Relatedness predicts phenotypic plasticity in plants better than weediness

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ABSTRACT

Background: Weedy non-native species have long been predicted to be more phenotypically plastic than native species.

Question: Are weedy non-native species more plastic than natives?

Organisms: Fourteen perennial plant species: *Acer platanoides*, *Acer saccharum*, *Bromus inermis*, *Bromus latiglumis*, *Celastrus orbiculatus*, *Celastrus scandens*, *Elymus repens*, *Elymus trachycaulus*, *Plantago major*, *Plantago rugelii*, *Rosa multiflora*, *Rosa palustris*, *Solanum dulcamara*, and *Solanum carolinense*.

Field site: Mesic old-field in Dryden, NY (42°27′49″N, 76°26′40″W).

Methods: We grew seven pairs of native and non-native plant congeners in the field and tested their responses to reduced competition and the addition of fertilizer. We measured the plasticity of six traits related to growth and leaf palatability (total length, leaf dry mass, maximum relative growth rate, leaf toughness, trichome density, and specific leaf area).

Conclusions: Weedy non-native species did not differ consistently from natives in their phenotypic plasticity. Instead, relatedness was a better predictor of plasticity.

Keywords: comparative ecology, competition, fertilization, old-field communities, phenotypic plasticity, plant invasion.

INTRODUCTION

Non-native species can negatively impact native ecosystems and are a source of concern for ecologists, land managers, and policy makers (Vitousek *et al.*, 1996; Lodge *et al.*, 2006). Biologists often try to identify traits of successful non-native species to understand the factors that have contributed to their success and to detect potential invaders before they become problematic (Mack, 1996; Lodge *et al.*, 2006). Phenotypic plasticity, an organism's ability to alter its phenotype in response to the environment, has been implicated as a potential characteristic of 'weeds' for almost 50 years (Baker, 1965; Richards *et al.*, 2006). Plasticity may aid in the establishment and spread of non-native species by allowing them to respond adaptively

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to the novel abiotic and biotic conditions in the introduced range (Bradshaw, 1965; Schlichting and Levin, 1986).

However, other plant characteristics may better predict variation in plasticity among species. One alternative hypothesis is that closely related species show more similar patterns of plasticity than distantly related species, regardless of non-native or invasive status (i.e. plasticity is evolutionarily conserved). Some evidence for this idea comes from Hoffmann and Franco (2003), who measured leaf trait plasticity in tropical forest and savanna species pairs, and found that genus explained up to 69% of the variation in plasticity among species. In another study, Kembel and Cahill (2005) combined data across 102 species from multiple families and found a strong signal of phylogenetic conservatism in how the species responded with root proliferation to soil nutrients patches (though not in other traits).

To address whether non-native weedy species are more plastic than native species, as well as account for variation in plasticity that is due to evolutionary history, we require comparisons of related species that differ in weediness. We conducted a field experiment using seven pairs of native and non-native congeners from six different plant families. We determined the plasticity of plants to four environments (a 2×2 factorial manipulation of competition and nutrients). We chose to manipulate competition and nutrients because successful non-native species are thought to respond strongly to human disturbance, which often reduces competition and increases nutrient availability in the environment (Hobbs and Huenneke, 1992; Davis et al., 2000). We used congeneric pairs to minimize variation in the comparison of weedy non-natives and related natives (Agrawal et al., 2005) and because each congeneric pair represents a phylogenetically independent test of the hypothesis that non-native weeds are more plastic than natives.

METHODS

Species

We employed seven congeneric pairs (Table 1) of natives and non-natives (non-natives listed first in all cases): *Acer platanoides* and *A. saccharum* (Aceraceae), *Bromus inermis* and *B. latiglumis* (Poaceae), *Celastrus orbiculatus* and *C. scandens* (Celastraceae), *Elymus repens* and *E. trachycaulus* (Poaceae), *Plantago major* and *P. rugelii* (Plantaginaceae), *Rosa multiflora* and *R. palustris* (Roaceae), and *Solanum dulcamara* and *S. carolinense* (Solanaceae). All species occur in Tompkins County, New York (USA) where the experiment was conducted. Also, all the species can be found in old-fields or around field margins and thus grow in habitats similar to our experimental conditions.

Analyses of how plasticity facilitates the establishment and spread of non-native species can focus on either invasive/native or invasive/non-invasive non-native comparisons (Richards et al., 2006). The latter approach asks why some non-native species become invasive and others do not, and whether plasticity contributes to this difference (Richards et al., 2006). In contrast, we chose to test weedy non-native species against native species because we were interested in how differential plasticity impacts plant performance in this primarily native plant community.

The species pairs were selected for several reasons. First, the congeners have similar habitats, morphologies, and life histories (see Appendix), but are native to different continents. All the non-native species have been described as 'invasive' in the scientific

literature and are considered 'noxious' species in the USDA Plants Database (available at: http://plants.usda.gov/). However, the 'invasive' moniker is becoming increasingly controversial (Brown and Sax, 2004; Davis *et al.*, 2011), so we have instead employed the terms non-native and weedy to describe the species studied here. There is some evidence that *Acer platanoides* (Wyckoff and Webb, 1996; Reinhart, 2003), *Bromus inermis* (Otfinowski *et al.*, 2007; Dillemuth *et al.*, 2009), and *Rosa multiflora* (Meiners *et al.*, 2001) are highly invasive in that they can displace native vegetation. The remaining non-native species may be more appropriately called weedy because they grow vigorously and spread rapidly, particularly in disturbed environments, but it is unknown whether they displace native species (Palmer and Sagar, 1963; Hawthorn, 1974; Dreyer *et al.*, 1987; Steward *et al.*, 2003; Moffatt *et al.*, 2004).

We mostly used field-collected seeds from Tompkins County (New York, USA) and southern Ontario (Canada) to establish our experimental plants. Seeds for woody species (*Celastrus*, *Acer*, and *Rosa*) were surface-sterilized in 10% bleach for 10 min, sprayed with fungicide to prevent moulding (Ortho Multi-Purpose Fungicide; Daconil 2787), and cold-stratified (4°C) for 2.5 months to break dormancy. Non-woody seeds were cold-stratified for one week. All seeds germinated in moist petri dishes on a sunny windowsill.

In mid-May 2007, we sowed individual seedlings into 500 mL pots filled with potting soil (Pro-mix 'BX' with biofungicide, Premier, Quakertown, PA) and grew the species in a hoop house. Seeds for three of the woody species did not germinate, including both *Acer* species and the native *Celastrus scandens*. To compensate, we collected naturally germinated *Acer* seedlings at the cotyledon stage from beneath adult trees. We purchased *Celastrus scandens* seedlings from a nursery that specializes in local, native plants (Plantsmens Nursery, Groton, NY). These seedlings were planted in the hoop house with the other experimental seedlings.

Environments

Our field site was a mesic, abandoned agricultural field in Dryden, NY (42°27′49″N, 76°26′40″W) that was fenced to exclude deer. The resident vegetation in the entire field was initially and uniformly trimmed to a height of 0.25 m. This field was then divided into 0.75×0.75 m plots ($N = 612$) and environmental manipulations were applied randomly to each individual plot. We used a 2×2 full factorial design such that some plots received no manipulation (control), some received either fertilizer or reduced competition, and others received both fertilizer and reduced competition.

To achieve 'low-competition' treatments, we sprayed herbicide (2% glyphosate, Monsanto) to kill all vegetation 2 weeks before planting and maintained low competition throughout the experiment by clipping weeds at the soil surface (Fig. 1). We did not uproot weeds to avoid additional soil disturbance. To achieve 'high competition' plots we did not control the surrounding vegetation (Fig. 1), because we wanted to employ a competitive environment that was more realistic and more closely matched conditions in which these species naturally grow. Although realism trades off with control, our treatments and plants were arrayed randomly throughout the field, so we do not believe we introduced any bias due to differential growth of the naturally occurring vegetation. For 'high nutrient' plots, we placed slow-release fertilizer (~16 g Osmocote Vegetable & Bedding Smart-Release Plant Food; 14:14:14 N:P:K, Scotts Company) at the base of each experimental seedling's root ball as it was planted. The 'low nutrient' plots received no fertilizer. In June 2007, we

Fig. 1. A photograph of two adjacent experimental plots, both containing an individual *Plantago* sp. On the left is a high competition plot, and on the right a reduced competition plot. Arrows indicate the experimental plant.

planted a single individual plant in the middle of each plot. We assumed that mortality within the first 2 weeks was due to transplant stress and replaced dead seedlings with plants of equal age.

Replication

Replication depended on germination and survival rates, but was generally comparable within a genus ($N = 612$ plants in total; see Appendix). *Rosa* and *Bromus* spp. had low replication, so we planted these species randomly with respect to treatment and species in a small block to minimize spatial variation. The remaining 12 species were arrayed randomly with respect to treatment and species in a much larger block that was directly adjacent to the *Bromus* and *Rosa* block. We ran the statistical analyses without *Rosa* and *Bromus* to determine whether the block effect qualitatively changed the results. As it did not, we included them with the rest of the data in the final analysis.

Traits

To assess phenotypic plasticity of the plants in the different environments, we measured six traits representing plant growth (maximum growth rate (RGR_{max}), total plant length, total leaf biomass, specific leaf area (SLA)), and palatability to herbivores (leaf toughness and trichome density; SLA also affects palatability). Successful non-native species were predicted to respond strongly to the increased nutrient availability that results from increased soil fertility and reduced competition (Davis *et al.*, 2000). Changes in growth traits in response to the environmental manipulations should reflect this ability to capitalize on nutrient flushes. We were also interested in how leaf palatability traits would change in

response to the environmental manipulations, as the success of non-natives has also been attributed partly to release from the natural enemies that regulate plant growth in the native range (Keane and Crawley, 2002). Enemy release may interact with resource availability to facilitate the spread of non-native plants, because plants in high-nutrient environments can be more palatable/less defended and thus benefit more from enemy release (Blumenthal, 2006).

To measure RGR_{max} we calculated changes in height (or in leaf length for *Plantago* spp.) that occurred between six sampling dates (planting date, 8 July, 17 July, 1 August, 27 August, harvest date), using the formula:

$$RGR_i = \frac{ht_t - ht_{t-1}}{ht_{t-1}} \times \frac{1}{\text{days}}.$$

This resulted in five measures of *RGR*. In our statistical model, we used the highest measure (RGR_{max}) for each plant. *Total plant length* is a measure of the spread of a plant, either how much it branches or how broad its footprint is on the soil. For most plants, total length was the cumulative length of all branches on a plant, except for the grasses (*Elymus* spp. and *Bromus* spp.), for which total length is equal to plant height, and *Plantago* spp., for which total length is the length of the longest leaf in each rosette. *Total leaf biomass* is a measure of primary productivity and plant performance. We collected leaf biomass in September to October, when plants had reached peak growth, and species within each genus were always harvested at the same time. We dried the tissue in drying ovens (65°C, 4 days) before weighing it to the nearest 0.001 g. *Toughness* affects palatability to herbivores, indicates leaf structural investment, and tends to decrease in shade or with fertilizer (Coley, 1983; Hemmi and Jormalainen, 2002). We assessed the toughness of the youngest fully formed leaf on each plant using a penetrometer (Type 516, Chatillon Corp., NY), which records the amount of force needed to puncture a leaf. *Trichome density* is involved in resistance to herbivores and water relations, where hairy leaves are less damaged and lose less water via evapotranspiration (Woodman and Fernandes, 1991). To measure trichome density, we took a 29.29 mm² hole punch from the tip of the youngest fully expanded leaf, centred on the mid-vein and used a dissecting scope to count trichomes on the top and bottom of each fresh leaf disc. Only 10 of the 14 species had trichomes: *Acer* spp. and *Celastrus* spp. did not. *SLA* is a measure of leaf thickness. To measure *SLA* ($mm^2 \cdot mg^{-1}$), the leaf discs from the trichome count were dried at 45°C overnight and weighed to determine dry mass. Higher *SLA* values indicate thinner leaves and thinner leaves are expected in shaded conditions to maximize leaf area for light capture.

Analyses

We present two separate analyses. The first analysis examines plasticity indirectly to determine whether origin explains patterns of plasticity. The second analysis directly quantifies plasticity.

Analysis I: Does origin explain patterns of plasticity?

To account for both correlations among traits and the inflated risk of type I error due to multiple tests, we initially analysed all of the trait data with a multivariate analysis of variance (MANOVA). The main effects in the model included competition (low or high), nutrients (no addition or addition), origin (native or non-native), and genus (7 genera). The

MANOVA was followed by univariate analyses of variance (ANOVAs) in which we considered all effects as fixed. All analyses were conducted with JMP (Version 7, SAS Institute Inc., Cary, NC).

Note that this analysis does not directly quantify the magnitude of the plastic response, but rather focuses on interaction terms for evidence of plasticity. A significant main effect of origin (or genus) indicates that natives and weedy non-natives (or genera) differ in their trait *means*, while an origin × genus interaction indicates that *species* differ in their trait *means*. A significant main effect of competition or nutrients indicates that plasticity has occurred (i.e. the environmental manipulation impacted trait values). A significant origin × competition or origin × nutrients interaction indicates that natives and weedy non-natives differentially responded to the environmental manipulations, and would thus suggest that weediness is a good predictor of plasticity. A significant genus × competition or genus × nutrients interaction would suggest that genera vary in their plastic responses.

We excluded the four-way interaction and two of the three-way interactions because they were not significant in the MANOVA or the ANOVAs. We did not, however, exclude the genus × origin × environment interactions, because they were important to our interpretation of the results. If either of these three-way interactions was significant, that would indicate that species differed in their plasticity, and thus that plasticity was not conserved within genera.

Finally, because there were 12 tests each of the hypotheses that origin or genus best explained plasticity (i.e. 6 traits × 2 origin-by-environment terms or 6 traits × 2 genus-by-environment terms), we addressed the inflated risk of type I error with a binomial expansion test (Sokal and Rohlf, 1994).

For Analysis I, we ln + 1 transformed all data to improve the normality of the residuals and then standardized trait values by converting them to *z*-scores, using $(x_i - \mu_x)/\sigma$, where x_i is the data point, μ_x is the mean trait value for a given species, and σ is the standard deviation of that trait and species. We standardized the data to address two issues. First, we were concerned that the large variation in trait means across all 14 species would drive the patterns of plasticity we saw and obscure origin × environment interactions. Second, some of the traits (total length and RGR_{max}) were measured differently on different species, because of variation in morphology (i.e. rosettes vs. branching plants). Standardizing the traits within species would facilitate comparisons across species. Running the model with data that were not standardized did not change our final interpretation of our results.

Analysis II: Direct estimation of the plastic responses

Our indirect measure of plasticity depends on the genus × environment interaction term. If only one genus responded to the environmental manipulations, we would still detect a significant genus × environment interaction. Thus, to *directly* assess differences in plasticity, we also quantified the amount and direction of plasticity for each species using within-study factorial meta-analysis techniques (Gurevitch *et al.*, 2000; Van Zandt, 2007). While there are many metrics for quantifying plasticity (Valladares *et al.*, 2006), the metric employed in a factorial meta-analysis, Hedges' *d*, offers several advantages. First, Hedges' *d* corrects for sample size and sampling variance, so we were able to take into account the differences in replication among the species employed in this experiment. Second, Hedges' *d* measures the strength and direction of a trait response in units of standard deviation, making it easier to compare the plasticity of different traits on the same scale. One can also calculate 95% confidence intervals around a Hedges' *d* value to enable comparisons across traits and species.

Table 1. Multivariate analysis of variance on six plant traits

	Effect	d.f.	*F*	*P*
	whole model	**180**	**3.1**	**< 0.0001**
Did native or non-natives, or genera or	origin	6	0.9	0.499
species, differ in trait means?	**genus**	**24**	**4.3**	**< 0.0001**
	genus × origin	24	1.5	0.054
Did the traits respond to competition	**competition**	**6**	**9.6**	**< 0.0001**
or nutrients?	**nutrients**	**6**	**9.8**	**< 0.0001**
	competition × nutrients	6	1.9	0.073
Did native and non-natives differ	origin × competition	6	0.7	0.648
in plasticity?	origin × nutrients	6	0.7	0.631
Did genera differ in plasticity?	**genus × competition**	**24**	**5.8**	**< 0.0001**
	genus × nutrients	**24**	**3.2**	**< 0.0001**
Did species within genus differ in	genus × origin × competition	24	0.6	0.934
plasticity?	genus × origin × nutrients	24	1.1	0.344

Note: *F*-values were approximated from Wilks' λ. Significant model factors are highlighted in **bold**.

RESULTS

The MANOVA (Table 1) indicated that plants responded to the environmental manipulations, and that competition and nutrients independently impacted plant traits. Natives and non-natives did not generally differ in plasticity (i.e. non-significant origin × competition and origin × nutrients terms). In contrast, relatedness was a good predictor of variation in plasticity (i.e. significant genus × competition and genus × nutrients interaction terms) and species within a genus had similar plasticity (non-significant genus × origin × environment interaction terms).

Univariate ANOVAs (Table 2) showed that plant traits responded plastically to the environmental manipulations. In response to reduced competition, the plants gained 73% more leaf mass (2.6 ± 0.2 g vs. 1.5 ± 0.1 g with competition; mean ± S.E.), grew 28% larger (total length: 72.5 ± 8.3 cm vs. 56.7 ± 5.8 cm), and produced 9% denser leaves (SLA: 19.7 ± 0.4 mm$^2 \cdot$mg^{-1} vs. 21.6 ± 0.5 mm$^2 \cdot$mg^{-1}). In response to the addition of fertilizer, plants grew 9% more rapidly (RGR_{max}: 0.038 ± 0.003 cm$\cdot$cm$^{-1}\cdot$day^{-1} vs. 0.035 ± 0.004 cm$\cdot$cm$^{-1}\cdot$day^{-1} without fertilizer) and produced 8% thinner leaves (SLA: 21.4 ± 0.5 mm$^2 \cdot$mg^{-1} vs. 19.9 ± 0.4 mm$^2 \cdot$mg^{-1}). They also produced 115% more leaf mass (2.8 ± 0.2 g vs. 1.3 ± 0.1 g) and grew 93% longer (total length: 85.5 ± 9.2 cm vs. 44.3 ± 4.3 cm).

As in the MANOVA, the univariate ANOVAs found that origin predicted very little of the plasticity. Natives and non-natives only differed significantly in the plasticity of specific leaf area to fertilizer addition and this single significant effect may have occurred due to chance (binomial expansion test, $P = 0.341$). Genus, in contrast, was a good predictor of the plasticity of total length, RGR_{max}, SLA, and trichomes in response to competition, and of plasticity of leaf mass (Fig. 2), total length, and RGR_{max} in response to nutrients (Table 2). Seven significant genus × environment effects are highly unlikely to have occurred by chance

Table 2. Results of ANOVA for five plant traits

	Effect	Trait	d.f.	*F*	*P*
Did traits respond to competition or nutrients?	competition	**leaf mass**	1	50.9	**< 0.0001**
		length	1	4.9	**0.028**
		relative growth rate	1	1.4	0.236
		specific leaf area	1	13.0	**0.0003**
		toughness	1	1.1	0.289
		trichomes	1	0.5	0.471
	nutrient	**leaf mass**	1	40.0	**< 0.0001**
		length	1	51.4	**< 0.0001**
		relative growth rate	1	16.1	**< 0.0001**
		specific leaf area	1	5.7	**0.018**
		toughness	1	2.4	0.123
		trichomes	1	3.0	0.084
	competition × nutrient	leaf mass	1	0.0	0.983
		length	1	1.0	0.327
		relative growth rate	1	2.2	0.138
		specific leaf area	1	3.3	0.069
		toughness	1	2.9	0.091
		trichomes	1	0.0	0.993
Did trait means differ among native and non-natives, among genera or among species?	origin	leaf mass	1	2.7	0.102
		length	1	0.4	0.531
		relative growth rate	1	0.9	0.353
		specific leaf area	1	0.0	0.926
		toughness	1	0.0	0.879
		trichomes	1	0.1	0.761
	genus	**leaf mass**	1	3.1	**0.005**
		length	1	3.4	**0.002**
		relative growth rate	1	5.3	**< 0.0001**
		specific leaf area	1	0.1	0.990
		toughness	1	0.3	0.922
		trichomes	1	7.1	**< 0.0001**
	genus × origin	leaf mass	1	0.7	0.622
		length	1	0.3	0.913
		relative growth rate	1	2.4	**0.028**
		specific leaf area	1	0.1	0.999
		toughness	1	0.1	0.998
		trichomes	1	0.2	0.957
Did native and non-natives differ in plasticity?	origin × competition	leaf mass	1	1.2	0.267
		length	1	0.1	0.783
		relative growth rate	1	2.3	0.128
		specific leaf area	1	0.4	0.530
		toughness	1	0.0	0.885
		trichomes	1	1.7	0.196

Table 2.—*continued*

	Effect	Trait	d.f.	*F*	*P*
	origin × nutrient	leaf mass	1	0.0	0.835
		length	1	0.0	0.965
		relative growth rate	1	0.2	0.654
		specific leaf area	1	6.1	**0.014**
		toughness	1	0.3	0.575
		trichomes	1	0.5	0.502
Did genera differ in plasticity?	genus × competition	leaf mass	1	1.4	0.232
		length	1	19.1	**< 0.0001**
		relative growth rate	1	2.3	**0.033**
		specific leaf area	1	3.6	**0.002**
		toughness	1	1.8	0.089
		trichomes	1	2.9	**0.021**
	genus × nutrient	**leaf mass**	1	6.5	**< 0.0001**
		length	1	5.6	**< 0.0001**
		relative growth rate	1	3.4	**0.003**
		specific leaf area	1	1.9	0.075
		toughness	1	1.2	0.311
		trichomes	1	2.4	0.0512
Did species within genera differ in plasticity?	genus × origin × competition	leaf mass	6	1.1	0.372
		length	6	1.1	0.337
		relative growth rate	6	1.0	0.401
		specific leaf area	6	1.9	0.077
		toughness	6	0.6	0.710
		trichomes	4	0.4	0.818
	genus × origin × nutrients	leaf mass	6	0.8	0.580
		length	6	1.5	0.164
		relative growth rate	6	0.8	0.600
		specific leaf area	6	1.6	0.156
		toughness	6	0.6	0.725
		trichomes	4	3.7	**0.006**

Note: Significant model factors highlighted in **bold**.

(binomial expansion test, *P* < 0.0001). Also, species within genera never varied in their trait plasticities, suggesting that plasticity may be evolutionarily conserved (Table 2).

When we directly quantified plasticity using Hedges' *d*, we again found highly variable plasticity across genera (Table 3, Fig. 3): the difference between the most negative and most positive plasticity for a given trait and environment ranged from 1.1 to 3.1 units of standard deviation (Table 3).
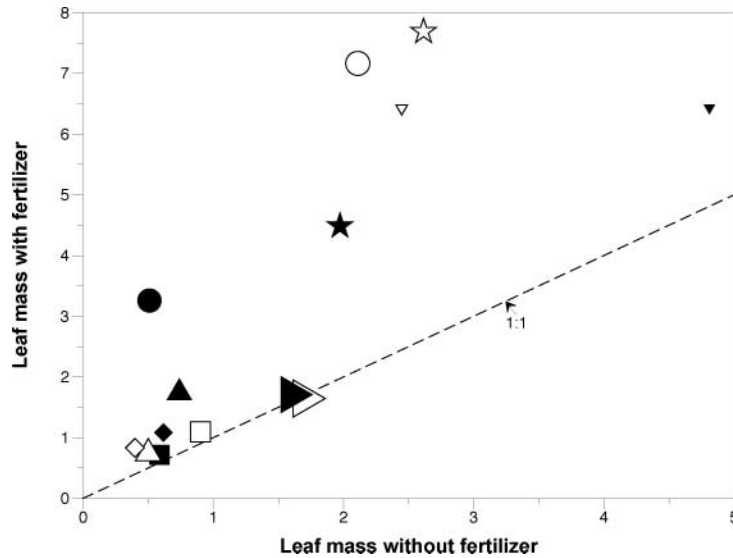
Fig. 2. Mean leaf mass in plots with fertilizer versus plots without fertilizer. Each point represents a species: open symbols = non-natives and closed symbols = natives. Congeneric pairs share symbols (*Acer* – squares, *Bromus* – circles, *Celastrus* – triangles, *Elymus* – diamonds, *Plantago* – large right-facing arrowheads, *Rosa* – small inverted triangles, *Solanum* – stars). The dashed line indicates a 1:1 line. If a point falls along this line, then that species had no plasticity of leaf mass to the fertilizer (i.e. equal leaf mass in fertilizer and no fertilizer treatments). Species within genus had similar plasticity (Table 2 ANOVA: genus × nutrients, $F = 6.5$, $P < 0.0001$). Within four genera (*Acer*, *Celastrus*, *Elymus*, and *Plantago*), the native and non-native pair cluster closely and show limited plasticity to fertilizer. For the remaining three genera, plasticity is larger and more variable within genus.

DISCUSSION

In this experiment, we employed seven pairs of native and weedy non-native plant congeners to determine whether origin predicted variation in plasticity among species. We found very little evidence that weedy non-natives were more plastic than related natives for the traits and environments tested. Instead, we found more evidence that genera differ in their plasticity, suggesting that plasticity may be conserved among related species.

Several recent analyses of plasticity in invasive species have reported results consistent with ours. Palacio-López and Gianoli (2011) conducted a meta-analysis of plasticity in 93 species pairs (of which 43% were congeneric pairs) and found that invasives were no more plastic than natives or non-invasive non-natives to light, nutrients, water, CO_2, herbivory or the presence of a climbing support upon which to grow. Godoy *et al*. (2011) examined plasticity to light and nutrients in 20 invasive–native pairs (of which 25% were congeners), and also found that invasives were not generally more plastic than natives. In contrast, Davidson *et al*. (2011) conducted a meta-analysis with 75 pairs of species, a quarter of which were congeners. They found that the invasives had higher plasticity than natives or non-invasive non-natives to nutrients, light, water, competition, disturbance, CO_2, presence of a climbing support, and presence of soil biota. Differences among these studies may be a function of the traits analysed, as plastic responses are specific to the traits measured and

Table 3. Direct measures of trait plasticity using Hedges' *d* in units of standard deviation

Trait	Genus	Species	Plasticity to C	Plasticity to N
Leaf mass	*Acer*	*platanoides*	1.113 (0.634, 1.592)	0.381 (−0.09, 0.852)
		saccharum	1.231 (0.735, 1.727)	0.514 (0.027, 1.001)
	Bromus	*inermis*	0.806 (−0.107, 1.718)	1.403 (0.472, 2.333)
		latiglumis	0.255 (−0.658, 1.168)	0.688 (−0.231, 1.607)
	Celastrus	*orbiculatus*	0.757 (−0.021, 1.535)	0.45 (−0.324, 1.223)
		scandens	1.397 (0.759, 2.036)	1.007 (0.377, 1.637)
	Elymus	*repens*	0.142 (−0.45, 0.735)	0.71 (0.113, 1.307)
		trachycaulus	0.428 (−0.124, 0.979)	0.35 (−0.201, 0.901)
	Plantago	*major*	0.678 (−0.049, 1.406)	−0.068 (−0.791, 0.655)
		rugelii	0.359 (−0.167, 0.884)	0.052 (−0.473, 0.576)
	Rosa	*multiflora*	1.26 (0.326, 2.194)	1.355 (0.418, 2.292)
		palustris	1.637 (0.425, 2.848)	0.631 (−0.542, 1.804)
	Solanum	*dulcamara*	0.187 (−0.321, 0.695)	1.237 (0.717, 1.757)
		carolinense	0.806 (0.29, 1.321)	0.906 (0.389, 1.423)
RGR	*Acer*	*platanoides*	0.257 (−0.202, 0.717)	0.074 (−0.385, 0.533)
		saccharum	−0.118 (−0.584, 0.347)	0.181 (−0.284, 0.647)
	Bromus	*inermis*	−0.032 (−0.936, 0.871)	0.973 (0.056, 1.889)
		latiglumis	0.173 (−0.695, 1.041)	0.721 (−0.154, 1.595)
	Celastrus	*orbiculatus*	−0.244 (−0.951, 0.464)	0.41 (−0.299, 1.119)
		scandens	0.61 (−0.013, 1.234)	0.891 (0.263, 1.518)
	Elymus	*repens*	−0.776 (−1.338, −0.214)	0.032 (−0.525, 0.588)
		trachycaulus	0.018 (−0.507, 0.542)	−0.099 (−0.623, 0.426)
	Plantago	*major*	0.337 (−0.381, 1.055)	−0.087 (−0.804, 0.63)
		rugelii	0.684 (0.165, 1.203)	−0.246 (−0.762, 0.27)
	Rosa	*multiflora*	0.063 (−0.85, 0.975)	0.112 (−0.8, 1.025)
		palustris	1.035 (−0.079, 2.149)	0.482 (−0.618, 1.581)
	Solanum	*dulcamara*	0.332 (−0.167, 0.831)	−0.078 (−0.577, 0.42)
		carolinense	0.174 (−0.332, 0.681)	0.229 (−0.277, 0.736)
Length	*Acer*	*platanoides*	0.876 (0.405, 1.347)	0.249 (−0.217, 0.715)
		saccharum	0.785 (0.295, 1.274)	0.491 (0.004, 0.978)
	Bromus	*inermis*	−0.904 (−1.888, 0.08)	0.168 (−0.804, 1.141)
		latiglumis	−1.27 (−2.177, −0.363)	0.916 (0.019, 1.813)
	Celastrus	*orbiculatus*	0.718 (−0.06, 1.495)	0.706 (−0.071, 1.483)
		scandens	1.247 (0.612, 1.881)	1.01 (0.381, 1.64)
	Elymus	*repens*	−1.19 (−1.795, −0.585)	0.638 (0.042, 1.234)
		trachycaulus	−0.924 (−1.481, −0.367)	0.148 (−0.402, 0.698)
	Plantago	*major*	−0.422 (−1.141, 0.297)	0.663 (−0.058, 1.384)
		rugelii	−0.404 (−0.934, 0.127)	0.208 (−0.322, 0.738)
	Rosa	*multiflora*	1.86 (0.901, 2.819)	1.28 (0.345, 2.215)
		palustris	1.406 (0.206, 2.606)	0.608 (−0.565, 1.781)
	Solanum	*dulcamara*	−0.226 (−0.729, 0.277)	1.264 (0.749, 1.779)
		carolinense	0.374 (−0.19, 0.938)	0.893 (0.324, 1.462)

Table 3.—*continued*

Trait	Genus	Species	Plasticity to C	Plasticity to N
SLA	*Acer*	*platanoides*	0.283 (−0.187, 0.753)	0.308 (−0.162, 0.778)
		saccharum	−0.628 (−1.116, −0.14)	0.369 (−0.117, 0.855)
	Bromus	*inermis*	−0.234 (−1.164, 0.697)	−0.447 (−1.38, 0.485)
		latiglumis	0.062 (−0.823, 0.948)	0.38 (−0.508, 1.267)
	Celastrus	*orbiculatus*	−1 (−1.783, −0.217)	0.873 (0.093, 1.653)
		scandens	−0.119 (−0.739, 0.501)	0.595 (−0.028, 1.218)
	Elymus	*repens*	−0.468 (−1.062, 0.126)	0.592 (−0.004, 1.187)
		trachycaulus	−0.619 (−1.167, −0.071)	0.807 (0.257, 1.357)
	Plantago	*major*	−1.189 (−1.919, −0.459)	−0.556 (−1.276, 0.164)
		rugelii	−1.443 (−1.996, −0.891)	0.537 (−0.001, 1.074)
	Rosa	*multiflora*	0.215 (−0.698, 1.128)	0.085 (−0.827, 0.998)
		palustris	0.348 (−0.821, 1.516)	0.198 (−0.969, 1.365)
	Solanum	*dulcamara*	0.125 (−0.383, 0.632)	0.123 (−0.384, 0.63)
		carolinense	−0.604 (−1.158, −0.05)	0.101 (−0.45, 0.652)
Toughness	*Acer*	*platanoides*	−0.198 (−0.664, 0.268)	−0.129 (−0.595, 0.337)
		saccharum	0.229 (−0.257, 0.714)	0.19 (−0.295, 0.676)
	Bromus	*inermis*	0.346 (−0.627, 1.32)	0.305 (−0.668, 1.278)
		latiglumis	−0.009 (−0.895, 0.877)	0.493 (−0.395, 1.382)
	Celastrus	*orbiculatus*	−0.364 (−1.121, 0.394)	−0.174 (−0.93, 0.583)
		scandens	0.158 (−0.462, 0.778)	−0.487 (−1.109, 0.135)
	Elymus	*repens*	0.366 (−0.333, 1.065)	−0.224 (−0.922, 0.475)
		trachycaulus	0.494 (−0.107, 1.095)	0.046 (−0.552, 0.645)
	Plantago	*major*	0.572 (−0.148, 1.292)	−0.222 (−0.94, 0.495)
		rugelii	0.459 (−0.073, 0.991)	−0.598 (−1.131, −0.064)
	Rosa	*multiflora*	0.215 (−0.698, 1.127)	−0.005 (−0.918, 0.907)
		palustris	−0.284 (−1.381, 0.813)	−0.532 (−1.632, 0.569)
	Solanum	*dulcamara*	−0.251 (−0.754, 0.252)	−0.627 (−1.133, −0.121)
		carolinense	−0.3 (−0.831, 0.231)	−0.233 (−0.764, 0.297)
Trichomes	*Acer*	*platanoides*	N.A.	N.A.
		saccharum	N.A.	N.A.
	Bromus	*inermis*	−0.611 (−1.546, 0.324)	−0.535 (−1.469, 0.398)
		latiglumis	0.285 (−0.602, 1.172)	0.084 (−0.802, 0.97)
	Celastrus	*orbiculatus*	N.A.	N.A.
		scandens	N.A.	N.A.
	Elymus	*repens*	−0.656 (−1.245, −0.068)	0.015 (−0.569, 0.6)
		trachycaulus	−0.157 (−0.702, 0.388)	−0.021 (−0.565, 0.524)
	Plantago	*major*	−0.031 (−0.748, 0.686)	1.019 (0.292, 1.745)
		rugelii	0.056 (−0.468, 0.581)	0.354 (−0.172, 0.879)
	Rosa	*multiflora*	0.541 (−0.375, 1.458)	1.171 (0.24, 2.102)
		palustris	0.534 (−0.637, 1.706)	0.402 (−0.768, 1.571)
	Solanum	*dulcamara*	0.346 (−0.158, 0.849)	0.59 (0.085, 1.095)
		carolinense	0.689 (0.134, 1.244)	−0.483 (−1.035, 0.07)

Note: Numbers in parentheses respresent the lower and upper bound of 95% confidence intervals. Tinted boxes indicate Hedges' *d*-values that are significantly different from zero.
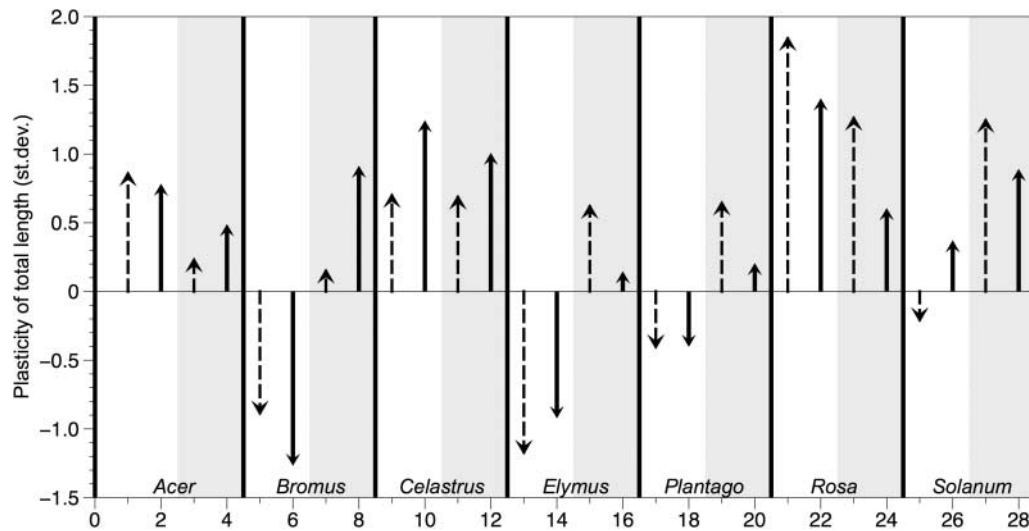
Fig. 3. The plasticity of total plant length to competition and nutrients. To illustrate the conservation of plasticity with genus, we show here Hedges' *d*, which directly quantifies the plasticity of total length to competition and fertilizer. The length of the arrow indicates the magnitude of trait change in response to the environmental treatments. Light columns indicate plasticity to competition and dark columns indicate plasticity to fertilizer. Columns are organized by genus, with the non-native species first (dashed arrows) and the native species second (solid arrows). The full dataset (with 95% confidence intervals) for each of the traits is given in Table 3.

the environments in which they are measured (Bradshaw, 1965; Schlichting, 1986). However, it is clear that weedy or invasive species are not consistently more plastic than non-weedy natives or non-natives.

While native and weedy non-native species did not differ in their plasticity in the present experiment, genera did. This suggests that related species share similar patterns of plasticity. Nonetheless, some research examining a single genus has reported differential plasticity among closely related species. For example, Valladares *et al.* (2000) reported highly variable plasticity among 16 tropical shrubs from the genus *Psychotria* and attributed differences in plasticity to their affinity for gap or understory habitats. Other single-genus studies have found differential plasticity among congeners and have attributed those differences to the invasive status of the species (e.g. Schweitzer and Larson, 1999; Brock *et al.*, 2005; Geng *et al.*, 2006; Leicht-Young *et al.*, 2007; Davidson *et al.*, 2011). These examples of differential plasticity among closely related species suggest that phenotypic plasticity evolves rapidly, in which case we would not expect to see a phylogenetic signal for plasticity. However, if plasticity evolves within a genus only to a limited extent and is ultimately constrained by evolutionary history, then we would detect a phylogenetic signal when comparing species at a broader phylogenetic scale (e.g. across genera). Indeed, Kembel and Cahill (2005) measured root plasticity in 102 species from multiple families and found a strong signal of phylogenetic conservatism for root proliferation in response to nutrients. Ultimately, a more extensive phylogenetic study would help elucidate patterns of plasticity evolution and show at what level of relatedness we might expect to see conservation versus lability of plasticity.

All of the species we studied grow in relatively open fields and may share patterns of plasticity due to similar habitat affinities rather than shared evolutionary history. Plasticity in plants has long been attributed to the type of habitat in which the plant grows (Grime, 1977). For example, Van Zandt (2007) compared nine pairs of congeners where each pair contained a species from a resource-limited glade habitat and a species from a more productive, non-glade habitat. He found that species from non-glade habitats generally had higher plasticity in chemical defences than those from glade habitats. Thus, in this example, habitat was a better predictor of plasticity than phylogenetic relatedness. However, others have compared species from very different habitats and found that evolutionary history still explained a significant portion of the variation in plasticity (Hoffmann and Franco, 2003). Because the 14 species in our experiment are from very similar habitats, we removed variation due to habitat affinity, thus providing additional control in our test of the impacts of evolutionary history and weediness on plasticity.

In conclusion, genus was a better predictor of plasticity than origin for the combination of traits, species, and environments that we tested. These results suggest that it may be better to examine evolutionary relationships rather than continental origin when trying to predict species traits. If plasticity does indeed contribute to the spread of non-native species, then a potential invader that is closely related to highly plastic natives may be of more concern than one that is related to less plastic natives.

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APPENDIX

Species information for the 14 species employed

Family	Species	Origin	Growth type	$N_{..}$	$N_{C.}$	$N_{.F}$	N_{CF}
Aceraceae	*Acer platanoides*	No	tree	16	22	17	19
	Acer saccharum	Na	tree	21	16	16	19
Celastraceae	*Celastrus orbiculatus*	No	vine	6	7	10	9
	Celastrus scandens	Na	vine	10	10	10	10
Poaceae	*Bromus inermis*	No	C3 grass	5	5	4	5
	Bromus latiglumis	Na	C3 grass	5	4	6	6
	Elymus repens	No	C3 grass	11	12	14	13
	Elymus trachycaulus	Na	C3 grass	15	14	14	13
Plantaginaceae	*Plantago major*	No	forb	12	9	11	4
	Plantago rugelii	Na	forb	14	14	16	14
Solanaceae	*Solanum dulcamara*	No	vine	16	15	15	16
	Solanum carolinense	Na	forb	15	15	15	15
Rosaceae	*Rosa multiflora*	No	shrub	4	5	6	4
	Rosa palustris	Na	shrub	3	3	3	4

Note: Under Origin, No = non-native and Na = native. Samples sizes in the four treatments are given for each species (no competition/no nutrient (••), competition only (C•), nutrient only (•F), and competition/nutrient (CF)).