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REPORT

Reduced competitive ability in an invasive plant

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Abstract

One explanation for successful plant invaders is that they evolved to be more competitive. An intuitive prediction of this Evolution of Increased Competitive Ability (EICA) hypothesis never previously tested is that invasive populations should outcompete their native 'ancestors' in a common environment. We tested this idea in a diallel competition experiment with *Alliaria petiolata* where offspring from native and invasive populations were grown alone or in all pairwise combinations. While without competition, there were no differences between native and invasive populations, native populations outperformed invasive ones when competing against each other. Our results contradict the EICA hypothesis and we conclude that it does not not hold for *Alliaria petiolata*. Instead, we formulate a new ERCA (Evolutionary Reduced Competitive Ability) hypothesis: if there is less competition in the invasive range and competitive ability involves traits that have a fitness cost, then selection might act against it, thereby reducing intraspecific interactions too.

Keywords

Alliaria petiolata, biological invasions, competitive ability, Evolution of Increased Competitive Ability, Evolutionary Reduced Competitive Ability, genetic differentiation, intraspecific competition, microevolution, native and introduced populations.

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INTRODUCTION

Evolutionary change can be rapid and therefore relevant to ecological studies (Thompson 1998). In this context, invasive, non-indigenous species offer excellent model systems (Thompson 1998; Mooney & Cleland 2001; Sakai *et al.* 2001; Lee 2002). In fact, there are several reasons why evolutionary processes might be expected to play a role in invasions: First, invasive species are brought into environments that are characterized by novel selection pressures (Mooney & Cleland 2001). Second, only few of those species introduced actually become invasive (Williamson 1996), suggesting selection upon key characters. Third, many of the species that become invaders do so after a lag time (Mack *et al.* 2000; Sakai *et al.* 2001), possibly after evolutionary adjustments to the novel environments (Weber & Schmid 1993; Mooney & Cleland 2001). Understanding such evolutionary mechanisms might be crucial for the successful management of biological invasions.

One evolutionary hypothesis to explain plant invasions is based on the observation that introduced species are often released from many of their specialized herbivores and pathogens (Maron & Vilà 2001; Keane & Crawley 2002; Wolfe 2002; Mitchell & Power 2003). At the same time, some invasive plants appear to perform better in their introduced than in their native range (e.g. Crawley 1987). Invoking a trade-off between plant growth and defence (Herms & Mattson 1992), Blossey & Nötzold (1995) proposed that this might be caused by rapid evolution. In the absence of specialized enemies selection might favour less defended but more competitive invader genotypes. This Evolution of Increased Competitive Ability (EICA) hypothesis makes two major predictions: when compared with native populations in a common environment, plants from the introduced range should be (1) less resistant to (specialized) enemies but (2) more competitive where enemies are excluded.

Recent tests of the EICA hypothesis were often restricted to one of the predictions and compared fitness (usually biomass) or resistance of offspring from native and invasive populations in a common environment (Blossey & Nötzold 1995; Daehler & Strong 1997; Willis & Blossey 1999; Willis *et al.* 1999, 2000; Siemann & Rogers 2001; van Kleunen & Schmid 2003; Leger & Rice 2003; Vilà *et al.* 2003). Another simple, albeit intuitive prediction has never been tested: if invasive genotypes have evolved to be more competitive, they should be able to outcompete their 'ancestors' from the native range. We tested this idea in a greenhouse study with garlic mustard (*Alliaria petiolata*), a European herb that is a serious invader in North American deciduous forests. We used a diallel design in which offspring from several native and invasive populations were either grown alone or in all pairwise combinations in a herbivore-free environment.

Our approach differed in two ways from previous EICA studies: First, it allowed separating fitness in the absence of competition from different aspects of competitive ability. Second, our focus on intra- rather than interspecific competition avoided the problem of competitor choice. If local adaptation, species-specific interactions and possibly coevolution play a role in plant invasions (Callaway & Aschehoug 2000; Klironomos 2002; Prati & Bossdorf 2004), then using one or few interspecific competitors from either of the two ranges will give a biased picture.

We asked the following questions: (1) when grown alone, do plants from invasive *Alliaria* populations have a higher fitness than plants from native populations? (2) do plants from invasive *Alliaria* populations outperform plants from native populations in competition? (3) is there a correlation between the mean performance of *Alliaria* populations in the absence of competition and their performance in competition?

Table 1 Native and invasive populations of *Alliaria petiolata* that were used in this study. For each, the numbers of surviving plants used in analyses of 'singles' (one plant per pot) or 'pairs' (two plants per pot) are given

ID	Location	Longitude	Latitude	Singles	Pairs
Native					
BRU	Bruck, AT	12°49′ E	47°18′ N	13	15
BUD	Budweis, CZ	14°29′ E	48°58′ N	11	19
HAL	Halle, D	11°58′ E	51°28′ N	15	18
IAS	Iasi, RO	27°38′ E	47°09′ N	12	20
KOP	Copenhagen, DK	12°34′ E	55°43′ N	7	19
MON	Montpellier, F	03°53′ E	43°36′ N	4	11
PAR	Ascot, UK	00°41′ W	51°25′ N	15	22
SOY	Soyhières, CH	07°22′ E	47°24′ N	1	7
Invasive					
CAS	Ipswich, MA	70°51′ W	42°41′ N	8	25
FF	McLean, IL	89°00′ W	40°29′ N	12	18
HF	Petersham, MA	72°17′ W	42°54′ N	4	2
HW	Mahomet, IL	88°09′ W	40°23′ N	5	16
OHA	Athens, OH	82°83′ W	39°20′ N	14	16
OHB	Athens, OH	82°07′ W	39°19′ N	15	20
VRO	Danville, IL	87°37′ W	40°09′ N	9	12
WI	Milwaukee, WI	87°53′ W	43°05′ N	14	14

MATERIAL AND METHODS

Study species

Garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara and Grande] is a member of the mustard family (Brassicaceae) native to the Eurasian temperate zone where it grows in mesic semi-shade habitats such as forest edges and moist woodlands. Plants typically germinate in early spring, form a rosette in the first year, overwinter as rosette, develop flowering stems in the following spring, produce seeds in June/July, and die. The species was first introduced to North America in the middle of the 19th century. Microsatellite data suggest that several independent introductions have occurred since then (O. Bossdorf, unpublished data). Over the last few decades, the species rapidly expanded its range and is now present in at least 34 US states and four Canadian provinces (Nuzzo 2000). Garlic mustard invades the understory of North American deciduous forests where it may displace native plant species (McCarthy 1997) and disrupt plant–insect associations (Porter 1994; Huang *et al.* 1995). In a recent study, we found that invasive US populations of garlic mustard are less resistant to a specialist herbivore than native European populations (Bossdorf *et al.* 2004).

In this study, we used seeds from eight European and eight US populations (Table 1). The species is self-compatible and primarily autogamous (Anderson *et al.* 1996), so that most genetic variation is found between rather than within populations (Meekins *et al.* 2001; O. Bossdorf, unpublished data). In both continents, the populations came from a mixture of forest, forest edge and roadside habitats. We regard them to be random samples within continents. Based on a long-term data set of climatic records (New *et al.* 2000), European and US populations did not differ in mean elevation, annual temperature, or precipitation (two-sample t-tests, $n = 14$, all $P > 0.1$). In autumn 2000, mature siliques were collected from several mother plants in each population. The seeds were cleaned and stored under cold, dry conditions.

Experimental design

In January 2001, seeds from 20 maternal families per populations were placed in petri dishes filled with a sterilized 1 : 1 mixture of sand and seeding compost (Composana® Anzuchterde, Compo GmbH, Münster, Germany) and dark stratified at 4 °C for 100 days. Hereafter the petri dishes were placed in a climate chamber with a 12/12 h light/dark cycle at 15/10 °C, where germinated seedlings were transferred to planting trays filled with a 1 : 1 mixture of sand and potting soil (Latterra® Typ P, Hawita-Gruppe GmbH, Vechta, Germany; a peat-based substrate with *c.* 150 mg N, 150 mg P_2O_5 and 250 mg K_2O per litre). At the end of May, the seedlings were taken to an unheated greenhouse and planted into 0.5-litre pots filled with the same substrate as above. In addition, each pot received 5 g of slow-release fertilizer (Osmocote® Plus 3–4 M with 15% N, 11% P_2O_5, 13% K_2O, 2% MgO + trace elements, Scotts International BV, Geldermalsen, The Netherlands). The final size and seed output of plant individuals in our experiment was similar to that of plants in a typical natural population, so we assumed our common environment to be a reasonable match of the nutrient-rich natural habitats (Nuzzo 2000) of garlic mustard.

Each population was grown in monoculture at two densities (one plant per pot and two plants per pot), and in pairwise mixture with each of the other populations (two plants per pot). There were three replicates for each treatment yielding a total of 456 pots and 864 plants. Within each population, plants were chosen at random from the available seed families. As a result of unequal germination success and chance, we eventually used 9–16 families per population. We measured the lengths of all leaves on each plant and calculated a sum of squared leaf lengths which was used as an estimate of initial plant size. A pilot study showed that this was a reasonable predictor for seedling biomass ($r^2 = 0.884$, $n = 100$).

The pots were randomly arranged on two benches in an unheated greenhouse, watered as needed, and re-randomized twice in the course of the experiment. In November 2001, all pots were taken to an experimental garden where they were packed into bark mulch and overwintered. By the end of March 2003, when the plants were returned to the greenhouse, 413 of all plants had survived (see Table 1). Similar rates of rosette mortality are possible in natural *Alliaria* populations (Nuzzo 1993). Winter mortality, analysed by logistic regression (McCullagh & Nelder 1989), was random across competition treatments and continents (all $P > 0.2$) but did range from 11–69% between populations within continents ($P < 0.001$). In April, all pots were treated with a systemic insecticide (Bi-58; BASF AG, Ludwigshafen, Germany). The plants were harvested at fruit maturity. For each one we measured plant height and counted the number of siliques. Siliques and the remaining aboveground parts were dried separately at 80 °C and weighed. Total aboveground biomass was calculated as the sum of the two fractions.

To estimate the precision of different fitness estimates we randomly chose 10 siliques on each plant, weighed them and removed the seeds which were counted and weighed. There were close correlations between silique biomass and seed number ($r^2 = 0.729$, $P < 0.001$) and silique biomass and seed biomass ($r^2 = 0.864$, $P < 0.001$), suggesting that silique biomass is a reasonable predictor for fitness in terms of seed output in *Alliaria*.

Statistical analyses

The winter mortality among plants caused our final data set to be unbalanced with missing values, including the loss of some population monocultures. This ruled out a calculation of traditional competition indices (Weigelt & Jolliffe 2003) and a full diallel analysis (McGilchrist 1965). Instead, we tested the effects of the target and neighbour plant origins by analysis of variance (Schmid & Bazzaz 1987). The target effect is the mean fitness of a population *i*, averaged over all neighbour populations. Likewise, the neighbour effect is the mean fitness of all plants that have population *i* as neighbour. Although target and neighbour effect are conceptually similar to competitive response and effect (Goldberg 1990), they differ in that they are not independent from each other. Each plant in a pair is used to estimate both target and neighbour effect.

Plant fitness (height, aboveground biomass, silique number and silique biomass) was analysed with a nested ANOVA. We carried out one analysis of the full data set that included all harvested plants, then we split up the data into single plants and plant pairs, and analysed each set separately. With the full data set, the ANOVA model included initial plant size as a covariate, and plant density, target continent and neighbour continent nested within density as fixed effects. Target and neighbour population were random effects nested within continent. We used after-winter density (one or two plants per pot) rather than initial density, as the latter had no significant effect on any of the dependent variables (all $P > 0.2$), i.e. plants that had been growing alone since the start of the experiment did not differ from those that ended up alone because of winter mortality. With single plants, the model included initial plant size, continent and population of origin. With plant pairs it included initial plant size and the nested target and neighbour effects. In all three analyses we used type-III sum of squares as the data were unbalanced (SAS Institute 2001).

Although the variables analysed were not independent, we did not carry out a multivariate analysis of variance (MANOVA), because this would have been difficult with unbalanced, nested data, and MANOVA is sensitive to departures from multivariate normal distribution of data (Kendall 1980; Cole *et al.* 1994). To account for multiple statistical tests of the same hypothesis, we calculated the expected probabilities of finding significant results and compared these with observed frequencies instead of using overly conservative Bonferroni procedures (Moran 2003).

To examine the relationship between plant fitness in the absence and presence of competition, we extracted the population least-square means from the analysis of singles, and the population least-square means of target and neighbour effects from the analysis of plant pairs. Similar to regression analyses for maternal and paternal arrays in genetic diallels (Mather & Jinks 1982), we calculated Pearson's product-moment correlations between the fitness of singles, target effects and neighbour effects with regard to plant height, aboveground biomass, silique number and silique biomass. In this analysis, a perfect negative correlation is expected between population target and neighbour effects if competitive interactions were fully reciprocal whereas a weaker, absent, or even positive correlation indicates departure from full reciprocity (Assémat & Oka 1980). One population (HF) was excluded because it was an extreme outlier based on only two surviving plants in pairs.

RESULTS

Single plants produced 67% more aboveground biomass, 66% more silique biomass, and 99% more siliques than plants in pairs, suggesting that there was strong competition for soil resources in our experiment (Table 2, Fig. 1). Plant fitness also strongly depended on the population of origin (Tables 2 and 3) and its interaction with density (Table 2). Thus, fitness had a genetic component.

In the analyses of the full data set, native plants were significantly taller than plants from the invasive range (Table 2, term 'Continent'). The differences between continents were revealed more clearly in the analysis restricted to plant pairs. Plants of native origin growing in pairs were significantly taller (+22%) and produced significantly more siliques (+48%) (Table 3, term 'Continent'). In addition, the neighbour effects of native plants were stronger than those of American plants, i.e. the former reduced the fitness of target plants with respect to silique number and silique biomass more than did the latter (Table 3, term 'Neighbour Continent'). When single plants were analysed separately, there was hardly any genetic variation detectable. Apart from a population effect on silique number ($F_{14,142} = 3.45$, $P < 0.001$), all continent and population effects were non-significant. Overall, single plants were remarkably similar in terms of their size and fecundity.

As expected, there was a strong negative correlation between target and neighbour effect for total aboveground biomass and silique biomass (Table 4). However, there was no correlation between the mean fitness of populations as singles and their mean target and neighbour effects in plant pairs for any of the traits investigated (Table 4, Fig. 2).

In a table with four statistical tests of the same hypothesis, the probability of finding a particular effect to be significant by chance is $1-0.95^4 = 0.185$ (Moran 2003), i.e. less than one of four tests. As in our analysis of plant pairs (Table 3) both continent and neighbour continent effect were significant twice, we are confident that the observed differences between native and invasive populations are not a product of chance.

DISCUSSION

A major prediction of the EICA hypothesis is that because of resource re-allocation from defence to growth, plants from the invasive range will be more competitive than those from the native range. In this study we found that under optimal, competition-free conditions there were no differences between native and invasive populations of *Alliaria petiolata*. When plants were competing against conspecifics, however, native populations outperformed those from the invasive range. This completely contradicts the EICA hypothesis and we therefore conclude that it does not hold for *Alliaria petiolata*.

A potential caveat of this study could be that we assume no adaptive evolution to environmental conditions, except for the absence of herbivores, in the introduced range.

Table 2 Summary of analyses of variance of the full data set with all harvested plants. Square brackets indicate nesting of terms. Degrees of freedom in parentheses are for silique biomass. Levels of significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

		Height		Total biomass		Silique number		Silique biomass	
Source	d.f.	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*
Initial plant size	1	19.1	0.04	1.69	0.11	0.74	0.16	1.41	0.50
Density	1	3043.2	6.95**	1784.27	111.04***	470.80	103.06***	277.72	98.56***
Continent	1	7792.6	4.66*	79.11	1.99	53.92	3.55	5.60	0.82
Population[C]	14	1670.9	3.82***	39.82	2.48**	15.19	3.32***	6.81	2.42**
D × C	1	1012.9	1.85	39.98	1.94	14.13	1.64	15.46	3.09
D × P[C]	14	548.0	1.25	20.59	1.28	8.63	1.89*	5.01	1.78*
Neighbour Continent[D]	1	86.4	0.14	79.33	3.10	12.52	3.20	16.98	4.19
Neighbour Population[NC, D]	14	606.6	1.39	25.57	1.59	3.91	0.86	4.05	1.44
C × NC[D]	1	787.6	1.51	3.23	0.25	4.99	1.02	0.00	0.00
P[C] × NP[NC, D]	120 (118)	521.4	1.19	12.67	0.79	4.90	1.07	2.15	0.76
Residual	244 (240)	437.8		16.07		4.57		2.82	

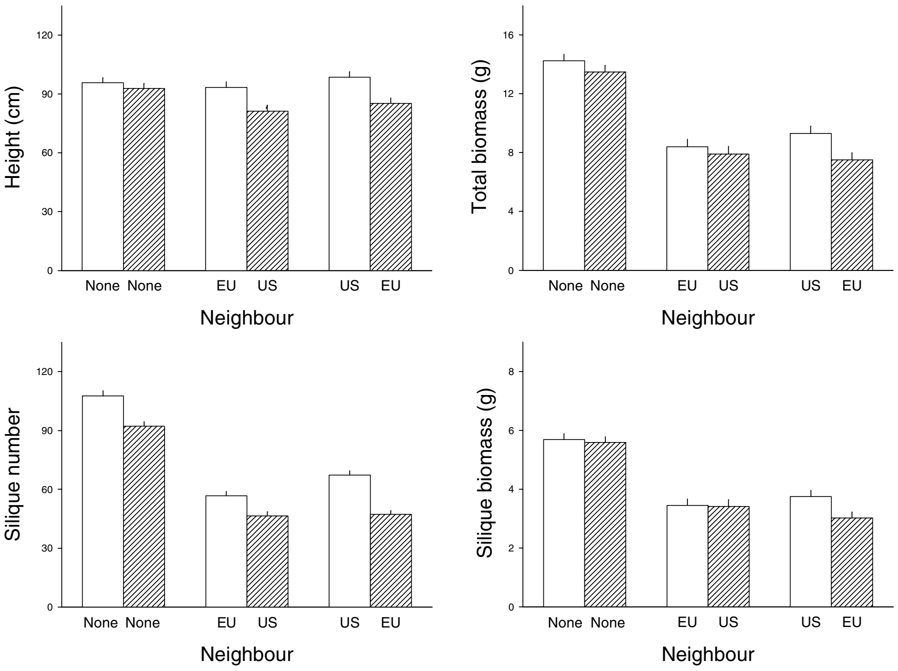

Figure 1 Mean size and fitness (+SE) of native European (open bars) and invasive North American (hatched bars) plants of *Alliaria petiolata* in an intraspecific competition experiment. Plants were either grown without neighbours (None) or in pairs with neighbours from the same or the other continent (EU, US).

Table 3 Summary of the analyses of variance of plant pairs. Square brackets indicate nesting of terms. Degrees of freedom in parentheses are for silique biomass. Levels of significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

		Height		Total biomass		Silique number		Silique biomass	
Source	d.f.	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*
Initial plant size	1	225.0	0.40	27.56	1.50	0.69	0.16	1.671	0.59
Continent	1	8224.2	5.11*	153.54	3.99	68.85	5.36*	24.977	3.13
Population[C]	14	1608.3	2.84**	38.47	2.09*	12.84	2.89**	7.974	2.80**
Neighbour Continent	1	127.1	0.21	91.47	3.55	20.30	5.94*	19.064	4.67*
Neighbour Population[NC]	14	616.9	1.09	25.76	1.40	3.42	0.77	4.082	1.43
C × NC	1	688.0	1.35	1.42	0.12	1.17	0.29	0.104	0.05
P[C] × NP[NC]	120 (118)	508.8	0.90	11.67	0.64	4.05	0.91	2.015	0.71
Residual	101 (97)	567.2		18.38		4.45		2.846	

Although we have shown that the source environments of native and invasive populations were comparable with regard to several important climatic variables, we cannot exclude the possibility that local adaptation to other environmental factors is reponsible for the observed differences. Another limitation of our study is that winter mortality substantially reduced the sample size, so the results should be viewed with some caution.

Many recent tests of the EICA hypothesis compared native and invasive populations in competition-free environments. Results were ambiguous: invasive populations had a greater fitness in *Lythrum salicaria* (Willis & Blossey 1999) and *Sapium sebiferum* (Siemann & Rogers 2001), but

Table 4 Correlations among 15 populations of *Alliaria petiolata* between the mean fitness when growing alone and the mean target and neighbour effects when growing in pairs. The values are correlation coefficients; *P*-values in parentheses

	Height	Total biomass	Silique biomass	Silique number
Fitness alone – target effect	0.189 (0.499)	0.372 (0.172)	0.182 (0.516)	0.405 (0.134)
Fitness alone – neighbour effect	0.148 (0.598)	0.026 (0.927)	0.131 (0.642)	0.303 (0.272)
Target effect – neighbour effect	−0.149 (0.595)	−0.798 (0.000)	−0.786 (0.001)	−0.251 (0.366)

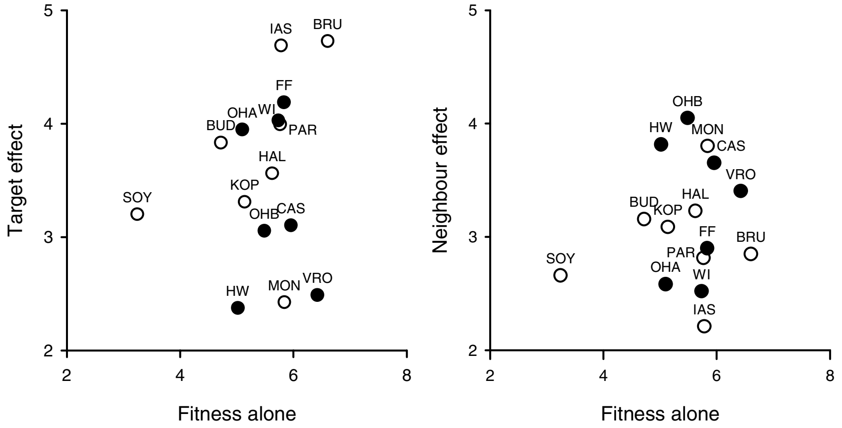

Figure 2 The relationship between mean fitness of European (white circles) and North American (black circles) populations of *Alliaria petiolata* when growing alone and their mean target and neighbour effects when growing in pairs. All values are ANOVA least-square means of silique biomass (g). See Table 1 for population details.

there were no differences in four invasive biennials (Willis *et al.* 2000). Still, fitness in the absence of competition might not necessarily translate into competitive ability, for instance if the ability of a plant to rapidly exploit resources has a different mechanistic basis than its ability to tolerate low resource levels (e.g. Grime 1979; Goldberg 1996). There was no relationship between the average fitness of *Alliaria* populations when growing alone and their competitive ability in pairs (Fig. 2). Had our experiment been restricted to plant singles, we would have concluded that there are no differences among native and invasive *Alliaria* populations.

To date, few studies used a competitive environment when testing for EICA. Leger & Rice (2003) found that invasive populations of *Eschscholzia californica* were superior only when grown without competition by horticultural poppies. Vilà *et al.* (2003) used a native grass as competitor and found no differences between native and invasive populations of *Hypericum perforatum*. Here, we have argued that interspecific competitors might give a biased picture, and that one way to tackle this problem is to focus on *intra*specific competition instead. Interestingly, those two studies that did so found counterevidence for EICA. Invasive populations of *Solidago canadensis* had a lower fitness than native ones when growing in dense monospecific stands (van Kleunen & Schmid 2003). In our study, native populations of *Alliaria petiolata* outperformed invasive populations in a competition diallel.

Reduced competitive ability could be the consequence of a genetic bottleneck with subsequent inbreeding depression or random changes through genetic drift (Barrett & Husband 1990). Both processes could have caused changes in traits that confer competitive ability. However, we think that this explanation is rather unlikely as *Alliaria* has a high selfing rate (Anderson *et al.* 1996) with low within-population genetic variation in both its introduced and native range (Meekins *et al.* 2001; O. Bossdorf, unpublished data). Also, significant differentiation among invasive populations suggests sufficient genetic variation for evolutionary responses.

Another explanation for reduced competitive ability in invasive populations would be directional selection. If there are fewer or weaker competitors in the North American habitats invaded by *Alliaria petiolata*, and at the same time resource competition involves traits that have a fitness cost – such as a particular growth form, allocation scheme, or physiological apparatus – then there might be selection against it in the invasive range. Furthermore, if plants in invasive populations have usually more intra- than interspecific neighbours, an Evolutionary Reduced Competitive Ability (ERCA) may increase stand-level fitness (King 1990) by reducing intraspecific interactions, too. It is conceivable that ERCA allows invasive populations of *Alliaria* to use the savings not spent for resource competition in other processes that may contribute to their invasion success, such as plasticity, tolerance to herbivory (Bossdorf *et al.* 2004), or allelopathy (Prati & Bossdorf 2004). Clearly further research is needed to test this new ERCA hypothesis.

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