AN INVASIVE PLANT ALTERS PHENOTYPIC SELECTION ON THE VEGETATIVE GROWTH OF A NATIVE CONGENER[1]

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- *Premise of the study:* The ecological consequences of plant competition have frequently been tested, but the evolutionary outcomes of these interactions have gone largely unexplored. The study of species invasions can make an important contribution to this field of research by allowing us to watch ecological and evolutionary processes unfold as a novel species is integrated into a plant community. We explored the ecological and evolutionary impact of an invasive jewelweed, *Impatiens glandulifera*, on a closely related native congener, *I. capensis* and asked: (1) Does the presence of the invasive jewelweed alter the fitness of native jewelweed populations? (2) Does the invasive jewelweed affect the vegetative growth of the native congener? and (3) Does the invasive jewelweed alter phenotypic selection on the vegetative traits of the native congener?
- *Methods:* We used a greenhouse competition experiment, an invasive species removal field experiment, and a survey of natural populations.
- *Key results:* We show that when the invasive jewelweed is present, phenotypic selection favors native jewelweed individuals investing less in rapid upward growth and more in branching and fruiting potential through the production of nodes.
- *Conclusions:* This research demonstrates that invasive plants have the potential to greatly alter natural selection on native competitors. Studies investigating altered selection in invaded communities can reveal the potential evolutionary impact of invasive competitors, while deepening our understanding of the more general role of competition in driving plant evolution and permitting species coexistence.

   Key words: competition-driven evolution; *Impatiens capensis*; *Impatiens glandulifera*; invasive species; selection analysis; vegetative competition.

Extensive research has been directed at understanding how herbivores, light availability, climate, pollinator preferences, and a wide variety of other environmental stimuli affect the evolutionary trajectory of plant communities (Agrawal, 2005; Benitez-Vieyra et al., 2006; Montague et al., 2008; von Wettberg et al., 2008). Meanwhile, studies of plant-plant interactions have largely focused on the ecological consequences of competition without investigating the potential for subsequent evolutionary change (Thorpe et al., 2011). This gap in the literature may be a response to long-standing ecological theory that downplays the importance of plant-plant interactions in shaping communities and instead supports abiotic or random processes (Gleason, 1926; Hubbell, 2005). Recent studies of

competition-driven plant evolution suggest that evolutionary responses to plant-plant interactions may play a larger role in shaping plant communities than previously recognized (Thorpe et al., 2011). A deeper investigation into the evolutionary consequences of plant-plant interactions is essential for a more complete understanding of the forces that drive plant morphological change and permit species coexistence.

Species invasions provide an excellent study system for exploring the evolutionary consequences of plant competition (Strauss et al., 2006). Invasive plants reduce the biodiversity of native plant communities through strong vegetative competition, often outcompeting native plants for sunlight and water, and overwhelming native communities through high reproductive output (Martin, 1999; Adams and Engelhardt, 2009; Vilá et al*.,* 2011). The intense competitive environment shaped by these species may create a strong selective force for adaptive evolution in native plants (Leger and Espeland, 2010).

Some studies already suggest that adaptive evolution in response to invasive competitors is possible (Lau, 2006; Mealor and Hild, 2007; Leger and Espeland, 2010; Oduor, 2013). For example, seedlings of the native grass, *Elymus multisetus* Burtt Davy (Poaceae), grown from seeds from communities invaded by the invasive grass, *Bromus tectorum* L. (Poaceae), grew larger when competing with the invasive than those from uninvaded areas (Rowe and Leger, 2011). Similarly, seedlings of the native herb, *Pilea pumila* Liebm. (Piperaceae), grown from

seed from areas invaded by the invasive biennial, *Alliaria petiolata* M. Bieb. (Brassicaceae), were more successful competitors than those from uninvaded communities (Lankau, 2012).

While these studies demonstrate the potential for native plant evolution in response to invasive competitors, many questions remain. It is unclear whether these evolutionary responses are common, and under what conditions they are likely to occur. Additionally, the underlying mechanisms driving evolutionary responses to invasive plant competitors often go unexplored. For example, few studies look directly at how natural selection on specific native plant vegetative traits is altered in the presence of an invasive competitor (but see Lau, 2008).

A deeper exploration of whether and how native plants evolve in response to invasive competitors will not only further our basic understanding of the role of competition in driving plant evolution, but may also aid in conservation efforts. For example, understanding the underlying evolutionary mechanisms at play in invaded communities can aid in predicting which plant populations will survive an invasion and which require remediation efforts (Rowe and Leger, 2011).

Here, we test whether an invasive jewelweed, *Impatiens glandulifera* Royle, alters phenotypic selection on the vegetative traits of a closely related native congener, *I. capensis* Meerb. We expected that the invasive jewelweed had the potential to direct evolutionary change in the native plant because the two species frequently grow intermixed and share a similar niche space (Tabak and von Wettberg, 2008). Additionally, *I. capensis* has previously been shown to evolve at a microenvironmental scale to changes in light availability (Dudley and Schmitt, 1995). Because the invasive jewelweed nearly always grows taller than the native congener, we predicted that the native jewelweed would experience selection for a reduced shade avoidance response, much as it does under a dense forest canopy (Dudley and Schmitt, 1995).

We addressed the following questions using a greenhouse competition experiment, an invasive species removal field experiment, and a survey of natural populations: (1) Does the presence of the invasive jewelweed alter the fitness of native jewelweed populations? (2) Does the invasive jewelweed affect the vegetative growth of the native congener? and (3) Does the invasive jewelweed alter phenotypic selection on the vegetative traits of the native congener?

MATERIALS AND METHODS

Study species—*Impatiens capensis* (Balsaminaceae), spotted jewelweed, is an annual plant native to much of the United States and Canada. It germinates in early May and continues to grow until first frost, often reaching a height of up to 1.5 meters. Flowering from late June onward, it produces fruits from both open, chasmogamous flowers and closed, cleistogamous flowers. *I. capensis* senses the shift in red to far-red radiation that occurs when sun shines through a competitor and can respond with what is known as the "shade avoidance syndrome" (Dudley and Schmitt, 1995). This response is characterized, in part, by greater investment in elongation through the extension of internodes at the cost of branching and fruiting (Smith and Whitelam, 1997). *I. capensis* populations under dense woodland shade have been shown to evolve in response to strong selection to suppress this elongation response (Dudley and Schmitt, 1995). In shaded settings, plants exhibiting rapid upward growth pay the cost of limited branching and fruiting without receiving the benefit of increased access to light.

Native jewelweed seedlings experience strong intraspecific vegetative competition. The early season density can reach well over 2000 individuals per square meter (Schmitt et al., 1987a). A height hierarchy develops early in the growing season as the fastest growing individuals inhibit the growth of neighbors

(Schmitt et al., 1987b). Reaching the top of this height hierarchy is critical for survival and seed production.

Native to the Himalayas, *Impatiens glandulifera* was introduced to the northeastern United States in the late 1800s, and now grows intermixed with *I. capensis* along roadsides, stream banks, and woods edges (Tabak and von Wettberg, 2008). The invasive jewelweed germinates synchronously with the native congener, and because it can reach a height of nearly 3 meters, it often towers over the native jewelweed by the end of the growing season.

Greenhouse competition study—We conducted a greenhouse competition study to test whether *Impatiens glandulifera* alters phenotypic selection on *I. capensis* in a controlled environment. In mid-September 2011, we collected and pooled seed from approximately 50 *I. capensis* individuals in a population uninvaded by *I. glandulifera* at the Hitchcock Center for the Environment in Amherst, Massachusetts, USA. On the same day, we collected and pooled seed from approximately 30 *I. glandulifera* individuals in a population about 30 km away in Petersham, Massachusetts. In early October, we placed the *I. capensis* seeds in cold stratification at 4°C on moistened filter paper in petri dishes. Because *I. glandulifera* seeds require a shorter cold stratification period, we waited until mid-November to place them in the same conditions.

Seeds of both species began germinating in cold stratification in mid-January 2012. In late January, we planted the seeds into trays with $3 \times 3 \times 4.5$ cm wells in Metro Mix 200 potting medium (Sun Gro Horticulture, Agawam, Massachusetts, USA) and placed them in the greenhouse at the University of Virginia. One week later, while seedlings were at the cotyledon stage, we transplanted them into 10 cm-square by 34.5 cm-deep pots filled with Fafard 3B potting medium (Sun Gro Horticulture) in the following three treatments with 85 replicates each:

(1) No competition—a focal *Impatiens capensis* seedling in the center of the pot without competitors.

(2) Conspecific competition—a focal *I. capensis* seedling surrounded by four conspecifics.

(3) Invasive competition—a focal *I. capensis* seedling surrounded by four *I. glandulifera* seedlings.

We randomly assigned pots to 17 blocks across 3 benches. In each block, we placed five replicates of each treatment together, with the order of treatments alternating across blocks. We spaced blocks 20 cm apart and treatments within blocks 15 cm apart. Within each competition treatment, we spaced pot sides 10 cm apart with the corners of adjacent pots touching. In the no-competition treatment, we spaced pot sides 10 cm apart with corners 8 cm apart. To minimize edge effects, we placed a wire around each competition treatment group in each block to restrict plants from growing into the open space between treatment groups.

We measured the height of focal plants at the date of transplanting into the treatments and then once a week for the duration of the experiment. We measured the length of the hypocotyl and first internodes of focal plants in late March after their elongation was complete. In mid-April, as plants across all treatments were just beginning to show signs of senescence, we estimated the total number of fruits produced by each focal plant by counting the number of buds, flowers, fruits, and pedicels with dehisced fruit (Dudley and Schmitt, 1996). We also counted the total number of internodes along the main axis. We then harvested the focal plants, dried them at a constant temperature, and weighed them to obtain aboveground biomass.

Analysis of fitness effects—We compared the effects of competition treatment on *Impatiens capensis* total fruit production, final height and aboveground biomass using mixed model ANOVAs with PROC GLM (SAS Institute, 2013). We included block and treatment by block interactions as random effects. Because individual plants within the same treatment and block were not independent of one another, we designated the block by treatment interaction as the error term for testing the significance of the treatment effect. We used independent contrasts for pairwise comparisons of treatments and corrected P values using a Tukey adjustment. We logarithmically transformed fruit and aboveground biomass to improve normality of residuals.

Analysis of vegetative response to competition—To find whether *Impatiens capensis* vegetative traits responded plastically to the presence of competition with conspecifics and with *I. glandulifera*, we tested whether they differed across treatments using mixed model ANOVAs in PROC GLM (SAS Institute, 2013). The vegetative traits included early growth rate, hypocotyl length, first internode length, and total internode number. Early growth rate was estimated as the average gain in height (cm) per day over the first quarter of the growing

season. As in the analysis of fitness effects, we included block and treatment by block interactions as random effects and designated block by treatment interaction as the error term for significance testing. We used independent contrasts for pairwise comparisons of treatments with Tukey-adjusted P values.

Selection analysis—To understand how competition with *Impatiens glandulifera* alters selection on the *I. capensis* vegetative traits included in the above analysis, we estimated standardized linear selection gradients (β) for each trait in each of the two competition treatments (Lande and Arnold, 1983). Within each treatment, we used relative fruit production as the fitness measure for each individual and regressed this value over vegetative trait values standardized to a mean of zero and standard deviation of one. We also included block in each multiple regression. Because total fruit set was not normally distributed, we tested the significance of selection gradients using a generalized linear model that assumed a Poisson error distribution with untransformed data (Formica et al., 2011). We calculated the standard errors for selection gradients using the formula outlined in McGlothlin et al. (2010).

To test whether selection gradients differed significantly between treatments, we used an analysis of covariance (ANCOVA) with untransformed data. The model included fruit set as the dependent variable and treatment, all vegetative traits, block, all treatment by trait interactions, and the treatment by block interaction as the independent variables. This model also assumed a Poisson error distribution. We used PROC GLIMMIX for all selection analyses (SAS Institute, 2013).

Invasive species removal study—To test whether *Impatiens glandulifera* alters phenotypic selection on *I. capensis* vegetative traits in a natural plant community, we designed an invasive species removal experiment in a community where the two jewelweeds grow intermixed. In early May 2013, while the jewelweeds were at the cotyledon stage, we set up 30, 0.5×1 m blocks along a damp 55 m ditch in Camden, Maine, USA. We placed blocks in areas densely covered with a mixture of *I. capensis* and *I. glandulifera* seedlings (mean initial number of *Impatiens* seedlings per block: 302.20, SE: 26.32). Blocks were no less than one meter apart. We divided each block into two, 0.5×0.5 m plots and randomly assigned one plot to the *I. glandulifera* removal treatment and the other to the control. We removed all *I. glandulifera* seedlings from the removal treatment plot by cutting the seedlings at the stem base with scissors. In each plot, we marked up to ten *I. capensis* seedlings by inserting a numbered swizzle stick in the ground near the base of the plant and wrapping a wire loosely around the stick and plant. To minimize edge effects, we only marked seedlings that were 10 cm or more from the edge of the plot. Because of the height reached by *I. glandulifera* plants by the end of the growing season, the potential for some shading from the invasive plant in the removal treatment remained. Estimates of differences in selection or fitness between treatments, therefore, are conservative. While we initially marked 550 plants, we were only able to gather data throughout the entire growing season on 22 blocks, for a total of 394 plants.

We tracked marked plants for the duration of the growing season. At the start of the experiment, we measured plant height. We continued to measure plant height once a month through September. Each month, we also recorded the survival of each marked plant and estimated the total number of fruits produced up to that point by counting the total number of pedicels, including those with buds, flowers, fruit, or dehisced fruit. At the August and September censuses, we measured the height of the hypocotyl and first internode, and counted the total number of internodes along the main axis. In early September, we harvested all surviving plants. We dried them at a constant temperature and then estimated their aboveground biomass.

Analysis of fitness effects—We tested for fitness differences in total fruit production, height, and aboveground biomass between the removal and control treatments using mixed model ANOVAs in PROC GLM (SAS Institute, 2013). As in the greenhouse experiment, we included block and treatment by block interactions as random effects and designated the block by treatment interaction as the error term for significance testing. The fruit and height models included all plants that were included in the selection analysis. The aboveground biomass model included only plants that survived to the September census. We logarithmically transformed all fitness components to improve normality of residuals.

We also compared survival to harvest between treatments using PROC LOGISTIC with survival as the dependent variable and treatment, block, and the treatment by block interaction as independent variables (SAS Institute, 2013).

Analysis of vegetative response to competition—We estimated plastic responses to the different competition treatments using the same statistical techniques as

in the greenhouse study. To improve normality, we square-root transformed early growth rate and hypocotyl length, and $\log^{10}$-transformed internode number.

Selection analysis—We compared phenotypic selection on vegetative traits in the removal and control treatments using the same statistical techniques that we used in the greenhouse selection analysis. We included all plants that survived to the August census. Early-season growth rate was again estimated as the average gain in height (cm) per day over the first quarter of the growing season. Because fruit numbers were not normally distributed, we tested the significance of selection gradients and the significant difference between selection gradients across treatments using models that assumed a Poisson error distribution (Formica et al., 2011).

We also measured selection in each treatment with models that used the estimated total seed number as the fitness measure. We estimated seed number for each plant by multiplying the total number of chasmogamous and cleistogamous fruits by the average number of seeds produced by each fruit type in the population. Because this alternative fitness measure resulted in similar selection gradients as the first, we do not present the results of this analysis here.

Natural populations' survey—We conducted a survey of *Impatiens capensis* populations growing with and without the invasive jewelweed. The first goal of this survey was to test whether the invasive jewelweed affects the fitness and vegetative growth of the native congener similarly across multiple natural plant communities. Then, if we found trait differences between populations growing with and without the invasive, we could compare these differences to the results from our greenhouse and removal experiments. If traits differed between populations growing with and without the invasive species in the same direction as differences in selection on these same traits in the greenhouse and removal experiment, then this would suggest the possibility of an evolutionary response to the altered selection imposed by the invasive species.

In late August and early September, toward the end of the *Impatiens* growing season, we visited 16 *I. capensis* populations across coastal Maine in the northeastern United States (Appendix 1). Eight populations grew intermixed with *I. glandulifera* and eight grew without the invasive plant. Whenever possible, we selected pairs of populations, that were in close proximity to each other, growing with and without the invasive plant. These paired populations were spaced a minimum of 30 m apart. In each population, we laid 50 m of transect and sampled the *I. capensis* plant closest to each meter mark. When populations were narrower than 50 m, we ran multiple parallel transects no closer than 3 m apart. We sampled up to 50 plants per population for a total of 723 plants. For each sample, we measured plant height, the length of the hypocotyl and first internode, and counted the total number of internodes along the main axis. We also estimated total fruit production by counting the total number of pedicels.

Statistical analysis—We tested for differences in total fruit number and vegetative traits between populations of *Impatiens capensis* growing with and without *I. glandulifera* using PROC GLIMMIX with models that included invasion status as a fixed effect, and population as a random effect. Because microsite environmental conditions varied greatly even within paired populations, we did not treat these pairs as blocks in the analysis. To improve normality, we logarithmically transformed fruit number and square-root transformed height and hypocotyl length.

RESULTS

Greenhouse competition study—*Fitness effects*—The competition treatments significantly affected the fitness of focal *Impatiens capensis* plants. Total fruit production was reduced by over 50% in both the conspecific and invasive competition treatments compared to the no-competition treatment (no competition vs. conspecific: $F_{1,16} = 72.99$, $P < 0.0001$; no competition vs. invasive competition: $F_{1,16} = 91.43$, $P < 0.0001$; Fig. 1). There was, however, no significant difference in fruit production between the conspecific and invasive competition treatments ($F_{1,16} = 0.92$, $P = 0.60$; Fig. 1). Conspecific competitors reduced plant height relative to the no-competition
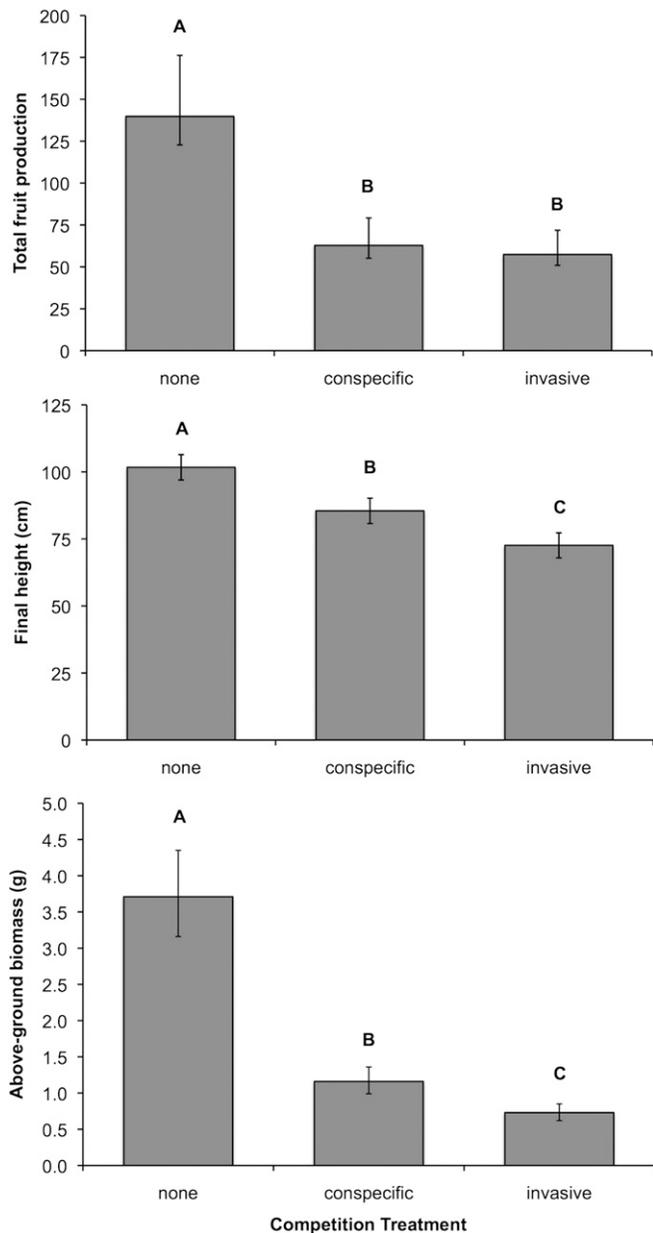
Fig. 1.   Means of fitness effects (± 95% confidence limits) by treatment in greenhouse competition study. Treatments with different letters are significantly different (Tukey adjustment for multiple comparisons: $P < 0.05$).

treatment ($F_{1,16c} = 23.00$, $P < 0.0001$), and invasive competitors further reduced plant height relative to the conspecific competition treatment ($F_{1,16} = 14.65$, $P = 0.001$; Fig. 1). Aboveground biomass was similarly reduced by competition with conspecifics relative to the no-competition treatment ($F_{1,16} = 104.19$, $P < 0.0001$) and further reduced by competition with the invasive jewelweed relative to the conspecific competition treatment ($F_{1,16} = 17.23$, $P = 0.0001$; Fig. 1).

Vegetative responses to the invasive competitor—The competition treatments also significantly affected the vegetative traits of the focal *Impatiens capensis* plants (Table 1). Individuals growing without competition had slower early growth rates (no competition vs. conspecific: $F_{1,16} = 12.33$, $P = 0.002$; no competition

vs. invasive competition: $F_{1,16} = 10.67$, $P = 0.004$). They also had shorter hypocotyls (no competition vs. conspecific: $F_{1,16} = 10.40$, $P = 0.004$; no competition vs. invasive competition: $F_{1,16} = 4.62$, $P = 0.08$), and shorter first internodes (no competition vs. conspecific: $F_{1,16} = 47.78$, $P < 0.0001$; no competition vs. invasive competition: $F_{1,16} = 52.24$, $P < 0.0001$). Finally, they had a significantly greater number of internodes (no competition vs. conspecific: $F_{1,16} = 67.47$, $P < 0.0001$; no competition vs. invasive competition: $F_{1,16} = 152.39$, $P < 0.0001$).

Vegetative traits of the native jewelweed did not differ greatly when competing with the native jewelweed vs. conspecifics (Table 1). Internode number, however, was reduced by the invasive competitor ($F_{1,16} = 16.59$, $P = 0.0002$).

Selection analysis—Although there was no difference in fruit production between the two treatments with competitors, the presence of the invasive jewelweed altered selection on a number of *Impatiens capensis* vegetative traits (Table 2). Under competition with conspecifics, selection favored *I. capensis* individuals with faster early growth rates. Under competition with the invasive jewelweed, however, there was no significant selection on this trait, and the selection gradients differed significantly between treatments (Table 2). When competing with conspecifics, there was also positive selection on the length of the first internode, but this trait had no effect on fruit production under invasive competition. The selection gradients on first internode length differed significantly between treatments (Table 2). *Impatiens capensis* plants in both competition treatments experienced positive selection on the number of internodes. Selection on this trait, however, was over twice as strong when plants competed with the invasive jewelweed, with the selection gradients on this trait also differing significantly between treatments (Table 2). An additional selection analysis that included height as a covariate did not change the pattern of altered selection on early growth rate or internode number (data not shown).

Invasive species removal study—*Fitness effects*—The presence of the invasive competitor reduced the fitness of the native jewelweed. Both total fruit production ($F_{1,21} = 9.81$, $P < 0.01$) and final height ($F_{1,21} = 8.39$, $P < 0.01$) were increased in the removal treatment (Fig. 2). Aboveground biomass also increased in the removal treatment, but this fitness measure did not differ significantly between treatments ($F_{1,18} = 1.64$, $P = 0.22$; Fig. 2). Survival to harvest was increased from 32% in the control treatment to 47.76% in the removal treatment ($\chi^2 = 7.99$, $P = 0.005$). For both treatments, most mortality occurred in the second half of the growing season (removal treatment survival to July: 89.76%, control treatment survival to July: 89.16%).

Vegetative response to the invasive competitor—*Impatiens capensis* plants in the control treatment demonstrated some plastic responses to the invasive competitor (Table 1). The presence of the invasive resulted in increased early growth rate ($F_{1,21} = 5.69$, $P = 0.03$) and decreased internode number ($F_{1,21} = 20.37$, $P = 0.0002$).

Selection analysis—The presence of the invasive jewelweed altered selection on the native jewelweed (Table 2). As in the greenhouse experiment, plants growing without the invasive in the removal treatment experienced significant positive selection

TABLE 1. Means with 95% confidence limits for vegetative traits in greenhouse competition study, field invasive species removal study, and natural populations survey. Within each study, treatment effects with different letters are significantly different ($P < 0.05$).

Study	Competition Treatment	Early Growth Rate (cm/day)	Hypocotyl (cm)	First internode (cm)	Internode number
Greenhouse (df = 1, 16)	conspecific	0.65 (0.63-0.68)[A]	6.07 (5.86-6.28)[A]	12.04 (11.46-12.62)[A]	11.14 (10.68-11.59)[A]
	invasive	0.65 (0.63-0.67)[A]	5.90 (5.69-6.11)[A, B]	12.15 (11.58-12.73)[A]	9.81 (9.36-10.26)[B]
	none	0.59 (0.57-0.62)[B]	5.58 (5.36-5.79)[B]	9.17 (8.59-9.75)[B]	3.82 (13.37-14.28)[C]
Field (df = 1, 21)	removal	0.61 (0.58-0.62)[A]	5.15 (4.88-5.38)[A]	12.42 (11.92-12.92)[A]	10.47 (9.55-11.22)[A]
	control	0.67 (0.65-0.71)[B]	5.20 (4.93-5.48)[A]	13.15 (12.65-13.65)[A]	7.94 (7.41-8.71)[B]
Natural populations' survey (df = 1, 706)	uninvaded	*	4.80 (4.24-5.38)[A]	11.23 (9.20-13.26)[A]	15.24 (13.77-16.70)[A]
	invaded	*	5.15 (4.57-5.76)[A]	13.43 (11.40-15.46)[A]	13.27 (11.80-14.73)[A]

*$P < 0.05$.

on early growth rate, while those competing with the invasive did not experience selection on this trait. Selection on early growth rate differed significantly between treatments (Table 2). Also as in the greenhouse study, the magnitude of selection on internode number was greatest when plants competed with *Impatiens glandulifera*. There was not, however, a significant difference in selection between treatments for this trait (Table 2). Unlike the greenhouse study where only the conspecific competition treatment produced positive selection on first internode length, plants growing both with and without the invasive competitor experienced positive selection on this trait (Table 2). An additional selection analysis that included height as a covariate did not change the pattern of altered selection on early growth rate or internode number (data not shown).

Natural populations' survey—*Impatiens capensis* populations growing with and without the invasive competitor did not differ in fruit production (mean and 95% CIs with the invasive = 22.42, 16.28-30.88; without the invasive = 29.37, 21.54-40.45; $F_{1, 707}$ = 1.41, $P = 0.23$) or in late season height (mean and 95% CIs with the invasive = 80.28, 69.56-91.78; without the invasive = 71.57, 61.46-82.45; $F_{1, 707}$ = 1.27, $P = 0.26$). We also detected no difference in vegetative traits across population types (Table 1).

DISCUSSION

The invasive jewelweed significantly altered selection on the vegetative traits of the native jewelweed. In both the greenhouse and field, when the invasive jewelweed was present, phenotypic selection favored native jewelweed individuals investing

less in rapid upward growth through a fast early growth rate and more in the production of nodes, which offer the potential for flowering and branching. In *Impatiens capensis*, fruit production and branching, which offers the potential for even greater fruit production, both occur at nodes. These results match our initial hypothesis that, in the presence of the taller invasive species, selection would favor a reduction in the shade avoidance response. A previous study showed that *I. capensis* populations adapted to sunny locations elongate their first internodes in response to competitors, while those adapted to forest canopies suppress this response (Dudley and Schmitt, 1995). In the controlled conditions of the greenhouse, we also found strong positive selection for elongation of the first internode under intraspecific competition, but no selection on this trait under shading from the invasive species. In the field, where conditions were less controlled, there was overall positive selection on elongation of the first internode in both treatments.

The greenhouse and field experimental designs were similar in that they enabled us to measure selection on *Impatiens capensis* both in the presence and absence of the invasive jewelweed. One important difference between these studies was that the greenhouse study maintained overall plant density between treatments while the field study did not. Density is often an important factor in determining the ecological consequences of plant competition (Goldberg et al., 2001; Treberg and Turkington, 2010) and may influence selection on vegetative traits (Dudley and Schmitt, 1996). Despite not controlling for density in the field, however, the field results matched the greenhouse study. The presence or absence of the invasive species, therefore, was more important than the density differences between treatments.

TABLE 2. Greenhouse and field studies directional selection gradients ($\beta \pm SE$) on *Impatiens capensis* vegetative traits in the presence and absence of *I. glandulifera*. The interaction shows whether selection gradients significantly differed between treatments. Significant selection gradients and interactions are shown in bold.

| Study	Trait	*I. glandulifera* presence		Interaction		
		− ($\beta \pm SE$)	+ ($\beta \pm SE$)	F	P	df
Greenhouse	Early growth rate	**0.09 (± 0.02)**	0.003 (± 0.002)	**4.38**	**0.04**	1, 122
	Hypocotyl length	**-0.04 (± 0.02)**	−0.01 (± 0.03)	0.76	0.39	1, 122
	Internode 1 length	**0.15 (± 0.02)**	0.04 (± 0.02)	**8.35**	**0.005**	1, 122
	Number of internodes	**0.14 (± 0.01)**	**0.36 (± 0.02)**	82.74	<0.0001	1, 122
Field	Early growth rate	**0.15 (± 0.03)**	−0.09 (± 0.11)	**3.93**	**0.049**	1, 222
	Hypocotyl length	−0.07 (± 0.07)	−0.10 (± 0.12)	0.09	0.76	1, 222
	Internode 1 length	**0.07 (± 0.03)**	**0.22 (± 0.10)**	0.17	0.68	1, 222
	Number of internodes	**0.79 (± 0.03)**	**1.04 (± 0.05)**	0.88	0.35	1, 222
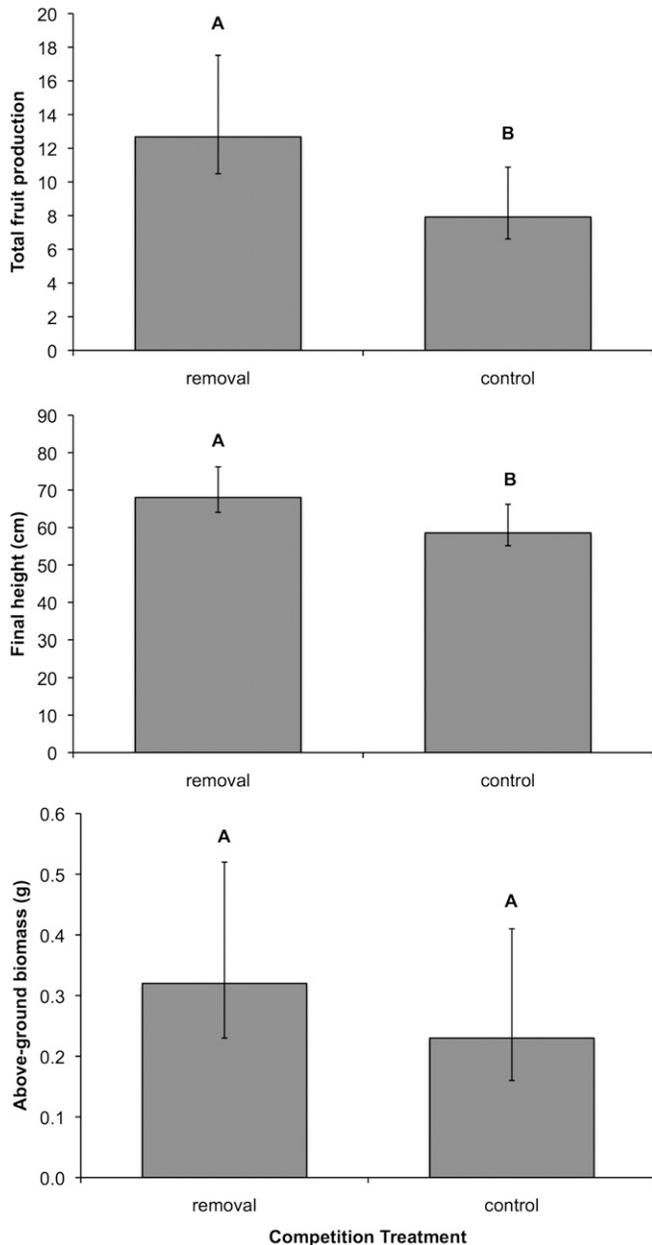
Fig. 2. Means of fitness effects (± 95% confidence limits) by treatment in field invasive species removal study. Treatments with different letters are significantly different ($P < 0.05$).

One potential drawback to estimating selection in natural plant communities is that the estimates may be biased by environmentally induced correlations between fitness and traits (Rausher, 1992). For example, plants that by chance grow near less vigorous neighbors might have greater fitness and faster growth rates than those growing in more competitive environments. This bias may also occur in the greenhouse since it is impossible to create a completely uniform competitive environment across all pots within a treatment. Although we cannot entirely rule out the possibility of environmentally induced correlations in our own studies, we believe that this potential bias alone could not fully explain the differences in selection between our treatments. We do not have estimates of competitor biomass for our field study. In our greenhouse study, however, we found that any significant

correlations between the aboveground biomass of competitors and fitness or trait values were similar across treatments (Appendix 2). Differences in selection, therefore, could not be explained solely by differences in the relationship between the intensity of competition and fitness or trait values.

The results of our removal experiment differ from those of a study that tested whether selection on *Impatiens capensis* vegetative traits was altered by the removal of a diverse array of heterospecific competitors (McGoey and Stinchcombe, 2009). This previous study found, for example, that there was positive selection on early growth rate in both the heterospecific competition and the removal treatments, while we found positive selection on this trait only under intraspecific competition. One possible explanation for the differences in our findings is that the strength and direction of competition-driven phenotypic selection on *I. capensis* may depend on the specific identity of the competitor species.

The results of the invasive species removal experiment show that *Impatiens glandulifera* has the potential to reduce fruit production in the native plant through vegetative competition. In the greenhouse, however, there was no difference in fruit production between native jewelweed individuals competing with their own species and with the invasive competitor. This lack of treatment response may be the result of the more protective environment of the greenhouse relative to the field. Plants in both greenhouse competition treatments experienced zero mortality and produced about six times as many fruits as plants in the field study.

In our natural populations' survey, we found no significant differences in fruit production, height, or other vegetative traits between native jewelweed populations growing with and without the invasive competitor. This result was surprising given the strong influence of the invasive on these fitness measures in the field removal experiment. It is possible that we were unable to detect an effect of the invasive jewelweed in invaded communities because the native jewelweed populations have already evolved in response to the competitor. The surveyed populations likely had 50 or more generations to respond to the invasive jewelweed (Tabak, 2005). If this evolutionary response has occurred, however, it did not result in fixed differences in any of the traits we measured between natural populations growing with and without the invasive jewelweed. Some other unmeasured traits may have evolved to enhance the competitive ability of the native jewelweed. Alternatively, it is possible that plastic responses to the presence of the invasive jewelweed may obscure genetic differences between population types. For example, our removal experiment showed that selection favored more internodes when the invasive species was present. Yet the plastic response to competition with the invasive was to produce fewer internodes.

It is also possible that the native jewelweed's evolved and plastic responses to other environmental variables overwhelm any response to a single-plant competitor. For example, populations of the native plant *Lotus wrangelianus* Fisch. & C.A.Mey. (Fabaceae) evolved in response to the invasive competitor *Medicago polymorpha* L. (Fabaceae), but this evolutionary response could only be detected when plants were protected from an invasive herbivore (Lau, 2006). *Impatiens capensis* populations may each respond to variables such as water availability (Heschel et al., 2002) and canopy cover (von Wettberg and Schmitt, 2005) that vary greatly across the range and could limit our ability to detect an evolutionary response to the invader. A reciprocal transplant experiment is an important next step for testing whether an evolutionary response has occurred.

Whether competition plays a role in plant evolution has frequently been questioned (Gleason, 1926; Hubbell, 2005). There is currently, however, resurgence in support for competition as a central force in driving adaptive plant evolution (Thorpe et al., 2011; Beans, 2014). The study of species invasions can make an important contribution to this field of research by allowing us to watch ecological and evolutionary processes unfold as a novel species is integrated into a plant community. Our research demonstrates that invasive plants can greatly alter natural selection on native competitors. Competition, therefore, may play an important role in determining the evolutionary trajectory of these plant communities. The fact that the same results were found in the greenhouse and the field suggests that invasive plant competitors may influence selection on native plants relatively constantly across different densities and populations. Studies investigating altered selection in invaded communities can reveal the potential evolutionary impact of invasive competitors, while deepening our understanding of the more general role of competition in driving plant evolution.

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