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Evidence that phylogenetically novel non-indigenous plants experience less herbivory

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19 **Abstract**

20 The degree to which biotic interactions influence invasion by non-indigenous species may be
21 partly explained by the evolutionary relationship of these invaders with natives. Darwin's
22 Naturalization Hypothesis controversially proposes that non-native plants are more likely to invade if
23 they lack close relatives in their new range. A possible mechanism for this pattern is that exotics that
24 are more closely related to natives are more likely to share their herbivores, and thus will suffer more
25 damage than phylogenetically isolated species.

26 We tested this prediction using exotic plants in Ontario, Canada. We measured herbivore
27 damage to 32 species of exotic plants in a common garden experiment, and 52 in natural populations.
28 We estimated their phylogenetic distances from locally-occurring natives in three ways: as mean
29 distance (age) to all native plants, mean distance to native members of the same family, and distance to
30 the closest native species.

31 In the common garden, the proportion of leaves damaged and the average proportion of leaf
32 area damaged declined with mean phylogenetic distance to native family relatives by late summer.
33 Distance to native confamilials was a better predictor of damage than distance to the closest native
34 species, while mean distance to the entire native plant community failed to predict damage. No
35 significant patterns were detected for plants in natural populations, likely because uncontrolled site-to-
36 site variation concealed these phylogenetic trends.

37 To the extent that herbivory has negative demographic impacts, these results suggest that exotics
38 that are more phylogenetically isolated from native confamilials should be more invasive; conversely,
39 native communities should be more resistant to invasion if they harbour close familial relatives of
40 potential invaders. However, the large scatter in this relationship suggests that these often are likely to
41 be weak effects; as a result, these effects often may be difficult to detect in uncontrolled surveys of
42 natural populations.

43

44 **Key words:** Biological invasions, biotic resistance, community phylogenetics, enemy release, natural
45 enemies.

46

47 **Introduction**

48 Invasions by non-indigenous (exotic) plants now have affected most ecosystems around the
49 world (Mack *et al.* 2000; Pimentel *et al.* 2000; Crall *et al.* 2006). Despite their pervasiveness,
50 predicting the invasion potential of exotic species remains difficult. Some of this difficulty may stem
51 from the complexity of interactions between potential invaders and their natural enemies and
52 competitors in the invaded region. Numerous theories have been proposed to describe these biotic
53 interactions (Mitchell *et al.* 2006), of which one of the most prominent is the Enemy Release
54 Hypothesis (ERH) (Keane and Crawley 2002; Torchin and Mitchell 2004). The ERH proposes that
55 exotic species leave behind natural enemies in their native range, resulting in an advantage relative to
56 native competitors (Keane and Crawley 2002; Torchin and Mitchell 2004). Despite its apparent
57 promise, tests of the ERH have found variable results (Colautti *et al.* 2004; Liu and Stiling 2006): some
58 invaders apparently do benefit from reduced damage, but many do not (*e.g.*, Agrawal *et al.* 2003;
59 Parker & Hay 2005; Liu *et al.* 2007).

60 One reason that enemy release often fails is that exotic plants rapidly can accumulate enemies in
61 invaded regions, replacing those lost in the invasion process (*e.g.*, Parker and Hay 2005; Parker *et al.*
62 2006; Hawkes 2007). This accumulation may be more likely for exotics with close native relatives in
63 the invaded area, since shifts of enemies should be more likely among closely related hosts (Strong *et*
64 *al.* 1984; Lewinsohn *et al.* 2005). Numerous studies provide evidence that phytophagous insects are
65 more likely to be shared as the phylogenetic distance between hosts declines (*e.g.*, Novotny *et al.* 2002;
66 Novotny and Basset 2005; Odegaard *et al.* 2005). For instance, in an extensive survey of host use by
67 herbivorous tropical insects, Weiblen *et al.* (2006) found that 25% of the variance in herbivore
68 community similarity was explained by the phylogenetic proximity of their hosts. Such trends extend
69 to other taxa of natural enemies as well: by experimentally transferring fungal pathogens among plants,
70 Gilbert & Webb (2007) showed the likelihood that disease symptoms developed decreased with the
71 phylogenetic separation of the species used as the source and target of the inoculum. If natural enemies

can readily spread from natives to related exotics, then non-native plants with close relatives in the native flora might experience reduced enemy release and ultimately diminished invasiveness.

The idea that phylogeny might affect invasion success is not new. Darwin (1859) predicted that exotics related to native species would be better invaders, since they would be expected to thrive in environments similar to those that these natives evidently found suitable. He was surprised to find that in fact they were less frequently successful, a pattern which has been termed Darwin's Naturalization Hypothesis (Daehler 2001). Empirical support for Darwin's Naturalization Hypothesis varies: Daehler (2001) and Duncan and Williams (2002) rejected the idea, but other studies have had positive results (e.g., Rejmánek 1996; Diez *et al.* 2008). One potential problem is that all of these studies used a taxonomic, rather than a phylogenetic approach. In one of the few studies which has used a phylogenetic analysis, Strauss *et al.* (2006) found that invasive exotic grasses in California are more likely to belong to lineages that have lower native species diversity, though they did not identify the mechanism responsible for this pattern. One possibility is competition: if closely related species compete more strongly, as Darwin (1859) argued, then exotics might be competitively excluded from areas where native congeners occur. Whether the assumptions underlying this explanation are realistic is unclear, however; for example, Cahill *et al.* (2008) found only weak evidence that closer relatives compete more strongly. An attractive alternative is provided by shared natural enemies: if enemy release is less effective for exotics with close relatives in the invaded community, as suggested above, then the result could be the patterns observed by Strauss *et al.* (2006) and Darwin (1859).

The only studies to date which have tested whether herbivory is greater for exotics with native relatives have produced both positive (Dawson *et al.* 2009) and negative (Cappuccino and Carpenter 2005) results; none has attempted a phylogenetic approach. In our study, we used a common garden experiment and surveys of natural populations to determine whether the herbivore damage experienced by exotic plants is correlated with their phylogenetic relationship to native species. We predicted that the foliar damage experienced by an exotic species (1) decreases with phylogenetic distance to the

97 closest locally-occurring native species, (2) decreases with phylogenetic distance to native members of
98 the same family, and (3) decreases with phylogenetic distance to the entire native community. We
99 provide evidence that damage declines with increasing distance to native confamilials, and possibly
100 with distance to the closest native species. These results suggest that herbivory may contribute to the
101 patterns suggested by Darwin's Naturalization Hypothesis. As well, they suggest both a reason for
102 variation in the applicability of the Enemy Release Hypothesis, and potential avenues for improving the
103 precision and predictiveness of this hypothesis.

104

105 **Materials and Methods**

106 *Study site*

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

113 *Common garden experiment*

114 We conducted a common garden experiment using 32 exotic old-field species (Table 1) selected
115 on the basis of their presence in the KSR flora, taxonomic diversity, and availability. Twenty-six of our
116 experimental species were germinated in a greenhouse from seed collected in southern Ontario and
117 grown for 6-8 weeks before transplantation into the field. These were supplemented with six additional
118 species transplanted from local populations; t-tests on damage measurements between transplanted and
119 non-transplanted species confirm that there was no difference between seed-grown and transplanted
120 individuals ($p = 0.244$ and $p=0.205$, respectively). In June 2005, six plants of each species were
121 randomly assigned to one of eight 50m x 8m plowed and disked common gardens located in different

122 old field sites. Landscape fabric was laid over the plowed plots to reduce the density of competitors.
123 Dominant species adjacent to the plots included *Bromus inermis* Leyss., *Chrysanthemum*
124 *leucanthemum* L., *Cirsium arvense* (L.) Scop., *Daucus carota* L., *Poa compressa* L., and *Solidago*
125 *canadensis* L.

126 We measured herbivore damage to all plants twice during the 2005 growing season: once shortly
127 after transplantation in late June (early summer), and once in late August (late summer). We made no
128 effort to distinguish damage by particular species; this is appropriate since we wished to integrate net
129 damage to plants by the entire herbivore community. On each date, the proportion of leaves damaged
130 per plant was measured; if the total number of leaves was greater than 50, this proportion was
131 estimated from a haphazard sample of 50 leaves. We also examined photographs of 1 to 5 haphazardly
132 chosen damaged leaves per plant to visually estimate the fraction of leaf area consumed (to the nearest
133 5%). Accuracy of this method was assessed by comparing visual estimates with digital estimates of the
134 minimum area removed for a subset of 380 leaves ($r^2 = 0.84$ for comparison of visual and digital
135 assessment). The proportion of leaves damaged and the proportion of area removed per damaged leaf
136 were combined to produce an index of the fraction of leaf area damaged per plant:

137 proportion of leaf area damaged = proportion of leaves damaged $\times$ average proportion of
138 area removed from damaged leaves.

139 *Natural population surveys*

140 We also conducted a survey of damage in natural populations of 52 exotic species at KSR (Table
141 1); between 2 and 30 plants from between 2 and 6 populations per species (as available) were sampled
142 during July and August 2005. Since our aim was to be as inclusive as possible, we measured damage to
143 species that are found in forest understory and riparian/wetland habitats, as well as in old fields.
144 Damage was measured using the same approach as in the common gardens, except that the leaf area
145 damaged was measured in the field instead of using photographs in the lab.

146 *Estimating relationship*

147 Reconstructing phylogenetic history using molecular information has been standard for over two
148 decades (Hillis 1987); however, many comparative ecological studies still rely on traditional taxonomic
149 ranks as a surrogate for phylogenetic relationship (*e.g.*, Agrawal *et al.* 2005; Diez *et al.* 2008). Here,
150 we used phylogenetic approaches to quantify each exotic species' relationship to locally occurring
151 natives (*i.e.*, those recorded on the KSR checklist: <http://www.ksr.utoronto.ca/>: site accessed 8 October
152 2008). We chose this small geographic scale because biotic interactions such as competition and
153 herbivory are expected to be important only if the potentially interacting species locally co-occur (Diez
154 *et al.* 2008; Proches *et al.* 2008).

155 For our phylogenetic analyses, we created a composite phylogeny of all the plants present at KSR
156 using the "Maximally Resolved Seed Plant" tree in the program PHYLOMATIC (Webb and Donoghue
157 2005: <http://www.phylodiversity.net/phyloomatic/>). The resulting tree had many polytomies at the
158 family level, but we resolved within-family relationships for our study species using the following
159 published phylogenies: Apiaceae (Downie *et al.* 2000), Asteraceae (Funk *et al.* 2005), Boraginaceae
160 (Långström and Chase 2002), Brassicaceae (Bailey *et al.* 2006), Caryophyllaceae (Oxelman *et al.* 1996;
161 Smissen *et al.* 2002), Lamiaceae (Wagstaff *et al.* 1998; Paton *et al.* 2004), Orchidaceae (Freudenstein *et al.*
162 2004), Plantaginaceae (Ronsted *et al.* 2002), Ranunculaceae (Ro *et al.* 1997), Rosaceae (Smedmark
163 and Erickson 2002; Potter *et al.* 2007), Rubiaceae (Natali *et al.* 1995), Scrophulariaceae (Olmstead *et al.*
164 2001). Branch lengths for the resulting tree were adjusted using the "bladj" function in
165 PHYLOCOM (Webb and Donoghue 2005: <http://www.phylodiversity.net/phylocom/>), which calibrates
166 unknown node ages by linear interpolation of ages from Wikstrom *et al.* (2001).

167 Three measures of the phylogenetic relatedness of our exotics to the native species at KSR were
168 then extracted from this tree: 1) mean evolutionary distance (in years of divergence between tips of the
169 tree) of each exotic to all native plants occurring at KSR; 2) the mean distance from each exotic to all
170 locally co-occurring native family members (in the absence of family members, the distance of each
171 exotic to the next nearest lineage were used); and 3) the distance of each exotic to the closest native

172 species. Distance to all native plants provides a description of each exotic's isolation from the entire
173 native community (e.g., Strauss et al. 2006); distance to native confamilials recognizes that enemies are
174 often shared at the family level (Novotny and Basset 2005; Odegaard *et al.* 2005; Weiblen *et al.* 2006).
175 Regressing damage against each of these distance measures provides a test of the hypothesis that
176 damage declines with this measure of phylogenetic isolation, consistent with the patterns predicted
177 from Darwin's Naturalization Hypothesis.

178 *Statistical analyses*

179 Since we primarily were interested in interspecific variation in herbivory, we treated species
180 means as data points. These were calculated by computing plot means (common garden experiment) or
181 population means (field survey) for damage to individuals of each species, then averaging those values.
182 This approach also allowed us to avoid pseudoreplication and to simplify our comparative analyses,
183 which are difficult to apply to spatially replicated datasets. The proportion of leaves damaged and the
184 average leaf area damaged were analyzed separately, since they are algebraically nonindependent.
185 Damage measurements were probit transformed to linearize proportional measurements; arcsin
186 transformation produced very similar results. All phylogenetic distance measurements were
187 transformed using their natural logarithm to better meet statistical assumptions of normality and
188 homoscedasticity. Statistical analyses were conducted using the programs R (R Development Core
189 Team 2006) and JMP v5.0. (SAS Institute Inc. 2002). Results are reported as mean $\pm$ standard error.

190 Linear regression was used to test whether damage declined with phylogenetic distance from
191 native relatives, for both the common garden experiment and the field survey. In the case of the
192 common garden data, June and August samples were analyzed independently, since they effectively
193 tested different hypotheses: June samples acted as a control to test for unwanted and unexpected initial
194 differences among newly-transplanted plants, while August samples provided useful data since they
195 recorded cumulative damage over the summer. Since the plants sampled in the field survey had not
196 been transplanted, an initial sampling was unnecessary. We compared the predictive power of our three

197 competing measures of phylogenetic distance (distance to nearest native species, native confamilials,
198 and native community) by using Akaike's Information Criteria (Burnham and Anderson 2002): for
199 cases where at least one competing model was statistically significant, the combination of high Akaike
200 weights and high strength of fit (r^2) identifies the simplest and most powerful model.

201 To determine whether the inclusion of multiple species from some families biased any significant
202 results, we ran regressions of damage vs. distance using all possible combinations of species, subject to
203 the constraint that only one species was used to represent each family. This resulted in 432 and 84480
204 models for the common garden experiment and the survey respectively. The value of the regression
205 slope when all species were included compared to the distribution of slopes from models lacking
206 within-family replication allowed us to determine if our results were biased by family-level
207 phylogenetic nonindependence.

208

209 **Results**

210 At the June sampling of the common garden there were no significant effects of phylogenetic
211 distance on damage (Table 2), indicating no unwanted initial differences. By the August sampling,
212 however, the proportion of leaves damaged (mean $\pm$ SE: 0.44 ± 0.05) and the leaf area damaged (mean
213 $\pm$ SE: 0.05 ± 0.003) both declined significantly with mean phylogenetic distance from native
214 confamilials, respectively explaining 12% and 18% of variation (Fig 1, Table 2). As well, there was a
215 marginally significant negative relationship between leaf area damaged and distance to the closest
216 native species ($p = 0.083$, $r^2 = 7\%$; Table 2). Models including only one species per family were
217 consistent with these results: 95% quantiles for slopes of these reduced models did not include 0, but
218 did include the slopes estimated in our significant regressions; this indicates our significant results were
219 not an artefact of including multiple species per family. In contrast, there was no statistical relationship
220 between either damage measurement and mean distance to all locally-occurring natives. Mean distance

to native family members was a much stronger predictor of damage than the other distance measures, as indicated by lower AIC and higher Akiake weights (w) and r^2 values (Table 2).

In contrast with the common garden results, damage to exotics in natural populations was not significantly related to any of the phylogenetic distance measures (Table 2; Fig. 2). In all cases, adjusted r^2 values were very low or slightly negative (Table 2), indicating that essentially none of the variation in damage could be explained by phylogenetic distance to native relatives.

Discussion

Does damage decline with phylogenetic distance between natives and exotics?

We predicted that herbivore damage to exotics would decline with phylogenetic distance from native relatives. Few tests of related hypotheses have been performed. Working in Tanzania, Dawson et al. (2009) found herbivory in introduced plants increased with both the presence of native congeners and the diversity of native confamilials, though this was apparently unrelated to invasiveness. In contrast, also working in Ontario, Cappuccino and Carpenter (2005) found that herbivore damage to exotic plants was unrelated to the number of native congeners or confamilial native genera. Neither of these studies employed a phylogenetic approach, but using methods based on phylogenetic distance rather than the number of congeneric or confamilial native species, we found that both the proportion of leaves damaged and the average proportion of leaf area damaged declined with phylogenetic distance from confamilials (Fig. 1). As well, the leaf area damaged showed a nearly significant decline with phylogenetic distance from the nearest native species (Fig. 1). Remarkably, we were able to detect these patterns despite both phylogenetic uncertainty and the high level of noise resulting from interspecific variation in damage; nonetheless, the strength of these relationships was low ($r^2 < 0.2$), suggesting the effects of native relatives often may be small relative to other factors affecting both herbivore damage and invasiveness.

245 In contrast with our common garden results, we found no significant phylogenetic trends in
246 damage to wild populations (Fig. 2). The most plausible explanation is that uncontrolled variation in
247 damage among natural populations was greater than any phylogenetic trend, and therefore masked the
248 effects of phylogenetic distance. This does not necessarily mean phylogenetic influences are
249 unimportant in natural populations; only that they operate in addition to other sources of background
250 variation. Herbivore communities are highly spatially variable and often differ among habitats (e.g.,
251 DeWalt *et al.* 2004). We sampled scores of natural populations in a wide range of habitats; site-to-site
252 variation in background levels of herbivore damage thus likely varied considerably. In contrast,
253 experimental plants in our common gardens all shared the same environment, minimizing unwanted
254 site effects. This reduction of environmental noise is one of the principal advantages of common
255 gardens, since it can allow the detection of subtle trends that may be difficult to demonstrate in field
256 surveys. Interestingly, the only other study we are aware of that shows an effect of phylogenetic
257 isolation on herbivory (Dawson *et al.* 2009) was conducted in a botanical garden: effectively a
258 common-garden approach.

259 Generally speaking, closer relatives share more of the herbivore community (Novotny *et al.*
260 2002; Novotny and Basset 2005; Odegaard *et al.* 2005; Weiblen *et al.* 2006); therefore, we expected
261 that distance to the nearest relative (often a congeneric) would be the strongest predictor of damage.
262 The stronger predictive value of family relatedness than distance to the nearest native relative was
263 unexpected. There are several possible explanations for our result. First, many characteristics of plants
264 that are important to herbivores are shared at the family level (chemistry, morphology, etc.); perhaps
265 the single closest relative is less important than the suite of confamilials sharing such characteristics.
266 There is some evidence that family-level characters can be more important in determining herbivore
267 communities than variation among species within a family; for example, Cappuccino and Carpenter
268 (2005) provide evidence that, although invasive exotic plants tend to be chemically more unusual than
269 non-invasive exotic species, phytochemical uniqueness may only be weakly correlated with phylogeny

below the family level. Second, deeper phylogenetic nodes where ecological or functional similarities are conserved may represent greater species diversity than a single nearest neighbour; thus, relatives at the family level may harbour a greater diversity of insects potentially able to colonize a new invader than does a single close relative. While Cappuccino and Carpenter (2005) found damage to exotics to be unrelated to the diversity of native relatives, Dawson et al. (2009) did find that herbivore damage increased with the diversity of native confamilials, consistent with this prediction. Finally, the stronger effect of family relationship may occur because estimates of topology and branch lengths below the family level are less accurate than that above the family level. This is likely, both since finer relationships are often more difficult to resolve, and because we were forced to use an interpolation procedure to estimate node ages.

Taxonomy often represents poly- or paraphyletic groupings of taxa, and also fails to account for taxon age, while a reliable phylogeny minimizes these problems; thus, phylogeny should be more powerful in detecting factors correlated with relationship. Nonetheless, it is important to realize that phylogenies are hypotheses about evolutionary history, and should be treated accordingly when incorporated into comparative analyses (Webb *et al.* 2002). As well, fully resolved phylogenies are still not available for most plant communities, forcing some degree of reliance on taxonomic information: in our case, we still used taxonomy to inform our choice of node ages to include as predictors.

Enemy Release and Darwin's Naturalization Hypothesis.

The Enemy Release Hypothesis states that escape from enemies may contribute to the success of exotic species (Keane and Crawley 2002; Torchin and Mitchell 2004; Liu and Stiling 2006). Tests of this hypothesis have produced variable results: exotic plants often do experience reduced levels of damage in new areas but there are numerous exceptions to this rule (Liu & Stiling 2006). Our results suggest one source of this variation: escape from enemies may depend on the phylogenetic relationship between an invader and members of the invaded community. An exotic plant closely related to natives in the invaded community thus may experience more damage than a phylogenetic outlier. The effects

295 we found were modest, and even substantial damage does not necessarily translate to reduced
296 invasiveness or demographic performance (Maron and Vilá 2001; Liu *et al.* 2007; Dawson *et al.* 2009);
297 nonetheless, in at least some cases, this biotic resistance might reduce the abundance or spread of an
298 exotic.

299 If natural enemies are more likely to attack exotics with close native relatives, this could provide
300 a mechanism for Darwin's Naturalization Hypothesis. Although we did not have the data to explicitly
301 test Darwin's Naturalization Hypothesis, evidence in the literature is mixed (Rejmanek 1996; Daehler
302 2001; Duncan and Williams 2002; Diez *et al.* 2008); however, this variation may partly reflect the
303 influence of opposing ecological forces operating at different spatial scales (Proches *et al.* 2008). At
304 regional scales, exotics and close native relatives may positively co-occur because of a requirement for
305 similar physical environments, as Darwin predicted; at local scales, negative biotic interactions such as
306 competition and herbivory may produce negative co-occurrence, as Darwin actually reported (Proches
307 *et al.* 2008). Diez *et al.* (2008) found exactly this pattern: at regional scale, the abundance of exotic
308 plants near Auckland, New Zealand was positively correlated with the abundance of native congeners,
309 while at a local (within-habitat) scale this pattern was reversed. Thus, community-scale studies (such as
310 ours) may be required to elucidate the contribution of biotic factors to the patterns discussed by
311 Darwin.

312 *Links with community phylogenetics*

313 Darwin's Naturalization Hypothesis represents a precursor to community phylogenetics: the
314 recent theory that communities are in part structured by patterns of evolutionarily conserved traits
315 among component taxa (Webb *et al.* 2002). Many such studies assume that competition and
316 environmental filtering are the dominant forces structuring communities (*e.g.*, Webb 2000; Cavender-
317 Bares *et al.* 2004; Cavender-Bares *et al.* 2006; Webb *et al.* 2006; Swenson *et al.* 2007). For example,
318 where close relatives do not co-occur (*i.e.*, a community is "phylogenetically overdispersed"), the
319 mechanism is assumed to involve limiting similarity resulting in competitive exclusion. However,

320 experimental evidence suggests that strong competition among close relatives may not in fact be a
321 leading determinant of community structure (Cahill *et al.* 2008). Instead, a negative association among
322 relatives could be explained by apparent competition (Holt 1977; Holt and Lawton 1994): the
323 suppression of one species by the enemies of another. Where natural enemies are shared among close
324 relatives, this also could result in phylogenetic overdispersion; our experimental results suggest this
325 may be a plausible alternative. Thus, a century and a half after it was originally proposed, Darwin's
326 Naturalization Hypothesis may lead to a better understanding of the role that phylogeny plays in
327 structuring natural communities, and the mechanisms involved in the success or failure of exotic
328 species.

329

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337

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483 **Table 1.** List of exotic plants sampled in common gardens and natural populations. Bolded families
 484 have native members at the study site (the Koffler Scientific Reserve). Nomenclature follows Morton
 485 and Venn (1990)

486

Family	Species	Common Garden	Natural Populations
Amaranthaceae	<i>Amaranthus retroflexus</i> L.		X
Apiaceae	<i>Daucus carota</i> L.	X	X
Asclepiadaceae	<i>Cynanchum rossicum</i> (Kleopov) Borh.		X
Asteraceae	<i>Arctium minus</i> (Hill) Bernh.	X	X
Asteraceae	<i>Centaurea jaceae</i> L.		X
Asteraceae	<i>Cirsium arvense</i> (L.) Scop.	X	X
Asteraceae	<i>Cirsium vulgare</i> (Savi) Tenore		X
Asteraceae	<i>Cichorium intybus</i> L.	X	X
Asteraceae	<i>Chrysanthemum leucanthemum</i> L.	X	X
Asteraceae	<i>Hieracium aurantiacum</i> L.	X	
Asteraceae	<i>Hieracium caespitosum</i> Dumort.		X
Asteraceae	<i>Inula helenium</i> L.		X
Asteraceae	<i>Sonchus arvensis</i> L.		X
Asteraceae	<i>Tragopogon dubius</i> Scop.		X
Asteraceae	<i>Tragopogon pratensis</i> L.	X	
Asteraceae	<i>Tussilago farfara</i> L.		X
Boraginaceae	<i>Cynoglossum officinalis</i> L.		X
Boraginaceae	<i>Echium vulgare</i> L.	X	X
Brassicaceae	<i>Alliaria petiolata</i> (M. Bieb.) Cav. & Gr.		X

Brassicaceae	<i>Capsella bursa-pastoris</i> (L.) Medikus	X	
Brassicaceae	<i>Erysimum cheiranthoides</i> L.		X
Brassicaceae	<i>Hesperis matronalis</i> L.		X
Brassicaceae	<i>Lepidium campestre</i> (L.) R.Br.	X	
Brassicaceae	<i>Sinapis arvensis</i> L.		X
Brassicaceae	<i>Thlaspi arvense</i> L.	X	
Campanulaceae	<i>Campanula rapunculoides</i> L.		X
Caryophyllaceae	<i>Dianthus armeria</i> L.	X	
Caryophyllaceae	<i>Saponaria officinalis</i> L.		X
Caryophyllaceae	<i>Silene latifolia</i> Poiret	X	X
Caryophyllaceae	<i>Silene noctiflora</i> L.		X
Caryophyllaceae	<i>Silene vulgaris</i> (Moench) Garcke	X	X
Chenopodiaceae	<i>Chenopodium album</i> L.	X	X
Clusiaceae	<i>Hypericum perforatum</i> L.	X	X
Convolvulaceae	<i>Convolvulus arvensis</i> L.		X
Dipsacaceae	<i>Dipsacus sylvestris</i> Hudson	X	
Euphorbiaceae	<i>Euphorbia cyparissias</i> L.	X	X
Fabaceae	<i>Lotus corniculatus</i> L.	X	X
Fabaceae	<i>Medicago lupulina</i> L.		X
Fabaceae	<i>Medicago sativa</i> L.		X
Fabaceae	<i>Melilotus alba</i> Medikus	X	X
Fabaceae	<i>Melilotus officinalis</i> (L.) Pallas		X
Fabaceae	<i>Trifolium pratense</i> L.	X	X
Fabaceae	<i>Vicia cracca</i> L.		X

Fabaceae	<i>Vicia tetrasperma</i> (L.) Moench	X	
Lamiaceae	<i>Glechoma hederaceae</i> L.		X
Lamiaceae	<i>Leonurus cardiaca</i> L.		X
Lamiaceae	<i>Mentha X piperita</i> L.		X
Lamiaceae	<i>Nepeta cataria</i> L.	X	X
Lythraceae	<i>Lythrum salicaria</i> L.		X
Orchidaceae	<i>Epipactis helleborine</i> (L.) Crantz		X
Papaveraceae	<i>Chelidonium majus</i> L.	X	X
Plantaginaceae	<i>Plantago lanceolata</i> L.		X
Plantaginaceae	<i>Plantago major</i> L.	X	X
Polygonaceae	<i>Rumex crispus</i> L.	X	X
Ranunculaceae	<i>Ranunculus acris</i> L.	X	X
Rubiaceae	<i>Galium verum</i> L.	X	X
Rosaceae	<i>Potentilla recta</i> L.	X	X
Scrophulariaceae	<i>Linaria vulgaris</i> Hill	X	X
Scrophulariaceae	<i>Verbascum thapsus</i> L.	X	X
Solanaceae	<i>Solanum dulcamara</i> L.	X	X
Total species		32	52

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Table 2. Regression and AIC results for herbivory (proportion of leaves damaged and leaf area damaged) vs. phylogenetic distance to native species occurring at KSR. Damage variables were probit transformed and phylogenetic distance measures were natural logarithm transformed before analysis. Headers represent degrees of freedom (df) used to test the significance of the regression slope (F, p), and Akaike's information criteria (AIC), Akaike weights (w), and variance explained (r^2) to determine the best phylogenetic distance model

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Data	Phylogenetic distance	Proportion of Leaves Damaged						Leaf Area Damaged				
		df	F	p	AIC	w	r^2	F	p	AIC	w	r^2
Common Garden (June)	All native taxa	1,30	0.030	0.865	74.700	0.30	0.00	0.041	0.840	48.706	0.26	0.00
	Native family taxa	1,30	0.544	0.467	74.156	0.40	0.00	1.302	0.263	47.391	0.49	0.01
	Closest native	1,30	0.000	1.000	74.731	0.30	0.00	0.004	0.953	48.746	0.25	0.00
Common Garden (August)	All native taxa	1,30	0.138	0.713	99.203	0.06	0.00	0.955	0.336	36.121	0.03	0.00
	Native family taxa	1,30	5.299	0.028	94.145	0.78	0.12	7.957	0.008	29.597	0.86	0.18
	Closest native	1,30	1.939	0.174	97.346	0.16	0.03	3.214	0.083	33.867	0.10	0.07
Survey	All native taxa	1,50	2.232	0.142	22.715	0.59	0.00	0.003	0.956	81.079	0.31	0.00
	Native family taxa	1,50	0.003	0.958	24.983	0.19	0.00	0.000	0.997	81.082	0.31	0.00
	Closest native	1,50	0.341	0.562	24.633	0.22	0.00	0.440	0.510	80.626	0.39	0.00

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Figure legends

Fig. 1 Proportion of leaves damaged in the common garden experiment versus phylogenetic distance to a) all native species, b) native family members, c) closest native relative, and proportion of leaf area damaged against phylogenetic distance to d) all native species, e) native family members, f) closest native relative. All damage measures were made during August 2005, and phylogenetic distances are based on tip-to-tip distances between exotic and native species present at KSR. Points represent means for each species. Intact lines indicate regressions significant at $p < 0.05$, the broken line indicates significance at $p < 0.1$

Fig. 2 Proportion of leaves damaged in naturally occurring populations at KSR versus phylogenetic distance to a) all native species, b) native family members, c) closest native relative, and proportion of leaf area damaged against phylogenetic distance to d) all native species, e) native family members, f) closest native relative. All damage measures were made during July and August 2005, and phylogenetic distances are based on tip-to-tip distances between exotic and native species present at KSR. Points represent means for each species included in the survey. No regressions were significant ($p > 0.1$)

Figure 1

Figure 2