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Post-print/Accepted manuscript

Steven Burton Hill

Peter M. Kotanen


The final publication is available at Springer via http://dx.doi.org/10.1007/s00442-009-1403-0

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Evidence that phylogenetically novel non-indigenous plants experience less herbivory

Steven B. Hill¹* and Peter M. Kotanen²

Department of Ecology and Evolutionary Biology
University of Toronto at Mississauga
3359 Mississauga Road N
Mississauga ON
L5L 1C6
Canada
tel: 905-828-5365; fax: 905-828-3792

¹e-mail: sb.hill@utoronto.ca
²e-mail: peter.kotanen@utoronto.ca

* Author for correspondence
Abstract

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

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

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

To the extent that herbivory has negative demographic impacts, these results suggest that exotics that are more phylogenetically isolated from native confamilials should be more invasive; conversely, native communities should be more resistant to invasion if they harbour close familial relatives of potential invaders. However, the large scatter in this relationship suggests that these often are likely to be weak effects; as a result, these effects often may be difficult to detect in uncontrolled surveys of natural populations.
Key words: Biological invasions, biotic resistance, community phylogenetics, enemy release, natural enemies.
Invasions by non-indigenous (exotic) plants now have affected most ecosystems around the world (Mack et al. 2000; Pimentel et al. 2000; Crall et al. 2006). Despite their pervasiveness, predicting the invasion potential of exotic species remains difficult. Some of this difficulty may stem from the complexity of interactions between potential invaders and their natural enemies and competitors in the invaded region. Numerous theories have been proposed to describe these biotic interactions (Mitchell et al. 2006), of which one of the most prominent is the Enemy Release Hypothesis (ERH) (Keane and Crawley 2002; Torchin and Mitchell 2004). The ERH proposes that exotic species leave behind natural enemies in their native range, resulting in an advantage relative to native competitors (Keane and Crawley 2002; Torchin and Mitchell 2004). Despite its apparent promise, tests of the ERH have found variable results (Colautti et al. 2004; Liu and Stiling 2006): some invaders apparently do benefit from reduced damage, but many do not (e.g., Agrawal et al. 2003; Parker & Hay 2005; Liu et al. 2007).

One reason that enemy release often fails is that exotic plants rapidly can accumulate enemies in invaded regions, replacing those lost in the invasion process (e.g., Parker and Hay 2005; Parker et al. 2006; Hawkes 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). 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). For instance, in an extensive survey of host use by herbivorous tropical insects, Weiblen et al. (2006) found that 25% of the variance in herbivore community similarity was explained by the phylogenetic proximity of their hosts. Such trends extend to other taxa of natural enemies as well: by experimentally transferring fungal pathogens among plants, Gilbert & Webb (2007) showed the likelihood that disease symptoms developed decreased with the 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
closest locally-occurring native species, (2) decreases with phylogenetic distance to native members of
the same family, and (3) decreases with phylogenetic distance to the entire native community. We
provide evidence that damage declines with increasing distance to native conspecifics, and possibly
with distance to the closest native species. These results suggest that herbivory may contribute to the
patterns suggested by Darwin's Naturalization Hypothesis. As well, they suggest both a reason for
variation in the applicability of the Enemy Release Hypothesis, and potential avenues for improving the
precision and predictiveness of this hypothesis.

Materials and Methods

Study site

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, 300m
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 may be found at http://www.ksr.utoronto.ca/jh.html/.

Common garden experiment

We conducted a common garden experiment using 32 exotic old-field species (Table 1) selected
on the basis of their presence in the KSR flora, taxonomic diversity, and availability. Twenty-six of our
experimental species were germinated in a greenhouse from seed collected in southern Ontario and
grown for 6-8 weeks before transplantation into the field. These were supplemented with six additional
species transplanted from local populations; t-tests on damage measurements between transplanted and
non-transplanted species confirm that there was no difference between seed-grown and transplanted
individuals (p = 0.244 and p=0.205, respectively). In June 2005, six plants of each species were
randomly assigned to one of eight 50m x 8m plowed and disked common gardens located in different
old field sites. Landscape fabric was laid over the plowed plots to reduce the density of competitors. Dominant species adjacent to the plots included *Bromus inermis* Leyss., *Chrysanthemum leucanthemum* L., *Cirsium arvense* (L.) Scop., *Daucus carota* L., *Poa compressa* L., and *Solidago canadensis* L.

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

$$\text{proportion of leaf area damaged} = \text{proportion of leaves damaged} \times \text{average proportion of area removed from damaged leaves.}$$

*Natural population surveys*

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

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

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

Three measures of the phylogenetic relatedness of our exotics to the native species at KSR were
then extracted from this tree: 1) mean evolutionary distance (in years of divergence between tips of the
tree) of each exotic to all native plants occurring at KSR; 2) the mean distance from each exotic to all
locally co-occurring native family members (in the absence of family members, the distance of each
exotic to the next nearest lineage were used); and 3) the distance of each exotic to the closest native
species. Distance to all native plants provides a description of each exotic's isolation from the entire native community (e.g., Strauss et al. 2006); distance to native confamilials recognizes that enemies are often shared at the family level (Novotny and Basset 2005; Odegaard et al. 2005; Weiblen et al. 2006). Regressing damage against each of these distance measures provides a test of the hypothesis that damage declines with this measure of phylogenetic isolation, consistent with the patterns predicted from Darwin's Naturalization Hypothesis.

Statistical analyses

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

Linear regression was used to test whether damage declined with phylogenetic distance from native relatives, for both the common garden experiment and the field survey. In the case of the common garden data, June and August samples were analyzed independently, since they effectively tested different hypotheses: June samples acted as a control to test for unwanted and unexpected initial differences among newly-transplanted plants, while August samples provided useful data since they recorded cumulative damage over the summer. Since the plants sampled in the field survey had not been transplanted, an initial sampling was unnecessary. We compared the predictive power of our three
competing measures of phylogenetic distance (distance to nearest native species, native confamilials, and native community) by using Akaike's Information Criteria (Burnham and Anderson 2002): for cases where at least one competing model was statistically significant, the combination of high Akaike weights and high strength of fit ($r^2$) identifies the simplest and most powerful model.

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

### Results

At the June sampling of the common garden there were no significant effects of phylogenetic distance on damage (Table 2), indicating no unwanted initial differences. By the August sampling, however, the proportion of leaves damaged (mean ± SE: 0.44 ± 0.05) and the leaf area damaged (mean ± SE: 0.05 ± 0.003) both declined significantly with mean phylogenetic distance from native confamilials, respectively explaining 12% and 18% of variation (Fig 1, Table 2). As well, there was a marginally significant negative relationship between leaf area damaged and distance to the closest native species ($p = 0.083, r^2 = 7\%$; Table 2). Models including only one species per family were consistent with these results: 95% quantiles for slopes of these reduced models did not include 0, but did include the slopes estimated in our significant regressions; this indicates our significant results were not an artefact of including multiple species per family. In contrast, there was no statistical relationship 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 Akaike 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.
In contrast with our common garden results, we found no significant phylogenetic trends in damage to wild populations (Fig. 2). The most plausible explanation is that uncontrolled variation in damage among natural populations was greater than any phylogenetic trend, and therefore masked the effects of phylogenetic distance. This does not necessarily mean phylogenetic influences are unimportant in natural populations; only that they operate in addition to other sources of background variation. Herbivore communities are highly spatially variable and often differ among habitats (e.g., DeWalt et al. 2004). We sampled scores of natural populations in a wide range of habitats; site-to-site variation in background levels of herbivore damage thus likely varied considerably. In contrast, experimental plants in our common gardens all shared the same environment, minimizing unwanted site effects. This reduction of environmental noise is one of the principal advantages of common gardens, since it can allow the detection of subtle trends that may be difficult to demonstrate in field surveys. Interestingly, the only other study we are aware of that shows an effect of phylogenetic isolation on herbivory (Dawson et al. 2009) was conducted in a botanical garden: effectively a common-garden approach.

Generally speaking, closer relatives share more of the herbivore community (Novotny et al. 2002; Novotny and Basset 2005; Odegaard et al. 2005; Weiblen et al. 2006); therefore, we expected that distance to the nearest relative (often a congeneric) would be the strongest predictor of damage. The stronger predictive value of family relatedness than distance to the nearest native relative was unexpected. There are several possible explanations for our result. First, many characteristics of plants that are important to herbivores are shared at the family level (chemistry, morphology, etc.); perhaps the single closest relative is less important than the suite of confamilials sharing such characteristics. There is some evidence that family-level characters can be more important in determining herbivore communities than variation among species within a family; for example, Cappuccino and Carpenter (2005) provide evidence that, although invasive exotic plants tend to be chemically more unusual than 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
we found were modest, and even substantial damage does not necessarily translate to reduced
invasiveness or demographic performance (Maron and Vilá 2001; Liu et al. 2007; Dawson et al. 2009);
nonetheless, in at least some cases, this biotic resistance might reduce the abundance or spread of an
exotic.

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

*Links with community phylogenetics*

Darwin's Naturalization Hypothesis represents a precursor to community phylogenetics: the
recent theory that communities are in part structured by patterns of evolutionarily conserved traits
among component taxa (Webb et al. 2002). Many such studies assume that competition and
environmental filtering are the dominant forces structuring communities (*e.g.*, Webb 2000; Cavender-
Bares et al. 2004; Cavender-Bares et al. 2006; Webb et al. 2006; Swenson et al. 2007). For example,
where close relatives do not co-occur (*i.e.*, a community is "phylogenetically overdispersed"), the
mechanism is assumed to involve limiting similarity resulting in competitive exclusion. However,
experimental evidence suggests that strong competition among close relatives may not in fact be a leading determinant of community structure (Cahill et al. 2008). Instead, a negative association among relatives could be explained by apparent competition (Holt 1977; Holt and Lawton 1994): the suppression of one species by the enemies of another. Where natural enemies are shared among close relatives, this also could result in phylogenetic overdispersion; our experimental results suggest this may be a plausible alternative. Thus, a century and a half after it was originally proposed, Darwin's Naturalization Hypothesis may lead to a better understanding of the role that phylogeny plays in structuring natural communities, and the mechanisms involved in the success or failure of exotic species.

Acknowledgements

This research was supported by NSERC Research and Equipment Grants (PMK), an NSERC PGS-D (SBH), and the Koffler Scientific Reserve at Jokers Hill. Thanks to Kateryna Kostyukova for her continuous help, to Nathalie Taraban-Lagois, Gilbert Tang, James McKay, and Andrew MacDonald for their support, discussions, and field assistance, and to two anonymous reviewers for valuable suggestions on an earlier version of this manuscript. This is a publication of the Koffler Scientific Reserve. All of the experiments conducted in this study comply with the current laws of Canada.
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Table 1. List of exotic plants sampled in common gardens and natural populations. Bolded families have native members at the study site (the Koffler Scientific Reserve). Nomenclature follows Morton and Venn (1990).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common Garden</th>
<th>Natural Populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaranthaceae</td>
<td><em>Amaranthus retroflexus</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Apiaceae</td>
<td><em>Daucus carota</em> L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asclepiadaceae</td>
<td><em>Cynanchum rossicum</em> (Kleopov) Borh.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Arctium minus</em> (Hill) Bernh.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Centaurea jacea</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Cirsium arvense</em> (L.) Scop.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Cirsium vulgare</em> (Savi) Tenore</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Cichorium intybus</em> L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Chrysanthemum leucanthemum</em> L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Hieracium aurantiacum</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Hieracium caespitosum</em> Dumort.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Inula helenium</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Sonchus arvensis</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Tragopogon dubius</em> Scop.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Tragopogon pratensis</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Tussilago farfara</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td><em>Cynoglossum officinalis</em> L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td><em>Echium vulgaris</em> L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Brassicaceae</td>
<td><em>Alliaria petiolata</em> (M. Bieb.) Cav. &amp; Gr.</td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>
Brassicaceae  Capsella bursa-pastoris (L.) Medikus  X
Brassicaceae  Erysimum cheiranthoides L.  X
Brassicaceae  Hesperis matronalis L.  X
Brassicaceae  Lepidium campestre (L.) R.Br.  X
Brassicaceae  Sinapis arvensis L.  X
Brassicaceae  Thlaspi arvense L.  X
Campanulaceae  Campanula rapunculoides L.  X
Caryophyllaceae  Dianthus armeria L.  X
Caryophyllaceae  Saponaria officinalis L.  X
Caryophyllaceae  Silene latifolia Poiret  X  X
Caryophyllaceae  Silene noctiflora L.  X
Caryophyllaceae  Silene vulgaris (Moench) Garcke  X  X
Chenopodiaceae  Chenopodium album L.  X  X
Clusiaceae  Hypericum perforatum L.  X  X
Convolvulaceae  Convolvulus arvensis L.  X
Dipsacaceae  Dipsacus sylvestris Hudson  X
Euphorbiaceae  Euphorbia cyparissias L.  X  X
Fabaceae  Lotus corniculatus L.  X  X
Fabaceae  Medicago lupulina L.  X
Fabaceae  Medicago sativa L.  X
Fabaceae  Melilotus alba Medikus  X  X
Fabaceae  Melilotus officinalis (L.) Pallas  X
Fabaceae  Trifolium pratense L.  X  X
Fabaceae  Vicia cracca L.  X
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>X</th>
<th>Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fabaceae</td>
<td><em>Vicia tetrasperma</em> (L.) Moench</td>
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<td><em>Glechoma hederacea</em> L.</td>
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<td>Lamiaceae</td>
<td><em>Leonurus cardiaca</em> L.</td>
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<td>Lamiaceae</td>
<td><em>Mentha × piperita</em> L.</td>
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<td>Lamiaceae</td>
<td><em>Nepeta cataria</em> L.</td>
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<td>Lamiaceae</td>
<td><em>Lythrum salicaria</em> L.</td>
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<td>X</td>
</tr>
<tr>
<td>Orchidaceae</td>
<td><em>Epipactis helleborine</em> (L.) Crantz</td>
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<tr>
<td>Papaveraceae</td>
<td><em>Chelidonium majus</em> L.</td>
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<td>Plantaginaceae</td>
<td><em>Plantago lanceolata</em> L.</td>
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<td>X</td>
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<tr>
<td>Plantaginaceae</td>
<td><em>Plantago major</em> L.</td>
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<td>Polygonaceae</td>
<td><em>Rumex crispus</em> L.</td>
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<td>Ranunculaceae</td>
<td><em>Ranunculus acris</em> L.</td>
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<td>Rubiaceae</td>
<td><em>Galium verum</em> L.</td>
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<td>Solanaceae</td>
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</table>

Total species: 32

487
488
489
490
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.

<table>
<thead>
<tr>
<th>Data</th>
<th>Phylogenetic distance</th>
<th>Proportion of Leaves Damaged</th>
<th>Leaf Area Damaged</th>
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<tr>
<td></td>
<td>df</td>
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<td>p</td>
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<td>Common Garden</td>
<td>All native taxa</td>
<td>1,30</td>
<td>0.030</td>
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<td></td>
<td>Native family taxa</td>
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<td></td>
<td>Closest native</td>
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<td>0.000</td>
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<tr>
<td>Survey</td>
<td>All native taxa</td>
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<td></td>
<td>Native family taxa</td>
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<td>5.299</td>
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<td>Closest native</td>
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<td>1.939</td>
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<td>All native taxa</td>
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<td>Native family taxa</td>
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<td></td>
<td>Closest native</td>
<td>1,50</td>
<td>0.341</td>
</tr>
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</table>
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

Proportion of leaves damaged vs. Distance to all native species (ln(MYa))

Proportion of leaf area damaged vs. Distance to native family members (ln(MYa))

Proportion of leaf area damaged vs. Distance to closest native species (ln(MYa))
Figure 2

(a) Proportion of leaves damaged vs. distance to all native species (ln(MYa)).
(b) Proportion of leaf area damaged vs. distance to native family members (ln(MYa)).
(c) Proportion of leaf area damaged vs. distance to closest native species (ln(MYa)).