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What happens in Europe stays in Europe: apparent evolution by an invader does not help at home

Robert W. Pal,[1,2,6] John L. Maron,[3] David U. Nagy,[2] Lauren P. Waller,[3] Ambra Tosto,[4] Huixuan Liao,[5] and Ragan M. Callaway[3]

[1]*Department of Biological Sciences, Montana Technological University, Butte, Montana 59701 USA*
[2]*Institute of Biology, Faculty of Sciences, University of Pecs, H-7624 Pecs, Hungary*
[3]*Division of Biological Sciences and the Institute on Ecosystems, The University of Montana, Missoula, Montana 59812 USA*
[4]*Centre for Crop System Analysis, Wageningen University, 6708 PB Wageningen, The Netherlands*
[5]*School of Life Sciences, Sun Yat-sen University, Guangzhou 510006 China*

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Abstract. Some invasive plant species rapidly evolve greater size and/or competitive ability in their nonnative ranges. However, it is not well known whether these traits transfer back to the native range, or instead represent genotype-by-environment interactions where traits are context specific to communities in the new range where the evolution occurred. Insight into transferability vs. context specificity can be tested using experiments performed with individuals from populations from the native and nonnative ranges of exotic invasive species. Using a widespread invasive plant species in Europe, *Solidago gigantea*, we established reciprocal common garden experiments in the native range (Montana, North America; $n = 4$) and the nonnative range (Hungary, Europe; $n = 4$) to assess differences in size, vegetative shoot number, and herbivory between populations from the native and nonnative ranges. In a greenhouse experiment, we also tested whether the inherent competitive ability of genotypes from 15 native and 15 invasive populations differed when pitted against 11 common native North American competitors. In common gardens, plants from both ranges considered together produced five times more biomass, grew four times taller, and developed five times more rhizomes in the nonnative range garden compared to the native range garden. The interaction between plant origin and the common garden location was highly significant, with plants from Hungary performing better than plants from Montana when grown in Hungary, and plants from Montana performing better than plants from Hungary when grown in Montana. In the greenhouse, there were no differences in the competitive effects and responses of *S. gigantea* plants from the two ranges when grown with North American natives. Our results suggest that *S. gigantea* might have undergone rapid evolution for greater performance abroad, but if so, this response does not translate to greater performance at home.

Key words: biogeography; common garden experiment; competition; EICA hypothesis; invasion; reintroduction; Solidago gigantea*; transcontinental research.*

Introduction

When plants are relocated to new biogeographic ranges, individuals are often larger in comparison to conspecifics from the native range (Siemann and Rogers 2001, Jakobs et al. 2004, Bossdorf et al. 2005, Ridenour et al. 2008, Callaway et al. 2012, Graebner et al. 2012, Felker-Quinn et al. 2013, Rosche et al. 2019). This suggests that greater size and competitive ability may be selected for and thus evolve in the new ranges of many exotic plant species (Blossey and Nötzold 1995, Blair and Wolfe 2004, Joshi and Vrieling 2005). This rapid evolution has been proposed to contribute to the invasiveness of some exotic species (Sakai et al. 2001, Stockwell et al. 2003, Lambrinos 2004, Barrett et al. 2008, Keller and Taylor 2008, Dudeque Zenni et al. 2016); however, the consequences of such evolutionary responses in both the native and nonnative ranges of invasive species are poorly understood.

One important knowledge gap in our understanding of how rapid evolution influences invasive species is whether this evolution confers a general superiority in performance if these species are taken back to their native range. In other words, if invasive species evolve larger size or greater fecundity compared to native conspecifics, are they similarly larger with enhanced performance when translocated back home? Alternatively, there might be a genotype-by-environment interaction whereby evolution that occurs in nonnative ranges might only confer superior performance in the ecological

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[6] E-mail: rpal@mtech.edu

context of that range. Of the few such biogeographic comparisons that have been conducted, experiments have produced mixed results. Maron et al. (2004) compared the size and fecundity of *Hypericum perforatum* from native and nonnative populations in common gardens in both the native and nonnative ranges. They found that across gardens introduced genotypes were neither universally larger nor more fecund than native genotypes. In a reciprocal common garden experiment, Williams et al. (2008) found that *Cynoglossum officinale* plants from populations in the nonnative range were larger and more fecund, but only in a common garden in the native range.

Thus, the few studies of the responses of exotic species from native and nonnative populations in native and nonnative ranges do not show a consistent pattern. Regardless, if plants do evolve larger size or competitive ability in the introduced range, it is reasonable to expect that this might not translate to similar high performance if these plants are brought home. The enemy release hypothesis (ERH) posits that the specialist enemies of invaders are absent or reduced in areas where they have been introduced, which enables exotic species to escape consumption, in turn leading to increases in distribution and abundance (Maron and Vilà 2001, Keane and Crawley 2002). Derived from the ERH, the EICA hypothesis (evolution of increased competitive ability; Blossey and Nötzold 1995) predicts that escape from specialist herbivores may put a selective premium on increased competitive ability, as fewer resources are needed for defense. This suggests that the evolution of larger size and/or competitive ability in the nonnative range may make plants from populations in the nonnative range more susceptible to the herbivores and pathogens that occur in their native ranges (Blossey and Nötzold 1995, Daehler and Strong 1997, Blair and Wolfe 2004, Joshi and Tielbörger 2012, Qin et al. 2013; but see Bossdorf et al. 2005, Ridenour et al. 2008, Cronin et al. 2015). Thus, reintroduction to the native range may result in reduced overall performance. However, results in support of EICA's predictions have been indeed mixed. In a meta-analysis Felker-Quinn et al. (2013) found no support across the studied invasive plants for defense or competitive ability. On the other hand, a second meta-analysis by Rotter and Holeski (2018) found partial support for the reduction of herbivore resistance in nonnative populations and for a trade-off between herbivore resistance and increased fitness.

We examined the performance of *Solidago gigantea*, a widespread invasive plant species in Europe that is native to North America, in common gardens in native and nonnative ranges. In gardens in both ranges, we assessed differences in size, vegetative shoot number, and herbivory. Other studies indicate that *S. gigantea* populations in nonnative ranges can differ distinctly in growth form and size from conspecifics in the native range. In a common garden, Güsewell et al. (2006) found that European *S. gigantea* plants produced, on average, more shoots than American plants (also see Jakobs et al. 2004, Meyer, Clare and Weber2005). We established multiple common gardens in each range to determine (1) whether introduced genotypes of *S. gigantea* have evolved greater size and/or fecundity in the invaded range and (2) whether herbivore resistance in the native range varies between native and introduced populations, and (3) to test the inherent competitive ability of *S. gigantea* from native and nonnative populations against species from the native range of *S. gigantea*.

METHODS

Species

Solidago gigantea (giant goldenrod) is a tall (30–280 cm), rhizomatous perennial herb in the Asteraceae family. Its yellow flower heads can range from 190 to 1,200, which produce up to 19,000 achenes that are dispersed by wind (Schmid et al. 1988, Weber and Jakobs 2005). Because of its clonal growth, shoot densities can reach 29–167 shoots/m^2, and significantly impact native plant diversity in the nonnative range (Jakobs et al. 2004, Pal et al. 2015). *Solidago gigantea* has three different cytotypes in the native range, of which the $2n = 4x$ is to be found in the nonnative range (Schlaepfer et al. 2008).

The species is one of the most widespread and problematic invasive plant species in central Europe (Weber and Jakobs 2005, Botta-Dukát and Balogh 2008, Lambdon et al. 2008). It is native to North America and was introduced to Europe in the 18th century as an ornamental, and became invasive roughly 100 yr later. Although *S. gigantea* prefers rich and moist soils, such as riverside habitats at lower altitudes, it can also be found in drier ruderal areas, especially in its nonnative range (Weber 2001, Weber and Jakobs 2005, Botta-Dukát and Dancza 2008). In the nonnative range the species is an aggressive invader of disturbed mesic sites and tree plantations, and often forms dense monodominant stands in abandoned fields (Török et al. 2003, Güsewell et al. 2005, Weber and Jakobs 2005, Láníková et al. 2009, Bartha et al. 2014).

Field common garden experiment

We collected seeds from six populations of *S. gigantea* in part of its native range (western Montana; 46°51’ N 113°57’ W–47°52’ N 114°01’ W), and from six populations in part of the nonnative range (southwestern Hungary; 46°01’ N 18°27’ E–46°07’ N 17°53’ E; Table 1). Within each range, the minimum distance among sampled populations was 3 km, whereas the maximum was 150 km. Individual plants from which seed was collected were located at least 10 m from each other, which reduced the risk of resampling the same clone. For each population, we sampled 10 maternal plants, and

Table 1. Source populations of *Solidago* seeds used in the common garden experiment.

Region	Nearby settlement	Elevation (m)	Latitude	Longitude	Original habitat
Hungary (nonnative range)					
1	Máriakéménd	152	46°01’ N	18°27’ E	Disturbed grassland
2	Somberek	96	46°03’ N	18°39’ E	Wetland
3	Almáskeresztúr	132	46°06’ N	17°51’ E	Disturbed grassland
4	Mozsgó	124	46°06’ N	17°50’ E	Wetland
5	Almáskeresztúr	143	46°06’ N	17°53’ E	Disturbed grassland
6	Mozsgó	128	46°06’ N	17°51’ E	Wetland
Montana (native range)					
1	Moiese	789	47°22’ N	114°14’ W	Grassland
2	Moiese	786	47°22’ N	114°14’ W	Ripparian area
3	Moiese	810	47°22’ N	114°15’ W	Grassland
4	Yellow Bay	904	47°52’ N	114°01’ W	Disturbed grassland
5	Missoula	986	46°51’ N	113°57’ W	Disturbed grassland
6	Missoula	974	46°51’ N	113°57’ W	Ripparian area

offspring from the same maternal plants were considered as replicates throughout our entire experiment on both ranges. To explore responses across a potential range of microsite variability, we established four common gardens in the native range in southwest Montana ([a] 47°22’ N 114°14’ W; [b] 47°22’ N 114°14’ W; [c] 47°29’ N 114°07’ W; [d] 47°29’ N 114°07’ W) and four common gardens in the nonnative range in southwest Hungary ([a] 46°01’53" N 18°08’ E; [b] 46°01’ N 18°08’ E; [c] 46°03’ N 18°15’ E; [c] 46°03’ N 18°15’E). Gardens were marked and signed visibly, but no protecting fences were established against large herbivores, as they were not problematic in either range. Only small rodents and insects damaged some of our plants. Latitudes of the sites on both continents were similar, but the elevation of our common gardens, and consequently their climates, varied. The average elevation of the Hungarian sites was 150 m above sea level (asl), with mean annual temperature ranging from 10 to 11°C and mean annual precipitation ranging between 650 and 700 mm (Bihari et al. 2009). The average elevation of the Montana sites was 800 m asl, with a mean annual temperature ranging from 7 to 8°C and mean annual precipitation between 345 and 405 mm per year (WRCC 2014). The general soil properties of the gardens in the two ranges can be found in Appendix S1: Table S1.

We initially grew eight seedlings (one for each garden) from each maternal plant from each population from each range for 3 months in naturally lit greenhouses at the University of Montana (USA) and the Directorate of Plant Protection and Soil Conservation in Baranya County, Pécs (Hungary). Plants were transplanted in early May 2009 and 2010 to the four common gardens in each range. Before transplanting, gardens were marked, and the existing natural vegetation was cut back to the ground level. In both ranges resident plant communities were dominated by perennial grasses, therefore competitive environments were quite similar. The only annual species among these plants was *Erigeron annuus.* In Appendix S1: Table S2. we have listed the 15 most dominant plant species in the resident plant communities of the common gardens in both ranges.

Each garden contained 120 plants (two continents × six populations × 10 maternal plants per population) in a 50 × 50 cm grid. We maintained the common gardens in both ranges for two seasons, letting natural vegetation regrow to mimic natural circumstances. Data collection took place in August before the plants started to flower and potentially before their vegetative shoots reached maximal height. Data on survival rate, height, number of vegetative shoots, and the magnitude of herbivory (percentage of the number of leaves per plant damaged by herbivores) were recorded in the first year. In the second year, aboveground biomass of *S. gigantea* was collected and weighed after two days of drying at 60°C. All test plants in the common gardens were eliminated at the end of the experiment with COLOMBUS* EC (Dow AgroSciences) herbicide.

Greenhouse competition experiment

We compared competitive effects and responses of *S. gigantea* from the native and invaded ranges when grown with and without North American native species. We used seeds collected from 15 *S. gigantea* populations from each of the native and invaded ranges (Table 2), and the seeds of 11 common native competitor species (*Achillea millefolium*, *Apocynum cannabinum*, *Artemisia ludoviciana*, *Carex nebrascensis, Geum macrophyllum*, *Helianthus maximiliani*, *Juncus arcticus*, *Leymus cinereus*, *Monarda fistulosa*, *Rudbeckia laciniata*, *Solidago canadensis*; more info on species trait can be found in Appendix S1: Table S3). The competitor species were selected on the basis of a biogeographic plot survey by Pal et al. (2015), from which we picked the most frequent native species co-occurring with *S. gigantea* that do not require long stratification treatments. The seeds of all target species were germinated in separate Petri dishes and transplanted to 250-mL rocket pots in autoclaved alluvial soil and sand mixture (50:50). We grew

TABLE 2. Source populations of *Solidago* seeds used for the greenhouse experiment.

Region	Country/State	Elevation (m)	Lat	Long	Habitat
Europe (nonnative range)					
INV	Austria	703	47°41’ N	16°18’ E	Dry
INV	Austria	116	47°50’ N	16°48’ E	Wet
INV	Switzerland	450	46°56’ N	08°17’ E	Wet
INV	Switzerland	742	46°55’ N	09°43’ E	Dry
INV	Czech Republic	248	49°50’ N	18°19’ E	Dry
INV	Croatia	147	45°27’ N	18°02’ E	Wet
INV	Croatia	341	45°25’ N	17°58’ E	Wet
INV	Hungary	193	46°06’ N	18°18’ E	Dry
INV	Germany	499	47°49’ N	12°22’ E	Dry
INV	Germany	500	47°49’ N	12°23’ E	Wet
INV	Poland	215	50°04’ N	19°51’ E	Wet
INV	Romania	293	46°28’ N	24°27’ E	Dry
INV	Romania	487	45°49’ N	25°36’ E	Dry
INV	Slovakia	117	48°49’ N	18°14’ E	Dry
INV	Serbia	77	45°17’ N	19°53’ E	Dry
North America (native range)					
NAT	Colorado	1,632	40°13’ N	105°15’ W	Wet
NAT	Idaho	450	46°08’ N	115°35’ W	Wet
NAT	Idaho	1,422	43°26’ N	112°06’ W	Dry
NAT	Iowa	315	42°01’ N	096°01’ W	Wet
NAT	Maine	135	44°37’ N	069°58’ W	Dry
NAT	Minnesota	287	46°45’ N	096°31’ W	Wet
NAT	Montana	970	46°52’ N	114°00’ W	Wet
NAT	Montana	964	46°50’ N	114°02’ W	Dry
NAT	North Dakota	375	46°54’ N	098°01’ W	Dry
NAT	North Dakota	695	46°55’ N	103°31’ W	Wet
NAT	Nebraska	778	40°53’ N	100°07’ W	Dry
NAT	Nebraska	323	41°03’ N	96°20’ W	Dry
NAT	South Dakota	392	45°32’ N	96°59’4" W	Wet
NAT	South Dakota	1,629	43°52’ N	103°37’ W	Wet
NAT	Wyoming	1,227	44°29’ N	104°46’ W	Wet

genotypes from each population in competition against each native competitor and also added 7 pots containing *S. gigantea* alone and 10 pots containing each native species alone. In total we established 15 *S. gigantea* populations × 2 ranges × 11 native competitors + 15 *S. gigantea* populations × 2 ranges in seven replications alone + 11 × 10 native competitors alone; $n = 650$ pots. The experiment was set up in February 2013 in a greenhouse in Missoula, Montana and harvested after 5 months. Above- and belowground biomass was weighed after two days of drying at 60°C.

Statistical analysis

All statistical analyses were carried out in R (version 3.5.2) (R Development Core Team 2018). For the common garden experiment data, we ran general linear mixed-effect models (LMM) testing the effect of the following fixed factors: (1) destination garden (Hungary, Montana), (2) origin of seeds (Hungary, Montana), and (3) the destination garden × origin interaction on aboveground biomass, plant height, vegetative shoot number, and the magnitude of herbivory with population (nested within continent) and garden site (nested within continent) as random factors. All models were fitted using the lme4 package. Binomial variables (mortality) were analyzed by generalized mixed-effect linear model (GLMM) using Pearson’s chi-square test. Data were transformed to fit normal distribution and reduce variance heterogeneity according to the graphical evaluation of the models (Crawley 2015). We used independent contrasts for pairwise comparisons with Tukey-adjusted P values using multcomp package. Significance for all statistical analyses was accepted at $P < 0.05$.

For the analyses of the greenhouse experiment, RII (relative interaction index) values for individual plants were calculated using the following equation from Armas et al. (2004):

$$\mathrm{RII} = \left(\frac{\mathrm{Biomass}_{\mathrm{withcompetition}} - \mathrm{Biomass}_{\mathrm{withoutcompetition}}}{\mathrm{Biomass}_{\mathrm{withcompetition}} + \ \mathrm{Biomass}_{\mathrm{withoutcompetition}}\mathrm{Biomass}_{\mathrm{withcompetition}} + \mathrm{Biomass}_{\mathrm{withoutcompetition}}}\right).$$

The RIIs of *S. gigantea* represented the responses to competition, and the RIIs of North American species represented the competitive effects of *S. gigantea*. We ran a general linear mixed-effect model testing the effect of the following fixed factors: (1) destination garden (nonnative, native), (2) competitive response/effect of *S. gigantea*, and (3) the garden destination × competitive response/effect, with population (nested within continent) and the identity of the native competitors as random factors. Because RIIs are negative values, the model was run with a normal distribution.

RESULTS

Field common garden experiment

In nonnative (Hungarian) gardens, the mortality of native (Montana) plants was 5.2% higher ($\chi^2 = 14.86$, $P < 0.0001$) than that of Hungarians. In contrast, in the native range, mortality of the Hungarian plants was 19% higher ($\chi^2 = 20.32$, $P < 0.0001$) than plants from Montana. Thus, survivorship suggests that plants from each range are better adapted to conditions in the range they currently inhabit compared to the recipient range into which we transplanted individuals.

In the nonnative range, plants from nonnative populations were larger than plants from native populations. However, this pattern did not hold up in Montana. There, native and nonnative populations were smaller than in Hungary, and not different from each other. Thus, increased size of nonnative populations that was manifest in Hungary did not transfer to Montana. Across gardens, populations exhibited differences in total biomass, height, and the number of vegetative shoots as indicated by highly significant destination garden × plant origin interactions. For biomass, the effect of origin was not significant, but the effect of range, that is, the range in which plants were grown, and the interaction between seed origin and range was (Table 3). Hungarian plants in Hungary had higher biomass (t value = −10.25, $P < 0.0001$) than Hungarian plants in Montana, and the biomass of Montana plants was also larger (t value = −5.39, $P < 0.0001$) in Hungary than in their native range (Fig. 1). The mean biomass of *S. gigantea* from nonnative populations was 59% higher in Hungary (post hoc, t value = −7.25, $P < 0.0001$) than plants from Montana populations. The mean biomass of Hungarian populations in Montana was not different (t value = 0.84, $P = 0.83$) than that of plants from Montana. The mean untransformed biomass of the Hungarian populations in Hungary was 23.86 ± 1.34 g, and it was 14.19 ± 0.64 g in the Montana populations. The mean untransformed biomass of the Hungarian populations in Montana was 2.59 ± 0.14 g, and it was 4.57 ± 0.25 g in the Montana populations.

For shoot number, the effect of seed origin was not significant, and neither was the effect of the range in which plants were grown. The interaction, however, between origin and range was highly significant (Table 3). Hungarian plants in Hungary had significantly higher (post hoc t = −17.12, $P < 0.0001$) numbers of vegetative shoots than Hungarian plants in Montana, whereas the shoot number of Montana plants was also higher in Hungary (post hoc t value = −6.09, $P < 0.0001$; Fig. 2). In Hungary Hungarian *S. gigantea* populations produced 49% (post hoc t value = −9.313, $P < 0.0001$) more vegetative shoots than plants from Montana. The shoot number (post hoc t value = 1.61, $P = 0.73$) of Hungarian *S. gigantea* populations in Montana was not different than that of plants from Montana. The mean untransformed shoot number for the Hungarian populations in Hungary was 4.22 ± 0.15 and 2.62 ± 0.12 for the Montana populations. The mean untransformed shoot number of the Hungarian populations in Montana was 1.37 ± 0.03, and it was 1.63 ± 0.04 for the Montana populations.

Plant height showed a similar trend in the first year. The effect of seed origin was not significant, but the effect of the destination garden and the interaction between these two factors was highly significant (Table 3). Hungarian plants in Hungary were significantly taller (t value = −22.48, $P < 0.0001$) than Hungarian plants in Montana, whereas the height of Montana plants was also greater (t value = −18.76, $P < 0.0001$) in Hungary than in their native range. In Hungary Hungarian *S. gigantea* populations grew 14% taller (t value = −3.83, $P = 0.01$) than plants from Montana. The height of Hungarian populations in Montana was not different (post hoc t value = 0.35, $P = 0.99$) than that of plants from Montana (Appendix S1:

TABLE 3. Results of the ANOVA testing for plant biomass, number of vegetative shoots, plant height, and the magnitude of herbivory between common gardens in Hungary and Montana.

	df	*F*	*P*
Biomass			
Origin of seeds	1, 9.996	0.369	0.557
Destination garden	1, 2.000	36.078	**0.027**
Origin of seeds × destination garden	1, 943.11	71.16	**<0.0001**
Number of vegetative shoots			
Origin of seeds	1, 11.49	1.66	0.2228
Destination garden	1, 2.128	12.15	0.0671
Destination garden × origin of seeds	1, 695.1	18.57	**<0.0001**
Plant height			
Origin of seeds	1, 9.987	1.83	0.2064
Destination garden	1, 1.992	135.89	**0.0074**
Destination garden × origin of seeds	1, 1385	36.47	**<0.0001**
Magnitude of herbivory			
Origin of seeds	1, 12.18	16.425	**0.0015**
Destination garden	1, 1.5	37.057	**0.049**
Origin of seeds × destination garden	1, 915.27	20.463	**<0.0001**

Note: Significant values ($P < 0.05$) highlighted in bold.

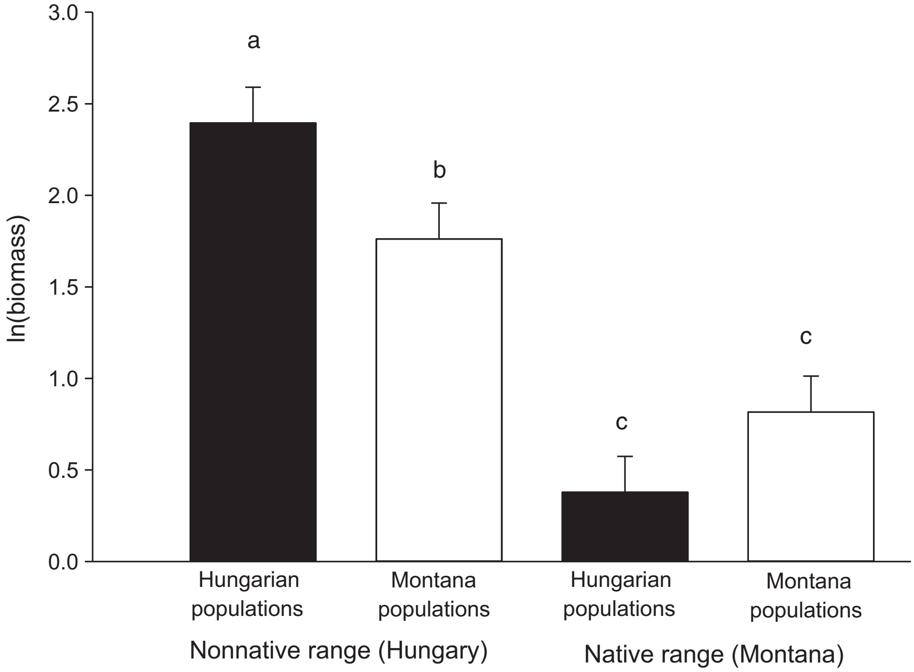

FIG. 1. Aboveground biomass of different *Solidago gigantea* populations in the second year of the experiment (values are represented by least-squares means and one SE). Different letters show significant differences based on Tukey pairwise comparisons.

Figure S1.). The mean untransformed plant height of the Hungarian populations in Hungary was 38.63 ± 0.73 cm, and 33.49 ± 0.71 cm for the Montana populations. The mean untransformed plant height of the Hungarian populations in Montana was 5.87 ± 0.17 cm, and 6.37 ± 0.14 cm for the Montana populations.

For aboveground herbivory, the effect of seed origin, the range in which plants were grown, and the interaction of these two factors were significant (Table 3). In

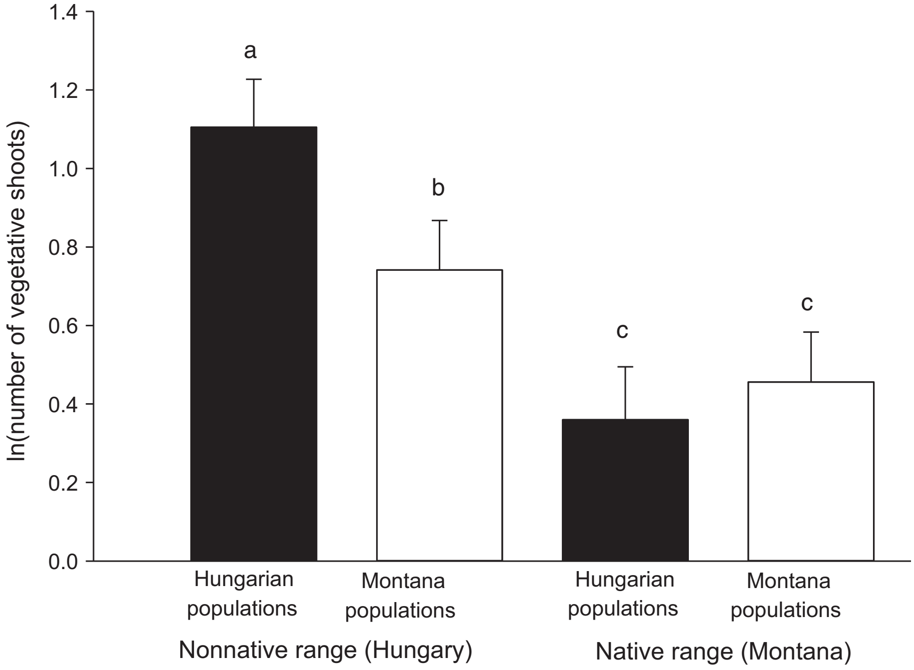

FIG. 2. Number of vegetative shoots of *Solidago gigantea* plants in the first year of the experiment (values are represented by least-squares means and SE). Different letters mean significant differences based on the Tukey pairwise comparisons.

the nonnative range, Montana populations experienced 51.8% higher herbivory than Hungarian populations (*z* value = 7.54, $P < 0.0001$). In the native range, herbivory on *S. gigantea* from Montana did not differ from that on *S. gigantea* from Hungary (*z* value = 0.37, $P = 0.979$). In the nonnative range an average of 41% of leaves per plant were damaged on Montana populations, and only 27% of leaves per plant were damaged on Hungarian populations. In the native range an average of 8% of leaves per plant were damaged on Montana plants and 7% were damaged on Hungarian plants (Appendix S1: Figure S2.).

Greenhouse competition experiment

The origin of *S. gigantea* seeds (native vs. nonnative range) did not affect either the competitive response or effect of *S. gigantea* when planted with 11 North American native species ($F_{1,28.01} = 2.30$, $P = 0.140$) (Table 4). However, the mean RII for the response of *S. gigantea* from Europe to competition from North American species was significantly different from zero (*t* value = −2.54, $P < 0.01$), suggesting that plants from the nonnative range were weaker competitors against North American species. In contrast, the response of *S. gigantea* from North America was not significantly different from zero (*t* value = −0.27, $P = 0.79$). The mean RII for the competitive effect of both native (*t* value = −22.67, $P < 0.0001$) and nonnative (*t* value = −23.79, $P < 0.0001$) *S. gigantea* populations was significantly different from zero. *Solidago* substantially outcompeted North American species with the difference between the competitive response and effect of *S. gigantea* populations being highly significant ($F_{1,614.07} = 1649.94$, $P < 0.001$). There was no significant difference ($F_{1,11.881} = 0.5592$, $P = 0.4691$) between the total biomass of the native and nonnative *S. gigantea* genotypes in the absence of competition (Fig. 3).

DISCUSSION

As other studies have found, in the nonnative range invasive plants from nonnative populations outperformed congeners from the native range (Siemann and Rogers 2001, Callaway et al. 2012, Shah et al. 2014, Ledger et al. 2015, Pal et al. 2015). Few studies, however, have asked how consistent these results are if the same plants are also evaluated against each other in the native range. We found that in the native range the patterns detected in the nonnative range did not hold; *S. gigantea* plants from nonnative populations in the native range underperformed relative to congeners from the native range. Although our results are consistent with rapid evolution resulting in increased size of *S. gigantea* in Hungary, we cannot rule out the possibility that founder effects play an important role in our results (Felker-Quinn et al. 2013). In other words, the populations may have been selected for or adapted locally without individuals in those populations becoming better competitors in general. Others have shown that the evolution of local adaptation might be an important mechanism enabling survival and rapid spread of plant species in their new ranges (Sakai et al. 2001, Barrett et al. 2008, Keller and Taylor 2008).

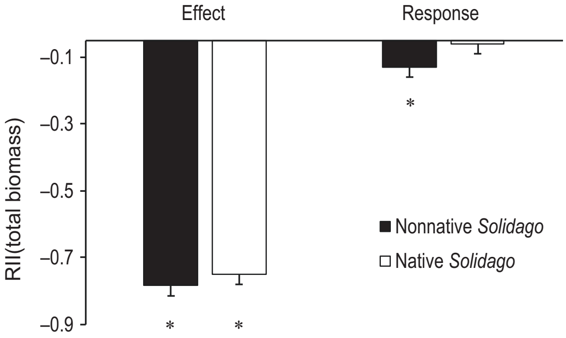

FIG. 3. Mean RIIs for competitive effects of *Solidago gigantea* from either Hungary or Montana on 10 North American plant species, and for the responses of *S. gigantea* to the North American native plant species. Asterisks indicate significant differences from zero.

TABLE 4. Results from an ANOVA, testing the difference in the competitive ability of the native and nonnative *Solidago* populations.

	df	*F*	*P*
RII (total biomass)			
Origin of seeds	1, 28.04	2.30	0.140
Origin of seeds × competitive effect/response	1, 614.07	1.15	0.285

There are several important limitations of our study. First, despite similar latitudes, there were differences in climate in the locations of the common gardens in the native and nonnative ranges. Thus, it could be that there are unknown climate-by-range interactions that may have influenced our results. Second, our common garden study only compared six populations from each range, from Montana and Hungary. Clearly a broader geographic sampling of populations would be desirable, something we tried to accomplish in the greenhouse portion of this study. Finally, we did not account for within-range adaptation to climatic conditions and demographic history that may lead to nonadaptive evolution (see Rosche et al. 2019).

Despite clear evidence of strong costs of returning home for exotic genotypes that showed genetically based size advantages in the nonnative range, we do not know the mechanisms that might drive these costs. Our salient finding—that large growth of Hungarian plants in Hungary did not translate to greater performance of these plants in Montana—was not driven by the loss of resistance and heavy herbivory in Montana, at least as suggested by our analyses. Plants from Montana populations were more damaged in the nonnative range than were plants from Hungary. In contrast, in Montana native and nonnative populations were equally damaged by aboveground herbivores (mainly Lygaeidae, Cicadellidae, and different leaf miner species). This is partially consistent with a meta-analysis conducted by Felker-Quinn et al. (2013; also see Bossdorf et al. 2005) which found little support for consistent loss of defense in populations in the nonnative ranges of exotic species. However, they found that nonnative populations consistently demonstrated increased growth relative to native populations in noncompetitive environments. Ridenour et al. (2008) found that the apparent evolution of larger size and competitive ability by *Centaurea stoebe* corresponded with an *increase* in defense to both specialist and generalist insects. As for many exotic invasive plant species (Kulmatiski et al. 2008, Lekberg et al. 2018), *S. gigantea* in Europe may benefit greatly by escaping the negative effects of soil biota. For example, sterilizing soil from the native range increased the biomass of a congener, *Solidago canadensis*, by 61%, but sterilization of soil from the nonnative range had no effect (R. Pal, *unpublished data*). Maron et al. (2015) compared the magnitude of plant–soil feedbacks experienced by *S. gigantea* plants from the native and nonnative ranges in soil collected across the western part of the species' native range in the United States. They found that both native and nonnative *S. gigantea* suffered consistently negative plant–soil feedbacks, but there were no differences in feedback responses between plants from the native and nonnative ranges. Thus, introduced *S. gigantea* does not appear to have lost resistance to the negative effects of soil biota, and these results do not suggest an alternative mechanism for the cost of returning home.

Our competition experiments, albeit in controlled conditions, did not show a clear relationship between larger growth and greater competitive ability. In this experiment, *S. gigantea* plants from the nonnative range did not differ in size in comparison to plants from the native range. There was no difference in the competitive effects of *S. gigantea* plants from the native and nonnative ranges on a suite of North American species. In fact, based on the differences in RIIs from zero, North American competitors suppressed *S. gigantea* from Hungary more than *S. gigantea* from Montana, emphasizing the lack of evidence for increased competitive ability as a mechanism.

Other studies have found, in common gardens, that plants grown from seed collected in the nonnative ranges of exotic species are larger than plants grown from seeds from native ranges (Crawley 1987, Jakobs et al. 2004). Colautti et al. (2009) conducted a meta-analysis of 32 common garden studies with 28 plant species and found that overall, plants from nonnative range populations exhibited increased growth and reproduction compared to conspecifics from native ranges. There is less evidence for such increases in growth corresponding to reduced allocation to defense. Joshi and Tielbörger (2012) found that the nonnative populations of *Lythrum salicaria* were attacked by herbivores more than native populations, but their final size did not reflect attack rates. Ridenour et al. (2008) demonstrated that nonnative *Centaurea maculosa* populations were better defended against insect herbivores than native populations. Johnson et al. (2007) found differences in foliar terpenoid composition between native and nonnative populations of *S. gigantea*, which suggested decreases in chemical defense in the latter. Hull-Sanders et al. (2009) found that a generalist herbivore grew better on *S. gigantea* from the nonnative range than congeners from the native range, but a specialist herbivore did not show any preferences. Others found that the compensatory growth of *S. gigantea* in response to herbivory was not consistent with the EICA hypothesis (Meyer and Hull-Sanders 2008).

Importantly, biogeographic correlative comparisons of impact, which did not directly compare congeners from native and nonnative ranges, show that increasing stem density of *S. gigantea* corresponds with significant decreases in native species diversity in the nonnative range; but not in the native range (Pal et al. 2015). Our results indicate that this might be due to increased size in the nonnative range, but we have no direct evidence of inherent differences in competitive ability between native and nonnative *S. gigantea* populations. But in summary, our results suggest that *S. gigantea* may have undergone rapid evolution for greater performance abroad, but this response appears to be context-specific, with a cost to growth performance in the native range.

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