LETTER

Biotic resistance to plant invasions? Native herbivores prefer non-native plants

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Abstract

In contrast to expectations of the enemy release hypothesis, but consistent with the notion of biotic resistance, we found that native generalist crayfishes preferred exotic over native freshwater plants by a 3 : 1 ratio when plants were paired by taxonomic relatedness. Native crayfishes also preferred exotic over native plants when tested across 57 native and 15 exotic plants found growing sympatrically at 11 sites throughout the southeastern USA. Exotic grass carp that share little evolutionary history with most of these plants exhibited no preference for native vs. exotic species. Analyses of three terrestrial data sets showed similar patterns, with native herbivores generally preferring exotic plants, while exotic herbivores rarely exhibited a preference. Thus, exotic plants may escape their coevolved herbivores only to be preferentially consumed by the native generalist herbivores in their new ranges, suggesting that native herbivores may provide biotic resistance to plant invasions.

Keywords

Enemy release, herbivore feeding preferences, increased susceptibility, new associations, novel resistance.

Ecology Letters (2005) **8**: 959–967

INTRODUCTION

The enemy release hypothesis is one of the most commonly accepted theories to explain the success of invasive species. It posits that exotic species become invasive because they are liberated from consumer control in their new ranges (Darwin 1859; Elton 1958). The absence of coevolved specialist enemies and the preferential consumption of native species by native generalists putatively gives exotic species a competitive advantage over their native counterparts (Maron & Vila 2001; Keane & Crawley 2002; Shea & Chesson 2002). Native consumers are predicted to prefer native prey because evolutionarily novel, exotic species may be inadequate or distasteful prey (Siemann & Rogers 2003; Lankau *et al.* 2004). Recent studies confirm that exotic species commonly harbour fewer species of specialized parasites, pathogens and consumers in their introduced vs. their native ranges (Wolfe 2002; Mitchell & Power 2003; Torchin *et al.* 2003). However, a lower diversity of enemies need not translate into less damage (Maron & Vila 2001).

Although enemy release has traditionally assumed that native consumers will be better adapted to consuming native than exotic prey, this perspective ignores the alternative possibility that exotic prey may be poorly adapted for deterring native consumers. As exotic prey share no evolutionary history with native enemies, they will not have experienced selection from these consumers and may therefore lack effective defences, i.e. the 'new associations' or 'increased susceptibility' hypotheses (Hokkanen & Pimentel 1989; Colautti *et al.* 2004). If native consumers prefer exotic over native prey, this suggests that native consumers could limit invasions, as suggested by the biotic resistance hypothesis (Elton 1958).

Despite these competing predictions, we know little about preferences of native consumers for native vs. exotic prey, leading to little predictive power for the likelihood of native consumers to influence biological invasions (Maron & Vila 2001; Keane & Crawley 2002; Shea & Chesson 2002; Colautti *et al.* 2004). However, in contrast to expectations from the enemy release hypothesis, one recent field test found that exotic plants in an experimental meadow suffered greater, rather than lesser, damage from naturally recruited herbivores than did related native plants (Agrawal & Kotanen 2003).

Here, we report an experimental study of the feeding preferences of three generalist aquatic consumers (two native and one non-native species) for native vs. exotic freshwater plants from throughout the southeastern USA.

Exotic plants are particularly common in freshwater habitats, and although herbivory on freshwater macrophytes was previously assumed to be insignificant, numerous reviews show that herbivory in freshwater systems rivals or exceeds herbivory in marine and terrestrial ecosystems (Lodge 1991; Newman 1991; Cyr & Pace 1993; Lodge *et al.* 1998). We focus on generalist rather than specialist herbivores because generalists: (i) commonly have stronger impacts on plant community structure in marine (Hay & Steinberg 1992; Hay 1997), freshwater (Lodge *et al.* 1998), and terrestrial systems (Crawley 1989), (ii) are often the relevant consumers in freshwater ecosystems, where specialist herbivores are rare (Lodge *et al.* 1998, but see Solarz & Newman 1996, 2001), and (iii) are more likely than specialists to feed on and thus impact exotic plants. In laboratory feeding assays we use both a phylogenetic approach, pairing 10 exotic plants with related natives to control for some evolutionary variance in morphology, chemistry and other traits that might differ between unrelated taxa (Mack 1996), and a community approach, comparing consumer feeding preferences for 57 native and 15 exotic plant species that we found growing in sympatry at 11 sites scattered throughout South Carolina, Georgia, and Florida in the southeastern USA. Additionally, we extended our study to other ecosystems by re-analysing data from the literature on the feeding preferences of four native (three

grasshoppers and one slug) and four exotic (slugs) terrestrial herbivores when presented with subsets of 234 species of native and 51 species of exotic plants. These data sets were not phylogenetically controlled but were comparable with our community-level analyses of freshwater systems. We hypothesized that if the evolutionary history of the plant–herbivore interaction was important, then native consumers would prefer, rather than avoid, exotic plants because these plants would not have been selected to resist these herbivores. In contrast, exotic consumers that share little evolutionary history with either native or exotic plants should have no preference as a function of plant origin.

METHODS

Phylogenetically paired assays

We tested whether native consumers preferred to feed on native or exotic plants by conducting choice feeding assays in the laboratory with 10 phylogenetically paired native and exotic plants (Table 1). To find suitable pairings, we examined over 50 separate wetlands, ponds, lakes, streams and rivers in several southeastern states of the USA for co-occurring, taxonomically related native and exotic species. In most cases, we selected pairings based on the first closely related taxa that we encountered, resulting in four

Table 1 Species used in the phylogenetically paired feeding assays

Plant origin		Consumer species	
Native	Exotic	*P. spiculifer*	*P. acutus*
1. *Vallisneria americana* Lake Juliette, GA	*Egeria densa* Lake Juliette, GA	$t = -9.15$, $P < 0.0001$	$t = -9.51$, $P < 0.0001$
2. *Vallisneria americana* Lake Juliette, GA	*Hydrilla verticillata* Lake Juliette, GA	$t = -4.59$, $P < 0.0001$	$t = -4.91$, $P < 0.0001$
3. *Myriophyllum pinnatum* Chattahoochee River, GA	*Myriophyllum spicatum* Lake Juliette, GA	$t = -2.86$, $P = 0.013$	$t = -2.82$, $P = 0.014$
4. *Pontederia cordata* Lake Jackson, FL	*Eichhornia crassipes* Lake Blackshear, GA	$t = -2.65$, $P = 0.019$	$t = -10.12$, $P < 0.0001$
5. *Ludwigia palustris* Johnson Ferry, GA	*Ludwigia hexapetala* Lake Blackshear, GA	$t = 0.21$, $P = 0.839$	$t = 2.13$, $P = 0.051$
6. *Myriophyllum heterophyllum* Lake Jackson, FL	*Myriophyllum aquaticum* Lake Blackshear, GA	$t = -0.63$, $P = 0.536$	$t = -2.21$, $P = 0.044$
7. *Peltandra virginica* Lake Griffin, FL	*Colocasia esculenta* Lake Griffin, FL	$t = -5.04$, $P < 0.0001$	$t = -4.67$, $P < 0.0001$
8. *Peltandra virginica* Lake Griffin, FL	*Pistia stratiotes* Lake Griffin, FL	$t = -4.54$, $P < 0.0001$	$t = -3.33$, $P = 0.005$
9. *Panicum hemitomon* Little Lake Harris, FL	*Panicum repens* Little Lake Harris, FL	$t = -3.28$, $P = 0.005$	$t = -1.41$, $P = 0.179$
10. *Commelina virginica* Chattahoochee River, GA	*Murdannia keisak* Chattahoochee River, GA	$t = -8.15$, $P < 0.0001$	$t = -7.29$, $P < 0.0001$

The designation numbers refer to the taxonomic pairs shown in Fig. 1; location of collection is beneath each species. Results are shown for individual paired *t*-tests on each species pair for each consumer species ($n = 15$ for all pairings).

congeneric comparisons and six confamilial comparisons (for exotic taxa that lacked native congeners). We found two exotic and two native species in the genus *Myriophyllum*; we paired these so that the native and exotic plants most closely resembled each other morphologically. Twice we had to use one native species in two different contrasts. This occurred because: (i) we could find only one native plant (*Peltandra virginica*) that was confamilial with *Colocasia esculenta* and *Pistia stratiotes*, and (ii) we could find only one native plant (*Vallisneria americana*) that was a submersed species similar to the exotic species in the same family (*Hydrilla verticillata* and *Egeria densa*). Although all of these plants are commonly found growing in sympatry across the southeastern USA (USDA 2004), in the time frame of this study we were only able to find exotic and related natives co-occurring at the same location for six of our 10 contrasts; in the other four contrasts, the paired relatives could only be found at different locations, potentially confounding site effects with plant origin effects for these four pairs. To be sure that we were not confounding plant origin effects with site of collection effects, and that we were not biasing our findings by using two native species in two paired assays each, we analysed not only the entire data set, but also subsets of the data after excluding contrasts that could have confounded our results.

To assess consumer preference, we fed plants to the native North American crayfishes *Procambarus spiculifer* and *Procambarus acutus*, both of which have native ranges that overlap the sites and types of habitats that we sampled (Hobbs 1981). Crayfishes are diverse and abundant foragers in aquatic habitats throughout North America, and they can dramatically reduce aquatic macrophyte biomass and fundamentally alter plant community composition (Lodge *et al.* 1998 and references therein). *Procambarus spiculifer* were collected from the Chattahoochee River (Atlanta, GA, USA); *P. acutus* were collected from an adjacent wetland. We housed each crayfish in a separate $12 \times 12 \times 10$ cm cubicle with perforated walls receiving recirculating, filtered water and fed them a diet of Bio-Blend Herbivore food 3–4 times per week.

For each native vs. exotic contrast, we offered 15 individuals of each crayfish species a portion (500 ± 100 mg) from a native and a related exotic macrophyte bound side-by-side in a binder clip. We ended each replicate when a consumer had eaten approximately half of either species. Controls for changes in plant mass unrelated to herbivory consisted of identical portions from the same individual plants (when permitted by the size of the plant), or portions of plants from the same collection, placed into the same water table but without herbivores. We calculated the mass of native and exotic plants eaten by individual consumers with: $(T_i \times C_f/C_i) - T_f$, where T_i and T_f were initial and final wet masses of tissue exposed to herbivores,

and C_i and C_f were initial and final wet masses of controls (as in Cronin & Hay 1996). Data were analysed with a mixed model ANOVA using each replicate consumer as a randomized block nested within each species pair, followed by planned, paired contrasts.

Feeding assays with regionally co-occurring macrophytes

The phylogenetic assays provide a powerful contrast because we could pair all plants by taxonomy and six of the 10 pairs by location of collection as well. However, the requirement for finding pairs of congeneric or confamilial species constrained our sample size to 10 pairs. To determine the robustness of the pattern found in the above assay, we also evaluated the willingness of each crayfish species to feed on each of 57 native and 15 exotic aquatic macrophytes that we found growing in sympatry across the southeastern USA. This approach allowed us to increase our sample size considerably but included many sources of variance (site, time of collection, phylogenetic history) that we largely avoided in our paired assays. Thus, our question here was whether we could still detect preference patterns for native vs. exotic prey despite these additional sources of variance. In addition to assays with crayfishes, we also conducted assays with the exotic herbivorous grass carp *Ctenopharyngodon idella*, a generalist herbivore from Asia that has been introduced throughout the USA (USGS 2005). This contrast included only the 33 native and 14 exotic macrophytes that we encountered after acquiring grass carp. Grass carp were not used in the previous, phylogenetically controlled assays because in pilot assays these consumers commonly took more than a week to acclimate and begin feeding in such trials. In contrast, crayfish trials were typically completed within a few hours.

For these assays, we collected the common native or exotic macrophyte species found growing sympatrically at 11 sites in South Carolina, Georgia and Florida, USA (see legend to Fig. 2 for sites). Plants were transported from the field to the laboratory in chilled coolers and kept chilled until fed to consumers, generally within 48 h. Because of the large number of species assayed (72 for crayfish and 47 for grass carp), we did not conduct cafeteria-style choice feeding assays. We instead determined acceptability as food by offering 15–22 individuals of each crayfish species a bite-sized portion of each macrophyte species and recorded whether each portion of food was eaten or rejected. If rejected, we fed consumers a piece of palatable aquatic macrophyte (generally *Ludwigia palustris*) to assure they were not satiated and rejecting all foods. If the palatable macrophyte was rejected, that replicate crayfish was not included in the assay because it appeared satiated. Grass carp would not feed when kept individually, so we housed three to five juveniles together in perforated 3.5 L buckets

with recirculating water and report results from the first fish that fed in each bucket as a replicate ($n = 13–16$ separate buckets). Order of macrophyte presentation was randomized separately for each replicate consumer. We then contrasted (using the Mann–Whitney test) the mean proportion of animals that were willing to feed on native vs. exotic plant species.

Re-analyses of previous literature

To provide a broader assessment of the relative palatability of exotic plants, we used the online database Web of Science (1945 to present) to find three studies that had fed numerous species of native and exotic plants to native and exotic generalist herbivores (Cates & Orians 1975; Otte 1975; Rathcke 1985). This approach added 285 plant species and eight consumer species to our analysis. Our intent here was to test whether the patterns we found in aquatic systems also held for terrestrial plants and their consumers.

None of these studies had focused on the palatability of native vs. exotic species. Instead, all had assessed the relationship between plant successional status and palatability, and all had found opposing patterns. Cates & Orians (1975) found that one native and one exotic slug in the Pacific Northwest preferred early successional species, Otte (1975) found that three native grasshoppers in Texas preferred later successional species, and Rathcke (1985) found no preference as a function of plant successional stage among three exotic slugs in the American northeast. We analysed their data as a function of plant origin (native vs. exotic species) rather than as a function of successional status. To determine whether plants were native or exotic in each particular study, we used the authors' own designations in Cates & Orians (1975) and Otte (1975), although we changed one species (*Rumex crispus*) in Otte (1975) from native to exotic based on its current classification status (USDA 2004). For Rathcke (1985), we assigned plant origin using the PLANTS database (USDA 2004). Feeding assays in all three studies were conducted by offering each consumer a choice between a treatment plant and a standardized control plant species, resulting in a metric of relative amount eaten (amount of treatment plant eaten relative to control plant). We analysed (Mann–Whitney tests) the relative amount eaten of all native and exotic plant species for each consumer in each study.

Although these studies found opposing influences of successional status on plant palatability, most of the exotic plants in each study were labelled early successional plants – 10 of 14 species in Otte (1975), all 27 species in Cates & Orians (1975), and all 13 species in Rathcke (1985), potentially confounding plant origin with successional status. Thus, we also analysed (Mann–Whitney tests) whether early successional exotic plants were more or less palatable than early successional native plants. We did not analyse these data with factorial ANOVAs (origin × successional status) because the near absence of late successional, exotic plants would render factorial analyses non-orthogonal and thus difficult to interpret.

RESULTS

In the 10 phylogenetically controlled feeding assays, both native crayfish showed a significant, 3-fold preference for exotic over native species (Fig. 1 insets; *P. spiculifer*: $F_{1,140} = 136.91$, $P < 0.0001$; *P. acutus*: $F_{1,140} = 147.51$,
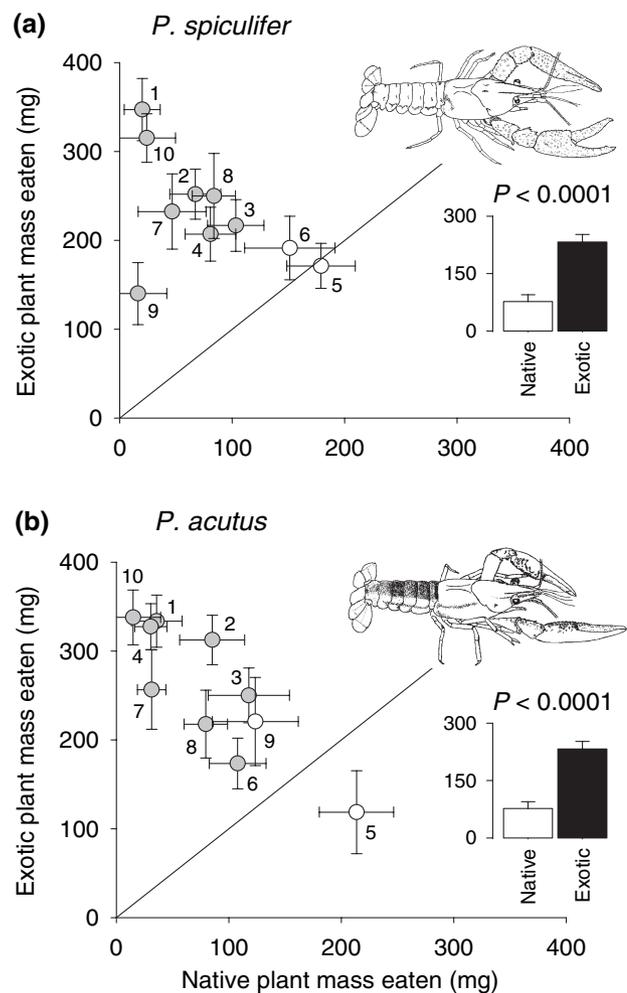

Figure 1 Mean (±SE) plant biomass consumed by the native crayfishes (a) *Procambarus spiculifer* and (b) *P. acutus* when offered a choice between phylogenetically paired (either congeneric or confamilial) native and exotic freshwater plants. Grey circles were statistically significant individual feeding assays ($P < 0.05$, paired *t*-tests; Table 1). Insets are the overall means between native and exotic plants, with standard errors corrected for the nesting factor. Numbers refer to taxonomic pairs in Table 1.

$P < 0.0001$). Each consumer significantly preferred exotic over native plants in eight of the 10 taxonomic pairs (Fig. 1; Table 1). Neither consumer ever preferred a native plant over its exotic relative, although one contrast trended in this direction (*Ludwigia* spp. comparisons for *P. acutus*; Fig. 1; Table 1). If the analyses excluded the non-sympatric species pairs or the contrasts with duplicative native species, we still found the same strong patterns. Native herbivores still strongly preferred exotic over native species ($P < 0.0001$ in all cases).

The above contrasts minimize uncontrolled variance because of taxonomy and, for six of the 10 paired contrasts, location. This allows a clear contrast of herbivore preference for similar native vs. exotic plants but constrains our sample size because of the difficulty of finding related native and exotic species growing sympatrically. We considerably improved our sample size by comparing the palatability of native vs. exotic species that we found growing at 11 locations across South Carolina, Georgia and Florida. Despite the potential for large uncontrolled variance due to taxonomic and site-specific effects on palatability, exotic species ($n = 15$) were significantly more palatable than native taxa ($n = 57$) to both species of native consumer (*P. spiculifer*: $P = 0.034$; *P. acutus*: $P = 0.033$, Mann–Whitney tests; Fig. 2), but not to the exotic grass carp ($P = 0.464$, $n = 14$ exotic and 33 native plants; Fig. 2). Although the 10 exotic species from the phylogenetic pairings were also included among the 15 species in the community comparisons, these 10 species did not appear to drive the community relationship as several of the plants not included in the phylogenetic pairings were highly palatable to both crayfishes (Fig. 2).

Our re-analyses of published data sets from terrestrial systems showed similar feeding preference patterns. Data of Cates & Orians (1975; their Tables 1–6) showed that both the native slug *Ariolimax columbianus* and the exotic slug *Arion ater* significantly preferred exotic ($n = 27$) over native
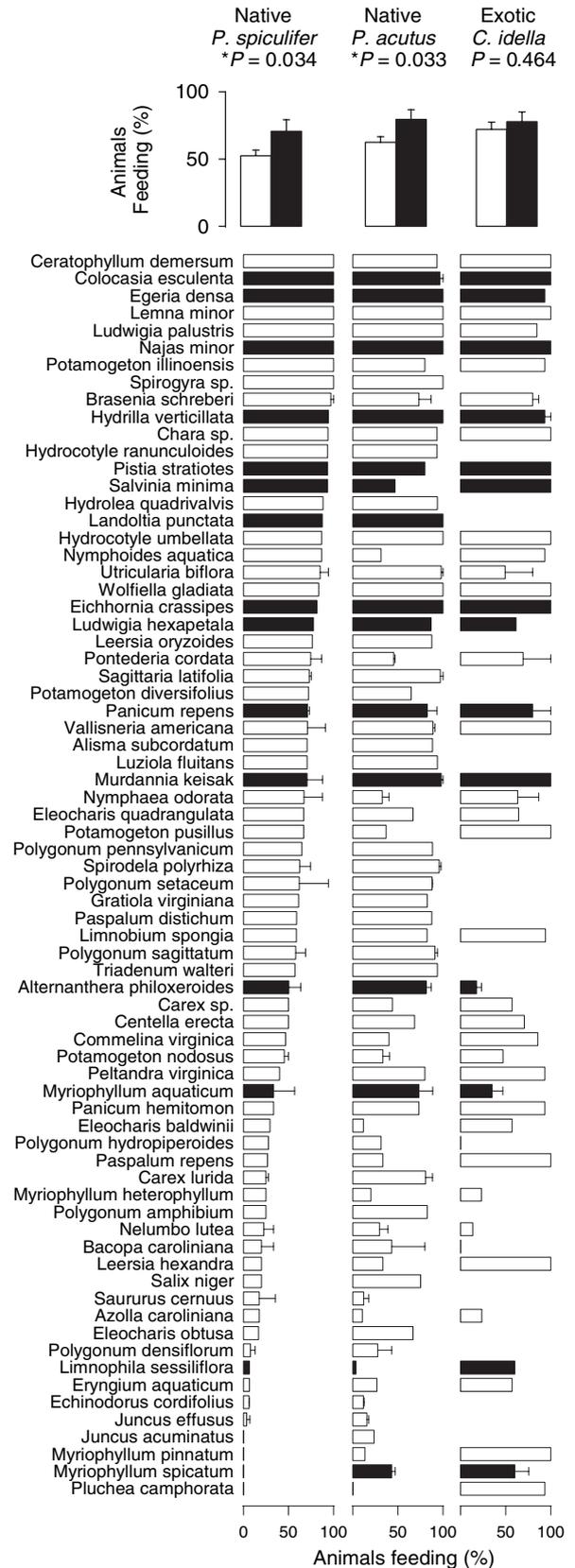
Figure 2 Mean (+SE) percentage of crayfish (*Procambarus spiculifer* and *P. acutus*) and grass carp (*Ctenopharyngodon idella*) feeding on all native (open bars) and exotic (filled bars) macrophyte species that were encountered during this study (statistics from Mann–Whitney tests). For a species at a given site, we averaged results from separate feeding assays if this plant had both submersed and emergent leaves; we then used this mean value to compute a mean palatability across sites. Standard errors represent the variance across sites, not among leaf types. The summary data presented at the top of the figure are based on 57 native and 15 exotic plant species for crayfishes; 33 native and 14 exotic species for grass carp. Sites of collection were: Rum Creek, GA; east and west Lake Juliette, GA; Lake Blackshear, GA, Johnson Ferry, GA, Lake Seminole, GA; Priests Landing, GA; Par Pond, SC; Pond 4, SC; Lake Bradshaw, FL; Little Lake Harris, FL.
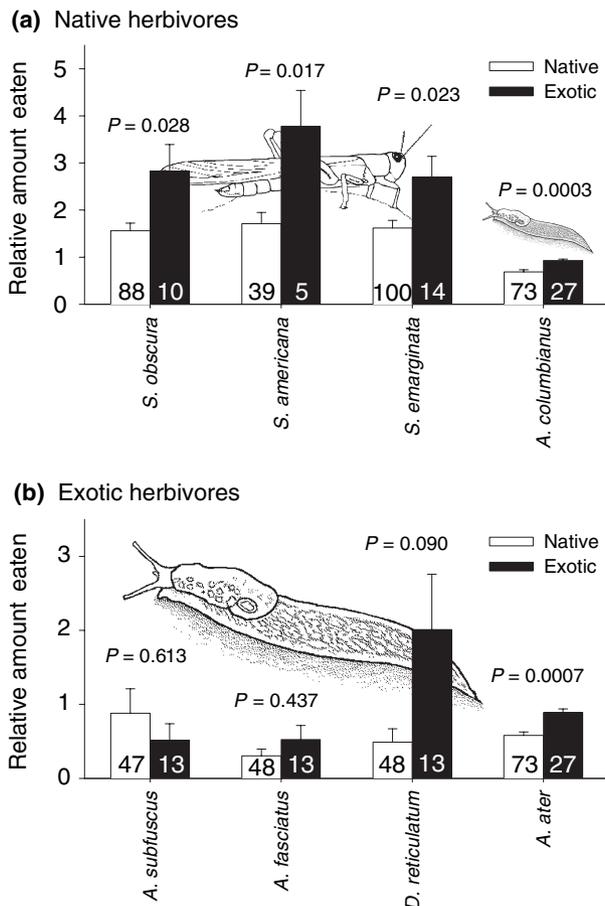
(a) Native herbivores

(b) Exotic herbivores

Figure 3 Mean (+SE) relative amount eaten of native (open bars) and exotic (filled bars) plant species by (a) native and (b) exotic consumers when offered a choice between an individual plant species and a standardized control plant species; see individual papers for methodological details. Statistics are from Mann–Whitney tests and numbers at bottom of bars are sample sizes.

plants ($n = 73$, $P \leq 0.0007$; Fig. 3a,b). Otte's study (1975; his Table 1) showed that all three native grasshoppers significantly preferred exotic over native plants (*Schistocerca obscura*: $n = 10$ exotic and 88 native plants, $P = 0.028$, Fig. 3a; *S. americana*: $n = 5$ exotic and 39 native plants, $P = 0.017$, Fig. 3a; *S. emarginata*: $n = 14$ exotic and 100 native plants, $P = 0.023$; Fig. 3a). Rathcke's (1985) study (her Appendix Tables 1–6) indicated that all three exotic slugs had no preference between exotic and native plants (*Arion subfuscus*: $n = 13$ exotic and 47 native plants, $P = 0.613$, Fig. 3b; *A. fasciatus*: $n = 13$ exotic and 48 native plants, $P = 0.437$, Fig. 3b; *Deroceras reticulatum*: $n = 13$ exotic and 48 native plants $P = 0.090$, Fig. 3b).

As many of the exotic species in the above studies were early successional plants, the native vs. exotic contrasts could be confounded by traits of early successional vs. late

successional species. When restricting the analyses to early successional species only, the native slug in Cates & Orians (1975) still strongly preferred early successional exotic plants ($n = 27$) over early successional native plants ($n = 36$; $P = 0.008$), whereas the exotic slug no longer showed a significant preference towards exotic plants, although it still trended in this direction ($P = 0.053$). The native grasshopper *Schistocerca emarginata* in Otte (1975) still preferred early successional exotic plants ($n = 10$) over early successional native plants ($n = 52$, $P = 0.007$), *S. obscura* trended in this direction ($n = 7$ exotic and 48 native plants, $P = 0.070$), and the remaining native grasshopper showed no significant preference ($n = 3$ exotic and 20 native plants, $P = 0.157$). However, the sample size in the latter contrast was too limited to be useful. By contrast, none of the exotic slugs in Rathcke (1985) distinguished between early successional exotic ($n = 13$) and native ($n = 8$) plants ($P \geq 0.171$ for *Arion subfuscus* and *A. fasciatus*), though *Deroceras reticulatum* trended towards preference of non-natives ($P = 0.054$). Thus, although these comparisons did not directly compare herbivore preferences as a choice between early successional exotic and native plants, two of the native consumers still found exotic plants more palatable than native plants unconfounded by successional status. None of the exotic consumers exhibited this pattern of preference.

DISCUSSION

Our results directly oppose the prediction of the enemy release hypothesis that native generalists will prefer native prey (Keane & Crawley 2002; Colautti *et al.* 2004). Instead, both species of native crayfishes significantly preferred exotic over native plants. This was true in both the phylogenetic pairings and in the region-wide assays of plant palatability (Figs 1 and 2). Results of analyses with terrestrial native consumers were similar. When we included all available data from our study and the terrestrial studies, six of six native generalist herbivores preferred exotic over native plants, while four of five exotic generalists did not (Figs 2 and 3). When we constrained the terrestrial data sets and evaluated only early successional native vs. exotic species, the patterns were less dramatic but similar in direction. Two of four native species significantly preferred exotic plants while none of the four exotic herbivores demonstrated any significant preference. Thus, exotic plants are more palatable than native plants to native generalist herbivores, suggesting the potential for native herbivores to provide biotic resistance to plant invasions.

As our native herbivores were two crayfishes, three grasshoppers, and one slug, while our exotic herbivores were one fish and four slugs, our analyses potentially confound consumer origin (native vs. exotic) with consumer type (e.g. grasshoppers vs. slugs). Contrasts with native vs.

exotic grasshoppers, native vs. exotic crayfishes, etc. would have been preferable but impossible in this case because: (i) the exotic crayfishes in North America are all range expansions (USGS 2005) that would have had a long evolutionary history with nearly all native flora, (ii) there are no native carp in North America (Nelson 1994), and (iii) there are no exotic grasshoppers in North America (Lockwood 1993). We did have one comparison among consumers of the same type. In Cates & Orians' (1975) study, both the native and the exotic slug preferred exotic over native plants (Fig. 3), but this pattern weakened and the exotic slug no longer significantly preferred exotic plants once we restricted the analysis to early successional plants (see Results). Despite limitations on the herbivores we could use, our analyses of the published terrestrial studies represent our best efforts to challenge our findings for freshwater systems, and they consistently support our finding that exotic plants are, on average, palatable and selectively consumed by native herbivores.

While our results were unanticipated within the framework of the enemy release hypothesis (Keane & Crawley 2002), they support a classic evolutionary hypothesis: exotic prey may be selectively attacked in their new ranges because they are defensively naïve against native consumers (Darwin 1859, p. 44), i.e. the 'new associations' principle (Hokkanen & Pimentel 1989). This hypothesis is predicated on the notion that native plants have evolved under selection from native herbivores, whereas exotic plants have not and thus are unlikely to be better adapted than native plants to resist native herbivores (Hokkanen & Pimentel 1989; Colautti et al. 2004). In fact, similar to our results for generalists, several papers have examined preferences of specialists for smaller groups of species and often found that native specialists can also prefer exotic plants over their native hosts (e.g. Thomas et al. 1987; Hokkanen & Pimentel 1989; Solarz & Newman 1996, 2001; Trowbridge & Todd 2001; Trowbridge 2004). These patterns suggest that prey are often vulnerable to novel consumers that they have not been selected to deter. Analogously, it is well documented that exotic generalist consumers such as ungulates, grass carp, gypsy moths, Nile perch, mongooses, cats, rats and snakes, following their introduction into new systems, often decimate naïve, native prey communities (e.g. Elton 1958).

All the exotic freshwater plants that we studied are considered pestiferous or noxious by at least one state in the USA (USDA 2004), and most of these plants were high preference prey to native consumers (Figs 1 and 2). Because it is the successful exotic plants that might be expected to best resist native consumers, our results are likely conservative (i.e. the most highly preferred exotic plants may have been eaten to local extinction and simply not been available for us to collect and study). Despite this potential bias, our findings clearly show that exotic plants are *on average* more

palatable than native species (Figs 1–3). There were, however, notable exceptions. Alligatorweed *Alternanthera philoxeroides* and the watermilfoils *Myriophyllum* spp. were relatively low preference prey (Fig. 2), suggesting that invasiveness in these species could result in part from their low palatability to native generalists. In other studies, however, Eurasian watermilfoil *Myriophyllum spicatum* is preferred over native milfoils and unrelated native macrophytes by both a native specialist weevil and an exotic generalist moth larva (Solarz & Newman 1996, 2001; Gross et al. 2001), perhaps leading to declines in the abundance of this aquatic weed (Creed 2000).

Our data address herbivore feeding preferences rather than impacts in the field. In some cases, laboratory-derived feeding preferences may be tempered or not expressed under more complex field conditions (e.g. Schmitz 1998). Despite these exceptions, feeding preferences commonly translate to impacts on plant community structure (Lubchenco & Gaines 1981; Hay 1997), and such impacts have been observed experimentally with crayfish (Dorn & Wojdak 2004), grass carp (McKnight & Hepp 1995), grasshoppers (Schmitz 1994) and slugs (Hanley et al. 1995). Moreover, when impacts to exotic plants in the field have been measured, the overall pattern has been equivocal, with some exotic plants heavily damaged by native herbivores and others apparently not (Maron & Vila 2001; Keane & Crawley 2002, and references therein). In most of these cases, however, only a single exotic species was studied, and it may be misleading to extrapolate the results from a few, potentially unusual, exotic species to exotic species *in general*, particularly when the underlying assumption of enemy release is that exotic plants are avoided by native herbivores by virtue of their evolutionary novelty. In fact, in the only study that we know of examining herbivore damage to a broad sample of native and exotic plants in a field setting, Agrawal & Kotanen (2003) found greater insect damage to 15 exotic vs. 15 related native plants, indicative of selective feeding on exotic plants by naturally recruited herbivores.

We examined a taxonomically diverse and environmentally disparate group of plants – 291 native and 66 exotic species – and 11 herbivore species, thus presumably avoiding the bias of studying any particular exotic species, and we found that native herbivores generally preferred exotic over native plants. Nevertheless, this general trend does not preclude the possibility that a few unusual invaders will have novel defences that are fortuitous pre-adaptations against local consumer species (analogous to Callaway & Aschehoug 2000). In these cases, evolutionary novelty may in fact impart a strong selective advantage for exotic over native species. Still, it remains to be tested whether the feeding preference patterns that we observed will translate to negative impacts on the distribution and abundance of exotic plants under field conditions.

Our results suggest that native, generalist consumers may suppress plant invasions via selective feeding on exotic plants. In some freshwater systems of Europe, native waterfowl and fishes nearly eliminate the North American invader *Elodea nuttallii* (Van Donk & Otte 1996), and numerous other studies document that generalist consumers limit the establishment and spread of exotic plants in a variety of systems (Maron & Vila 2001; Keane & Crawley 2002, and references therein). It appears rare, however, for generalist herbivores to preclude invasions entirely (Levine *et al.* 2004), suggesting that exotic plants may proliferate despite being vulnerable to the evolutionarily novel consumers in their new range. This could occur for several reasons. It may be rare to find intact, native herbivore assemblages or ecosystems unaltered by anthropogenic influences (Byers 2002), or the increased vulnerability of exotic plants to generalist herbivores may be offset by some other plant attribute, perhaps high growth rates, fecundity or consumer tolerance (e.g. Schierenbeck *et al.* 1994; Rejmanek & Richardson 1996). Additionally, in some cases escape from particularly damaging specialists could outweigh the effects of gaining new generalist enemies. These hypotheses remain largely untested but will be critical to determining the net impacts of native enemies on exotic plants.

The influence of herbivores on plant invasions is uncertain (Maron & Vila 2001), but the proposed mechanisms and the importance of enemy release have often been accepted without critical evaluation (see discussions in Keane & Crawley 2002; Shea & Chesson 2002; Colautti *et al.* 2004). In contrast to the common assumption that exotic plants are advantaged because native generalist herbivores will prefer native plants, we found no evidence to support this hypothesis. Whether we considered freshwater or terrestrial plants, we found that: (i) a diverse group of native consumers (including crayfish, grasshoppers and slugs) consistently preferred exotic over native plants (Figs 1–3; Table 1), whereas (ii) exotic consumers (including fish and slugs) rarely demonstrated a preference between native vs. exotic plants (Figs 2 and 3). Given that generalists typically have a larger impact on plant community structure than specialists (Crawley 1989; Hay & Steinberg 1992; Hay 1997; Lodge *et al.* 1998), the selective preference that we observed for exotic plants could negate the benefit of losing coevolved specialists, and native generalists could provide biotic resistance to plant invasions.

ACKNOWLEDGEMENTS

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