

Plant invasions, generalist herbivores, and novel defense weapons

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Abstract. One commonly accepted mechanism for biological invasions is that species, after introduction to a new region, leave behind their natural enemies and therefore increase in distribution and abundance. However, which enemies are escaped remains unclear. Escape from specialist invertebrate herbivores has been examined in detail, but despite the profound effects of generalist herbivores in natural communities their potential to control invasive species is poorly understood. We carried out parallel laboratory feeding bioassays with generalist invertebrate herbivores from the native (Europe) and from the introduced (North America) range using native and nonnative tetraploid populations of the invasive spotted knapweed, *Centaurea stoebe*. We found that the growth of North American generalist herbivores was far lower when feeding on *C. stoebe* than the growth of European generalists. In contrast, North American and European generalists grew equally well on European and North American tetraploid *C. stoebe* plants, lending no support for an evolutionary change in resistance of North American tetraploid *C. stoebe* populations against generalist herbivores. These results suggest that biogeographical differences in the response of generalist herbivores to novel plant species have the potential to affect plant invasions.

Key words: biological invasions; biotic resistance; enemy release; evolution of increased competitive ability; herbivorous invertebrates; novel associations; plant–herbivore interactions.

INTRODUCTION

One of the biggest mysteries in ecology is that some exotic plants occur at low densities in their native ranges but attain very high densities in their introduced ranges. These changes in community dominance suggest the existence of powerful but poorly understood ecological processes. The most obvious difference in biotic interactions invasive plants experience in their new ranges is the lack of specialist herbivores (Keane and Crawley 2002, Mitchell et al. 2006). But in their native ranges plants interact with a complex suite of herbivores that range from highly coevolved specialists to broad generalists. In nonnative ranges exotic plants no longer interact with specialists and encounter a new suite of generalist natural enemies with which they have no evolutionary past (Mitchell et al. 2006, Verhoeven et al. 2009). Because generalist herbivores are widespread and present in both the native and nonnative ranges of invaders and apparently cannot be escaped, ecologists have focused almost exclusively on the release of invaders from specialists and the potential of reintroducing specialists to control invaders (Müller-Schärer

and Schaffner 2008). However, there are few if any generalist consumers of plants that do not have preferences, and the preferences of generalists can completely transform the composition and diversity of plant communities (Huntly 1990, Strauss et al. 2009). Furthermore, recent studies have suggested that broad or single-family native generalists avoid some invasive plant species (Cappuccino and Carpenter 2005, Wikström et al. 2006, Parker and Gilbert 2007, Han et al. 2008, Jogesh et al. 2008, Tallamy et al. 2010; but see Lind and Parker 2010).

We do not yet understand the fundamental ecological and evolutionary consequences of the shift in the enemy complex that occurs with range expansion, but this shift is at the core of a suite of key hypotheses for why some introduced plant species become invasive. The enemy release hypothesis (ERH) predicts that introduced plants escape specialist herbivores and receive less damage from generalist natural enemies (Keane and Crawley 2002). The evolution of increased competitive ability hypothesis (EICA hypothesis), an evolutionary extension of the ERH, posits that decreased enemy attack selects for individuals that allocate less resources to herbivore defense and more to growth, driving the evolution of increased competitive ability in exotic populations (Blossey and Nötzold 1995). The novel weapons hypothesis (NWH), first put forward in the

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context of allelopathy (Callaway and Aschehoug 2000, Callaway and Ridenour 2004), proposes that invasive plants possess allelopathic chemicals that are relatively ineffective against their natural neighbors because of coevolution but that are highly inhibitory to naïve plants in the introduced range. More recently, the NWH has been extended to include biochemical interactions between invasive plants and soil microbes (Callaway et al. 2008). In contrast, the biotic resistance hypothesis (BRH) argues that introduced plants, because they share no evolutionary history with their competitors and new natural enemies in the introduced range, may lack effective defenses against the resident consumers in the introduced range (Parker and Hay 2005).

The lack of specialist herbivores in introduced ranges is the basic observation upon which the ERH and the EICA hypotheses are founded. However, all of the hypotheses mentioned above find common ground in ideas about the effects of generalist herbivores. In the context of the ERH, Keane and Crawley (2002) predicted that “generalists will have a greater impact on the native competitors,” however, soon after they also state that “... there is no obvious reason why generalist enemies should be less likely to attack exotics or to have a lower impact on exotics.” The NWH provides a reason: it predicts that native generalist herbivores will avoid or grow poorly on plant species with novel defense chemicals, thereby contributing to the invasiveness of these species (Cappuccino and Carpenter 2005). A review of the literature supports this idea showing that highly invasive exotic plant species in North America are more likely to have potent secondary compounds than exotics that are widespread, but not invasive (Cappuccino and Arnason 2006). The EICA hypothesis predicts that the lack of specialist herbivores should select for reduced anti-specialist defenses in invasive plants (Blossey and Nötzold 1995). However, if in the native range plants evolve intermediate defense traits as a result of differential selection by specialist and generalist herbivores, and if introduced plants are attacked by native generalist herbivores in the introduced range, anti-generalist defenses should actually increase rather than decrease in concentration (Müller-Schärer et al. 2004, Joshi and Vrieling 2005, Ridenour et al. 2008).

In the most thorough review of the literature on the role of generalist consumers in plant invasions to date, Parker et al. (2006) presented evidence that successful invaders may be poorly adapted to defend themselves against generalist herbivores native to the invaded ranges, and that healthy populations of native herbivores can provide biotic resistance to plant invasions. Thus there are three general hypotheses for how generalist herbivores might respond to exotics: (1) native generalists avoid and show reduced performance on exotic invaders because of their biochemical or other defense novelty, which would be consistent with the ER and the NW hypotheses, (2) native generalists prefer and

perform better on exotic invasive plants because exotic plants lack evolved defense traits against the native generalists, which would be in line with the BR hypothesis, and (3) plant populations in the introduced range have evolved a shift in allocation from defenses to growth, rendering them more suitable for generalist herbivores than plant populations from the native range. An increased growth rate of generalist herbivores on North American *C. stoebe* plants would provide support for the EICA hypothesis.

To disentangle these contradicting hypotheses, we carried out parallel laboratory feeding bioassays with generalist invertebrate herbivores from the native (Europe) and from the introduced (North America) range using native and nonnative tetraploid populations of spotted knapweed, *Centaurea stoebe* (Treier et al. 2009). *Centaurea stoebe*, a native to Europe, is highly invasive in temperate grasslands in North America and possesses at least one novel defense chemical, the sesquiterpene lactone cnicin, not yet found in plant species native to North America (Cappuccino and Arnason 2006).

METHODS

Species description and experimental design.—In its native range, *C. stoebe* occurs in a diploid (2 \times) and a tetraploid (4 \times) form, while all populations in the introduced range analyzed so far are tetraploids (Treier et al. 2009). We carried out parallel laboratory feeding bioassays with generalist herbivores from the native (Europe) and from the introduced (North America) range using seeds of native and introduced 4 \times populations of *C. stoebe* (Appendix A). All seeds were collected during extensive field surveys conducted in the native and the introduced range in 2005 (for details see Treier et al. 2009). We planted seedlings of eight native and nine introduced populations of *C. stoebe* individually in 1-L pots filled with a standard potting soil mixture. As a control, one lettuce (variety “Maikönig”) and one pea seedling (variety “Feltham First”; both varieties were purchased from MIGROS AG, Delémont, Switzerland, and used in both laboratories) each were planted together in 1-L pots. Feeding bioassays were conducted by setting up for each generalist one potted *C. stoebe* plant of each of the 17 populations as well as between 12 and 16 control pots, resulting in 29–33 trials for each herbivore species. All test and control plants had at least eight true leaves at the time they were used in the bioassays.

Generalist herbivores with a host-range comprising members of at least five different plant families (Appendix B) were collected from sites where *C. stoebe* was present, or purchased from companies that have laboratory rearings of generalist herbivores. Our approach was to test as many common generalist herbivores as possible that occur in habitats where *C. stoebe* is present, irrespective of whether they were recorded feeding on *C. stoebe* or not. This was intended

to provide some insight into putative generalist pressure that is characteristic for *C. stoebe* habitats in the native and the invaded range. In 2006 and 2007, eight European generalist herbivores and one North American generalist were tested at the CABI Europe-Switzerland Centre, Delémont, and nine North American generalists and one European generalist at the University of Montana, Missoula, USA (Appendix B). Potted *C. stoebe* and control plants were covered with a transparent mesh bag that was fixed to the pot with an elastic band, and placed in a randomized design onto a table in an unheated greenhouse. Prior to releasing the herbivores into the mesh bag, their fresh mass (most herbivores in Europe), body length (most herbivores in North America), or nymphal stage (all Hemiptera) was determined. One individual of a generalist herbivore species was transferred into each mesh bag and the mesh bag closed. Fresh mass, body length, or nymphal stage of the herbivores was determined and mortality recorded every 2–3 days over a period of 8–14 days. Relative growth rate was calculated as the slope of the linear regression of $\ln(\text{mass})$, $\ln(\text{body length})$, or nymphal stage plotted against number of days. Herbivore species were tested at different times, depending on availability, but for each herbivore species all treatments were set up simultaneously.

To assess whether the results of the experiments carried out in the two different laboratories were comparable, eggs of the generalist noctuid moth *Trichoplusia ni*, which has a holarctic distribution, were ordered from Cornell University, Geneva, New York, USA, and sent to both laboratories. *Trichoplusia ni* was the first insect tested in the two laboratories. Moreover, one of the North American generalist herbivores, the noctuid *Heliothis virescens* was also tested in Delémont (eggs were obtained from Syngenta, Stein, Switzerland).

Data analysis.—We tested the effects of herbivore origin and plant type using meta-analysis to examine the 18 individual bioassays carried out in Delémont and Missoula. To assess how the growth of European and of North American generalist herbivores is affected by *C. stoebe*, compared to a control, and whether *C. stoebe* plants from the introduced range affect herbivore growth differently than *C. stoebe* plants from the native range, we calculated the effect sizes for each herbivore species from the mean relative growth rate values (+1 to include zeros). The log response ratio, or $\ln(R)$, was used since it is a highly robust standardized measure using the means, standard deviation and sample sizes associated with each pair of treatments and controls (Hedges et al. 1999). This metric is calculated as the paired differences between the natural log of the treatment samples from the natural log of the mean control samples. Importantly for ecological datasets, the distribution of this metric is generally linear, relatively normal, and sensitive to changes in both the treatment and control groups (Hedges et al. 1999). The relative effect of plant origin, i.e., European vs. North American *C. stoebe*, was

contrasted to the set of controls (Oksanen 2001), while the effect of herbivore origin was contrasted by treating each origin as a separate, independent categorical variable (with *C. stoebe* origin collapsed where appropriate). Both meta-analyses were modeled as random effects, with 9999 resampling iterations, and bootstrapped 95% confidence intervals are reported. Heterogeneity within and between groups was inspected to determine if the groups adequately described the data (Higgins and Thompson 2002) and all statistics were done with MetaWin 2.1 (Rosenberg et al. 2000). Nonoverlapping confidence intervals between different groups or with zero indicates significant differences between groups in the former case and a significant effect (i.e., different from 0) in the latter case at the alpha level of $P < 0.05$. ANOVAs and Kruskal-Wallis test were performed in SPSS 16.0 for Windows (SPSS, Chicago, Illinois, USA).

RESULTS

North American generalist insects as a group grew much more slowly on *C. stoebe*, relative to their growth on control plants, than European generalists (Fig. 1), a results which is not consistent with the BRH (Parker et al. 2006) but is consistent with the NWH. This general biogeographic difference also extended to congeneric comparisons. *Spodoptera littoralis*, a broad generalist from Europe, grew as well on *C. stoebe* as on the control plants (Fig. 2A). In contrast, all individuals of the North American congener, *Spodoptera frugiperda*, placed on *C. stoebe* died. Moreover, while the growth rate of the European generalist *Heliothis peltigera* did not differ significantly between *C. stoebe* and the controls, the growth of the North American congener *Heliothis virescens* was reduced by 55–75% when grown on *C. stoebe* (Fig. 2B). In the third congeneric pair, the European *Lygus rugulipennis* maintained a higher growth rate on the European than on the North American 4× *C. stoebe*, but RGR on 4× *C. stoebe* did not differ from that on the control. However, RGR of the North American *Lygus* species (either *L. hesperus* or *L. lineolaris*) was significantly lower on *C. stoebe* than on the control (Fig. 2C). The European generalist *Chortipus* sp. showed the highest variation in performance on *C. stoebe*, with eight individuals dying and 10 individuals rapidly gaining mass during the bioassays (Fig. 1).

The growth rates of both North American and European generalists were equally affected by North American and European 4× *C. stoebe* plants (Fig. 3). In two out of 18 herbivores tested, RGR on the European 4× *C. stoebe* plants was significantly higher than that on the North American 4× *C. stoebe* plants (Fig. 2C; Appendix C). In the other sixteen herbivores RGR did not differ between European and North American *C. stoebe* plants. Hence, our results provide little support for an evolutionary change in resistance of North American 4× *C. stoebe* populations against generalist herbivores, as predicted by the EICA hypothesis.

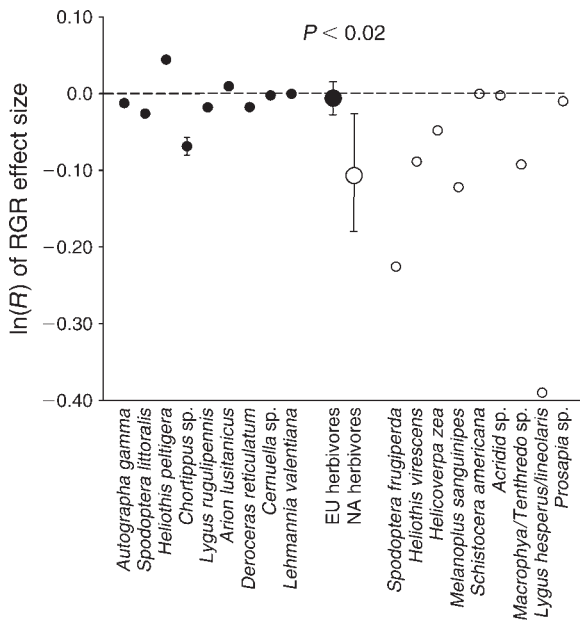


FIG. 1. The effects of *Centaurea stoebe* (European and North American populations collapsed) and control plants (mixture of *Pisum sativum* and *Lactuca sativa*) on the relative growth rate (RGR) of European ($N = 9$) and North American ($N = 9$) generalist herbivores. Given are the effect size measure (ϵ) and variance of RGR, $\ln(R)$, of the herbivore species tested, as well as the means of the effects sizes (EU herbivores, NA herbivores) and 95% confidence intervals, separated by herbivore origin. Positive values indicate a relative increase in growth of herbivores on *C. stoebe* plants, while negative values indicate decreased relative growth rate on *C. stoebe* compared to controls. For the effect sizes of individual herbivores, \pm SE is either shown or is smaller than the symbol. Means of effects are significant when the 95% confidence interval does not cross zero. P value is for the difference in effects of European vs. North American generalist herbivores.

The two initial bioassays with the cosmopolitan species *Trichoplusia ni* conducted in both laboratories revealed comparable patterns in relative growth rate among European 4 \times , North American 4 \times and control plants (Appendix D). Moreover, we intentionally tested generalist species that had already been introduced to Europe from North America or vice versa. For example, of the nine generalists tested in North America we included *Lehmannia valentiana*, a European slug, and found no significant difference in relative growth rate or final biomass when grown on *C. stoebe* (biomass 0.57 ± 0.06 g) than when grown on control plants, consistent with the overall lack of effect of *C. stoebe* on European generalists (biomass 0.73 ± 0.06 g; analysis of variance on relative growth rate for *C. stoebe* vs. control: $F_{1,30} = 0.317$, $P = 0.557$). We also tested the NA generalist *Heliothis virescens* in Missoula and in Delémont and found comparably strong inhibitory effects of *C. stoebe* in each laboratory, consistent with the overall negative effect of *C. stoebe* on North American generalists (Appendix E).

Because generalists were much easier to find in the vicinity of spotted knapweed in Europe than in North America, more of the European generalists were collected in the field (seven of eight) than North American generalists (five of nine; Appendix B). This raises the possibility that more European species had the opportunity to behaviorally acclimate to *C. stoebe*, thereby confounding any interpretation of adaptation. However, both field-collected North American generalists (three out of five species) and North American generalists obtained from laboratory rearings (three out of four species) showed significant negative effects when grown on *C. stoebe* (Appendices B and C). An alternative to the interpretation that North American species are less adapted to a novel weapon than European species, is that differences in the taxonomic composition of North American and European generalist herbivores caused higher consumption of *C. stoebe* by European species. For example, four of the European generalists were snails or slugs, whereas we could not find any native North American mollusks in the much drier grasslands of Montana. However, the mean of the effect sizes for both the European mollusks (-0.004) and the other European generalists (-0.017) were higher than that for North American generalists (-0.107 ; Table 1), indicating that the presence of mollusks in the set of European generalists does not fully explain the difference in response of generalist herbivores to *C. stoebe* found between the native and the introduced range.

DISCUSSION

Our experimental results are the first to indicate a strong biogeographical difference in the responses of generalist herbivores to an invasive species and are consistent with the NWH. This in turn provides the first empirical foundation for one of the fundamental predictions of the ERH, i.e., that generalists will have a greater impact on the native competitors than on the invasive plant (Keane and Crawley 2002). We found a difference in the effects of *C. stoebe* on North American and European generalists; yet, this does not necessarily mean that European generalists suppress *C. stoebe* more than North American generalists. This is an important distinction because successful invasion would ultimately depend on consumer effects, not responses. Nevertheless, increases in consumer mortality or decreases in the fitness of survivors would likely alter their effects on plant communities.

We controlled for substrate, *C. stoebe* genotype, and the seed source used for our control plants (a mixture of *Pisum sativum* and *Lactuca sativa*) but an inherent weakness in our experimental design is that most North American generalists were tested in North America and most European generalists were tested in Europe. This was unavoidable because of the ethical and legal problems with transporting generalist invertebrates between continents. However, when we tested the same two herbivores in parallel experiments in the two

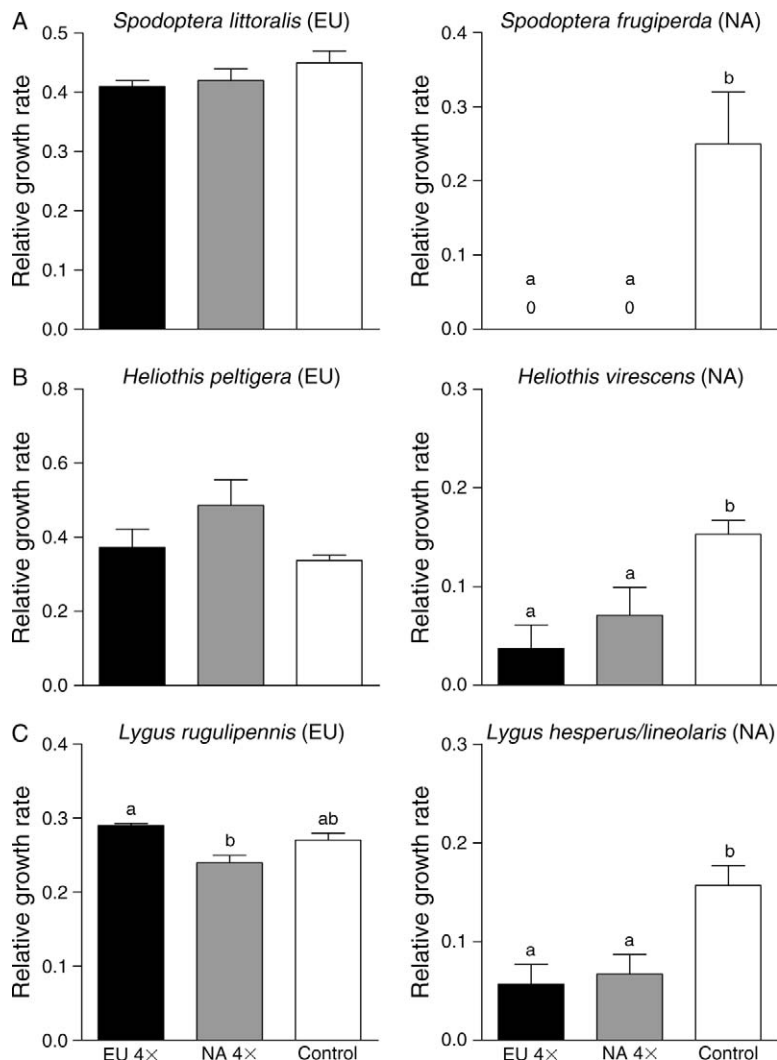


FIG. 2. Biogeographic comparisons of the relative growth rate (means \pm SE) of congenic pairs of generalist herbivores fed European tetraploid (EU 4 \times) *C. stoebe*, North American tetraploid (NA 4 \times), *C. stoebe*, or control plants (mixture of *Pisum sativum* and *Lactuca sativa*). (A) *Spodoptera littoralis*, ANOVA, $F_{2,24} = 1.039$, $P > 0.2$; *Spodoptera frugiperda*, Kruskal-Wallis chi = 13.310, $P < 0.001$. (B) *Heliothis peltigera*, ANOVA, $F_{2,24} = 2.514$, $P > 0.05$; *Heliothis virescens*, ANOVA, $F_{2,31} = 9.222$, $P < 0.001$. (C) *Lygus rugulipennis*, ANOVA, $F_{2,27} = 3.360$, $P < 0.05$; *Lygus hesperus/lineolaris*, ANOVA, $F_{2,23} = 7.135$, $P < 0.01$. Different letters indicate significant differences among the plant categories (Tukey test for ANOVAs, Mann-Whitney for Kruskal-Wallis).

laboratories and assessed performance of a European slug that was introduced into North America the results paralleled those of the entire data set.

Only a few other studies have taken explicit biogeographic approaches to the study of the effects of generalist consumers on invasive plants. In its native range in Europe, *Silene latifolia* is damaged more by generalist enemies than in North America where it is an invader (Wolfe 2002). Similarly, fewer generalist herbivores occur on the invasive seaweed *Fucus evanescens* in Sweden than on native seaweeds, but *F. evanescens* supports as many generalists in its native range in Iceland as other native seaweeds (Wikström et al. 2006). Furthermore, generalist herbivores native to Sweden preferred native species over the invasive *F. evanescens*,

whereas, in its native Iceland, *F. evanescens* was preferred by the two native generalists.

A number of studies have used feeding trials to compare the effects of generalists on native and invasive plant species in terrestrial ecosystems. For example, Jogesh et al. (2008) found that the generalist North American grasshoppers, *Schistocerca americana* and *Melanoplus femurrubrum*, caused much less damage to invasive *Centaurea* species in the field than to noninvasive congeners. Other studies have found similar patterns (Berenbaum 1981, Cappuccino and Carpenter 2005, Carpenter and Cappuccino 2005, Parker and Gilbert 2007, Han et al. 2008). Using an experimental approach, Agrawal et al. (2005) found that exotic plant species, on average, received less insect herbivory than

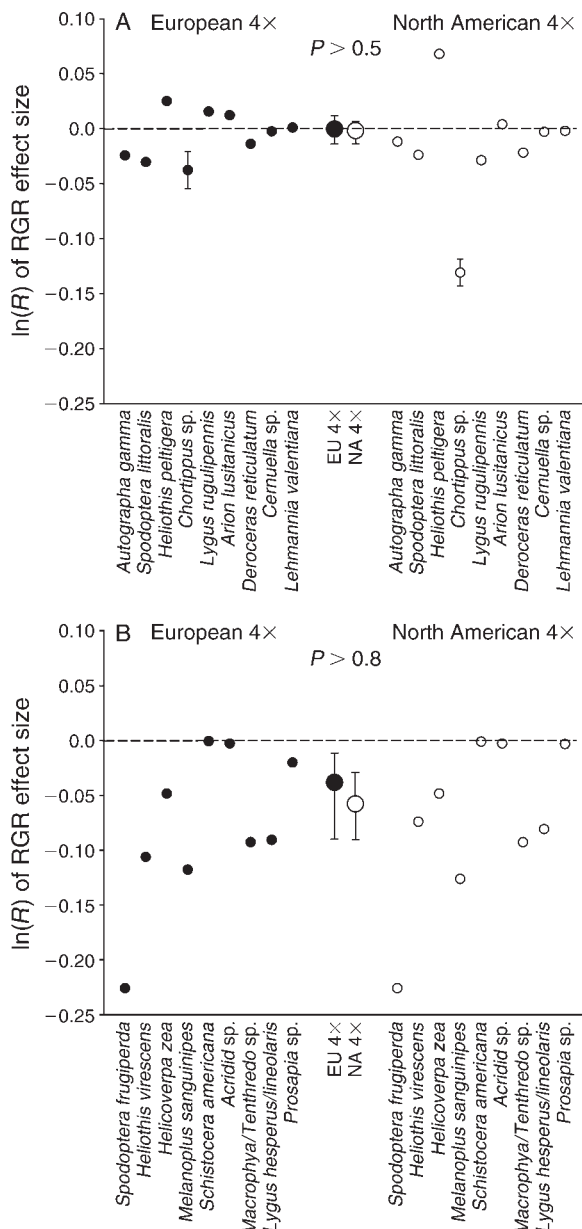


FIG. 3. Effects of European tetraploid (EU 4 \times) and North American tetraploid (NA 4 \times) populations of *Centaurea stoebe* on the relative growth rate of (A) European and (B) North American generalist herbivores. Given are the effect size measures (e_{++} and variance) of RGR, $\ln(R)$, of the herbivore species tested as well as the means of the effects sizes and 95% confidence intervals separated by *C. stoebe* origin. Positive values indicate a relative increase in growth of herbivores on *C. stoebe* plants, while negative values indicate decreased relative growth rate on *C. stoebe* compared to controls. For the effect sizes of individual herbivores, \pm SE is either shown or smaller than the symbol. Means of effects are significant when the 95% confidence interval does not cross zero. P values test difference in effects of European vs. North American tetraploid *C. stoebe*.

natives. Parker and Gilbert (2007) compared natural enemy attack among native and nonnative clovers in California and found that invertebrate herbivores caused more damage on native species, but the effects of the herbivores on mortality did not differ between native and introduced species. Also, the most invasive species showed greater infection and greater prevalence of herbivory from noninvasive introduced species. Tallamy et al. (2010) raised four generalist lepidopteran herbivores on a large number of native and invasive plant species and found that with few exceptions, the generalists either died or grew at very low rates on the leaves of exotic species. In contrast, Lind and Parker (2010) conducted choice tests with the extracts of native and invasive plant species and using the very broad generalist, *Pyrrharctia isabella* (woolly bear caterpillar), and found no preference for either invasive or native species (also see Parker and Hay 2005).

Our results, together with the studies cited above, suggest that diffuse regional ecological and evolutionary relationships may occur among generalist herbivores and plants and that these relationships may have important implications for plant invasions. The NWH posits that mismatches in plant–natural enemy interactions are based on novel, toxin-based plant defenses. Our results support this notion and suggest that such mismatches may not only occur between invasive plants and native plants (Callaway and Ridenour 2004) or microorganisms (Callaway et al. 2008), but also among invasive plants and generalist herbivores. Corollary to this, our results indicate that generalist herbivores may have unusually important and so far largely underestimated roles in the evolutionary trajectories of native communities.

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APPENDIX A

Origin and description of *Centaurea stoebe* populations used in the feeding bioassays (*Ecological Archives* E092-071-A1).

APPENDIX B

Taxonomy and origin of the North American (NA) and European (EU) generalist herbivores (*Ecological Archives* E092-071-A2).

APPENDIX C

Relative growth rate (means \pm SE) of European and North American generalist herbivores fed European tetraploid (*C. stoebe*), North American tetraploid (*C. stoebe*), or control plants (*Ecological Archives* E092-071-A3).

APPENDIX D

Relative growth rate of *Trichoplusia ni* (*Ecological Archives* E092-071-A4).

APPENDIX E

Relative growth rate of *Heliothis virescens* (*Ecological Archives* E092-071-A5).