defenses (e.g. leaf toughness) or phytochemical traits, as these are likely to have different effects on herbivores as well as differential costs of production (Koricheva 2002; Barton 2016). Feeding trial results were grouped by whether trials used specialist herbivores, generalist herbivores (as defined by the study authors), or assessed damage from ambient herbivores at the study site (i.e. studies that did not identify herbivores but rather used in situ damage).

We also divided plant fitness traits into categories: reproductive traits, developmental rates, belowground vegetative traits, aboveground vegetative traits, and total (final) biomass. These five categories represent common measurements to quantify fitness; multiple categories were used because competitive ability may be expressed differently for different plant species and environments. Reproductive traits included flower production (number), seed output, and other traits related to sexual reproduction. Rates of development included days until flowering, or growth per day. We considered traits such as root mass and length as belowground vegetative traits while shoot or stem length and shoot mass were used as aboveground vegetative traits. Total (final) biomass is the sum of belowground and aboveground biomass. Both vegetative traits and reproductive traits are directly relevant to competitive ability as they may allow increased domination of resources and/or a greater ability to produce progeny (Aarssen 2005; Lockwood et al. 2005; Traveset and Richardson 2006; Simberloff 2009; Younginger et al. 2017) These functional traits are thus meaningful proxies for ecological competiveness (Cornelissen et al. 2003). Due to a limited number of studies (four) that included direct plant–plant competition experiments we did not include these trials.

We extracted the time since introduction and the method of introduction for each plant species using information supplied by each study. We calculated time since introduction as the year in which a study was conducted relative to the first known record of the plant in the non-native area, as given by the authors. We noted whether each introduction was intentional (e.g., garden escapes, agriculture plants, bank stabilization), or accidental (e.g., weeds from grain stock, hay contamination). The effect of time since and method of introduction on plant fitness traits was assessed using random effects models, which compared heterogeneity to a Chi square distribution (Metawin Ver. 2.1, Rosenberg et al. 2000). All models were compared against a Chi square distribution for significance (i.e., a significant Q_T implies other (non-measured) variables are more explanatory for the model; Cooper and Lindsay 1998). All alpha levels were set at 0.05.

Inclusion of species with closely shared evolutionary history can bias meta-analysis results (Adams 2008). We tested for phylogenetic independence within our meta-analysis. We created a phylogenetic tree of the species included using a super tree from Phylomatic v. 3 (Webb and Donoghue 2004), pooled the fitness effect sizes for each species, and tested for phylogenetic independence using the program Phylometa ver. 1.3 (Lajeunesse 2011). This program uses the Akaike information criterion (AIC) to indicate which model (phylogenetic independent model versus a traditional meta-analysis model) is the most efficient at reducing statistical error (Lajeunesse 2009). We found that our data was best described under a traditional meta-analysis model (traditional meta-analysis model AIC score = 54.50; phylogenetic independent AIC score = 56.75), thus we proceeded without any phylogenetic-related weights for the effect sizes.

EICA predicts a trade-off between allocations of resources to defense against herbivores versus traits related to competitive ability. We used meta-regression (OpenMEE; Wallace et al. 2017) to characterize the relationship between specific metrics of specialist herbivore performance and/or resistance traits versus fitness. Because many papers included independent studies of several herbivore species we included these as unique data points in the regressions. To avoid non-independence of our data we created an average fitness metric for the individual plant species used within each independent herbivore trial within studies. We used a random-effects model with a maximum likelihood estimator to evaluate models.

Lastly, we tested for publication bias using the effect size of fitness. We evaluated publication bias through three methods. First, we plotted our effect sizes against their standard error to create a funnel plot. A symmetrical data shape indicates that there is no publication bias, this assumes that studies with larger variance are less precise than studies with smaller variance. Secondly, to evaluate this symmetry we used Spearman's rank correlation test (Begg and Mazumdar 1994). Finally we used the Rosenberg's fail safe number to determine how many publications with effect sizes of zero would be needed to negate significant effect sizes of our study (Rosenberg 2005).

Results

Overall, resistance traits increased within non-native plant populations, relative to native populations of the same species (grand mean = 0.636, $p < 0.001$, Fig. 1a). The overall trend for resistance traits was driven in large part by phytochemical resistance traits and non-trichome physical defenses, which were higher in non-native populations than in native populations (grand mean = 0.446, $p = 0.033$ and grand mean = 1.378, $p = 0.002$, respectively, Fig. 1a). Levels of trichomes were measured in fewer studies (six total), with variable results across studies (grand mean = 0.393, $p = 0.321$, Fig. 1a).

Herbivores performed better on non-native populations than on native populations of the same species (grand mean = 0.556, $p < 0.001$, Fig. 1b). Although EICA was originally conceived to focus on relaxation of resistance against specialist herbivores, in feeding trials, we found no significant difference between generalist and specialist performance ($F_{1,\ 24} = 0.92$, $p = 0.41$). Generalist and specialist performance was highest on non-native, relative to native, populations, although this trend was significant only for generalists (generalist grand mean = 1.030, $p = 0.002$; specialist grand mean = 0.318, $p = 0.161$). Ambient herbivory also did not differ significantly between non-native vs. native populations (grand mean = 0.368, $p = 0.236$, Fig. 1b).

The manner in which an herbivore feeds, as well as its degree of specialization, can affect how particular

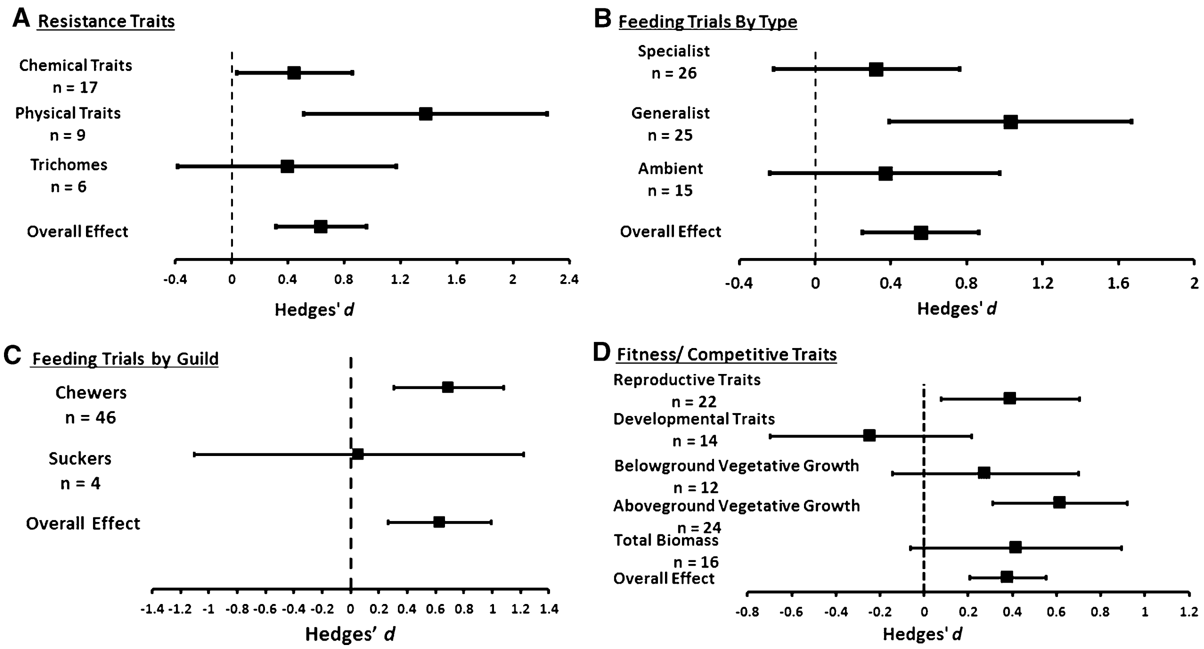

Fig. 1 Forest plots of effect sizes and 95% confidence intervals for each category of traits, as well as overall mean effect size. Panel **a** shows resistance trait results, Panel **b** displays feeding trial (herbivore performance) results, Panel **c** shows results for guilds of feeding styles, and Panel **d** displays fitness traits. Positive effect sizes represent an increase in trait values in non-native populations, relative to native

plant resistance traits influence its performance (e.g., Bossdorf et al. 2004), so we also examined differences in performance within subgroupings of herbivores (by feeding guild and order). Chewing insects tended to perform better on non-native populations relative to native populations (grand mean = 0.691, $p = 0.021$), and piercing/sucking insects tended to have a neutral response (grand mean = 0.058, $p = 0.922$; Fig. 1c). Considered at the order level, Lepidoptera and Coleoptera did better on non-native populations than on native populations of the same species (grand mean = 0.745, $p = 0.028$ and grand mean = 0.682, $p = 0.013$, respectively). Gastropods and Hemipterans had no significant differences in performance in native versus non-native plant populations (grand mean = 0.83, $p = 0.182$ and grand mean = 0.058, $p = 0.756$, respectively) (Fig 1S, supplemental information).

Consistent with EICA, fitness was higher within non-native plant populations, relative to native populations of the same species (grand mean = 0.380, $p < 0.001$, Fig. 1d). Within this overall trend, there was variation among categories of fitness traits. While four of the five subgroups showed a general increase of fitness in non-native populations (Fig. 1d), this increase was statistically significant for only two categories, reproductive traits and aboveground vegetative growth (grand mean = 0.392, $p = 0.015$, and grand mean = 0.616, $p < 0.001$ respectively). Trait values for belowground growth and total biomass were both generally higher in non-native populations than in native populations, but these positive effect sizes were not statistically significant (grand mean = 0.277, $p = 0.198$, grand mean = 0.418, $p = 0.086$, respectively). Development time also showed no significant difference in non-native populations, relative to native (grand mean = − 0.241, $p = 0.300$).

Time since introduction influenced the effect size of the fitness traits, with generally larger effect sizes for these traits in non-native plant populations that were introduced earlier (Q = 36.143, $p = 0.05$). Non-native populations included in this meta-analysis were introduced from 100 to 385 years before each study occurred. This suggests that changes predicted by EICA may take substantial amounts of time to occur. In contrast, the type of introduction did not seem to influence the magnitude or direction of effect sizes (Q = 35.662, $p = 0.151$).

In support of EICA, we found evidence for a trade-off between herbivore performance and average plant fitness ($R^2 = 0.455$, $p = 0.011$, Fig. 2). There was an outlier in this analysis, however this did not impact the outcome of the meta-regression (with outlier removed, $R^2 = 0.122$, $p = 0.010$). Similarly, we found a negative correlation between herbivore performance and belowground vegetative traits and herbivore performance and total biomass, although these latter two trends were also affected by an outlier data point ($R^2 = 0.187$, $p = 0.043$, and $R^2 = 0.45$, $p < 0.001$ respectively; Fig 2S). With the outlier removed, the relationship between herbivore performance and belowground vegetative traits became non-significant ($R^2 = 0.02$, $p = 0.229$) but that of herbivore performance and total biomass remained significant ($R^2 = 0.32$, $p = 0.009$ respectively). We found no relationship between herbivore performance and aboveground vegetative traits, developmental traits and reproductive traits ($R^2 = 0.156$, $p = 0.09$, $R^2 = 0.131$, $p = 0.821$, and $R^2 = 0.19$, $p = 0.411$ respectively). We also did not find a clear relationship across studies between any tested aspect of levels of resistance traits versus plant growth (Supplemental Table 1). Both phytochemical and physical resistance traits were negatively correlated with herbivore performance (Fig. 3).

We found no evidence of publication bias towards publications with relatively large effect sizes (Fig 3S; $R^2 = 0.203$, $p = 0.29$). Rosenberg's fail safe number was robust at N = 4131 ($p < 0.001$), indicating that a large number of studies with an effect size of zero would be needed in order to negate the significance of an observed effect size (Koricheva et al. 2013).

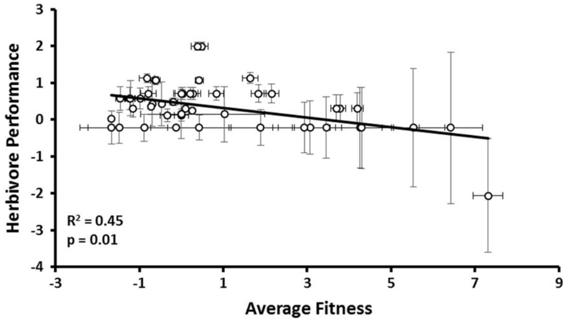

Fig. 2 Meta-regression plot of average plant fitness by herbivore performance. Points are effect sizes (Hedges' *d*)

Discussion

Do the predictions of EICA hold?

We found partial support for the two predictions of EICA in our assessment of genetic-based traits across studies. Evidence for the first EICA prediction, that escape from specialist herbivores in a new environment can lead to the evolution of reduction in resistance against these herbivores, was ambiguous. Generalist herbivore performance tended to be higher on non-native plant populations than on native populations of the same species. However, contrary to the first EICA prediction, measured resistance traits were also higher in non-native populations relative to native populations, although there was still an overall negative relationship between plant resistance traits and herbivore performance. Consistent with the second EICA prediction, we found partial, although not complete, evidence for a trade-off between herbivore performance and plant allocation to traits related to fitness. Fitness trait values were higher in non-native populations than in native populations of the same species. Evidence for EICA was strongest when we focused on direct measurements of herbivore performance, and non-existent when we assessed resistance traits, highlighting the complicated and often unknown relationship between defense traits and particular herbivores in many plant–herbivore systems.

Deviations from the EICA hypotheses for resistance traits and herbivore performance

We found an increase in both resistance traits and herbivore performance in non-native populations relative to native populations, although there was a negative relationship overall between plant resistance and herbivore performance. We assessed resistance traits and herbivore performance independently, similar to the Felker-Quinn et al. (2013) meta-analysis, while these were grouped in Bossdorf et al.'s (2005) narrative review. However, the previous meta-analysis did not find effect sizes significantly different from zero for either resistance traits or herbivore performance (Felker-Quinn et al. 2013). We included multiple studies that had not been published at the time of the Felker-Quinn et al. (2013) review, which may have driven these results.

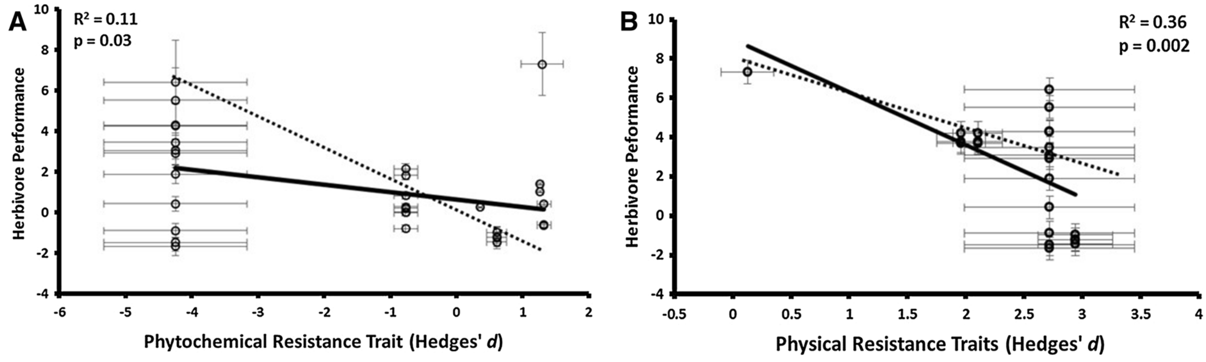

Fig. 3 Meta-regression plot of herbivore performance by **a**. Chemical resistance traits, and by **b**. Physical resistance traits. Dotted lines represent a 1:-1 tradeoff between plant fitness and herbivore performance as would be theoretically predicted by EICA. Points are effect sizes (Hedges' *d*)

The observed increase in resistance traits in non-native populations relative to native was unexpected and we propose several non-exclusive mechanisms to explain this result. First, the EICA-predicted release from specialist herbivory in a non-native environment may not necessarily always occur. Specialists on a native species can occasionally successfully utilize a closely related non-native species. For example, *Junonia coenia* (Nymphalidae) are specialist caterpillars that feed on native North American members of Plantaginaceae but often feed on introduced *Plantago* spp. (Scott 1992; Graves and Shapiro 2003). This host switching could maintain selection pressures on the non-native plant. While *Plantago* was not included in our review, the same phenomenon may be broadly relevant. For example, the Brassicaceae in our database that are non-native to North America may face specialist herbivores such as Pieridae that feed on native North American Brassicacea (Scott 1992). In other cases, particularly when the non-native plant is invasive, a specialist herbivore may have been introduced as a biocontrol (Rapo et al. 2010). Secondly, with evidence of generalist herbivores preferring non-native plants (Bossdorf et al. 2004; Parker and Hay 2005; Morrison and Hay 2011) an increase in resistance traits of non-native plants may be needed for these plants to succeed within a non-native environment, even if release from specialist herbivores were to occur. Novel phytochemical resistance compounds in the non-native range may be strongly selected for if the increase of these novel phytochemicals increases the overall fitness of the plant when faced with both generalists and specialist herbivores (Callaway and Aschehoug 2000; Zheng et al. 2015). This phenomenon, termed "the novel weapons hypothesis" has been observed across many non-native plants populations (see Cappuccino and Arnason 2006, Hill and Kotanen 2009). Finally, some studies incorporating nutrients into studies of invasions of non-native plants suggest that non-native plants are better at exploiting nutrient resources (Davis et al. 2000). This could result in more overall resources available to allocate to plant resistance traits, as well as to plant fitness traits, and contrast with the EICA assumption that nutrients are equally limited in both the native and non-native environments.

Although we did not find any direct trade-offs between defense traits and fitness, we did detect tradeoffs between herbivore performance and fitness. These results indicate that feeding trials can be an effective way to evaluate resistance within the EICA framework. Feeding trials can account for the effects of resistance traits that may not be easily quantifiable, are unknown, and/or resistance influenced by suites of traits (e.g., Agrawal and Fishbein 2006), via observed differences in insect performance. Simultaneous assessment of both resistance traits and herbivore performance can be important, however, in disentangling the effects of plant resistance from plant nutritional quality on herbivore performance. We were not able to assess plant nutritional quality in our meta-analysis due to the scarcity of studies that focus on both nutritional and herbivory-related aspects of non-native species.

Tests of fitness

As the ultimate measure of reproductive success and the growth or maintenance of population size, fitness traits are particularly relevant to EICA. These traits are involved in the spread of non-native species, allowing a greater ability to disperse to and colonize potentially suitable habitat in the non-native environment. Consistent with the predictions of EICA, we found an overall increase in fitness ability-related trait values in non-native populations, relative to native. In our analysis, any increase in a developmental trait in a non-native plant was scored as positive. This may be misleading because at times slower growth rates may be more ecologically beneficial to the plant (Herms and Mattson 1992).

The previous two reviews of fitness and/or competitive ability in the context of EICA found more equivocal results than did our study. In one, increased growth in non-native populations was found in just over half of studies done in common environments, while competition experiments did not yield consistent results (Bossdorf et al. 2005). In the other review, plant vegetative traits but not reproductive fitness or direct measures of plant competitive ability, were higher in non-native populations than in native, resulting in no overall EICA support (Felker-Quinn et al. 2013).

Evolutionary trade-offs and EICA

We found evolutionary trade-offs in many studies between herbivore performance and fitness, as predicted by EICA. Trade-offs between fitness and defense traits are often variable between species with different life histories and ecological systems, potentially varying in both direction and magnitude across abiotic and biotic environments (Bazzaz et al. 1987; Koricheva 2002). Our study suggests that, despite this variation, tradeoffs do take place under the EICA framework across a number of systems and environments.

While the predictions of EICA are generally supported in our meta-analysis, adherence to at least some of these predictions is clearly species and/or system dependent. For example, the most comprehensive test of EICA within the 30 studies included in this review quantified genetic differences in fitness traits, physical and phytochemical resistance traits, tolerance to herbivory, conducted feeding trials with specialist and generalist herbivores of differing orders, and included direct competition experiments (Ridenour et al. 2008). This study found evidence for increases in both plant defense and competitive ability, rather than the trade-offs predicted by EICA.

Additional factors influencing adherence to EICA

Although non-native plants have been shown to evolve rapidly in response to introduction (Whitney and Gabler 2008), we found that time since introduction did influence the magnitude of effect sizes for fitness traits. As time since introduction increased, from 100 years since introduction to over 350 years, non-native plants exhibited increased values for fitness traits. As most plants included in this meta-analysis were herbaceous plants with relatively short generation times, a fairly substantial number of generations would occur for a particular population during even the low end of the range for time-since-introduction. The difference in magnitude of effect sizes that was dependent on time since introduction could possibly be the result of gradual local adaptation to new selection pressures (Parker et al. 2003), repeated introductions and matings among plants introduced at different times (Ellstrand and Schierenbeck 2000), or other stochastic events that may take at least moderate amounts of time to occur.

Due to a lack of standard measures across studies, our meta-analysis did not include the degree to which a plant species is invasive, but this may be an important concept to evaluate in the context of the EICA hypothesis. Cappuccino and Carpenter (2005) found that within field sites in eastern North America plant species that are more ecologically aggressive (more invasive) had on average 96% less leaf damage than less aggressive species (less invasive). There may also be analogous predictable variation in resistance across invasive plants with varying degrees of invasiveness. The studies included in our meta-analysis range from ruderal weeds (such as *Lepidium draba*, Müller and Martens 2005) to aggressive, dominant plants that have changed entire landscapes (*Centaurea maculosa* Ridenour et al. 2008).

Our meta-analysis demonstrates a bias in the order and/or feeding guild of herbivores most often used; chewing insects from the Coleoptera and Lepidoptera are almost exclusively utilized. In addition, we found that the taxa or feeding guild of herbivores used may influence the results of a study. This result is compatible with previous studies demonstrating differential response of particular feeding guilds to particular resistance traits (e.g., Carmona et al. 2011). These differences may have fairly substantial influence on observed experimental patterns. The importance of choice of herbivores in designing feeding trials at the functional and phylogenetic level to understand plant resistance traits has been noted (Ali and Agrawal 2012). Our results suggest that these same methods should be applied to tests of EICA, with more studies of non-chewing herbivores generally needed, as well as guidance by the natural history of a particular system.

Conclusions

One of the persistent issues with understanding and predicting the success of invasive species is limited understanding of the traits that drive non-native plant success in their new environment (Pyšek and Richardson 2008). The EICA hypothesis provides as a series of testable ecological predictions within an evolutionary framework, and has helped promote understanding of the selection underlying traits that promote invasion success, but designing studies to comprehensively test EICA is not a simple process.

While our results show some support for the predictions of EICA across studies that focus on genetic-based trait variation and evolutionary tradeoffs between resistance to specialists and fitness, our sample size is still relatively small. We also found contradiction in EICA predictions by observing an overall increase in resistance traits in non-native plants. Results from additional common garden studies that include direct competition experiments (Bossdorf et al. 2005), or assessment of the effects of resistance traits as well as plant nutritional quality on herbivore performance, while also measuring fitness would be beneficial to assess broad support for EICA.

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