

# Phylogenetic structure predicts capitular damage to Asteraceae better than origin or phylogenetic distance to natives

Steven B. Hill · Peter M. Kotanen

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**Abstract** Exotic species more closely related to native species may be more susceptible to attack by native natural enemies, if host use is phylogenetically conserved. Where this is the case, the use of phylogenies that include co-occurring native and exotic species may help to explain interspecific variation in damage. In this study, we measured damage caused by pre-dispersal seed predators to common native and exotic plants in the family Asteraceae. Damage was then mapped onto a community phylogeny of this family. We tested the predictions that damage is phylogenetically structured, that exotic plants experience lower damage than native species after controlling for this structure, and that phylogenetically novel exotic species would experience lower damage. Consistent with our first prediction, 63% of the variability in damage was phylogenetically structured. When this structure was accounted for, exotic plants experienced significantly lower damage than native plants, but species origin only accounted for 3% of the variability of capitular damage. Finally, there was no support for the phylogenetic novelty prediction. These results suggest that interactions between exotic plants and their seed predators may be strongly influenced by their phylogenetic position, but not by their relationship to locally co-occurring native species. In addition, the influence of a species' origin on the damage it experiences

often may be small relative to phylogenetically conserved traits.

**Keywords** Asteraceae · Darwin's naturalization hypothesis · Community phylogenetics · Enemy release hypothesis · Invasion biology

## Introduction

The Enemy Release Hypothesis (ERH) predicts that non-indigenous (exotic) species leave many of their enemies behind in their native range, giving them an advantage over co-occurring native species in their invaded range (Keane and Crawley 2002; Torchin and Mitchell 2004; Mitchell et al. 2006). Tests of this hypothesis have found varying results: exotic species often experience reduced damage compared to natives (Torchin and Mitchell 2004; Liu and Stiling 2006), but exceptions are frequent (e.g., Agrawal and Kotanen 2003; Parker and Hay 2005; Liu et al. 2007; Chun et al. 2010). This variation reflects the fact that exotic plants are likely to encounter new enemies in their invaded range (Hawkes 2007). Since host-use by enemies is often phylogenetically conserved (Odegaard et al. 2005; Brändle and Brandl 2006; Weiblen et al. 2006; Gilbert and Webb 2007; Pearse and Hipp 2009), such accumulation of enemies may be more likely for exotics that have close relatives in their introduced range (Strong et al. 1984; Lewinsohn et al. 2005; Dawson et al. 2009; Pearse and Hipp 2009; but see Zuefle and Brown 2008).

The idea that the phylogenetic relationship between exotic and native species can influence invasion success is not new. Both de Candolle (1855) and Darwin (1859) reported that exotic plants in North America often belonged to novel genera, suggesting phylogenetically isolated

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S. B. Hill · P. M. Kotanen (✉)  
Department of Ecology and Evolutionary Biology,  
University of Toronto at Mississauga,  
3359 Mississauga Road N, Mississauga,  
ON L5L 1C6, Canada  
e-mail: peter.kotanen@utoronto.ca

S. B. Hill  
e-mail: sb.hill@utoronto.ca

species were better invaders; subsequently (Daehler 2001), this idea was named Darwin's Naturalization Hypothesis (DNH). Results of tests of this hypothesis vary; for instance, Daehler (2001) and Duncan and Williams (2002) found evidence against the idea, while other studies have found support (Strauss et al. 2006; Diez et al. 2008). Although other biotic interactions can potentially result in community-level patterns consistent with DNH, competition is usually assumed to be the mechanism (Darwin 1859; Webb et al. 2002). However, experimental evidence that compares competitive interactions among species based on their phylogenetic relatedness suggests that trends often tend to be weak; for instance, Cahill et al. (2008) found that there were only marginal relationships between competition and phylogenetic distance among a broad group of plants.

Alternatively, phylogenetically conserved interactions with natural enemies may cause patterns similar to those predicted by DNH through mechanisms such as apparent competition (Holt 1977; Mack 1996; Thuiller et al. 2010). Evidence that close relationship to native species affects the susceptibility of an invader to herbivory, however, is mixed (Cappuccino and Carpenter 2005; Dawson et al. 2009; Pearse and Hipp 2009; Hill and Kotanen 2009, 2010). For instance, we have previously shown that folivory on a diverse set of exotic plants in common gardens (but not natural populations) declined with increasing phylogenetic distance to native family members (Hill and Kotanen 2009). Despite this, we have found no relationship between phylogenetic isolation and folivory for natural populations of Asteraceae (Hill and Kotanen 2010).

Most studies evaluate enemy escape on plants using damage by folivorous insects (e.g., Agrawal and Kotanen 2003; Hill and Kotanen 2009, 2010). However, the phylogenetic component of enemy escape may be stronger for enemies that tend to have more specialized host-use (Frenzel and Brandl 2001; Joshi and Vrieling 2005); insects that consume seeds while still attached to the maternal plant (pre-dispersal seed predators) may offer a guild of such enemies. Also, damage by folivorous insects may only have weak effects on an invader's fitness or vigor (Crawley 1989; Parker and Gilbert 2007), whereas pre-dispersal seed predators can cause dramatic declines in seed production (e.g., Hawthorn and Hayne 1978), reducing fitness and in some cases negatively affecting population growth (e.g., Louda and Potvin 1995; Louda et al. 1997; Louda and O'Brien 2002).

We have discussed foliar damage to exotic Asteraceae in a related study (Hill and Kotanen 2010). Here, we use an improved approach to describe damage to common members of this family by a different set of enemies: pre-dispersal seed predators. We tested the hypotheses that: (1) patterns of seed loss are phylogenetically structured; (2) when accounting for this structure, pre-dispersal damage to

capitula is lower for exotic species than native species; and (3) that phylogenetically novel exotic species experience lower rates of seed damage than those more closely related to the native flora. Our results support the first hypothesis, and (weakly) the second, but we did not find that phylogenetically novel exotics experienced the least damage.

## Materials and methods

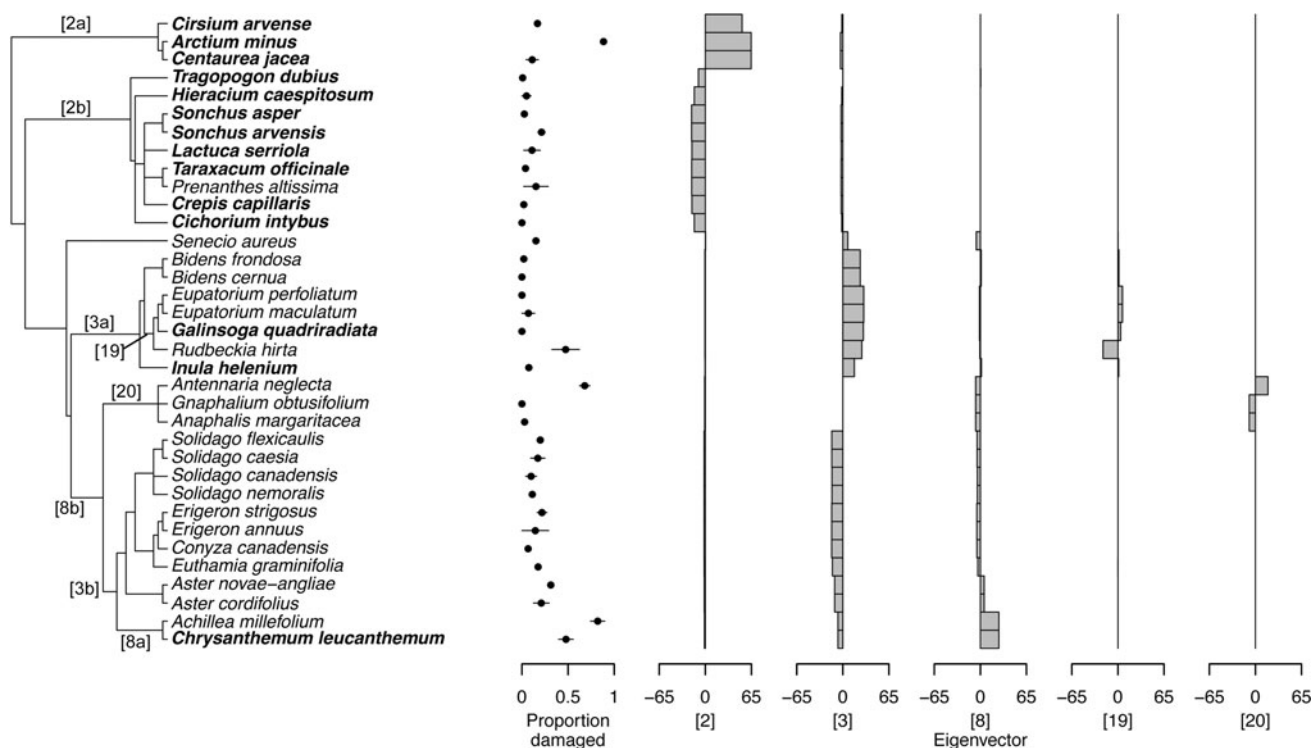
### Study site and natural history

This study was conducted at the University of Toronto's Koffler Scientific Reserve (KSR) at Jokers Hill, Regional Municipality of York, in southern Ontario, Canada (44°02'N, 79°31'W, 300 m ASL). This 350-ha site lies within the Oak Ridges Moraine, and is dominated by prominent hills with a thin organic layer over deep glacial sands. Vegetation is a mixture of old fields supporting a diverse range of native and exotic plants, hardwood (maple–beech–hemlock) forest, and conifer plantations. Further information on this site, including species lists, may be found at <http://www.ksr.utoronto.ca>.

An advantage of working at this site is that the local flora is well-known, allowing the construction of a complete community phylogeny (for species that were present between 1995 and 2008). We chose to work with plants in the Asteraceae because the phylogeny of this group is well understood (Funk et al. 2005), because this family includes many invasive species worldwide (Cadotte et al. 2009), and because it is well represented at KSR: 77 species (~12% of the local flora), of which 44 are native and 33 are exotic. We used species only if they were common enough to be reliably located; this potentially might bias against native and exotic species that were rare because of heavy damage, but provided a good representation of the most prominent invasive and native taxa. Various examples of our study species are present in all major habitats found on the site, including old-field meadows, forest understories, wet meadows, and ponds.

### Survey of capitular damage

From May to November 2008, we collected capitula for 35 representative species, including 21 natives and 14 exotics (Fig. 1); these species were chosen based on their abundance in the field and to represent as many habitats and lineages within the family as possible. Though all species were sampled at the same field site, we incorporated individuals from up to 5 locations whenever possible; for each species, sample locations were separated by at least 200 m. Capitula were collected from 2–10 randomly sampled individuals per species at each of these locations.



**Fig. 1** Plot of the community phylogeny of the 35 species of Asteraceae that were used in this study; exotics are indicated in *bold*. The first column of scores represents the untransformed mean proportion of capitula damaged by seed predators ( $\pm$ SE). The remaining columns are the eigenvector loadings for the 5 significant

eigenvectors used to explain the phylogenetic component of capitular damage (Table 1). Numbers next to lineages indicate where phylogenetic structure in damage was detected by the eigenvectors as referred to in the text. Nomenclature follows Morton and Venn (1990); 1–5 sites were sampled per species (mean = 2.4)

To allow time for colonization by seed predators, we collected the capitula for each species 2–4 weeks after first noting that flowering had begun. In the laboratory, capitula from each location were mixed together, and between 50 and 100 were randomly selected to count; the resulting measure of damage represented the average level of damage by pre-dispersal seed predators at the spatial scale corresponding to the 350-ha Koffler Scientific Reserve. Capitula were counted as damaged if larvae of any kind were found amongst the developing seeds or buried in the receptacle. We also counted damage where larvae were absent, but insect larvae had clearly caused damage. This included bore holes in seeds with missing endosperm, bore holes in the receptacle, and missing seeds in the presence of insect frass. We detected numerous taxa of seed predators, including Coleoptera, Diptera, and Hymenoptera, but did not attempt to distinguish between species or to differentiate between native and exotic taxa. This approach is appropriate since it captures the sum of pre-dispersal seed predation by all insects experienced by exotic plants: for enemy release to apply, total damage must be reduced, not just the damage caused by co-evolved specialists (Maron and Vilà 2001).

For statistical analyses, damage for each species was calculated as the ratio of the number of damaged capitula

to total capitula summed across conspecific locations. This measure represents the proportion of capitula attacked, rather than the proportion of seeds killed or the resulting reduction in fitness. However, it was common for all developing seeds within a damaged capitulum to be consumed, and in many cases damaged capitula were structurally disrupted (e.g., by gluing seed or pappus together), likely reducing the probability of normal dispersal of any remaining seeds, and potentially resulting in the abortion of flower heads (e.g., Louda 1983). Consequently, we feel our data provide an index of the intensity of seed loss, in addition to a measurement of the frequency of capitular damage; in fact, severe damage often made it impossible to determine how many seeds had been consumed, suggesting capitular damage may often be a more reliable measure of insect attack than estimates based on counts of surviving seeds. Data were transformed by calculating the associated Z score for the proportion of damaged capitula; when there were no capitula damaged, 0.001 was added to the zero-score to avoid undefined numbers (Crawley 2007). Z score transformations are similar to probit transformations, and linearize the response variable, which typically is more appropriate for linear models (Crawley 2007).

Previous work has indicated that rates of attack may be influenced by capitulum size in Asteraceae (Fenner et al.

2002). Therefore, prior to evaluating the relationship between the amount of damage and phylogeny among our study species, we evaluated the relationship between damage and capitulum size. For each species, we randomly selected 10 capitula to be measured. Each of these was dissected longitudinally, and the diameter measured using calipers. For all species, the Z-transformed proportion of damaged capitula was then regressed against average capitulum diameter.

### Community phylogeny

The backbone of the Asteraceae community phylogeny 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 v.4.0.1 (Webb and Donoghue 2005), with node age calibration points from a phylogeny based on *rbcl* and *ndhF* sequence data (Kim et al. 2005) (see Fig. 1). Origin was distributed unevenly over phylogeny in our dataset, reflecting our choice of species: some lineages were dominated by natives, and others by exotics.

### Statistical analyses

To evaluate the phylogenetic component of herbivory, we used an eigenvector decomposition method (Diniz-Filho and de Sant’Ana 1998; Desclaves et al. 2003). Using a principal co-ordinate analysis (PCoA) of the phylogenetic distance matrix from the Asteraceae community phylogeny, 34 eigenvectors were extracted to predict phylogenetically structured damage ( $n-1$  based on 35 species). These PCoA eigenvectors represent unique (orthogonal) potential predictors of phylogenetic structure in a trait (in this case capitular damage) based on distances between species at different phylogenetic scales. The approach is similar to spectral analysis in that the eigenvectors represent a series of sine waves with decreasing period (e.g., Borcard and Legendre 2002); the first eigenvector has the broadest period (large-scale phylogenetic structure), and the last eigenvector has the smallest period (fine-scale phylogenetic structure). Eigenvectors that were related to capitular damage ( $P \leq 0.10$ ) were selected based on a forward selection multiple regression. A  $P$  value of 0.1 is typically used for a step-wise multiple regression; this allows for a less conservative model, reducing the risk that potentially informative predictors are removed.

We then evaluated the independent contributions of origin (native vs. exotic) and phylogeny (significant eigenvectors) to patterns in capitular damage using the

function `varpart` from the vegetation analysis package `vegan` (Oksanen et al. 2009); this uses multiple regression to calculate variance components ( $r_{\text{adj}}^2$ ) associated with origin and phylogeny. This approach is the same as one used for detecting phylogenetically structured environmental variation in a trait (Desclaves et al. 2003). An analysis of covariance model was then used to test the hypothesis that exotic species experience lower damage than native species while accounting for phylogenetically structured variation. Origin was treated as a fixed factor, and each significant ( $P \leq 0.10$ ) eigenvector was treated as a predictor. Analysis of the residuals from the linear model met the assumptions of normality and homoscedasticity. We also used a one-tailed  $t$  test of phylogenetically independent contrasts (PICs) to test the hypothesis that exotic species experienced lower damage than native species (Felsenstein 1985); PICs were calculated using the function “aot” in the statistical package PHYLOCOM (Webb et al. 2002);  $t$  tests were calculated using Excel.

To determine if phylogenetically novel invaders experienced lower capitular damage than those more closely related to native Asteraceae at KSR, 4 predictors of phylogenetic novelty were calculated: (1) mean distance to all native and exotic Asteraceae, (2) mean distance to closest native or exotic relative, (3) mean distance to all native taxa, and (4) mean distance to closest native taxa. Distances among individual taxa (in years of divergence) were based on the tip-to-tip measurements given the branch lengths in the Asteraceae community phylogeny. Z-transformed capitular damage was then regressed against each of these predictors.

All analyses were completed using R (R Development Core Team 2006) or JMP v5.0 (SAS 2002).

## Results

### Capitulum size and damage

We were unable to detect an effect of capitulum size on rates of attack using regression ( $t_{33} = 0.753$ ,  $P = 0.457$ ). We therefore did not include this as a predictor in any further analyses.

### Origin versus phylogeny

The majority of variation in capitular damage was explained by phylogeny ( $r_{\text{adj}}^2 = 0.63$ ). Regressions between damage and eigenvector score often indicated clumping of data and/or isolated datapoints, in part as a consequence of the statistical approach used. Nonetheless, five eigenvectors were significantly related to damage (Fig. 2; Table 1) and were associated with phylogenetic structures at various

**Fig. 2** Plots of the Z-transformed proportion of capitula damaged for 35 species of Asteraceae, regressed against the five significant eigenvectors identified using forward selection multiple regression. Significance for each slope is as follows: **a** eigenvector 2, **b** eigenvector 3, **c** eigenvector 8, **d** eigenvector 19, and **e** eigenvector 20. Triangles represent mean damage for native species, and circles for exotic species. Test statistics, degrees of freedom, and *P* values are presented for slopes

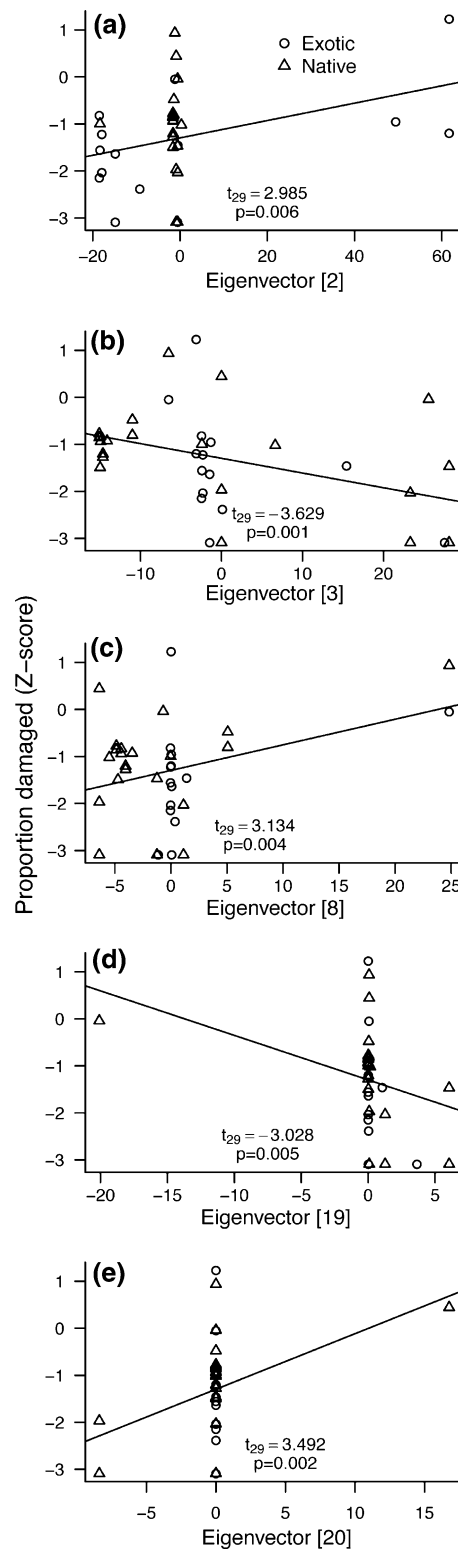
scales (Fig. 1): eigenvectors 2 and 3 were associated with relatively broad phylogenetic patterns in damage, eigenvector 8 was associated with intermediate phylogenetic patterns, and eigenvectors 19 and 20 were associated with fine-scale patterns in damage. The broader-scale eigenvectors detected higher rates of damage among species in lineage 2a compared to species in lineages 2b, and generally higher rates of damage in lineage 3a compared to 3b (Fig. 1). The intermediate-scale eigenvector detected higher rates of damage for *Achillea millefolium* and *Chrysanthemum leucanthemum*, versus other species in the same respective clades. The fine-scale eigenvectors detected higher damage for *Rudbeckia hirta*, compared to other species belonging to the same lineage, and higher damage for *Antennaria neglecta*, compared to other species in its lineage.

#### Native versus exotic

Capitular damage was similar for native and exotic species when no phylogenetic correction was made (one-tailed *t* test:  $t_{33} = -0.709$ ,  $P = 0.242$ ). When phylogenetic structure in damage was accounted for, however, damage to exotic species was less than damage to native species (one-tailed test:  $t_{28} = 1.865$ ,  $P = 0.036$ ) (Table 1). Despite the loss of degrees of freedom resulting from the clustering of native versus exotic species in our phylogeny, this result was further supported using phylogenetically independent contrasts of the difference between damage on native versus exotic plants (mean difference  $\pm$  SE:  $0.16 \pm 0.052$ ,  $t_4 = 3.073$ ,  $P = 0.019$ ). Nonetheless, species' origins accounted for a very low percent of explained variation in capitular damage ( $r_{\text{adj}}^2 = 0.03$ ). The variance partitioning approach also evaluated the combined influence of phylogeny and origin; however, essentially none of the variability in capitular damage was explained by this combination ( $r_{\text{adj}}^2 < 0.01$ ).

#### Phylogenetic novelty

The prediction of decreased capitular damage for phylogenetically novel exotic species was not supported. Damage was not statistically related to any of the four phylogenetic distance measures for exotic species: distance to all Asteraceae ( $F_{1,12} = 2.386$ ,  $P = 0.148$ ), distance to



closest Asteraceae ( $F_{1,12} = 0.011$ ,  $P = 0.916$ ), mean distance to all native Asteraceae ( $F_{1,12} = 1.290$ ,  $P = 0.278$ ), and mean distance to closest native Asteraceae ( $F_{1,12} = 1.177$ ,  $P = 0.299$ ) (Fig. 3). We suspected that capitular

**Table 1** ANCOVA model for 35 Asteraceae describing the relationship between the Z-transformed proportion of their capitula damaged by seed predators and their origin (exotic or native) plus the five significant phylogenetic eigenvectors identified using principal co-ordinate analysis

Term	Estimate	SE	$t_{28}$	$P$
Intercept	-1.565	0.182	-8.576	<0.001
Origin	-1.119	0.239	1.865	0.073*
Eigenvector 2	0.020	0.006	3.323	0.002
Eigenvector 3	-0.030	0.008	-3.656	0.001
Eigenvector 8	0.062	0.017	3.599	0.001
Eigenvector 19	-0.090	0.030	-3.000	0.006
Eigenvector 20	0.118	0.032	3.638	0.001

The overall variance explained by the eigenvectors was  $r_{\text{adj}}^2 = 0.63$ , versus  $r_{\text{adj}}^2 = 0.03$  for species' origins

Eigenvector numbers represent the rank of each eigenvector among the 34 used as potential phylogenetic predictors; lower numbers represent eigenvectors that have longer periods and explain broader patterns of phylogenetically structured variation (see Fig. 1)

\* One-tailed  $t$  test:  $P = 0.036$

damage on *Cirsium arvense* and *Arctium minus* were in part the result of introduced insects, possibly including biocontrol species (Zwölfer 1998; Mason and Huber 2002). For *Arctium*, much of the damage likely was inflicted by the burdock moth, *Metzneria lappella* Zeller (Gelechiidae), which was introduced to Canada in the nineteenth century and is now abundant (Gross et al. 1980); for *Cirsium*, the introduced weevil *Rhinocyllus conicus* Froeh. was common, and a variety of other native and introduced insects are possible (Moore 1975; Zwölfer 1998; Louda and O'Brien 2002; Louda et al. 2003). However, even when data for these two species were removed from the phylogenetic distance regressions, none had significant slopes ( $0.554 \leq P \leq 0.907$  for all cases).

## Discussion

Whether exotic species are likely to accumulate enemies may influence their success and invasiveness in new environments (Maron and Vilà 2001; Levine et al. 2004; Hawkes 2007). In this study, we predicted that capitular damage on locally co-occurring native and exotic Asteraceae would be phylogenetically structured, that after accounting for this structure, exotic species would experience lower damage than natives, and that exotics least closely related to native species would experience the lowest rates of damage. We show strong evidence that damage to common native and exotic Asteraceae is phylogenetically structured. After correcting for this phylogenetic structure in damage, we found that exotic species

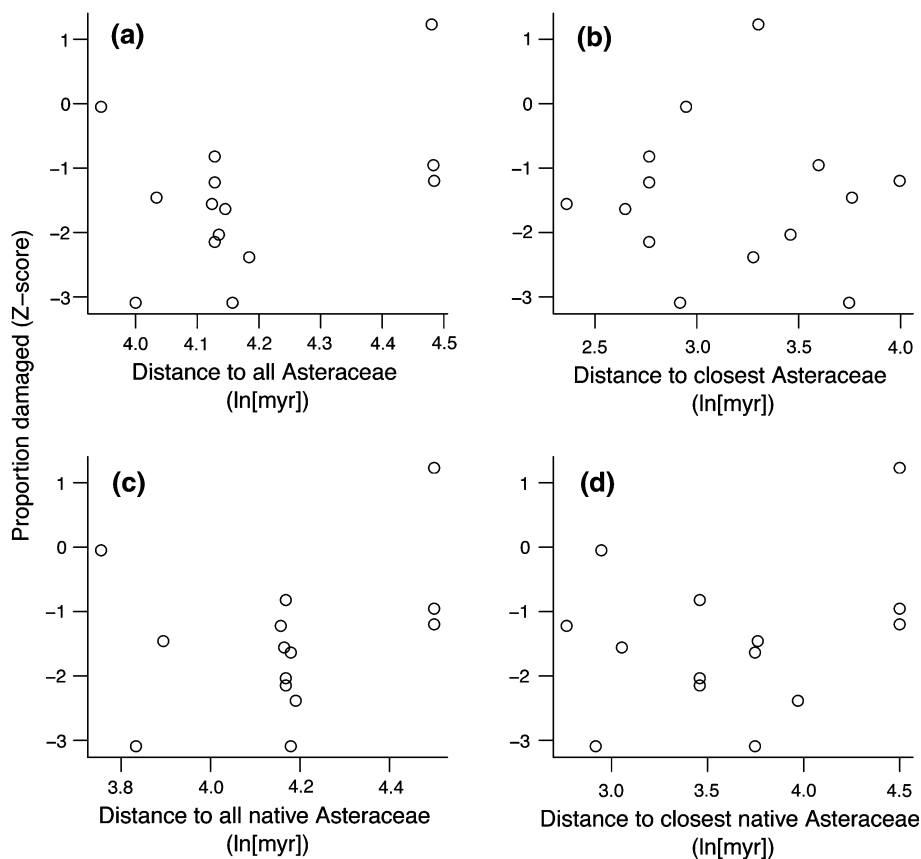
experienced significantly lower damage, though the fraction of variance explained was small. Our data, however, were not consistent with the prediction that phylogenetic novelty results in lower susceptibility to enemies: exotic species consistently experienced rates of damage that were independent of their evolutionary distance from locally co-occurring native and exotic confamilials.

The strong relationship between damage and phylogeny is convincing evidence that evolutionary history has a large impact on susceptibility to pre-dispersal seed predators of native and exotic plants within the Asteraceae. The eigenvector approach that was used also revealed that phylogenetically structured damage exists at multiple scales. Broad-scale patterns, for example, existed between plants in the tribes Cardueae and Lactuceae (lineages 2a and 2b; Fig. 1); at finer phylogenetic scales, *Rudbeckia hirta* and *Antennaria neglecta* both experienced higher rates of damage than other species in their respective lineages. The strength of phylogeny as a predictor of capitular damage suggests that evolutionary history may be a better predictor of damage by pre-dispersal seed predators than a host's place of origin.

The combined effect of origin and phylogeny (Desdesvires et al. 2003) did not explain any additional variation in capitular damage. Although some lineages in our dataset were dominated by exotics and others by natives, this result suggests that any association between exotic status and particular lineages did not consistently bias our results. However, since native and exotic species in our study set tended to be over-represented within different broad lineages, there were few fine-scale comparisons to be made.

We considered only relatively common exotics, which might be expected to have benefitted most from enemy release; nonetheless, even for these species, any reduction in damage relative to natives apparently was small. The lack of an effect of origin for non-corrected damage indicates that the exotic Asteraceae in this study have been colonized by pre-dispersal seed predators (including introduced insects) since their introduction to North America. This contrasts with the results of Fenner and Lee (2001), who found in a phylogenetically non-corrected analysis that exotic Asteraceae in New Zealand had greatly reduced rates of pre-dispersal seed predators compared to native populations. This discrepancy likely reflects the phylogenetic and geographical isolation of the New Zealand flora (Fenner and Lee 2001); in contrast, an European exotic plant in North America may be much more likely to encounter relatives, and the enemies of those relatives. In fact, in our study, capitular damage was higher in some exotics than in most native species. For instance, *Arctium minus* had the highest proportion (89%) of damaged capitula, even though it is an exotic, while native species such as *Bidens cernua*, *Eupatorium perfoliatum*, and

**Fig. 3** Plots of the Z-transformed proportion of capitula damaged for 14 exotic species of Asteraceae, versus phylogenetic distance (in millions of years) to other Asteraceae at KSR. All relationships were non-significant: **a** distance to all Asteraceae, **b** distance to closest Asteraceae, **c** mean distance to all native Asteraceae, **d** mean distance to closest native Asteraceae



*Gnaphalium obtusifolium* had no evidence of damaged capitula.

In contrast, we found exotics experienced lower rates of pre-dispersal seed predation than related native species when phylogenetic structure was accounted for. This indicates that exotics experience less damage than would be expected relative to related species; however, this was such a weak effect that it was masked by phylogenetic variability in the uncorrected dataset. This suggests that detecting reductions in enemy use, and therefore enemy release of exotic species, may be difficult without detailed knowledge of the local flora and the evolutionary history of a community to which an exotic is introduced.

The apparent lack of relationship between damage and phylogenetic distance of invaders to co-occurring family members suggests that the degree of evolutionary divergence among these plants had a minimal effect on their susceptibility to attack. This contrasts with studies which have found damage to exotics decreases with phylogenetic distance from natives in common gardens (Dawson et al. 2009; Hill and Kotanen 2009; Pearse and Hipp 2009), though this effect is often weak (e.g., Hill and Kotanen 2009). However, our results do resemble those from our study of folivory in Asteraceae (Hill and Kotanen 2010), which also failed to detect a decline in damage with phylogenetic distance in natural populations. These results

suggest that any effects of phylogenetic distance among these relatively closely-related (confamilial) species are too weak to be detected against a background of natural variation. Instead, the large component of variability in damage that was explained by the phylogenetic eigenvectors ( $r_{\text{adj}}^2 = 0.63$ ) is convincing evidence that processes that result in similar levels of capitular damage are conserved among sub-lineages within the family, regardless of their origin.

#### Implications for ERH and DNH

The idea that exotic species experience less damage than natives (Keane and Crawley 2002) is weakly supported here. However, this reduced enemy susceptibility was detected only when phylogenetic relatedness was controlled. This suggests that enemy release may best be considered a relative process: an exotic may experience less damage than expected based on its evolutionary relationship to co-occurring natives, rather than simply a reduction compared to the average native. Future tests of the ERH may benefit from including an explicit phylogenetic component; this may help to explain the varied results among case studies in the literature (Maron and Vilà 2001; Colautti et al. 2004; Liu and Stiling 2006; Chun et al. 2010).

The prediction that pre-dispersal seed predation would be negatively related to phylogenetic novelty was rejected for all 4 phylogenetic distance measures. This resembles the lack of effect we detected for folivory (Hill and Kotanen 2010), even though it might be expected that greater host-specificity by seed predators might have led to a stronger result. This implies that pre-dispersal seed predators are unlikely to produce the patterns of co-occurrence predicted by DNH. Since the proportion of capitula damaged nonetheless had a strong phylogenetic signal, phylogenetically conserved characters may be much more important for determining rates of seed predation than origin. One likely candidate is capitulum size: larger capitula tend to be at a greater risk of seed parasitism (Fenner et al. 2002). Nonetheless, our data did not support this pattern. Identifying the characters responsible for phylogenetic signals in rates of attack by enemies and how well they are conserved should help in prediction of susceptibility to enemies, and in understanding where DNH may or may not operate.

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