EVOLUTION OF COMPETITIVE ABILITY WITHIN *LONICERA JAPONICA'S* INVADED RANGE

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Factors influencing invasive taxa may change during the course of an invasion. For example, intraspecific competition is predicted to be more important in areas with older stands of dense monospecific invaders than at the margins of an invaded range. We evaluated evolution in response to predicted changes in competition by comparing the intraspecific competitive ability of North American populations of Japanese honeysuckle (*Lonicera japonica*) from areas established 100–150 yr ago, which make up the core of the invaded range, to populations from the northern range margin, established in the past 50 yr. Plants from populations in the core and margin regions of the invaded range were grown in two common garden studies. The first had three levels of intraspecific competition, and vines differed in their access to a lattice for climbing. The second asked whether plants from older core or newer margin populations were better competitors. Intraspecific competition decreased the size of plants from both core and margin regions. Contrary to predictions, there was no increase in climbing shoot frequency or size in plants from denser core populations, although these did increase in the presence of a lattice structure. Also contrary to predictions, plants from the margin of the invaded range were larger and stronger competitors than those from the core, regardless of competition level. Enhanced intraspecific competitive ability of plants from low-density margin populations is likely driven by selection for more rapid growth rate in the north, rather than direct selection on competitive ability. Results counter to prediction highlight the importance of considering the broader selective context to understand evolution. Furthermore, this differentiation across the invaded range is likely to enhance *L. japonica*'s invasive potential.

Keywords: intraspecific competition, invasive species, vine, population differentiation, Japanese honeysuckle.

Online enhancement: appendix table.

Introduction

Little is known about the long-term dynamics of plant invasions, particularly how factors influencing invasive taxa change during the course of an invasion. A typical view of an invasion is that after the initial "explosion," when invasive species expand rapidly as a result of enemy release, an abundance of available niche space, or exploitation of resources following human disturbance, further range expansion will occur due to adaptation (Sakai et al 2001; Dietz and Edwards 2006). Several types of adaptation may facilitate this further range expansion. First, selection may alter physiological tolerance in response to novel environmental conditions, which can result in taxa becoming adapted to local conditions (Sexton et al. 2002; Parker et al. 2003) or environmental clines in the invaded habitat (Kollmann and Banuelos 2004; Maron et al. 2004; Leger and Rice 2007; Alexander et al. 2009; Kooyers and Olsen 2012). Alternatively, selection may differ between the initial area of invasion and the edge of an invaded range

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(Sexton et al. 2009). For example, traits that promote colonization, such as those that improve dispersal ability (Simmons and Thomas 2004; Phillips et al. 2006, 2010; Geber 2008) and interspecific competition (Lankau et al. 2009), may evolve during the process of invasion, enhancing fitness at the advancing margin of the invaded range. In contrast, in older regions of the invaded range, selection may favor a different suite of traits, such as those that result in retaining local dominance. However, to date there has been little study of such evolutionary change over the course of an invasion (Lankau et al. 2009).

Competitive ability has a complex role in the invasion process. Interspecific competitive ability is key to range expansion, while long-term dominance of invasive species is expected to select for enhanced intraspecific competitive ability. Furthermore, these expectations may depend on the specific mechanism of competition. For example, invasive Garlic mustard (*Alliaria petiolata*) near the range edge, where it experiences interspecific competition, has greater allelopathic properties than older, denser populations, where high densities of conspecifics are the rule (Lankau et al. 2009). Such chemical-based competitive ability is more useful against other species than conspecifics, which are likely resistant. Alternatively, competitive ability based on plant size may be equally functional against interspecific and intraspecific competitors. On average, we expect traits that enhance intraspecific competitive ability to become increasingly important as invasive populations be-

come older and grow in size and density (Lankau and Strauss 2011). By virtue of their age, populations in the initially colonized region ("range core") are expected to be denser and therefore experience higher intraspecific competition than newly colonized populations. This will be particularly true for aggressive invaders that readily form high-density monospecific stands. Such high-density populations should favor greater intraspecific competitive ability. In total, selection pressures in a region are expected to change over time, favoring plants that are good colonizers early in the invasion (through enhanced colonization or interspecific competition) and those that grow well when surrounded by high densities of conspecifics later on (through enhanced intraspecific competition).

We tested this hypothesis using the invasive vine *Lonicera japonica* (Japanese honeysuckle) as a model system. In *L. japonica*'s invaded North American range, plants initially moved from cultivation into the wild 100–150 yr ago in the southeastern United States (Leatherman 1955; Nuzzo 1997). This area now represents the core of the invaded region. Populations at the northern margin of the invaded range colonized within the past 50 yr (Beans et al. 2012). When *L. japonica* from both regions was grown in common gardens in both locations, individuals from margin populations grew to a greater size and had better survival regardless of planting location. Furthermore, these differences were not due to genetic sampling during colonization (Kilkenny and Galloway 2013), indicating that evolution occurred during the invasion process.

The lack of evidence for adaptation to local environmental conditions by core plants and the overall advantage of margin plants in *L. japonica*'s invaded range may have been a product of the experimental design. The common gardens featured an open field design with no intraspecific competition (Kilkenny and Galloway 2013). Such conditions are more typical of the biotic environment of the range margin, where *L. japonica* densities are low (25% cover), than the range core, where *L. japonica* densities are much higher (60% cover; Kilkenny 2011). Margin habitats also had a greater percentage of open fields relative to forest edges than core habitats (56% open fields at the margin, 45% in the core; F. F. Kilkenny, unpublished data). Conspecific density may also affect growth pattern. Honeysuckle shoots can grow both vertically, by twining around a support structure ("climbing"), and horizontally, with shoots that traverse the ground ("running"; Larson 2000). The open field design of the previous study (Kilkenny and Galloway 2013) may have given an advantage to genotypes that produce runners and have a spreading, colonizing growth form, whereas the design may have provided less opportunity for genotypes predisposed to climbing, likely at an advantage in denser conspecific environments. As such, the design of the previous study may have reduced the probability of detecting local adaptation.

Here we evaluate response to intraspecific competition in *L. japonica*, testing whether plants from the older core of the invaded region have enhanced competitive ability relative to populations from the range margin. We conducted two experiments to address the following questions: (1) Do plants from the core and margin regions of the invaded range differ in their ability to resist intraspecific competition? (2) Do plants from the core and margin regions differ in their tendency to climb? (3) Are there differences in competitive ability between

plants from the two regions—that is, are plants from the core of the range better able to suppress growth in their conspecific neighbors than those from the range margin?

Material and Methods

Study System

Lonicera japonica (Japanese honeysuckle; Caprifoliaceae) is a woody vine native to Japan, China, and Korea (Schierenbeck 2004). During the nineteenth century, horticultural varieties were introduced into the United States and widely cultivated (Leatherman 1955; Nuzzo 1997). The species has since become widespread throughout the eastern half of the United States, particularly in the Southeast, where the first invasions occurred (Nuzzo 1997; Schierenbeck 2004). After rapidly expanding to most of its present range, *L. japonica* has continued to spread northward during the past ~50 yr (Leatherman 1955; Beans et al. 2012). The southeastern United States, where it initially established and populations are denser, represents the core of the invaded range, while the recently established, sparser northern populations represent the range margin. Populations experience climatic differences between the two regions, in particular colder temperatures in the margin region (Kilkenny 2011). However, there is no evidence of local adaptation to abiotic factors for populations in the core and margin regions (Kilkenny and Galloway 2013).

Lonicera japonica's growth characteristics make it a strong competitor (Larson 2000). It has a highly plastic growth form, with shoots growing straight when spreading across flat surfaces ("running") or twining upward on support structures, typically other plants ("climbing"). In addition, plants can send out shoots at any node and root at any node in contact with the ground, thus allowing for clonal spread. This rapid spread allows *L. japonica* to quickly fill available space, and plants may grow in high-density, nearly monospecific stands.

Intensity of Competition Experiment

We sampled multiple populations from the core and margin regions of *L. japonica*'s invaded range to evaluate evolution of competitive ability during the process of invasion. Plants for this study were originally collected as cuttings from 12 populations located in the core of the invaded range and 15 populations from the northern margin (see the appendix, available in the online edition of the *International Journal of Plant Sciences*, for population locations; see Kilkenny and Galloway 2013 for the collection process). Cuttings were rooted and the resulting plants grown under greenhouse conditions until early spring 2010, when clones of each individual were created through vegetative propagation. To do this, pieces of stem with several nodes were treated with rooting hormone, placed in pots filled with perlite, and kept moist. To generate target plants, one or two genotypes from each population were used to make clones (1.70 ± 0.47 SD genotypes per population; 46 total genotypes) and roughly 8 clones were made per genotype (7.8 ± 4.4 SD clones per genotype; 365 total clones for all treatments and experiments). In addition, 704 clones were generated to act as competitors for the target plants. All sample sizes reported here are final numbers from the conclusion of the experiment.

Table 1

ANCOVA of Running and Climbing Shoot Mass and Log-Linear Analysis of the Probability of Producing a Climbing Shoot and the Probability of Running and Climbing Shoots Flowering for *Lonicera japonica* Populations Originating from the Core and Margin Regions of Its Invaded Range

Source	df	Running shoot mass[a]	Climbing shoot mass[b]	Probability of climbing shoot	Running flowers	Climbing flowers
Competitor no.	2	15.79***	4.10*	.91	8.54*	.68
Target origin	1	4.38*	.37	1.14	.40	2.03
Target origin × competitor no.	2	1.29	.17	.08	.94	.39
Population (target origin)	...	1.53[+]	2.01*	...	...	...
Lattice	1	.23	18.67***	7.59**	11.40***	6.27*
Lattice × competitor no.	2	.35	.45	1.40	1.48	6.28*
Lattice × target origin	1	.03	.03	.52	1.28	1.28
Cohort	1	77.00***	6.66**	3.04[+]	4.54*	5.32*
Cohort × target origin	1	1.06	1.14	.84	1.78	.91
Initial mass	1	5.28*	1.86	...	...	...

Note. Plants were grown with three levels of intraspecific competition and differed in whether they had access to a lattice to climb. Cohort reflects planting date. For the ANCOVA, F ratios and Z values are given for fixed and random effects, respectively. For the log-linear analysis, χ^2 values are reported.

[a] Error df = 239, except target origin = 25.

[b] Error df = 140, except target origin = 25.

[+] $P < 0.1$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Two cohorts of clones were created. In the first cohort, rooted cuttings were removed from the perlite after a month and then bagged and briefly refrigerated. During refrigeration, a large number of clones accidentally froze. Surviving clones were weighed prior to planting and potted in 11.4-L pots filled with Fafard 3 mix. A second cohort of clones was made from the original plants to serve as replacements using the above process. When ready for transplant, clones were weighed (but not refrigerated) and immediately potted as described above. This second cohort was ∼6 wk younger than the first and had approximately twice as many plants. Plants from the core and margin of the range were evenly distributed between the two cohorts.

Three competition treatments were established. Clones were designated as "targets" or "competitors." Target plants were used for data acquisition and were planted in the center of each pot, while competitors planted in the same pot were used to create the experimental treatments. Competitors were arranged evenly around targets so that different densities would create different levels of below- and aboveground competition. Target plants were grown with four competitors, two competitors, or alone in a pot. Equal numbers of competitors from the core and margin regions were used so that any competitive differences between the two regions did not confound the results.

We also evaluated whether *L. japonica* from the core of the invaded range, where populations are denser, were more likely to take advantage of opportunities to climb. In each competition treatment, approximately two-thirds of the pots were given a lattice for climbing, while the others received no climbing structure. Climbing on the lattice was expected to provide increased access to light and may become more important as competitor number increases. On average, there were 30 replicates (range, 24–32) of each competition treatment for each target origin grown with lattice and 17 replicates without lattice (range, 14–20; 277 total target plants in experiment).

Plants were grown in a common garden in *L. japonica*'s invaded habitat located intermediate in latitude to the sampled core and margin populations (Blandy Experimental Farm; appendix). Pots were placed in a grassy field, a common habitat throughout the range and one that had been used in previous experimental work (Kilkenny and Galloway 2013). Without competition the site was more similar to northern habitats, while the high-competition treatments resembled the core of the range. In late June 2010, pots were placed 0.5 m apart in eight rows and partially buried in the ground to reduce drying and winter exposure. The rows were separated by 1 m, and 3.5 rows had a 1.2-m-tall lattice structure constructed over them (2.5 cm × 1.9 cm plastic mesh). The lattice was placed a few centimeters above the pots, close enough for plants to easily encounter it. All plants were protected from deer and watered regularly during the summer, but they were not fertilized.

Plants were harvested after a year of growth at the end of May 2011. The aboveground portions of the target plants were collected and separated into climbing shoots and straight running shoots. Climbing shoots were classified as any branch that demonstrated twining behavior by twisting around the lattice or nearby plants, even if the initial support structure collapsed, as was often the case when twining on grasses. Running shoots were classified as branches with no twining behavior at all. Because classification was performed on branches, as opposed to the entire architecture of a basal stem, basal stems often had a mixture of biomass allocated to climbing and running behaviors. Although it was not possible to directly observe circumnutation of the *L. japonica* shoot tips, the abundance of structure—in the form of the lattice, other plants, and conspecific shoots—made it likely that the majority of circumnutating shoot tips would have encountered a support of some kind, resulting in observable twining. Therefore, we are confident that nearly all running shoots demonstrated
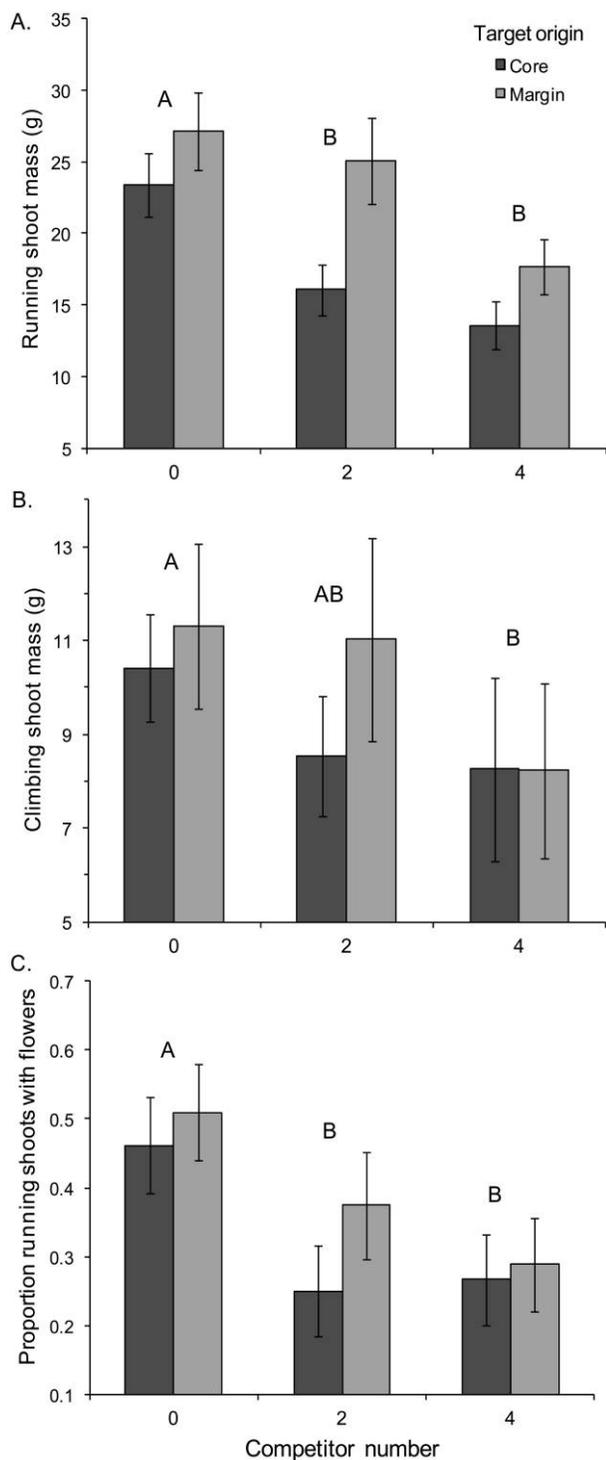
Fig. 1 Mean ($\pm$SE) mass of running (*A*) and climbing (*B*) shoots and the proportion of running shoots with flowers (*C*) for *Lonicera japonica* originating from the core and the margin of the invaded range and grown with differing numbers of intraspecific competitors. Competitor treatments with different letters are different at $\alpha = 0.05$ following a Tukey multiple comparison.

the low-circumnutation, prostrate, and unidirectional growth pattern that has been shown in other studies of *L. japonica* plasticity (Schweitzer and Larson 1999; Larson 2000). The abundance of structure also meant that many individuals had climbing shoots regardless of their lattice treatment. Some of the competitors died during the 11-mo experiment. The number remaining was noted for each pot at harvest. Shoots were dried and weighed, and the presence of flowers on each shoot type was recorded.

Source of Competition Experiment

We also evaluated differences in the competitive environment created by plants from core and margin populations for both core and margin target plants. Experimental plants were created using the procedures detailed above. For this study, two competitors from either core populations or margin populations were grown with target plants from either the core or the margin. No plants had access to the lattice. On average, there were 22 replicates (range, 20–24; 88 total target plants in experiment) for each target origin and competitor origin combination. Plants were grown and harvested as described above.

Statistical Analysis

Intensity of Competition Experiment

Vegetative and reproductive traits were compared across competitor densities for plants that originated from core and margin populations to determine whether *Lonicera japonica* has evolved different responses to competition across its invaded range. The mass of running and climbing shoots, both natural log transformed, were evaluated using ANCOVA (PROC MIXED; SAS Institute 2009). Target origin (core or margin region), competitor number, cohort, and lattice (whether a plant was provided a climbing structure) were included in the model as fixed effects. Population, nested in target origin, was treated as a random effect. Initial mass of target plants was used as a covariate. Interaction terms, target origin by competitor number, lattice by competitor number, lattice by target origin, and cohort by target origin were also included. Cohort was considered a blocking factor because we expected plants in the first cohort to be larger than those in the second cohort. Some competitors died during the study; therefore, the analyses were conducted using either the original competitor number or the final competitor number. The results between the two analyses were qualitatively similar, so original competitor number (0, 2, 4) was used for simplicity.

Dichotomous traits (presence of at least one climbing shoot, flowers on running shoots, and flowers on climbing shoots) were analyzed using a log-linear model with a binomial distribution (PROC GENMOD). Target origin, number of competitors, lattice, and cohort were included as factors. The interaction terms of target origin by number of competitors, target origin by cohort, target origin by lattice, and lattice by number of competitors were also included. Population was omitted from the model because there was insufficient variation within some populations for the likelihood analyses to converge.
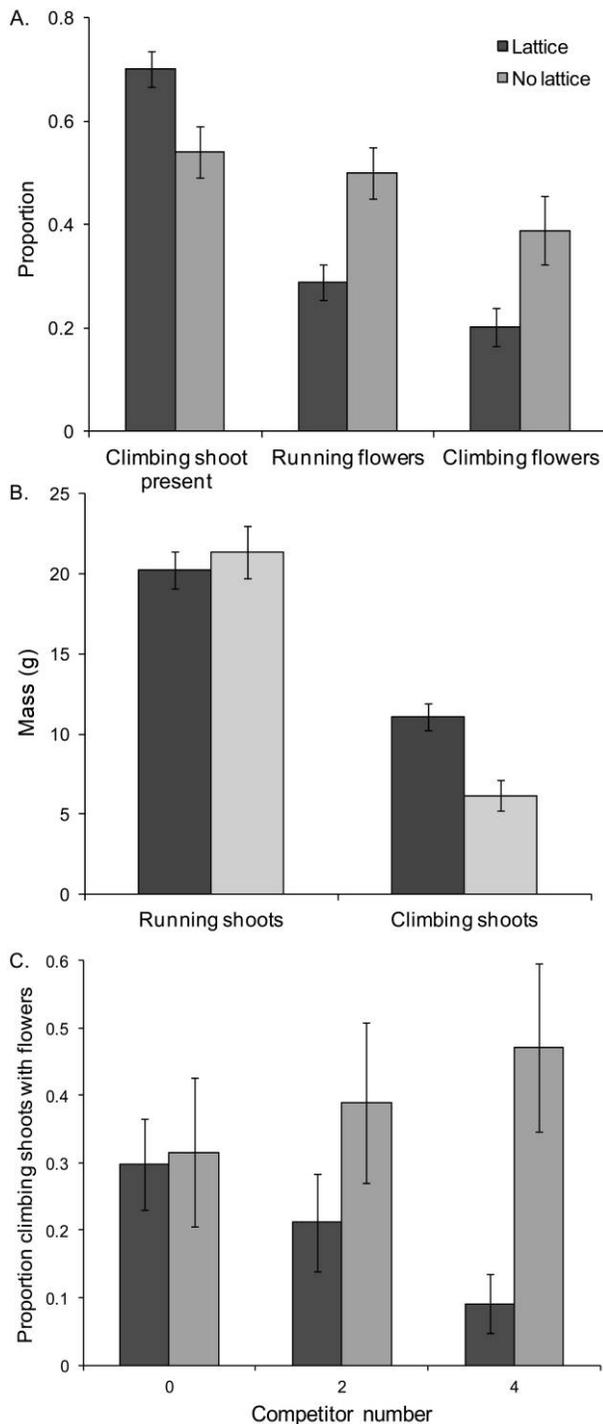
Fig. 2 *A*, Mean (± SE) proportion of *Lonicera japonica* producing climbing shoots, flowers on running shoots, and flowers on climbing shoots. *B*, Mass of running shoots and climbing shoots. *C*, Proportion of climbing shoots with flowers for plants that were grown with differing numbers of intraspecific competitors. Plants that had access to a lattice for climbing are shown separately from those that did not.

Source of Competition Experiment

To determine whether plants from the core and margin regions differ in their competitive ability, vegetative and reproductive traits were compared between targets from the core and margin regions of the range. Natural-log-transformed masses of running and climbing shoots were analyzed using ANCOVA (PROC MIXED) with target origin, competitor origin (core or margin region), and cohort as fixed effects and initial mass as a covariate. Population nested in target origin was included as a random effect. Target origin by competitor origin and target origin by cohort were included as interaction terms. The probability of producing a climbing shoot was analyzed using an analogous log-linear analysis but with the factor of population omitted. Sample size and modest reproduction precluded analysis of flowering for running and climbing shoots.

Results

Intensity of Competition Experiment

Increased competition decreased *Lonicera japonica* growth. When competitors were present, both running and climbing shoots were smaller (table 1; fig. 1*A*, 1*B*). In addition, a smaller proportion of running shoots flowered in the presence of intraspecific competitors (table 1; fig. 1*C*). However, competitor presence did not influence the probability of producing a climbing shoot or whether climbing shoots were reproductive.

Both climbing shoots and probability of reproduction were affected by the presence of a lattice. When a lattice was present, a plant was more likely to have climbing shoots, and climbing shoots were larger (table 1; fig. 2*A*, 2*B*). However, on average reproduction was less likely on both running and climbing shoots when a lattice was present (table 1; fig. 2*A*). For climbing shoots, this change in reproduction depended on the number of competitors. An increased competitor number resulted in fewer reproductive climbing shoots when a lattice was present but an increased number when it was absent (fig. 2*C*).

As expected, plants from the first cohort were larger and more likely to flower than those from the second cohort (table 1).

Intensity of Competition Experiment and Source of Competition Experiment

The geographic origin of *L. japonica* influenced its size and competitive effect. Running shoots of margin plants were heavier than those of core plants over all competition intensities (table 1; fig. 1*A*). However, when competitor origin was tested, running shoot mass depended on both the origin of target plants and the origin of the competitor (table 2). Running shoots of target plants from margin populations were of similar size regardless of whether competitors were from the core or the margin region (fig. 3). In contrast, running shoots of core plants were smaller when competitors were from margin populations than from core populations. There was also a modest effect of competitor origin on the presence of climbing shoots (table 2; $P < 0.078$). A smaller proportion of plants grown with margin competitors had climbing shoots (mean, 0.47; SD,

Table 2

ANCOVA of Running and Climbing Shoot Mass and Log-Linear Analysis of the Probability of Producing a Climbing Shoot for *Lonicera japonica* Populations Originating from the Core and Margin Regions of the Invaded Range

Source	df	Running shoot mass[a]	Climbing shoot mass[b]	Probability of climbing shoot
Competitor origin	1	2.38	1.95	3.11[+]
Target origin	1	1.27	.25	2.25
Target origin × competitor origin	1	8.52**	.31	2.24
Population (target origin)	...	2.05*	.62	...
Cohort	1	21.94***	.56	1.08
Cohort × target origin	1	1.30	.00	1.49
Initial mass	1	.08	.61	...

Note. Plants were grown with competitors from either the core or the margin region. Cohort reflects planting date. For the ANCOVA, F ratios and Z values are given for fixed and random effects, respectively. For the log-linear analysis, χ^2 values are reported.

[a] Error df = 58, except target origin = 23.
[b] Error df = 21, except target origin = 20.
[+] $P < 0.1$.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

0.08) than those with competitors from the core region (mean, 0.63; SD, 0.07).

Discussion

Increasing levels of intraspecific competition had a detrimental effect on *Lonicera japonica* growth, irrespective of whether plants originated from core or margin regions of the invaded range. On average, running shoots decreased in mass by 38% and climbing shoots by 24% when plants were grown with four competitors compared with being grown alone. This finding is consistent with other intraspecific and interspecific competition studies, where increasing levels of competition reduced individual size (reviewed in Gurevitch et al. 1992; see

Fig. 3 Mean (±SE) mass of running shoots in *Lonicera japonica* originating from the core and the margin of the invaded range when grown with intraspecific competitors from either the core or the margin of the range.

also Wassmuth et al. 2009; Blank 2010; Mangla et al. 2011). Competition also reduced the proportion of plants with running shoots that produced flowers. This too is consistent with other studies that have found that competition has a negative effect on reproductive potential (Leger and Rice 2003; Miller and Gorchov 2004; Bonser and Ladd 2011).

A reduction in individual size with greater intraspecific density supports the idea that invasive species are vulnerable to competition. Invasions typically begin in resource-rich, disturbed habitats, which are a boon for fast-establishing species that are able to rapidly increase and take advantage of the abundant available resources (Dietz and Edwards 2006). In such habitats, competition is initially modest. However, once the edge of a disturbed habitat is reached, resource availability decreases and competition increases (D'Antonio 1993). In particular, areas with relatively little open niche space and high levels of biodiversity are expected to hinder further spread of invasive taxa (Stohlgren et al. 1999; Kennedy et al. 2002; Godfree et al. 2004). *Lonicera japonica* fits this model as the species thrives in disturbed areas, such as forest light gaps, margins, and old fields (Schierenbeck 2004), and spreads rapidly, growing over existing vegetation. Our results suggest that the growth rate will be most rapid in open areas and decline as conspecific—and likely heterospecific—density increases.

Opportunities for climbing, provided by the presence of a lattice, increased allocation to twining shoots. In contrast, the proportion of biomass allocated to twining shoots was not influenced by competition. Increased allocation to climbing shoots in the presence of a vertical structure is consistent with previous work, supporting the conclusion that *L. japonica* exhibits a highly plastic growth form that is responsive to local environmental conditions (Schweitzer and Larson 1999). Interestingly, biomass allocated to running shoots was greater than that allocated to climbing shoots regardless of lattice treatment. Twining vines such as *L. japonica* tend to need more structural support for climbing shoots than tendril climbers but less support than other types of vines (Putz 1984), so it possible for allocation
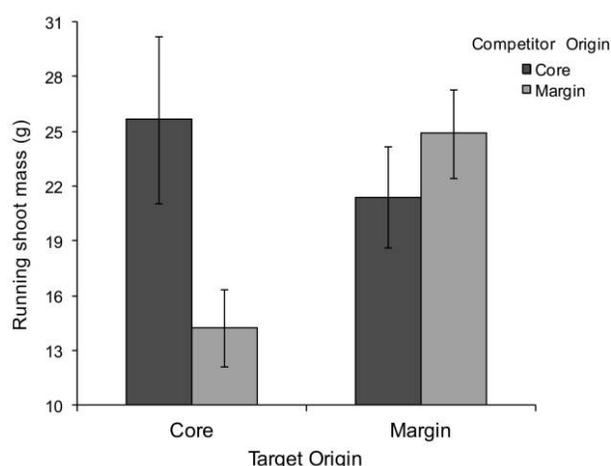
to climbing shoots to be reduced if available structural support is not adequate. Indeed, plants in this study climbed on all available structures, including grasses, which often collapsed under the mass of twining shoots. However, plants with available lattice, which acted as a strong support structure, also had greater allocation to running shoots than to climbing shoots, suggesting that a lack of adequate structural support was not the primary reason for this allocation bias. In forest environments, running shoots primarily act as a searching mechanism for available vertical structures (Peñalosa 1984). However, *L. japonica* in North America is often found at much higher densities along forest edges and in open fields, which have limited support availability (F. F. Kilkenny, personal observation), suggesting that running shoots may act as a primary means of vegetative spread.

We also found that the presence of a lattice decreased the overall probability of reproduction. However, it is unclear how general this result is, as reproductive output increased in the presence of a support structure in another invasive vine (Stansbury et al. 2007). While the presence of lattice decreased reproduction in general, the proportion of plants with climbing shoots that produced flowers increased with increasing competition in the presence of the lattice but decreased with increasing competition when no lattice was present. This suggests that *L. japonica* may be able to mitigate some of the density-dependent loss in reproductive capacity by allocating resources to climbing shoots when support is available. This finding supports studies showing that response to density can be complex in vines because flexibility in resource allocation can allow vines to escape the negative effects of high density in ways unavailable to plants with less plastic growth habits (Klimeš and Klimešová 1994; Leicht-Young et al. 2011).

There was no difference in the response to a lattice or the probability of producing climbing shoots between plants from the core and margin regions of the range. We predicted that plants from the core area would be more likely to take advantage of a support structure (lattice × target origin interaction) because conspecifics are much denser in the core and *L. japonica* frequently forms monospecific stands, climbing up and over itself and other taxa. Furthermore, we predicted that an increased allocation to climbing shoots in populations from the core region would results in a greater competitive ability. Despite differences in *L. japonica* density between core and northern margin populations, there was no difference between regions in the tendency to produce climbing shoots, in the plastic response to density, or in the response to a support structure. One possible reason for the lack of differentiation is that it is always advantageous to climb over other vegetation regardless of whether it represents intraspecific or interspecific competition. Therefore, the selective environments may be more similar between regions than we had expected. Alternatively, differentiation in these traits may be lacking due to inadequate genetic variation or to insufficient time for divergence, a possible result of *L. japonica*'s high propensity for clonal reproduction and therefore potentially long generation time. However, studies have found that the genetic diversity of North American *L. japonica* is comparable to that of other plants with similar life history characteristics (Schierenbeck et al. 1995) and that diversity is concentrated at the population level (Kilkenny 2011).

Lonicera japonica plants from the northern margin of the invaded range were larger and better competitors than plants from the core. Running shoot mass was greater for margin populations than for core populations, regardless of competitor number. In addition, running shoots of targets from the core region were smaller when competitors were from the margin than when competitors were from the core. However, running shoots of target plants from margin populations were similar in size regardless of competitor origin. Finally, margin competitors also tended to reduce the proportion of target plants with at least one climbing shoot. In total, these results suggest a genetic difference in competitive ability between populations from the core and margin regions. Larger size of plants from margin populations was also found in a study of *L. japonica* in which plants from a similar group of populations were grown in common gardens located in the core and the northern margin of the invaded range (Kilkenny and Galloway 2013).

In contrast to the prediction that greater intraspecific competitive ability would be favored at sites in the core where conspecific density is higher, plants from margin populations were better competitors than those from core populations. It seems unlikely that increased intraspecific competitive ability is favored by selection in margin populations because local *L. japonica* densities are low (25% cover) relative to those in the core of the range (60% cover; Kilkenny 2011). Indeed, if intraspecific competition was driving the evolution of competitive ability, we would expect plants from core populations to outcompete those from the margin. It seems more plausible that a larger plant size (or increased growth rate that results in larger plants) is favored by selection at the range margin and that the improved competitive ability of plants from margin populations is a consequence of their greater size.

There are several possible explanations for the greater size of plants from margin populations when grown in the same environment as plants from core populations. First, greater size in margin plants may be due to the evolution of more rapid growth in northern populations with a shorter growing season (i.e., countergradient variation; Conover and Schultz 1995; Laugen et al. 2003; Etterson 2004). The increased growth rate would result in larger size of northern populations when grown in the same environment as the core populations. Faster growth rates associated with countergradient variation similarly result in greater competitive ability of higher-latitude populations in frogs (Lindgren and Laurila 2010). Second, greater size of plants from margin populations may be a result of selection for traits that promote colonization, such as increased clonal spread (Geber 2008). The sites in the north are the most recently invaded and therefore are more likely to express the rapid growth associated with increased rates of clonal spread. Finally, in more recently invaded northern populations, interspecific competition is expected to be stronger than in core populations that have greater densities of *L. japonica*. If interspecific competition is a stronger selective agent than intraspecific competition and increased plant size increases competitive ability, plants from the northern range margin would be expected to be both larger and better competitors. In total, indirect evolution of competitive ability through selection for increased size represents a mechanism that enhances the invasive potential in novel habitats.

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