

Phylogenetically structured damage to Asteraceae: susceptibility of native and exotic species to foliar herbivores

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Abstract Invasive plants often lose natural enemies while moving to new regions; however, once established in a new area, these invaders may be susceptible to attack by locally occurring enemies. Such damage may be more likely for exotics with close native relatives in the invaded area, since shifts of enemies should be more likely among closely related hosts. In this study, we evaluated whether exotics experience less herbivore damage than natives, and whether phylogenetically novel exotics experience less damage than those that are more closely related to locally occurring family members. Foliar damage was measured on 20 native and 15 exotic Asteraceae that co-occur locally in southern Ontario, Canada. The phylogenetic structure of this damage was quantified using an eigenvector decomposition method, and the relationship between damage and phylogenetic novelty of exotics was evaluated based on phylogenetic distances to other locally occurring Asteraceae. Our results show that 32% of the variation in damage was explained by phylogenetic relationship; similarity in damage tended to be associated with tribes. As predicted, exotics experienced lower damage than

native species, even when the dataset was corrected for phylogenetic nonindependence. Contrary to our prediction, however, exotics that were more phylogenetically isolated from locally occurring relatives did not experience less damage. These results suggest that, though exotic Asteraceae may escape many of their natural enemies, this is not in general more likely for species phylogenetically distant from locally occurring native confamilials.

Keywords Asteraceae · Community phylogenetics · Enemy release hypothesis · Exotic species · Invasion biology

Introduction

Biotic interactions may have important consequences for biological invasions (Mitchell et al. 2006). How an invader interacts in its new range with native competitors (Naeem et al. 2000; Fargione and Tilman 2005), mutualists (Richardson et al. 2000), and enemies (consumers, herbivores, pathogens, and parasites) (Agrawal and Kotanen 2003; Agrawal et al. 2005; Parker and Hay 2005; Parker and Gilbert 2007) may strongly influence its success (Levine et al. 2004).

Many such biotic interactions may be affected by an invader's relatedness to species already occurring in its new range (Connor et al. 1980; Cappuccino and Carpenter 2005; Dawson et al. 2009). For instance, one of the key theories of invasion biology is the

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enemy release hypothesis (ERH) (Keane and Crawley 2002; Torchin et al. 2003; Mitchell and Power 2003). The ERH predicts that exotic species lose specialist enemies during invasion, giving them an advantage over co-occurring native competitors (Keane and Crawley 2002; Torchin et al. 2003). This hypothesis remains controversial, however: compared to co-occurring natives, many exotics do not experience lower levels of damage (Agrawal and Kotanen 2003; Colautti et al. 2004; Liu and Stiling 2006). In part, this can result from exotics rapidly accumulating new enemies in their invaded range (Hawkes 2007; Parker and Gilbert 2007). This accumulation may be more likely for exotics with close native relatives in the invaded area, since shifts of enemies should be more likely among closely related hosts (Strong et al. 1984; Lewinsohn et al. 2005; Gossner et al. 2009).

Numerous studies provide evidence that phytophagous insects are more likely to be shared as the phylogenetic distance between hosts declines (e.g., Novotny et al. 2002; Novotny and Basset 2005; Odegaard et al. 2005). There is also evidence that taxonomically isolated exotic species experience less damage by natural enemies (Connor et al. 1980; Dawson et al. 2009; Hill and Kotanen 2009). For instance, we previously have shown that folivory on a taxonomically diverse set of exotic plants declined with increasing phylogenetic distance to native family members (Hill and Kotanen 2009). Thus, whether ERH applies to a particular invader may depend in part on its relationship to native species; this suggests that incorporating phylogenetic structure into tests of ERH may help to resolve some of the uncertainty surrounding this hypothesis.

Despite these examples, not all studies have supported the hypothesis that phylogenetically novel invaders are more likely to escape their enemies (e.g., Cappuccino and Carpenter 2005); others have demonstrated relatively weak trends (including Hill and Kotanen 2009). In part, this may be because few studies have yet applied modern comparative methods to well-resolved phylogenies; for instance, Cappuccino and Carpenter (2005) quantified isolation by counting native congeners and confamilials; Hill and Kotanen (2009) did map herbivore damage onto a very large (>600 species) phylogeny, but with relatively low resolution. Here, we report a study in which we used a different approach to evaluate whether damage to exotic Asteraceae by foliar

herbivores is influenced by their phylogenetic relationship to co-occurring species. We hypothesized (1) that exotic species experience lower herbivory than natives, (2) that this is true when phylogenetic relationships are accounted for, and (3) that phylogenetically novel exotics experience less herbivory than those that are less isolated. We tested these hypotheses by measuring herbivore damage to native and exotic members of this family, and mapping these data onto a well-resolved phylogeny.

Methods

Study site and natural history

We conducted this study at the University of Toronto's Koffler Scientific Reserve (KSR) at Jokers Hill, in the Regional Municipality of York, southern Ontario, Canada (44°02'N, 79°31'W, 300 m ASL). KSR occupies 350 ha on the western reaches of the Oak Ridges Moraine. Soils are dominated by a thin organic layer over deep glacial sands. Vegetation on the western side of the property is dominated by old-fields, and on the eastern side by mixed forest consisting largely of maple, beech, and hemlock. Across the property, there are also numerous conifer plantations. Further site information can be found at <http://www.ksr.utoronto.ca/>.

We chose to work with native and exotic species in the Asteraceae, as they are well represented in the local flora (~12%), and because their evolutionary history is also relatively well resolved (Funk et al. 2005). Within the family, there are 44 and 33 locally occurring native and exotic species respectively. Members of the family can be found in all habitat types across the property, including old-fields, forest understory, and wetlands.

Herbivory survey

From May to November 2008, damage was measured on 20 native and 15 exotic species (Table 1); species were chosen to represent as many lineages within the family as possible. We used species only if they were common enough to be reliably located, and excluded both rare natives and exotics; this potentially might bias against native and exotic species which were rare

Table 1 Species of Asteraceae used for this study

Species	Origin	Proportion damaged	SE
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook.	Native	0.025	0.014
<i>Antennaria neglecta</i> Greene	Native	0.008	0.003
<i>Aster cordifolius</i> L.	Native	0.21	0.032
<i>Aster novae-angliae</i> L.	Native	0.078	0.017
<i>Bidens cernua</i> L.	Native	0.209	NA
<i>Bidens frondosa</i> L.	Native	0.179	0.007
<i>Conyza canadensis</i> (L.) Cron.	Native	0.031	0.003
<i>Erigeron annuus</i> (L.) Pers.	Native	0.056	0.026
<i>Erigeron philadelphicus</i> L.	Native	0.04	0.009
<i>Erigeron strigosus</i> Muh L.	Native	0.033	0.018
<i>Eupatorium maculatum</i> L.	Native	0.147	0.059
<i>Eupatorium perfoliatum</i> L.	Native	0.422	0.023
<i>Euthamia graminifolia</i> (L.) Salisb.	Native	0.078	0.007
<i>Gnaphalium obtusifolium</i> L.	Native	0.026	NA
<i>Prenanthes altissima</i> L.	Native	0.069	0.02
<i>Rudbeckia hirta</i> L.	Native	0.059	0.02
<i>Senecio aureus</i> L.	Native	0.074	0.024
<i>Solidago caesia</i> L.	Native	0.053	0.01
<i>Solidago canadensis</i> L.	Native	0.209	0.047
<i>Solidago flexicaulis</i> L.	Native	0.104	0.028
<i>Arctium minus</i> (Hill) Bernh.	Exotic	0.101	0.032
<i>Centaurea jacea</i> L.	Exotic	0.031	0.009
<i>Chrysanthemum leucanthemum</i> L.	Exotic	0.026	0.009
<i>Cichorium intybus</i> L.	Exotic	0.066	NA
<i>Cirsium arvense</i> (L.) Scop.	Exotic	0.088	0.037
<i>Crepis capillaris</i> (L.) Wallr.	Exotic	0.033	0.015
<i>Galinsoga quadriradiata</i> Ruiz & Pavon	Exotic	0.009	NA
<i>Hieracium caespitosum</i> L.	Exotic	0.02	0.005
<i>Hieracium pilosella</i> L.	Exotic	0.017	0.009
<i>Inula helenium</i> L.	Exotic	0.043	0.007
<i>Lactuca serriola</i> L.	Exotic	0.009	0.001
<i>Sonchus arvensis</i> L.	Exotic	0.062	0.037
<i>Sonchus asper</i> (L.) Hill	Exotic	0.058	0.026
<i>Tragopogon dubius</i> Scop.	Exotic	0.014	0.004
<i>Tussilago farfara</i> L.	Exotic	0.079	0.035

Origin, mean proportion of total foliar area damaged, and SE of damage are indicated for each species

“NA” indicates only one population of a species was sampled

because of heavy damage, but provided good representation of the most prominent invasive and native taxa. For each species, five to ten individuals were randomly sampled from one to three populations. For individual plants, the total number of leaves, the number of damaged leaves, and the percent of leaf area damaged for each damaged leaf were recorded. Percent leaf area damaged was estimated visually to the nearest 5%. The proportion of leaves damaged

and the mean proportion of area damaged per damaged leaf were then multiplied to give an index of plant-level damage; the product represents an estimate of the total proportion of foliar area lost to herbivory, and was used in all analyses. For all analyses, damage for individual species was pooled based on means for each population as we were interested in among-species variation and its relationship to phylogeny.

Our approach deliberately integrated the net effects of the entire herbivore community to evaluate plant-level damage. We therefore did not determine the identity of herbivores on a case-by-case basis; however, both specialists and generalists belonging to the Chrysomelidae (leaf chewing), Lepidoptera (leaf chewing), and Diptera (leaf mining) likely were causing much of the observed damage.

Community phylogeny

The backbone of the community phylogeny for this family was drawn from Funk et al. (2005). Where polytomies existed, we supplemented the topology based on the following studies: *Erigeron* (Noyes 2000), *Hieracium* (Gaskin and Wilson 2007), *Lactuceae* (Whitton et al. 1995), *Solidago* (Semple and Cook 2006). Node ages for the resulting tree were then estimated using the function “bladj” in PHYLOCOM (Webb et al. 2008), with node age calibration points from Kim et al. (2005).

Statistical analyses

To evaluate phylogenetically uncorrected differences in damage between native and exotic species we used one-tailed *t*-tests, as we expected a priori that exotics would experience less damage. To evaluate the phylogenetic component of herbivory, we used an eigenvector decomposition method (Diniz-Filho and de Sant’Ana 1998; Desclaves et al. 2003). We used principal coordinate analysis, “cmdscale” in R (R Development Core Team 2009), to extract 34 eigenvectors ($n - 1$, based on our 35 species) from a phylogenetic distance matrix derived from our community phylogeny of both native and exotic species. These summarize the phylogenetic structure of the dataset, and therefore represent potential predictors of phylogenetically structured trait variation (in our case herbivory); they are associated with broad to fine-scale patterns across the phylogeny based on their order (Diniz-Filho and de Sant’Ana 1998). Each eigenvector was then compared to the total proportion of foliar area damaged for each species; those that were significantly correlated at $P \leq 0.10$ were retained as predictors of phylogenetically structured patterns of foliar damage. We then calculated the residuals from a multiple regression of foliar damage versus the significant phylogenetic eigenvectors;

these residuals were used to represent non-phylogenetically structured foliar damage. One-tailed *t*-tests using these residuals were then used to evaluate the hypothesis that exotic species experienced lower herbivory than natives after correcting for their phylogenetic relationship. We also tested this hypothesis by calculating standard phylogenetically independent contrasts (Felsenstein 1985) using the function “aot” in the statistical package PHYLOCOM (Webb et al. 2008), and analyzing them using a one-tailed paired *t*-test.

To evaluate whether herbivory on exotic plants declines with phylogenetic isolation, foliar damage was compared to four phylogenetic distance measures: (1) mean distance to all locally occurring taxa (native and exotic), (2) mean distance to closest relative (native or exotic), (3) mean distance to all native taxa, and (4) distance to closest native taxon, or taxa in the case of ties. These analyses test different predictions based on phylogenetic scale (i.e., comparison to all family members and closest relative) and on whether interactions with both exotic and native species or just native species matter. Phylogenetic distances were based on tip-to-tip distances between exotic species and other family members. Separate linear regressions were used for each test.

For all statistical analyses, the proportion of plant-level foliar damage was transformed using the respective *Z*-score. This was used to better meet assumptions of the statistical tests and linearize the proportional measurement. As such, all figures are presented using this transformed measurement.

Results

Overall, the proportion of leaf area damaged was lower for exotics (mean \pm SE: 0.038 ± 0.02) than for natives (0.073 ± 0.04) (Fig. 1). Without considering phylogenetic relatedness among individuals, this supports the hypothesis that exotics tend to experience lower damage than native species ($t = -2.085$, $df = 32.87$, $P = 0.022$).

When the phylogenetic distance matrix from the community phylogeny was decomposed using a principal coordinate analysis, two eigenvectors were significantly correlated with herbivory (negatively for the first, and positively for the second) and explained

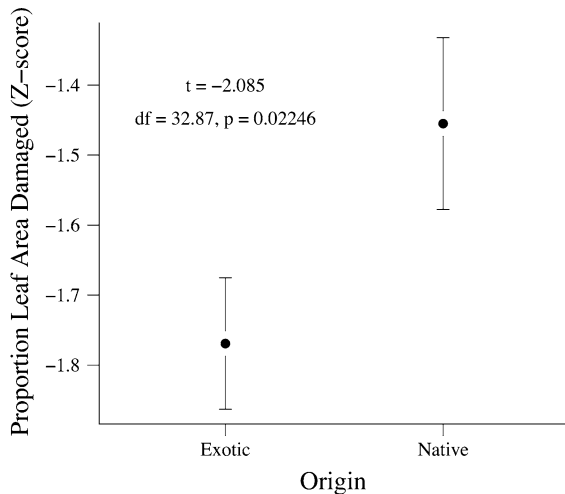


Fig. 1 Foliar damage (Z-transformed mean \pm SE) to native and exotic Asteraceae, without phylogenetic correction. Also indicated are results of a one-tailed Welch's *t*-test for unequal variances; this supports the hypothesis that exotic species experience less damage than native species

Table 2 Multiple regression results of foliar damage versus the eigenvectors from a principle coordinate analysis of community phylogeny that were significantly related to herbivory

Parameter	Estimate	SE	t_{32}	<i>P</i>
Intercept	-1.581	0.069	-22.776	<0.001
Eigenvector [6]	-0.020	0.008	-2.482	0.016
Eigenvector [25]	0.097	0.028	3.417	0.002

The sum of these eigenvector loadings is shown in Fig. 2. Numbers in square brackets represent the rank of each eigenvector among the 34 eigenvectors that were used to partition phylogenetic distances; lower numbers represent eigenvectors that explain broader patterns of phylogenetically structured variation

32% of variation in damage among species (Table 2; Fig. 2). In general, phylogenetically structured patterns of damage were associated with deeper nodes within the family lineage that tend to represent taxonomic tribes (Funk et al. 2005). The most apparent trends were associated with low damage in the lineage containing *Antennaria neglecta*, *Gnaphalium obtusifolium*, and *Anaphalis margaritacea* (Gnaphalieae) and relatively high damage in the lineage containing *Senecio aureus* and *Tussilago farfara* (Senecioneae). There was also a weak phylogenetic signal in damage associated with the

Astereae group (*Solidago* spp., *Erigeron* spp., *Conyza* sp., *Euthamia* sp., and *Aster* spp.). The exception to the broad phylogenetic trend in herbivory, however, was the fine-scale pattern predicted by eigenvector 25. This particular trend was represented by lower damage on *Galinsoga quadriradiata*, versus higher damage on the two *Eupatorium* species.

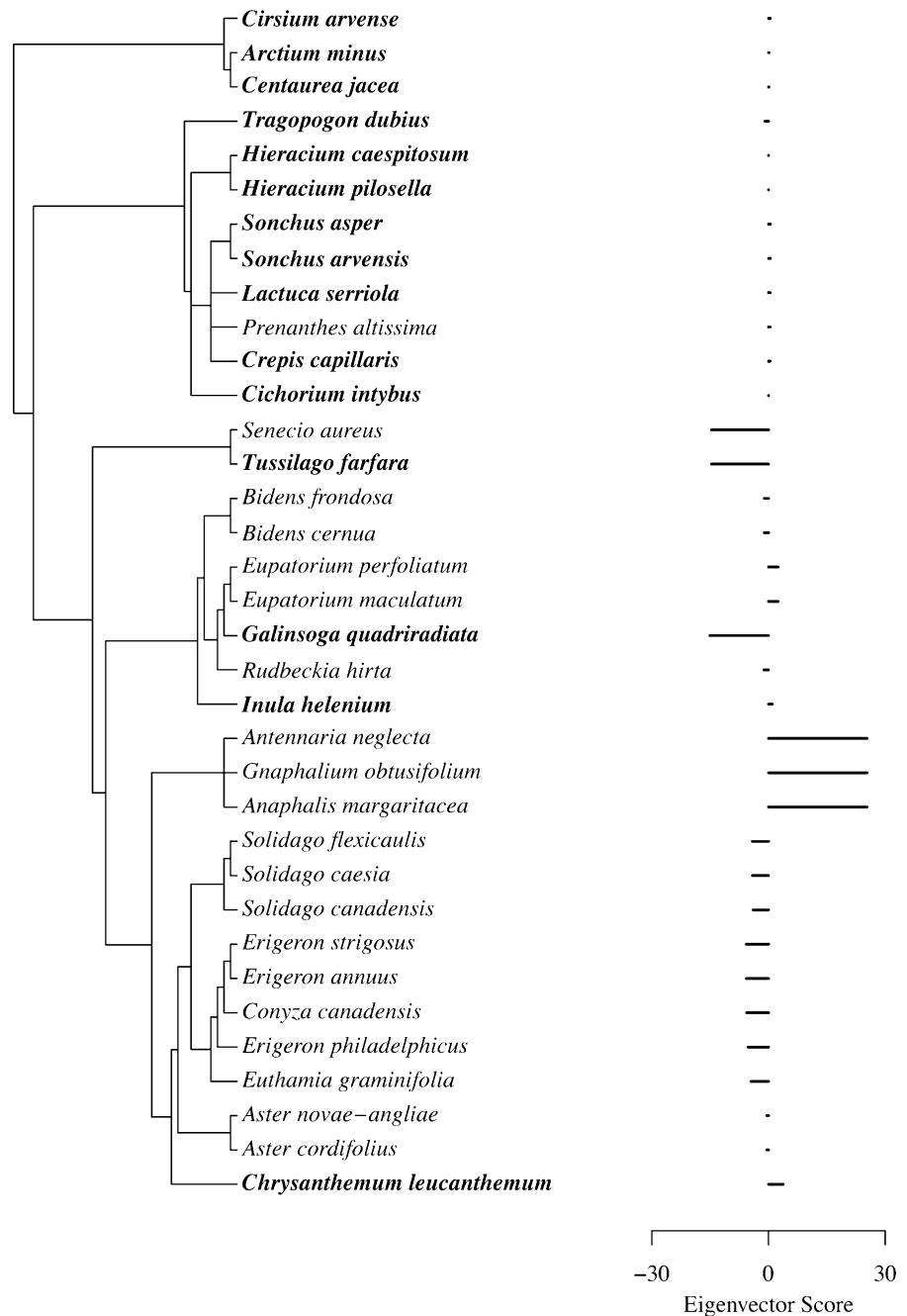
When the residuals of the multiple regression of damage on the phylogenetic eigenvectors were used to represent phylogenetically corrected damage, exotic species still experienced lower damage than native species ($P = 0.005$, Fig. 3). If degrees of freedom were further reduced to compensate for fitting the original regression (García-Berthou 2001), this result was essentially unchanged ($P = 0.005$). Phylogenetically independent contrasts also supported this pattern: the mean difference for contrasts of native and exotic species was 0.046 ± 0.025 ($t = 1.843$, $df = 3$, $P = 0.0695$) without considering branch lengths; when contrasts were standardized by branch lengths, the result became even stronger ($t = 2.975$, $df = 3$, $P = 0.020$).

Contrary to our prediction, phylogenetically novel exotic species tended to experience more damage than those that were closely related to natives (Table 3; Fig. 4). Statistically, however, these trends were weak for all phylogenetic distance predictors (Table 3); of the four measures, only distance to the closest native member of the Asteraceae was close to significance ($P = 0.092$). We suspected that these trends were influenced by high damage on *Cirsium arvense* and *Arctium minus* (Table 1; Fig. 2), which in part may have resulted from biocontrol insects (Mason and Huber 2002). When the analyses were run excluding these two species, there was no significant relationship between damage and any of phylogenetic distance measures, including the distance to closest native relative ($0.195 \leq P \leq 0.818$ for all cases).

Discussion

In this study, we show that exotic species in the Asteraceae experience less herbivory than co-occurring native confamilials. However, contrary to our prediction, phylogenetically novel exotics did not experience lower rates of herbivory than those more closely related to natives.

Fig. 2 Community phylogeny for the Asteraceae sampled. *Bars on the right* show the sum of the two eigenvectors describing phylogenetic structure that had a significant correlation with herbivory; together, these explained 32% of the variation in foliar damage (Table 2). *Bolding* indicates species are non-indigenous to North America



Implications for enemy release

Tests of the Enemy Release Hypothesis have produced variable results (Maron and Vila 2001; Agrawal and Kotanen 2003; Colautti et al. 2004; Liu and Stiling 2006; Parker and Gilbert 2007). Our data also indicate that damage to exotics can be

variable, and even greater than for native species; for example, exotic species such as *Arctium minus*, *Cirsium arvense*, and *Tussilago farfara* experienced higher damage than the majority of native species, while natives such as *Gnaphalium obtusifolium*, *Anaphalis margaritacea*, and *Antennaria neglecta* experienced damage that was similar to or lower than

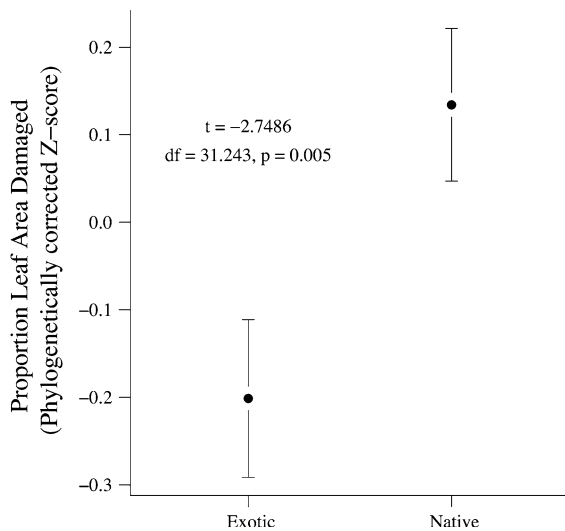


Fig. 3 Foliar damage to native and exotics, calculated as residuals (Z-transformed mean \pm SE) from a multiple regression of damage versus significant phylogenetic eigenvectors (Table 2). Also indicated are results of a one-tailed Welch's *t*-test for unequal variances; this supports the hypothesis that exotic species experience less damage than native species

the majority of exotic species. Nonetheless, on average exotics experienced less herbivory than natives; this also was true when phylogenetic relationships were accounted for using PICs or residual analysis, indicating that exotics experience less damage even when compared with close relatives. Since most of the exotic species we studied can be found in the same habitats as native species, these reductions in herbivory may give them a competitive advantage, potentially increasing their impact as an invader (Maron and Vila 2001; Keane and Crawley 2002; Colautti et al. 2004; Liu and Stiling 2006).

Some of the measured herbivory was phylogenetically structured. Where this was the case, damage tended to be correlated within lineages associated with taxonomic tribes (Funk et al. 2005), regardless

of species origin. For example the exotic *Chrysanthemum leucanthemum* experienced similar rates of damage to native species in the same lineage (*Erigeron* sp., *Conyza* sp., and *Solidago* spp.); similarly, damage to the native *Prenanthes altissima* was only slightly higher than damage to related exotics such as *Sonchus arvensis*, *Sonchus asper*, and *Crepis capillaris* (Table 1). There were exceptions, however; for example, damage on the native *Eupatorium* spp. tended to be very high, but the closely related *Galinsoga quadriradiata* experienced the lowest damage among all exotic species (Table 1).

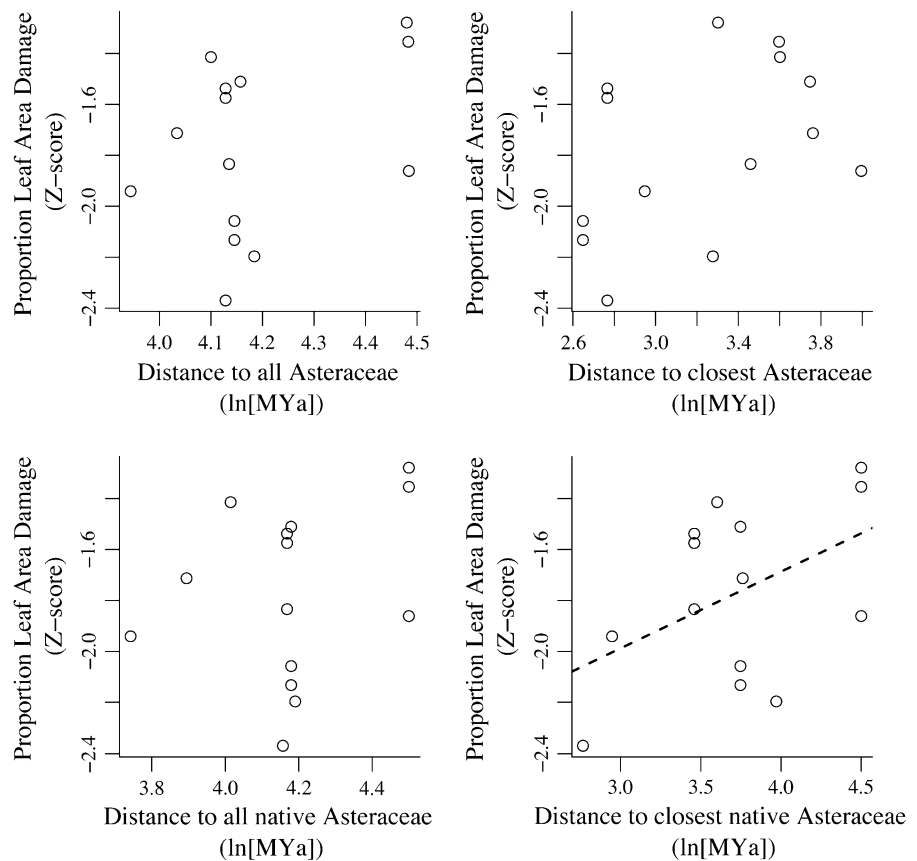
Contrary to our expectation, exotics that were less closely related to native species did not experience lower levels of herbivory. These results contrast with our previous work, in which we found that invaders more phylogenetically isolated from native confamilials experienced less foliar damage (Hill and Kotanen 2009). This different result may result from a difference in phylogenetic scale between these studies. Hill and Kotanen (2009) compared patterns across exotics from 25 families ranging from Orchidaceae to Asteraceae, as opposed to examining patterns within a single family; consequently, the results were largely driven by differences among families. Enemies often tend to be associated with particular plant families (Bernays and Chapman 1994; Futuyma and Mitter 1996; Odegaard et al. 2005; Weiblen et al. 2006), potentially leading to the patterns at this scale; results of the present study suggest detailed patterns within families may be less predictable. As well, even in Hill and Kotanen (2009), correlations of foliar damage versus phylogenetic distance of exotic species from natives were nonsignificant in natural populations; the only significant results came from common gardens, where background variation was controlled. Similarly, Dawson et al. (2009) demonstrated that exotic trees

Table 3 Regressions results of foliar damage versus different measures of phylogenetic uniqueness: mean distance to (1) all Asteraceae, (2) closest Asteraceae, (3) all native Asteraceae, and (4) closest native Asteraceae

Model	Slope	SE	$F_{1,12}$	<i>P</i>	r^2
All Asteraceae	0.747	0.541	1.909	0.192	0.07
Closest Asteraceae	0.309	0.189	2.676	0.128	0.11
All native Asteraceae	0.437	0.436	1.008	0.335	<0.01
Closest native Asteraceae	0.301	0.165	3.353	0.092	0.15

Distance to closest native Asteraceae is marginally significant and explains the most variation in damage (15%)

Fig. 4 Foliar damage to exotics (Z-transformed) versus phylogenetic novelty (ln-transformed distance to all Asteraceae, closest Asteraceae, all native Asteraceae, and closest native Asteraceae). Damage tends to increase with phylogenetic novelty, but was marginally significant only when distance to closest native relative was used as the predictor (see statistics in Table 3)



with native relatives experience more herbivory, but detected this pattern in a controlled (botanical garden) environment. It may be that phylogenetic patterns in herbivore damage are often too weak to be detected in natural populations.

The possibility that damage might in fact increase with phylogenetic isolation is surprising, though this pattern is weak. Some other studies have reported that herbivory tended to be higher on exotic plants belonging to novel rather than native genera (Parker et al. 2006; Ricciardi and Ward 2006). The reasons for this pattern are unclear, but it might be explained if novel invaders are evolutionarily naïve, lacking the necessary defenses to avoid or tolerate damage from the new enemies they encountered (Hokkanen and Pimentel 1989; Verhoeven et al. 2009). As well, some phylogenetically isolated exotics may experience more damage because they have been targeted for biocontrol. In particular, *Cirsium arvense*, in the sub-family Cardueae (Funk et al. 2005), has often been targeted because of its invasiveness in agricultural habitats (Mason and Huber 2002). Biocontrol

organisms that have been intended for use on *C. arvense* may colonize other species in the same tribe such as *Arctium minus*, and these two species experienced some of the highest rates of damage among the exotic species that we sampled (Mason and Huber 2002). Removing these two species from the analyses resulted in non-significant trends between foliar damage and all phylogenetic distances.

Phylogenetically structured herbivory

Although phylogenetic novelty was not a significant predictor of damage, a moderate proportion of herbivore damage was phylogenetically structured. Among native and exotic Asteraceae, just under a third of the observed variability in foliar damage was explained by shared evolutionary history. Therefore, even though exotic species tended to experience lower rates of damage than native species, patterns of damage were best explained by their evolutionary relationship to other Asteraceae.

Since phylogenetic distance measures were not strong predictors of damage, other aspects of evolutionary history must explain the phylogenetically structured patterns of herbivory that we observed. Identifying these characteristics may help to determine whether natural enemies are likely to attack invaders belonging to a particular lineage of plants. For example, rates of damage may be naturally low in lineages sharing an effective set of defenses. When an exotic from such a lineage is introduced into a new community, it might experience low rates of damage because it shares the same defenses as its successful native relatives, not because it has escaped previously effective enemies (Ricciardi and Ward 2006). Future tests of the role of natural enemies in invasions may benefit by considering phylogenetic trends in defence and attack for both exotics and co-occurring native species.

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