

LETTER

Trade-offs in non-native plant herbivore defences enhance performance

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Abstract

Non-native plants are typically released from specialist enemies but continue to be attacked by generalists, albeit at lower intensities. This reduced herbivory may lead to less investment in constitutive defences and greater investment in induced defences, potentially reducing defence costs. We compared herbivory on 27 non-native and 59 native species in the field and conducted bioassays and chemical analyses on 12 pairs of non-native and native congeners. Non-natives suffered less damage and had weaker constitutive defences, but stronger induced defences than natives. For non-natives, the strength of constitutive defences was correlated with the intensity of herbivory experienced, whereas induced defences showed the reverse. Investment in induced defences correlated positively with growth, suggesting a novel mechanism for the evolution of increased competitive ability. To our knowledge, these are the first linkages reported among trade-offs in plant defences related to the intensity of herbivory, allocation to constitutive versus induced defences, and growth.

KEYWORDS

constitutive defence, growth, herbivore pressure, induced defence, non-native plant invasion

INTRODUCTION

Non-native plant invasions have provided remarkable insights into rapid adaptation in defence allocation (Callaway & Maron, 2006; Lin et al., 2021; Waller et al., 2020). In part, this is because non-native species are often attacked less than natives, and are typically

released from specialist enemies (i.e., those that feed on one plant species or a small number of related plant species) in the introduced ranges but continue to be attacked by generalists (i.e., those that feed on multiple unrelated plant species)—articulated in the Enemy Release Hypothesis (ERH, Keane & Crawley, 2002). Thus, the most predictable change in herbivore communities in

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the introduced ranges, is a decline in herbivore pressure overall, at least until biocontrol agents are introduced (Heger & Jeschke, 2014; but see Colautti et al., 2004).

Generalist-dominated herbivory in introduced ranges commonly corresponds with non-native species developing greater qualitative defences against generalists relative to conspecifics in native ranges—the Shifting Defence Hypothesis (SDH, Joshi & Vrieling, 2005; Müller-Schärer et al., 2004). For example, a meta-analysis by Callaway et al. (2022) found that qualitative defences (generally cheaper toxins, e.g., pyrrolizidine alkaloids, glycosides) were greater in plants from introduced ranges, whereas quantitative defences (e.g., toughness) were lower. Qualitative defences may be constitutive or induced, but the poor understanding of selection for constitutive versus induced defences in the introduced ranges is a major knowledge gap in understanding defence allocation and plant invasions.

Plants are thought to maximize fitness by balancing resource allocation to defence with other functions (Mertens et al., 2021; Rotter & Holeski, 2018), and this allocation can be affected by herbivores (Stamp, 2003). Constitutive defences protect plants from attack without a time lag, but constitutive defences are costly in the absence of herbivores (Ali & Agrawal, 2012; Aljibory & Chen, 2018). Thus, when herbivore pressure is low, plant fitness might be maximized by investing less in constitutive defences. In contrast, induced defences appear to be cost-saving strategies where defences are expressed only in response to herbivore pressure (Agrawal & Hastings, 2019; Gatehouse, 2002). From the ‘quagmire’ (Stamp, 2003) of hypotheses for defence allocation in plants, a few possibilities emerge for how induced and constitutive defences might evolve in plant species in their introduced ranges. In a review of invasive plants, Orians and Ward (2010) suggested that induced defence should evolve to be more prevalent in introduced ranges where plants are attacked less frequently, but experimental evidence comparing non-native and native species is mixed (Beaton et al., 2011; Lin et al., 2021; Liu et al., 2020). Different non-native species often experience very different degrees of generalist herbivore pressure (Agrawal & Kotanen, 2003; Sims-Chilton et al., 2009). Such variation in herbivore pressure should lead to variation in defence traits (Coverdale & Agrawal, 2022; Wan et al., 2022) and less intense and frequent herbivory should select for allocation to induced defences (Bixenmann et al., 2016). However, how this variation in generalist herbivore pressure affects potential trade-offs in constitutive versus induced defensive strategies among non-native species is unknown.

Growth-defence trade-offs appear to derive from plasticity or adaptive variation in allocation that maintains fitness in a variable environment (Monson et al., 2022). Increased investment in defence may result in reduced growth (Hahn et al., 2021), leading to differential investment in growth or defence by species based on their evolutionary responses to environmental conditions (Coley

et al., 1985). Changes in selection due to herbivory selection may drive rapid evolution of non-native species through reallocation of resources from defence to growth and reproduction, which may promote invasion—the Evolution of Increased Competitive Ability Hypothesis (EICA, Blossey & Nötzold, 1995). Most studies have focused on how variation in herbivore pressure across geographical clines shapes evolution of plant defence (Moreira et al., 2018; Woods et al., 2012). However, these studies have not considered how range-based shifts in defence strategies might constrain growth.

Non-native species provide good systems for studying constitutive and induced defences. If non-native species are attacked less by herbivores than natives, we can test the prediction that (i) non-natives increase the expression of cheaper induced defences and decrease the expression of expensive constitutive defences (Figure S1). If non-native species are attacked disproportionately by herbivores, then this effect might permit a cleaner opportunity to test another prediction (ii) that the herbivore pressure a species experiences will increase expression of constitutive defences and decrease induced defences (Figure S1). We can then test the prediction (iii) that allocation to less expensive induced defence allow allocation to greater growth (Figure S1). To explore these predictions, we measured herbivore pressure on 27 non-native and 59 co-occurring native species in the field and on 12 pairs of non-native species and native congeners in a common garden. We also measured constitutive and induced defences and plant growth on species pairs from the common garden.

MATERIALS AND METHODS

Herbivore pressure in the field

To compare herbivore pressure on a wide range of non-native and native species under natural conditions, we conducted a field survey in abandoned agricultural fields at 28 sites in northern China (Table S1). At each site, we selected the three tallest plants of each species in a 5 × 10 m plot (Tables S2 and S3). To determine herbivore pressure, we calculated the percentage of leaves with damage by counting 10–50 leaves starting from the top of each plant, depending on the size of the plant. Leaves with holes, cuttings, transparent traces, and missing whole lamina were identified as damaged. We also measured herbivores biomass on non-native species to determine whether our broad measurements of herbivore damage correlated with herbivore biomass (Supplementary Methods S1).

Herbivore pressure in the common garden

We conducted a common garden experiment at Henan University, Kaifeng, China. We selected the 12 most

common non-native herbaceous species in the field survey and compared herbivory on these species and 12 co-planted native congeners (Table S4). There have been no classical biocontrol programmes for these non-native species in China, no record of accidental introduction of specialists, and we observed no specialists on non-native species in the field survey. Therefore, we assumed that all damage we found on non-native species was from generalists.

In the field survey, there was no significant effect of site on leaf damage for most non-native species or native congeners (Wald Chi-square test applied on a Generalized Linear Model, Tables S2 and S3). Therefore, we collected seeds from 2 to 3 individuals of each non-native species and their native congeners at each site and mixed them. We sowed seeds in trays (20 × 30 cm) and placed them in the greenhouse at 50–70% humidity, 16/8 hr light/dark cycle, 26°C at day and 20°C at night.

We established 144 1 × 1 m plots grouped into six blocks. Plots within each block were separated by 1.5 m and blocks were separated by 3 m. The 24 plots within each block were randomly assigned to one of the 24 species. We transplanted four similar sized seedlings (about 5 cm in height) of each species into each plot spaced 25 cm apart. All plants were exposed to naturally occurring herbivores.

Three months later, we evaluated the percentage of damaged leaf area for all plants. We cut 20 fully expanded leaves near the base of the petiole starting from the top of each plant. We measured damaged and total areas using Image Proexpress V.6.0 (Media Cybernetics, Inc.). Leaves with only petioles remaining were recorded as 100% damage. We also measured herbivore biomass for non-native species (Supplementary Methods S1). We used the average of herbivore damage and herbivore biomass of the four plants in each plot for data analysis, resulting in six replicates for each species.

Constitutive and induced bioassay defences

We used the same species as in the common garden to assess constitutive and induced defences (Table S4). We grew plants of each species individually in pots (15 cm diameter, 18 cm height) filled with 50% potting media (Pindstrup) and 50% topsoil in the greenhouse (at 50–70% humidity, 16/8 hr light/dark cycle, 26°C at day and 20°C at night). When plants had 20 leaves, we started the herbivory treatment for induced defences and the bioassays.

As the non-native species were mainly attacked by Lepidoptera in the field survey (Figure S2a) and common garden experiment (Figure S2b), we applied the generalist *Spodoptera littoralis* (Lepidoptera: Noctuidae), a species that feeds on more than 40 plant families (Kempel et al., 2011), as a bioassay. We obtained eggs

of *S. littoralis* from Keyun Biological Control Co., Ltd., China and used newly emerged larvae for the following bioassays.

To quantify constitutive defences, which can inhibit insect growth, we measured larval weight gain when fed on undamaged leaves harvested from undamaged plants. Specifically, we cut one fully expanded upper leaf near the base of the petiole and placed it in a Petri dish (9 cm diameter) with moist filter paper. Then, we added a newly emerged pre-weighed larva into the Petri dish. We replaced the previous leaf with a fresh one from another undamaged plant every day to ensure that larvae were not affected by food limitation. After 4 days we re-weighed the larva. There were 10 replicates (larvae) for each plant species.

To quantify induced defences, we measured larval weight gain on undamaged leaves that were harvested from plants possessing other leaves previously damaged by herbivores. Specifically, we placed 2–6 second instar larvae on two leaves at mid-height of each plant, depending on the size of different plant species, and covered them with a mesh bag (0.8 mm openings). After 2 days of feeding, we removed the larvae. The damage level was roughly 10%, consistent with the average leaf damage on all non-native species in common garden experiment ($11.5 \pm 1.2\%$). Plants were grown 4–8 days to produce new leaves. Using the same protocol described above for constitutive defences, we used these new undamaged leaves to quantify induced defences. There were 10 replicates (larvae) for each plant species.

Constitutive and induced chemical defences

Phenolics and terpenoids are important defensive chemicals that are constitutively present in plants, but can also be induced by herbivory (Mithöfer & Boland, 2012). Therefore, we measured total phenolics and total triterpenoids in leaves harvested from undamaged and herbivore-damaged plants for the same species as described above in the common garden (Table S4). Transplanting and herbivory treatments (only for induced defence) and growth conditions were the same as those in the bioassay. Total phenolics were quantified using the Folin-Ciocalteu method (Supplementary Methods S2). Total triterpenoids were measured by vanillin–glacial acetic acid–perchloric acid spectrophotometry (Supplementary Methods S2). These chemical concentrations were expressed as mg/g fresh leaf weight. There were 12 replicates (plants) for each species and defence type.

Growth rates

To evaluate the relationship between the strength of induced defences and plant growth, we measured the

absolute growth rate (hereafter growth rate) for the species in the common garden (Table S4). Transplanting and growth conditions were the same as in the bioassay. We randomly assigned individuals of each species to two groups. One group of plants were harvested 2 weeks after transplanting (weight_1 , 10 plants per species). The other group of plants were harvested 8 weeks after transplanting (weight_2 , 12 plants per species). All plants were dried at 70°C for 48 h, and weighed. We calculated growth rate for each species as $[(\text{weight}_2) - (\text{weight}_1)]/42$ days, resulting in 12 replicates for each species.

Statistical analysis

Herbivore pressure—To test for difference in herbivore pressure (binary data of undamaged versus damaged leaves in a cbind matrix) among the non-native species in the field survey, we used a generalized linear mixed model (GLMM) with a binomial distribution. Sites were random effects. We tested for difference in herbivore pressure (percentage of damaged leaf area) among the non-native species in the common garden experiment using a linear mixed model (LMM) with blocks as random effects. We conducted the same analyses for native species.

To test for difference in herbivore pressure between the non-natives and natives in the field survey, we used a GLMM with a binomial distribution that included origin (non-natives vs. natives) as a fixed effect, and sites and species nested in origin as random effects. Since the number of native species ($n=59$) was larger than that of non-natives ($n=27$) in the field survey, we used a bootstrap method that uses random sampling with replacement (1000 bootstrap estimates) to test again whether non-natives and natives were different when the numbers of non-natives and natives were equal. We also tested for difference in herbivore pressure in the common garden experiment using a LMM with origin as a fixed effect, and blocks and species nested in origin as random effects.

Furthermore, we used a GLMM with a binomial distribution that included random terms for sites and species to test whether percentage of damaged leaves depended on herbivore biomass for non-natives in the field survey. We also used a LMM that included random terms for blocks and species to test whether percentage of damaged leaf area depended on herbivore biomass for non-natives in the common garden experiment. Finally, we used Pearson correlations to examine the relationship between percentage of damaged leaves and percentage of damaged leaf area for non-native species in the field survey and common garden experiment using mean values for species.

Constitutive and induced defences—We used larval weight gain and chemical contents to assess defences.

For constitutive defence, we used larval weight gain on the leaves of undamaged plants. Using larval weight gain as a measurement of defence is common (Kempel et al., 2011), but does not always reflect the full cost of a plant's investment. Thus, it is a good measurement of the benefit of defence investment, but an indirect reflection of investment. For induced defence, we calculated the larval weight gain on the leaves of plants previously damaged by herbivores minus the mean of larval weight gain on the leaves of undamaged plants. Constitutive and induced chemical defences were evaluated using the same methods. We used the percentage of damaged leaf area for each species in the common garden experiment as herbivore pressure. To evaluate relationships among constitutive defence, induced defence and herbivore pressure, we carried out Pearson correlations where we multiplied larval weight gain with -1 since higher larval weight gain indicates lower defence. Mean values per species were used for above analyses and non-native and native species were analysed separately.

To test for differences in constitutive and induced defences between non-native and native species, we used a LMM with species as random effects. Finally, to test whether changes in chemicals might underly changes in herbivore growth, we conducted Pearson correlations across both herbivory treatments and all species to examine the dependence of larval weight gain on concentrations of total phenolics or total triterpenoids using mean values per species in each herbivory treatment. Although constitutive and induced defences of non-native and native species were different, herbivore performance was primarily dependent on chemical concentrations. Thus, data from undamaged and damaged plants of non-native and native species were analysed together.

Induced defence and plant growth—To test for difference in growth rate between non-native and native species, we used a LMM with species as a random effect. Furthermore, since induced defences should require less investment than constitutive defences, we compared the strength of induced defence for species to their growth rate using a Pearson correlation. Induced defence was calculated in terms of larval weight gain.

Homogeneity of variances and normality of distributions of data were checked before data analyses and P-values were corrected by False Discovery Rate (Benjamini & Hochberg, 1995). To account for phylogenetic relatedness in the analyses above, we first constructed a phylogenetic tree for the 12 non-native species, the 12 native species and all 24 species together based on ITS sequences from the NCBI database, respectively (Supplementary Methods S3). We then analysed data using the phylogenetic generalized linear mixed model (PGLMM). All significant associations were also significant when controlling for phylogenetic relatedness, thus we did not include phylogenetic relatedness in the analyses. All statistics were conducted in R (version 4.0.5) with the 'car' (Fox & Weisberg, 2011), 'lme4' (Bates

et al., 2014), 'RVAideMemoire' (Hervé et al., 2015) and 'phyr' (Li et al., 2020) packages.

RESULTS

Herbivore pressure on native and non-native plant species

In the field survey, 396 individuals of 27 non-native species and 678 individuals of 59 native species were evaluated. There were large differences among non-native species ($\chi^2=3744$, $p<0.001$, Figure 1a) and among native species ($\chi^2=3025$, $p<0.001$, Figure 1b) in herbivore damage, with non-natives damaged 46.2% less than natives ($\chi^2=22.63$, $p<0.001$, Figure 1c). The bootstrap test showed that even if sample size was the same between non-natives and natives, the damage between them was still significantly different [95% CI of p -value=(0.00032–0.00041)].

In the common garden experiment, herbivore damage varied by over an order of magnitude among non-native species ($\chi^2=100.29$, $p<0.001$, Figure 1d) and among native congeners ($\chi^2=86.36$, $p<0.001$, Figure 1e). Herbivore damage on non-natives was 41.5% less than on native congeners ($\chi^2=4.36$, $p=0.037$, Figure 1f).

Non-native species with higher herbivore damage also had more herbivore biomass on them in the field survey ($r=0.57$, $p<0.001$, Figure S3a) and in the common garden ($r=0.47$, $p<0.001$, Figure S3b), indicating that herbivore damage is a good proxy for herbivore abundance. Furthermore, there was a strong positive relationship between herbivore damage on non-native species in the field survey and the same species in the common garden experiment ($r=0.95$, $p<0.001$, Figure S4).

Herbivore pressure and constitutive and induced defences

Assessed by *S. littoralis* larval weight gain, constitutive defence ($-1 \times$ larval weight gain on leaves collected from healthy plants) was positively correlated with herbivore pressure across all 12 non-native species ($r=0.66$, $p=0.020$, Figure 2a), whereas there was no significant correlation for native congeners ($r=0.32$, $p=0.306$, Figure 2a). Induced defence was negatively correlated with herbivore pressure for non-native species ($r=-0.69$, $p=0.014$, Figure 2b), but no significant correlation was found for native congeners ($r=-0.49$, $p=0.106$, Figure 2b). Overall, constitutive defence of non-natives was 38.7% lower than that of native congeners ($\chi^2=4.28$, $p=0.039$, Figure 2a), while induced defence of non-natives was 55.3% higher than that of native congeners ($\chi^2=5.56$, $p=0.018$, Figure 2b).

For defences assessed by phenolics, results were similar to those assessed by larval weight gain. Constitutive

defence ($r=0.76$, $p=0.004$) and induced defence ($r=-0.84$, $p<0.001$) were positively and negatively correlated with herbivore pressure, respectively, across all 12 non-native species (Figure 2c,d). Whereas, for native congeners, there was no correlation between constitutive defence and herbivore pressure ($r=-0.20$, $p=0.525$, Figure 2c) or between induced defence and herbivore pressure ($r=-0.18$, $p=0.571$, Figure 2d). Overall, constitutive defence of non-natives was equal to that of native congeners ($\chi^2=0.02$, $p=0.885$, Figure 2c), whereas induced defence was higher than that of native congeners ($\chi^2=163.29$, $p<0.001$, Figure 2d). However, for defence assessed by triterpenoids, there was no relationship between constitutive defence and herbivore pressure (non-natives, $r=-0.08$, $p=0.807$; natives, $r=-0.20$, $p=0.527$), or between induced defence and herbivore pressure (non-natives, $r=-0.07$, $p=0.820$; natives, $r=0.01$, $p=0.970$) for non-natives and native congeners (Figure 2e,f). Constitutive defence ($\chi^2=0.03$, $p=0.852$) and induced defence ($\chi^2=2.15$, $p=0.143$) of non-natives was equal to that of native congeners (Figure 2e,f).

Across all herbivory treatments (leaves from undamaged and damaged plants) and plant species (non-natives and native congeners), larval weight gain was negatively correlated with phenolic content ($r=-0.29$, $p=0.047$, Figure 3a) and with triterpenoid content ($r=-0.29$, $p=0.044$, Figure 3b).

Trade-off between constitutive and induced defences

For defence assessed by larval weight gain, plant species that had higher constitutive defence had lower induced defence, resulting in a negative correlation across the 12 non-native species ($r=-0.85$, $p<0.001$) and the native congeners combined ($r=-0.58$, $p=0.048$) (Figure 4a). This pattern was similar for non-native species when defence was assessed by phenolic content ($r=-0.76$, $p=0.004$), but not for native congeners ($r=0.05$, $p=0.881$) (Figure 4b).

Induced defence and plant growth

Growth rate of non-native species was 1.6 times higher than that of native congeners ($\chi^2=19.08$, $p<0.001$, Figure 5a; Figure S5). Variation in growth rate was strongly positively correlated with variation in the strength of induced defence as measured by larval weight gain ($r=0.72$, $p=0.008$, Figure 5b).

DISCUSSION

Our results make two key conceptual contributions to understanding allocation of defences. First, we showed

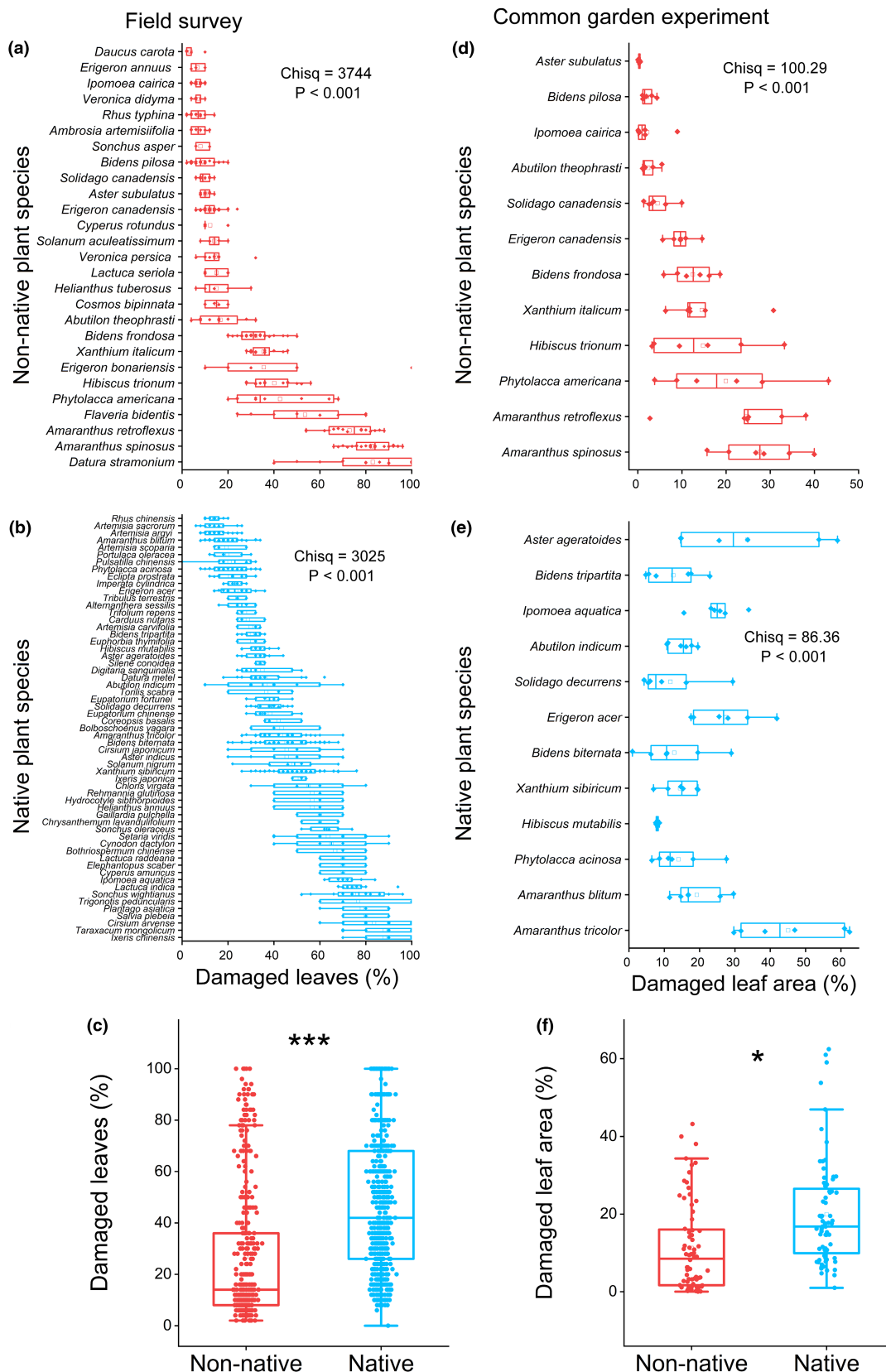


FIGURE 1 Herbivore pressure on non-native and native plant species. Percentage of damaged leaves on non-native species (a) and co-occurring native species (b) in the field survey, and percentage of damaged leaf area on non-native species (d) and native congeners (e) in the common garden experiment. Differences in the percentage of damaged leaves on non-native and co-occurring native species in the field (c) and in the percentage of damaged leaf area on non-native species and native congeners in the common garden (f). Boxplots represent the interquartile range and median, and points represent outliers. There were 27 non-native species measured ($n=3-66$ individuals per species depending on occurrence) and 59 native species measured ($n=3-54$ individuals per species depending on occurrence) in the field survey across 28 sites in China. The most common 12 non-native species and their native congeners were used in the common garden experiment ($n=6$ per species). * $p < 0.05$ and *** $p < 0.001$.

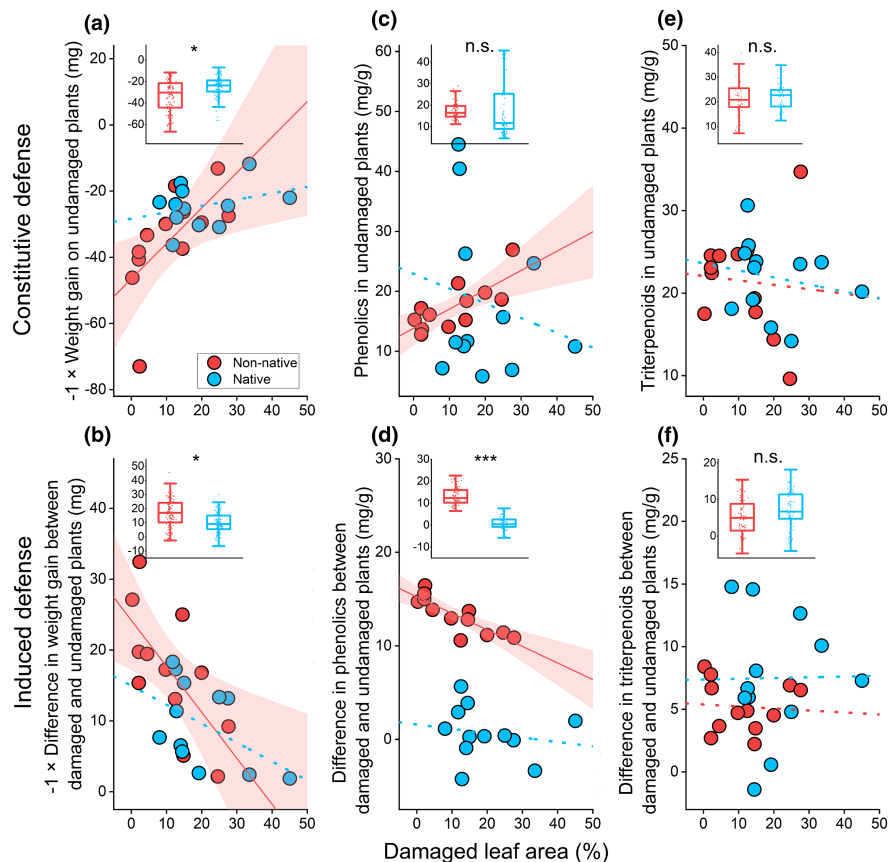


FIGURE 2 Correlations between constitutive or induced defences and herbivore pressure across 12 non-native plant species and 12 native congeners. Relationships between the percentage of damaged leaf area in the common garden experiment and constitutive defence assessed by generalist *Spodoptera littoralis* larval weight gain on the leaves of undamaged plants ($-1 \times$ larval weight gain on the leaves of undamaged plants, (a) and assessed by phenolics (c) and triterpenoids (e) contents in the leaves of undamaged plants. Relationships between the percentage of damaged leaf area in the common garden experiment and induced defence assessed by difference in *S. littoralis* larval weight gain on the leaves between undamaged and damaged plants [$-1 \times$ (larval weight gain on the leaves of damaged plant—average of larval weight gain on the leaves of undamaged plant), b], and assessed by differences in phenolics in the leaves between undamaged and damaged plants (content in the leaves of damaged plant—average of content in the leaves of undamaged plant, (d) and difference in triterpenoids on the leaves between undamaged and damaged plants (content in the leaves of damaged plant—average of content in the leaves of undamaged plant, (f). Each point represents individual non-native species (red points, $n = 12$) and native congeners (blue points, $n = 12$). Solid lines indicate significant linear relationships between defences and damage. Dotted lines represent non-significant relationships between variables. The embedding boxplots represent the comparison for each group of species overall. * $p < 0.05$ and *** $p < 0.001$.

that non-native species, which experienced much lower herbivory, had lower constitutive defences and higher induced defences, which correlated with higher growth rates as compared with native species. Second, non-native species showed a strong positive relationship between herbivore pressure and the strength of constitutive defence, and a strong negative relationship between herbivore pressure experienced by a species and the intensity of induced defences exhibited by that species. There are three novel aspects of these findings. Firstly, to the best of our knowledge no previous studies have presented evidence for strong trade-offs derived from the intensity of herbivory experienced by species, allocation to constitutive versus induced defences, and growth. Secondly, we know of no study that has explored relationships between the intensity of herbivory and induced versus constitutive defences for a large group of species

within a community. Thirdly, to our knowledge, no studies have explored these relationships and trade-offs in the context of non-native invasion, in our case comparing congeneric pairs.

Integrating these results suggests that reduced herbivore attack favoured allocation to induced defences instead of constitutive defences. Our results also suggest that induced defences are a “cheaper” overall strategy that favours higher growth rates. It appears that the generalist-dominated herbivore community that attacked non-native species drove a strong positive relationship between the intensity of herbivore pressure and allocation to constitutive defence among our target species. This finding supports long-held theory that has had minimal empirical support—intense or consistent herbivory should select for more expensive constitutive defences over cheaper induced defences (Ito & Sakai, 2009).

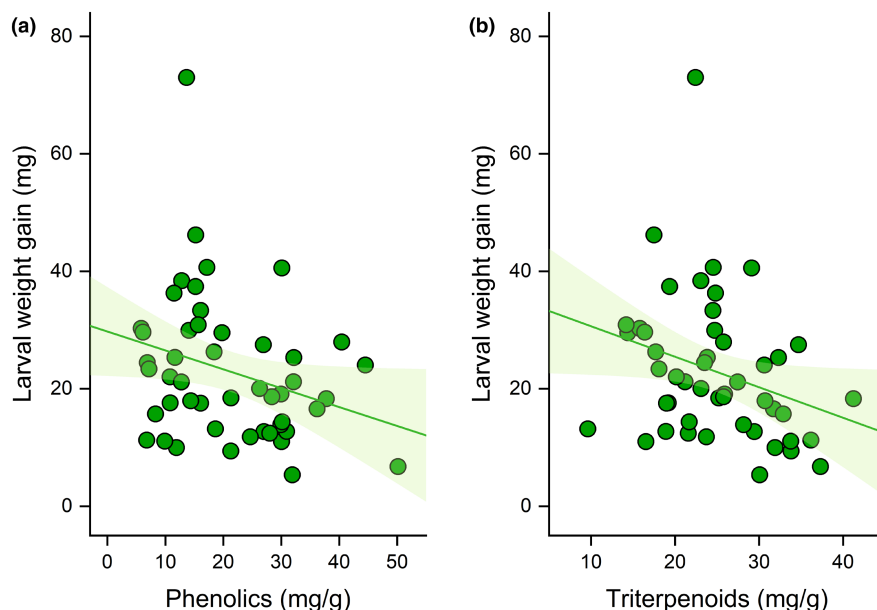


FIGURE 3 Correlations between the growth of *Spodoptera littoralis* larvae and leaf secondary chemicals across all plant species (12 pairs of non-native species and native congeners) and herbivory treatments (undamaged plants and larvae-damaged plants). Relationships between larval weight gain and leaf phenolic content (a) and leaf triterpenoid content (b). Data points represent mean values per species in each combination ($n=48$, 24 species $\times$ 2 herbivory treatments). Lines indicate significant linear relationships.

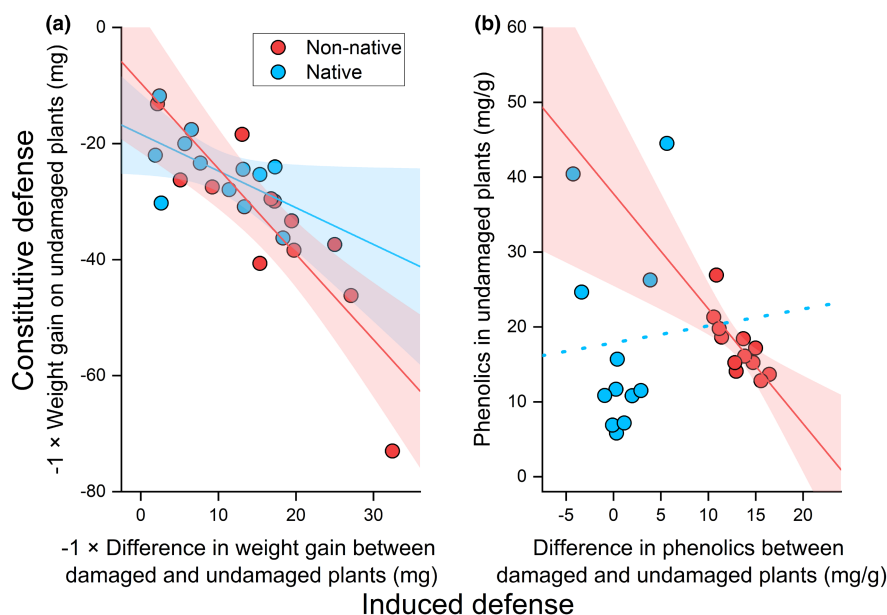


FIGURE 4 Trade-off between constitutive defence and induced defence across 12 pairs of non-native plant species and native congeners. Relationship between constitutive defence ($-1 \times$ larval weight gain on the leaves of undamaged plant) and induced defence [$-1 \times$ (larva weight gain on the leaves of damaged plant – average of larval weight gain on the leaves of undamaged plant)] assessed by generalist *Spodoptera littoralis* larval growth. Note the negative y axis (a). Relationship between constitutive defence (content in the leaves of undamaged plant) and induced defence (content in the leaves of damaged plant – average of content in the leaves of undamaged plant) assessed by phenolics (b). Blue points represent individual native species ($n=12$), and red points represent individual non-native species ($n=12$). Solid lines indicate significant linear relationships between constitutive and induced defences. Dotted line represents non-significant relationship between variables.

Generalist herbivore pressure

In our study, non-natives suffered less damage than natives, which is consistent with the ERH—non-native species are released from natural enemies (Keane &

Crawley, 2002). This difference may be because the absence of specialists or decreased attack by generalists, but our results could not make this distinction. Williams and Sahli (2016) also found that *Rubus phoenicolasius* and *Fallopia japonica* experienced less damage in their

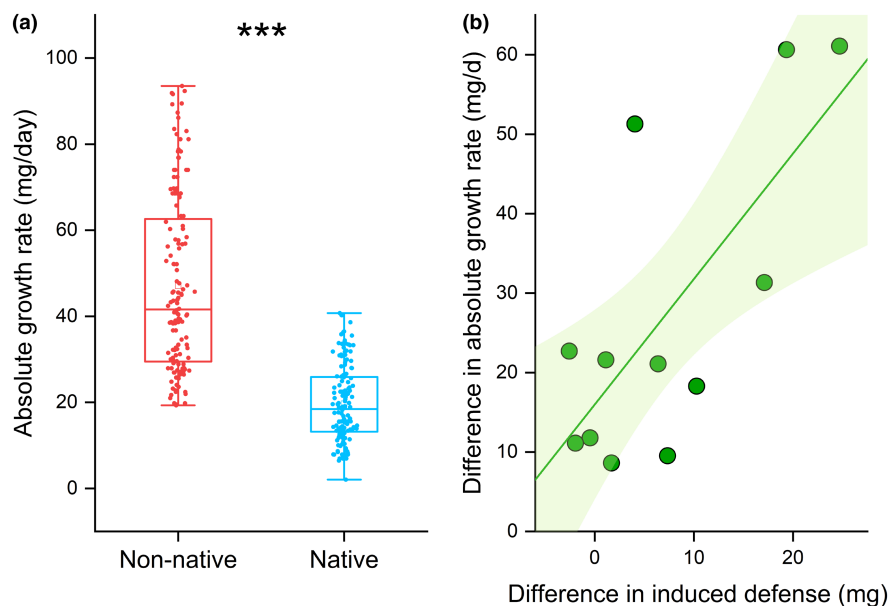


FIGURE 5 Growth rates of non-native plant species and native congeners (a). Boxplots represent the interquartile range and median, and points represent outliers. There were 12 non-native species and 12 native congeners ($n = 12$ plants per species). Relationship between the difference in the growth rate between non-native species and its corresponding native congener and the difference in the induced defence between non-native species and its corresponding native congener (b). Each point represents a non-native species and its native congener ($n = 12$). Growth rate was calculated as $[(\text{weight}_2) - (\text{average of weight}_1)]/42$ days. Induced defence was assessed by difference in *Spodoptera littoralis* larval weight gain on the leaves between undamaged and damaged plants $[-1 \times (\text{larval weight gain on the leaves of damaged plant} - \text{average of larval weight gain on the leaves of undamaged plant})]$. *** $p < 0.001$ (a). Line indicates significant linear relationship (b).

introduced range than congeneric native species, *F. scandens* and *R. occidentalis*. Decreased attack by generalist could be due in part to the novelty of taxa-specific defence chemicals produced by non-natives to which native generalists have not adapted (Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004; Inderjit, 2012; Schaffner et al., 2011). For example, Sedio et al. (2020) evaluated the biochemistry of 15 non-native plant species and found that the species that were the most chemically unusual were less attacked by herbivores. These, and other studies indicate that unusual or novel biochemicals of some non-native species may be why native herbivores avoid them (Inderjit et al., 2021).

Defence chemicals

Intense and predictable herbivory is thought to select for constitutive defences (Kalske & Kessler, 2020), whereas induced defences appear to be adaptive to less intense and infrequent herbivory (Agrawal & Karban, 1999; Ito & Sakai, 2009). The SDH posits that non-native species increase defence against generalists in the introduced ranges (Joshi & Vrieling, 2005; Müller-Schärer & Schaffner, 2004), but which defence strategies will be increased primarily by non-native species remains largely unknown. By comparing 12 non-native species with their native congeners, we found that non-native species showed lower constitutive defence and higher induced defence. Our finding that non-native species

increase induced defence refines the predictions of the SDH. More importantly, we found that non-native species that experienced more damage had higher constitutive defence and lower induced defence, compared with species that experienced less damage. To the best of our knowledge, we demonstrate for the first time that non-native species could further fine-tune defence strategies in response to herbivore pressure.

Recent results indicate that secondary metabolism plays key roles in the interactions between non-native plants and herbivores (Tian et al., 2021; Yu et al., 2022). We showed that weight gain of a generalist herbivore was negatively correlated with phenolic concentration across all species and herbivory treatments, suggesting that defence might derive from variation in constitutive and induced phenolic concentrations. Similar results were found for larval weight gain and triterpenoid content. However, triterpenoid content did not correspond with herbivore pressure. In this study, we only measured total triterpenoids, which have profound impacts on herbivores (Mithöfer & Boland, 2012). Some triterpenoids are directly toxic to herbivores and reduce herbivore digestibility, whereas others stimulate feeding and oviposition (González-Coloma et al., 2011). Thus, functional diversification of triterpenes may have masked simple defensive responses to herbivores. Future studies that measure specific defensive compounds will provide more clear evidence of shift from constitutive defence to induced defence of non-native plants. Furthermore, in addition to the two broad classes of secondary metabolites

we measured, primary metabolites (e.g., proteins) and morphological traits (e.g., trichomes) play important roles in plant defence against herbivores, but were not considered in this study.

Cost–benefit optimization

Optimal defence theory assumes that organisms are under strong natural selection to allocate resources to optimize cost–benefit ratios for fitness (Alba et al., 2012; Stamp, 2003). Much of this research has focused on a proposed evolutionary trade-off where non-native species experience relaxed selection on herbivore defence and evolve greater allocation to growth and competitive ability—EICA (Callaway et al., 2022; Zhang et al., 2020). Generalist herbivory can mediate defensive strategies and resource allocation (Müller-Schärer et al., 2004), thus, we suggest that the costs and benefits of induced defences should differ in low-versus high-damage risk environments. Such damage pressure-dependent defensive strategies could drive strong selection on defensive strategies (Maron et al., 2019) in ways that optimize plant defence and maximize plant fitness components for each non-native species. The striking positive relationship between herbivory experienced by different non-native species in the field and constitutive defence, and negative relationship between herbivory experienced by non-native species and induced defence, imply that non-native species may adopt cost-saving strategies balanced between constitutive and induced defences in response to herbivore pressure.

Plant species commonly show a trade-off between defence and growth (Lazzarin et al., 2021), but herbivore-driven changes in particular defensive strategies might alter the cost–benefit ratios of defence and growth allocation. Maintaining constitutive defence at high levels appears to require plants to invest substantial resources, potentially increasing the total cost of chemical defences. If induced defences are less costly than constitutive defences, perhaps relaxed selection on constitutive defence could allow greater growth, and such a trade-off might contribute to the dominance of some non-native species. To our knowledge, no study of EICA has experimentally integrated potential increased growth trade-offs of non-native plants derived from a shift from constitutive to induced defences. Our results support the defence strategies that have proposed such trade-offs between constitutive and induced defences where cheaper induced defences allow greater growth and reproduction (Mauch-Mani et al., 2017; Mumm & Hilker, 2006). Altogether, the results suggest that the defence strategy of stronger protection against generalist herbivores is a factor contributing to invasion success.

An important caveat is that we only used one generalist to explore the defensive strategy of non-native plants. Other studies indicate that generalist preferences and

impacts can vary a great deal among herbivore species (Schaffner et al., 2011). Our non-native species were occupied by many generalist species in the field, and thus our single-species bioassay is a limitation. We also emphasize that our binary approach to herbivore diet (generalist vs. specialist) was heuristic, and thus too simplistic (Hardy et al., 2020), but appeared to have allowed the detection of some fundamental ecological phenomena. Another caution is that we only measured two classes of defence compounds and total plant defences can be far more complex. Furthermore, our measurements of phenolics and triterpenoids cannot be easily extrapolated to theory related to either quantitative versus qualitative defence chemicals, although our conclusion about constitutive and induced defences should be solid. For example, phenolics consist of about 10,000 individual compounds (Tungmunnithum et al., 2018). Some are directly toxic to insects, such as flavonoids, more consistent with qualitative defences, whereas others reduce digestibility, such as tannins, and more consistent with quantitative defences. Finally, the best tests of hypotheses such as ours compare the same species in both the native and non-native ranges (Sheng et al., 2022), and it should be noted that studying defence-related trade-offs among native and non-native species in the same non-native range provides strong, but not the best, evidence for defence adaptations (van Kleunen et al., 2010). However, including many non-natives and native congeners increases the strength of inference for our results.

Integrating herbivore-related hypotheses for non-native species invasion

Two key hypotheses derived from non-native invasions are the ERH—that non-native species escape much of the herbivory experienced in their native ranges, primarily by specialists, and the related SDH—that non-native species increase defences, chiefly qualitative, against generalists. Our results show a shift to induced defences by non-native species, and that as herbivore pressure intensifies on non-native species, so does the strength of their constitutive defences. Our results also suggest new ways to consider EICA—perhaps the “cheaper” induced strategy adopted by non-natives allows more allocation to growth and competitive ability. Thus, our results suggest that all three hypotheses may be surprisingly integrated, but perhaps in ways that change over time (Figure 6). For example, in early invasions, herbivore pressure should be at its lowest and selection should immediately favour plants with reduced costly constitutive defence. This dynamic might rapidly lead to selection on growth. During or after this selection pressure, if generalist herbivory increases, there might be selection for increased induced qualitative defence, which tend to be cheaper, but they are not free. Thus, selection for increased growth may wane to some degree. The results of studies like ours may

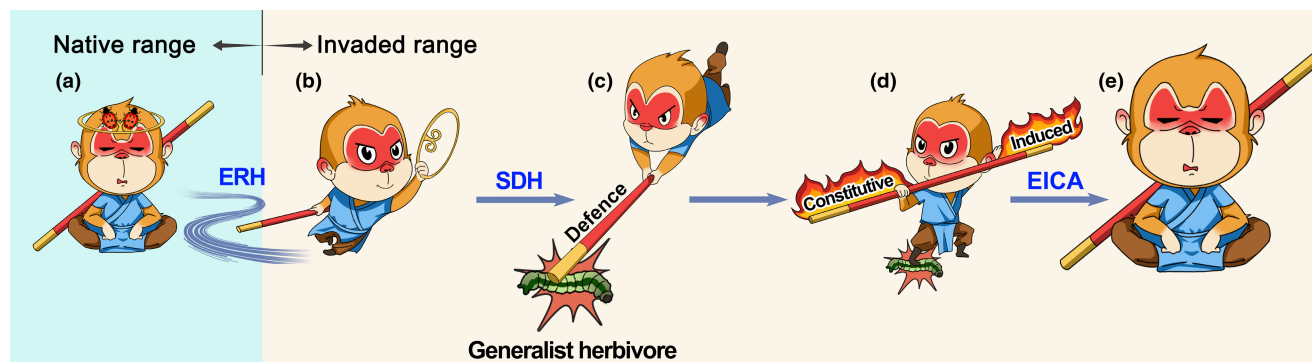


FIGURE 6 Appropriation of ancient Chinese folk mythology to illustrate integration of the ERH, SDH, and EICA hypotheses with variation in defence allocation. Sun Wukong, the monkey king (representing a plant species), possesses inherent strength that is limited by the incantation of the golden hoop (a) – specialist herbivores – which keeps him under control. However, when Sun Wukong undertakes a pilgrimage to the west (b) – non-native introduction – the golden hoop does not exist, allowing a rapid increase in defence capacity (c) – the golden cudgel he acquired on his journey – against the now predominant generalist herbivores. Simultaneously, removing the golden hoop allows a strong and consistent response to variation in generalist herbivore pressure, resulting in a positive correlation between herbivore pressure and allocation to cheaper induced defence (d). This reallocation leads to greater growth consistent with the Evolution of Increased Competitive Ability Hypothesis (e). 🐵: Sun Wukong. 📿: The golden hoop. 🐛: Generalist herbivore. 🐛: specialist herbivore. —: Golden cudgel, plant defence. ERH: Enemy Release Hypothesis. SDH: Shifting Defence Hypothesis. EICA: Evolution of Increased Competitive Ability Hypothesis.

depend on when in this dynamic process measurements are made. Regardless, our results expand insights into trade-offs in constitutive and induced defences and into how variation in herbivore communities might affect defence allocation in plants.

AUTHOR CONTRIBUTIONS

XS, JD, and WH conceived the idea. XS, WH, and JD designed the study. XS, YS, XC, XZ, and JW conducted experiments. RMC, SLF, XS, WH, and JD developed the conceptual structure and interpretation. XS, YS, and WH performed data analyses. XS, RMC, WH, YS, JD, and SLF drafted the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have declared that there is no conflict of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Raw data and code associated with this study are publicly accessible in the figshare (<https://doi.org/10.6084/m9.figshare.22670980.v1>).

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SUPPORTING INFORMATION

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