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Invasive exotic plants suffer less herbivory than non-invasive exotic plants

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We surveyed naturally occurring leaf herbivory in nine invasive and nine non-invasive exotic plant species sampled in natural areas in Ontario, New York and Massachusetts, and found that invasive plants experienced, on average, 96% less leaf damage than non-invasive species. Invasive plants were also more taxonomically isolated than non-invasive plants, belonging to families with 75% fewer native North American genera. However, the relationship between taxonomic isolation at the family level and herbivory was weak. We suggest that invasive plants may possess novel phytochemicals with anti-herbivore properties in addition to allelopathic and anti-microbial characteristics. Herbivory could be employed as an easily measured predictor of the likelihood that recently introduced exotic plants may become invasive.

Keywords: herbivory; invasive plants; introduced plants; alien plants; enemy release hypothesis

1. INTRODUCTION

Exotic plants are notorious for the damage they can do to natural communities. However, of the thousands of exotic plants established in North America, only a small proportion have become major pests in natural areas by forming monocultures and displacing native species (Williamson & Fitter 1996; Lockwood *et al*. 2001). The rest simply become naturalized and, although they may be widespread, they remain minor members of their new communities. The ability to predict which new exotic plants pose the greatest risk to native communities, and which will merely join the local flora with little impact, is crucial if we wish to develop proactive control strategies for emerging invaders (Mack 1996).

Although many studies have searched for common traits among invasive exotic plants, these studies have typically involved life-history traits rather than interactions between the plants and their natural enemies (Mack 1996). This does not reflect the belief that enemies have little influence on invasions. On the contrary, the idea that the success of introduced plants can be attributed to a lack of enemies in their new ranges—the enemy release hypothesis—has inspired a wealth of studies (Keane & Crawley 2002; Agrawal & Kotanen 2003 and references therein). The results of these studies have been mixed. Exotic plants sometimes experience considerably more

herbivory in their new ranges than expected, which is often interpreted as lack of support for the enemy release hypothesis. However, comparisons of herbivory on exotics and natives typically overlook the invasiveness status of the exotic plants. In two recent exceptions, plants that were more invasive tended to have fewer pathogens (Mitchell & Power 2003) and less leaf herbivory (Carpenter & Cappuccino 2005).

In the present study, we investigate the leaf herbivory of highly invasive plants and non-invasive plants to further test the hypothesis that invasiveness is negatively correlated with herbivory. We also test the hypothesis that taxonomically isolated species are more invasive than exotics with many native relatives (Lockwood *et al*. 2001).

2. MATERIAL AND METHODS

Nine terrestrial invasive plant species were chosen from a list of natural-area weeds published online by the USDA Forest Service (2004) Eastern Region (http://www.fs.fed.us/r9/wildlife/range/weed/index.php). The nine species were listed by the Forest Service as category 1, 'highly invasive plants that invade natural habitats and replace native species', or category 2, 'moderately invasive [plants] replacing native species…in local areas' (table 1). We also chose nine non-invasive plants that were not included in the list or included as either category 3, 'widespread non-native species' that are 'not especially invasive in undisturbed natural habitats', or category 4, 'plants of local concern' that are 'not currently known to be especially invasive' (table 1).

As an additional measure of invasiveness, we used Mitchell & Power's (2003) method to estimate the invasiveness of our 18 species (table 1). This involved a tally of American states in which a plant is listed as affecting natural areas according to the compilation of the Alien Plant Working Group (http://www.nps.gov/plants/alien/list/all.htm). The nine plants we designated as invasive were listed by 19–27 states (median $=22$), whereas those we considered to be non-invasive were listed by 0–15 states (median $=4$; table 1).

We included all species from the Forest Service category 1 list that were available, excluding only those that were included in our earlier study (three species), those that were fully aquatic (four species) and those that duplicated genera already included (six species). Our choice of 18 species from 17 families (table 1) allowed us to address how invasive species differ from non-invasive species in degree of taxonomic isolation. Higher taxonomic levels were not disproportionately represented in either invasiveness category (table 1). Two species of *Centaurea* were included because of our interest in the comparative ecology of invasive and non-invasive knapweed species.

In July and August 2004, plants were sampled from natural areas in the vicinity of Ottawa, Ontario, Canada; northern and central New York State, USA and eastern Massachusetts, USA (table 1). We tried to find two populations of each species that were separated by at least 5 km; however, three species were sampled from one site only (table 1). We randomly chose one leaf from each of 20 individuals from each population. The leaves were scanned using imaging software (Scion Image Beta 4.02, Scion Corporation, Frederick, Maryland, USA, http://www.scion-corp.com) to measure total leaf area and area damaged by chewing, gall-making or mining insects (O'Neal *et al*. 2002). Where two sites were sampled, a single damage measurement averaged over both sites was used in the analyses.

We consulted the USDA Plants Database (http://plants.usda.gov/; USDA 2004) to determine the number of congeners native to the continental United States for each exotic species, as well as the number of native confamilial genera. A genus was considered native if it contained at least one native species.

The three continuous response variables—the per cent of leaf damage, the number of native congeners and the number of native confamilial genera—were not normally distributed and their non-normality was not remedied by transformation. Non-parametric Wilcoxon tests were performed to address the difference between invasive and non-invasive exotics in the mean per cent of leaf damage, the number of native congeners and the number of native confamilial genera. The two *Centaurea* species were omitted from analyses involving taxonomy because they were purposely paired and are equivalent in degree of taxonomic isolation. Spearman's rank correlation was performed to examine relationships between

Table 1. Taxonomic affinities, invasiveness scores and sampling sites of nine invasive and nine non-invasive species sampled for leaf herbivory in July and August 2004.

species[a]	family	subclass	USDA-FS invasiveness category[b]	invasiveness category for our analyses	states listing plant as invasive[c]	number of samples taken	location of samples[d]
Berberis thunbergii DC	Berberidaceae	Magnoliidae	1	invasive	21	2	NY, MA
Celastrus orbiculatus Thunb.	Celastraceae	Rosidae	1	invasive	22	2	ON, MA
Centaurea biebersteinii DC. (the equivalent of *C. maculosa* Lam.)	Asteraceae	Asteridae	1	invasive	26	2	ON, NY
Elaeagnus umbellata Thunb.	Elaeagnaceae	Rosidae	1	invasive	22	2	NY, MA
Euphorbia esula L.	Euphorbiaceae	Rosidae	1	invasive	19	2	ON
Lonicera tatarica L.	Caprifoliaceae	Asteridae	1	invasive	21	2	ON
Lythrum salicaria L.	Lythraceae	Rosidae	1	invasive	27	2	ON
Rhamnus cathartica L.	Rhamnaceae	Rosidae	1	invasive	23	2	ON
Vinca minor L.	Apocynaceae	Asteridae	2	invasive	25	2	ON, NY
Campanula rapunculoides L.	Campanulaceae	Asteridae	3	non-invasive	1	2	ON
Centaurea jacea L.	Asteraceae	Asteridae	—	non-invasive	4	1	ON
Malus pumila P. Mill.	Rosaceae	Rosidae	—	non-invasive	8	2	ON, NY
Malva sylvestris L.	Malvaceae	Dilleniidae	—	non-invasive	1	1	ON
Medicago sativa L.	Fabaceae	Rosidae	3	non-invasive	7	1	ON
Origanum vulgare L.	Lamiaceae	Asteridae	—	non-invasive	0	2	ON
Rumex crispus L.	Polygonaceae	Caryophyllidae	3	non-invasive	15	2	ON
Solanum dulcamara L.	Solanaceae	Asteridae	3	non-invasive	8	2	ON
Viburnum opulus L. var. *opulus*	Adoxaceae	Asteridae	4	non-invasive	3	2	ON

[a] Taxonomy according to the USDA Plants Database (http://plants.usda.gov/; USDA 2004), which follows Cronquist, A. 1981. An integrated system of classification of flowering plants. The New York Botanical Garden. New York: Columbia University Press.
[b] USDA Forest Service (2004) Eastern Region Invasiveness categories (http://www.fs.fed.us/r9/wildlife/range/weed/Sec3B.htm): category 1: highly invasive plants that 'invade natural habitats and replace native species'; category 2: moderately invasive species; category 3: widespread non-native species that are 'not especially invasive' and category 4: plants of local concern that are 'not currently known to be invasive'. Dashes indicate species that were not on the USDA-Forest Service list.
[c] The number of American states in which species is listed as an invasive plant affecting natural areas according to the Alien Plant Working Group of the Plant Conservation Alliance (http://www.nps.gov/plants/alien/list/all.htm).
[d] ON: within 50 km of Ottawa, Ontario, Canada; NY: Tompkins or Jefferson County, New York, USA and MA: Norfolk or Plymouth County, Massachusetts, USA.

invasiveness (number of state lists a species occurs on), leaf damage and the two taxonomic variables.

3. RESULTS
Leaf damage on invasive exotic plants was similarly low at the two sampling sites for each species, even when those sites were as distant as Ottawa and eastern Massachusetts (*ca* 500 km). With the exception of *Berberis thunbergii*, which suffered 5.27% leaf herbivory in Massachusetts and only 0.36% in upstate New York, damage to the invasive species was always less than 1.0%. On the other hand, all of the non-invasive exotics, with the exception of *Campanula rapunculoides* at one site, experienced leaf damage greater than 1.0%. The nine invasive species suffered significantly less damage than the non-invasive species (figure 1; Wilcoxon test: chi square $=10.39$, d.f.$=1$, $p=0.0013$). In addition, plants listed by more states experienced less damage than those listed by fewer states (Spearman's rho$=-0.659$, $p=0.003$, $N=18$).

Invasive species did not have fewer native congeners than non-invasive species (Wilcoxon test: chi square$=0.07$, d.f.$=1$, $p=0.791$). However, invasive species belonged to families with fewer native genera than non-invasive species (figure 2; Wilcoxon test: chi square $=5.11$, d.f.$=1$, $p=0.024$). Plants listed by many states did not have significantly fewer native congeners (Spearman's rho$=-0.014$, $p=0.956$, $N=16$), nor did they belong to families with fewer native genera (Spearman's rho$=-0.333$, $p=0.178$, $N=16$).

The relationship between herbivore damage and the number of native congeners was not statistically significant (Spearman's rho$=0.09$, $p=0.739$, $N=16$). The relationship between herbivore damage and the number of native genera, although positive, was likewise non-significant (Spearman's rho$=0.421$, $p=0.104$, $N=16$).

4. DISCUSSION
A small but important fraction of exotic plants become highly aggressive invaders that have strong negative impacts on native species (Williamson & Fitter 1996). Most exotic plants, however, are non-invasive, minor members of local plant communities (Ortega & Pearson 2005). Our study highlights a potentially important difference between these two types of plants: highly invasive exotic plants suffered substantially lower leaf herbivory than non-invasive plants.
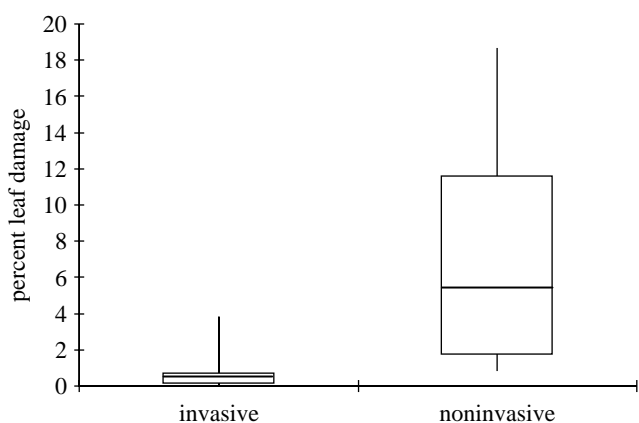
Figure 1. Per cent leaf damage of nine invasive and nine non-invasive exotic plants. Boxplots depict medians, 25th and 75th percentiles and minimum and maximum values.
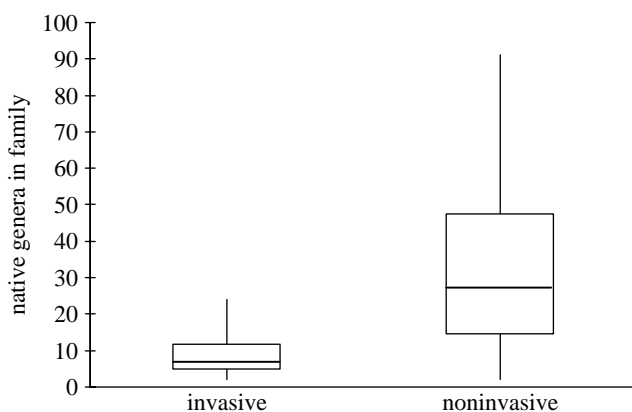

Figure 2. The number of native genera in the families of eight invasive and eight non-invasive exotic plants. Boxplots depict medians, 25th and 75th percentiles and minimum and maximum values.

Our comparison of herbivory on aggressive invaders and non-invasive exotic plants sheds light on the mixed results observed in tests of the enemy release hypothesis (Keane & Crawley 2002; Agrawal & Kotanen 2003). These mixed results may stem, in part, from the inclusion of non-invasive species, which escape herbivory to a lesser extent than highly invasive species. In one of the few studies that have considered differences in the invasiveness level of exotic plants, Mitchell & Power (2003) found that greater release from fungal pathogens was correlated with greater invasiveness in 473 European plant species naturalized in the United States. Likewise, our previous work revealed a negative correlation between herbivory and invasiveness (Carpenter & Cappuccino 2005).

Although it would be tempting to conclude that lack of herbivory is the key to the success of the highly invasive plants included in our study, we have not established a link between herbivory and plant performance. Evidence of successful biological control using enemies imported from the plants' native ranges would support the claim that herbivores matter. Biological control has been attempted for three of our species: purple loosestrife *Lythrum salicaria*, leafy spurge *Euphorbia esula* and spotted knapweed *Centaurea biebersteinii* (the equivalent of *Centaurea maculosa*). Control of purple loosestrife by

the leaf beetles *Galerucella calmariensis* and *Galerucella pusilla*, released in the mid 1990s, has been quite successful: at some release sites, native plant diversity has rebounded, as has use of the areas by nesting birds (Blossey *et al.* 2001). In the Ottawa region, the defoliation of loosestrife approaches 100% in many sites, so we were forced to move beyond the current range of the intentionally released *Galerucella* beetles to sample herbivory by other organisms.

Biological control of leafy spurge has been less successful, being achieved in some habitats but not others (Harris 1993). Control of spotted knapweed has not been achieved despite the release of 11 agents (Müller-Schärer & Schroeder 1993). Allelopathy, not enemy release, may be an important mechanism driving the enormous success of this species (Hierro & Callaway 2003). The allelopathic aggression of spotted knapweed has inspired Callaway & Ridenour's (2004) novel weapons hypothesis, which states that novel phytochemical compounds, to which native plants and soil organisms are not adapted, give some exotic plants a dramatic advantage in their new range. Of our nine highly invasive plants, evidence of allelopathy has been detected only in *C. biebersteinii* (the equivalent of *C. maculosa*) and a congener of *Euphorbia esula* (Alsaadawi *et al.* 1990). While we cannot exclude the possibility that some of the others possess strong allelopathic compounds as well, low herbivory indicates that they may possess novel defensive compounds, instead of, or in addition to, novel allelopathic agents. These hypotheses are complementary and could perhaps be combined under the umbrella of a 'novel phytochemistry hypothesis': exotic plants with potent secondary compounds that are unique or underrepresented in the plants' new range are more likely to become highly invasive.

Rather than conferring a single advantage on the plants that possess them, some novel phytochemicals may have multiple activities, protecting plants from herbivores as well as altering soil microbial communities and increasing competition via allelopathy. Examples of phytochemicals with multiple activities include cnicin in spotted knapweed (Kelsey & Locken 1987; Landau *et al.* 1994), glucosinolates in the Brassicaceae (Siemens *et al.* 2002) and monoterpenes in *Thymus vulgaris* (Linhart & Thompson 1999). If potent novel phytochemistry commonly manifests itself through multiple biological activities, leaf herbivory could be a useful proxy for allelopathy or antimicrobial activity in predicting invasiveness because it is simple to measure.

An even simpler attribute to measure is taxonomic isolation, which requires nothing more than counting native relatives. Lockwood *et al.* (2001) showed that taxonomic isolation is a good predictor of exotic plant invasiveness, possibly because it reflects phytochemical isolation. Taxonomic isolation has been shown to influence the size of the insect fauna of introduced trees; trees with fewer native relatives accumulate fewer herbivores than trees with many close relatives in their introduced range (Connor *et al.* 1980). Our results suggest that isolation at the family level is more important than isolation at the generic level. However, taxonomic isolation was not as strongly

associated with invasiveness as herbivory and the relationship between herbivory and taxonomic isolation was weak. Although taxonomic isolation might be indicative of phytochemical isolation in general, plants with many native relatives might nevertheless possess unique phytochemical adaptations. Spotted knapweed *Centaurea biebersteinii* (the equivalent of *C. maculosa*) is a good example. As a member of the Asteraceae, the largest North American plant family, it is not taxonomically isolated. However, it is highly isolated phytochemically; its allelopathic agent is a rare compound, (−)-catechin, which occurs in only a few other plants (Callaway & Ridenour 2004). Because of the possibility that other exotic plants from families with a large native contingent are similarly phytochemically unique, it would seem wiser to use phytochemistry or, as a proxy that is relatively easy to measure, herbivory to predict the invasiveness of newly introduced plants.

Over time, native organisms should adapt to even the most uniquely defended introduced plants. Within native herbivore populations, selection to utilise exotic hosts can be rapid (Singer *et al.* 1993; Thompson 1998). As the native biota adapts to an introduced plant, the plant's invasiveness might be expected to decline. Information on the original invasiveness levels of plants that were introduced to North America by the earliest European colonists is, unfortunately, lacking, largely because we have only recently become concerned with the phenomenon of exotic plants invading intact natural communities. Many of these earliest arrivals are considered by modern accounts to be less invasive than recently arrived plants; however, Carpenter & Cappuccino (2005) found no relationship between the date of introduction and herbivory. Greater pathogen attacks or decreased allelopathic effects as native plants adapted to the exotics cannot be ruled out to explain the lower invasiveness of longstanding exotics.

Agrawal, A. A. & Kotanen, P. M. 2003 Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol. Lett.* **6**, 712–715.

Alsaadawi, I. S., Sakeri, F. A. K. & Al-Dulaimy, S. M. 1990 Allelopathic inhibition of *Cynodon dactylon* (L.) Pers. and other plant species by *Euphorbia prostrata* L. *J. Chem. Ecol.* **16**, 2747–2754.

Blossey, B., Skinner, L. C. & Taylor, J. 2001 Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodivers. Conserv.* **10**, 1787–1807.

Callaway, R. M. & Ridenour, W. M. 2004 Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* **2**, 419–426.

Carpenter, D. & Cappuccino, N. 2005 Herbivory, time since introduction and the invasiveness of exotic plants. *J. Ecol.* **93**, 215–321.

Connor, E. F., Faeth, S. H., Simberloff, D. & Opler, P. 1980 Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecol. Entomol.* **5**, 205–211.

Harris, P. 1993 Effects, constraints and the future of weed biocontrol. *Ag. Ecosyst. Env.* **46**, 289–303.

Hierro, J. L. & Callaway, R. M. 2003 Allelopathy and exotic plant invasion. *Plant Soil* **256**, 25–39.

Keane, R. M. & Crawley, M. J. 2002 Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170.

Kelsey, R. G. & Locken, L. J. 1987 Phytotoxic properties of cnicin, a sesquiterpene lactone from *Centaurea maculosa* (spotted knapweed). *J. Chem. Ecol.* **13**, 19–33.

Landau, I., Müller-Schärer, H. & Ward, P. I. 1994 Influence of cnicin, a sesquiterpene lactone of *Centaurea maculosa* (Asteraceae), on specialist and generalist insect herbivores. *J. Chem. Ecol.* **20**, 929–942.

Linhart, Y. B. & Thompson, J. D. 1999 Thyme is of the essence: biochemical polymorphism and multi-species deterrence. *Evol. Ecol. Res.* **1**, 151–171.

Lockwood, J. L., Simberloff, D., McKinney, M. L. & Von Holle, B. 2001 How many, and which, plants will invade natural areas. *Biol. Invasions* **3**, 1–8.

Mack, R. M. 1996 Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.* **78**, 107–121.

Mitchell, C. E. & Power, A. G. 2003 Release of invasive plants from fungal and viral pathogens. *Nature* **421**, 625–627.

Müller-Schärer, H. & Schroeder, D. 1993 The biological control of *Centaurea* spp in North America: do insects solve the problem? *Pesticide Sci.* **37**, 343–353.

O'Neal, M. E., Landis, D. A. & Isaacs, R. 2002 An inexpensive, accurate method for measuring leaf area and defoliation through digital image analysis. *J. Econ. Entomol.* **95**, 1190–1194.

Ortega, Y. K. & Pearson, D. E. 2005 Weak versus strong invaders of natural plant communities: assessing invasibility and impact. *Ecol. Appl.* **15**, 651–661.

Siemens, D. H., Garner, A. S., Mitchell-Olds, T. & Callaway, R. M. 2002 Cost of defense in the context of plant competition: *Brassica rapa* may grow and defend. *Ecology* **83**, 505–517.

Singer, M. C., Thomas, C. D. & Parmesan, C. 1993 Rapid human-induced evolution of insect–host associations. *Nature* **366**, 681–683.

Thompson, J. N. 1998 Rapid evolution as an ecological process. *Trends Ecol. Evol.* **13**, 329–332.

USDA Forest Service. 2004. Eastern Region invasive plants, ranked by degree of invasiveness as based on information from states. http://www.fs.fed.us/r9/wildlife/range/weed/?open=Sec3B.htm. Eastern Region-R9, Milwaukee, WI, USA.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov), National Plant Data Center, Baton Rouge, LA, USA.

Williamson, M. & Fitter, A. 1996 The varying success of invaders. *Ecology* **77**, 1661–1666.