A comprehensive test of evolutionarily increased competitive ability in a highly invasive plant species

Srijana Joshi^{1,†}, Michal Gruntman^{1,*}, Mark Bilton¹, Merav Seifan² and Katja Tielbörger¹

¹Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany and ²Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 84990, Israel

* For correspondence. E-mail michal.gruntman@bot.uni-tuebingen.de

[†] Present address: International Centre for Integrated Mountain Development, GPO Box 3226, Kathmandu, Nepal

Received: 21 May 2014 Returned for revision: 11 July 2014 Accepted: 26 August 2014 Published electronically: 9 October 2014

• **Background and Aims** A common hypothesis to explain plants' invasive success is that release from natural enemies in the introduced range selects for reduced allocation to resistance traits and a subsequent increase in resources available for growth and competitive ability (evolution of increased competitive ability, EICA). However, studies that have investigated this hypothesis have been incomplete as they either did not test for all aspects of competitive ability or did not select appropriate competitors.

• **Methods** Here, the prediction of increased competitive ability was examined with the invasive plant *Lythrum salicaria* (purple loosestrife) in a set of common-garden experiments that addressed these aspects by carefully distinguishing between competitive effect and response of invasive and native plants, and by using both intraspecific and interspecific competition settings with a highly vigorous neighbour, *Urtica dioica* (stinging nettle), which occurs in both ranges.

• **Key Results** While the intraspecific competition results showed no differences in competitive effect or response between native and invasive plants, the interspecific competition experiment revealed greater competitive response and effect of invasive plants in both biomass and seed production.

• **Conclusions** The use of both intra- and interspecific competition experiments in this study revealed opposing results. While the first experiment refutes the EICA hypothesis, the second shows strong support for it, suggesting evolutionarily increased competitive ability in invasive populations of *L. salicaria*. It is suggested that the use of naturally co-occurring heterospecifics, rather than conspecifics, may provide a better evaluation of the possible evolutionary shift towards greater competitive ability.

Key words: Competitive effect, competitive response, evolution of increased competitive ability, EICA, intraspecific competition, interspecific competition, invasive species, *Lythrum salicaria*, purple loosestrife, stinging nettle, *Urtica dioica*.

INTRODUCTION

Invasive success has often been suggested to result from species' post-invasion evolution and their resulting adaptations to novel environments (Sakai *et al.*, 2001; Müller-Schärer *et al.*, 2004; Prentis *et al.*, 2008; Drenovsky *et al.*, 2012). For example, the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold, 1995) proposes that plants in their introduced range experience reduced damage by natural enemies, such as pathogens and specialist herbivores, which selects for reduced allocation to resistance traits and a consequent increase in resources available for growth and competitive ability (Blossey and Nötzold, 1995; Maron *et al.*, 2004; Bossdorf *et al.*, 2005; Doorduyn and Vrieling, 2011). The EICA hypothesis therefore predicts that, compared with their native conspecifics, invasive genotypes should exhibit an inherently reduced resistance to native-range enemies and a greater competitive ability when these enemies are excluded (Blossey and Nötzold, 1995; Doorduyn and Vrieling, 2011).

These predictions have been examined, often separately, in several studies (Vilà *et al.*, 2003; Franks *et al.*, 2008; Huang

et al., 2010; Beaton *et al.*, 2011; Alba *et al.*, 2012; Hanley, 2012; Wang *et al.*, 2013), but no general pattern has emerged, particularly regarding the evolution of increased competitive ability (Bossdorf *et al.*, 2005; van Kleunen *et al.*, 2010; Dostal, 2011; Felker-Quinn *et al.*, 2013). This may be due to the fact that, despite being a key component of the hypothesis, competitive ability has rarely been addressed in a manner consistent with current approaches in community ecology. Particularly, previous plant competition studies have suggested that a distinction should be made between the ability of plants to suppress the growth of their neighbours (i.e. competitive effect) and to tolerate their impact (i.e. competitive response) (Goldberg and Fleetwood, 1987; Goldberg and Landa, 1991; Cahill *et al.*, 2005). Competitive effect and response are not necessarily correlated (Goldberg and Landa, 1991; Keddy *et al.*, 1994; Cahill *et al.*, 2005) and could be governed by different traits, such as high resource-capture rate and resource-use efficiency, respectively (Cahill *et al.*, 2005). In an invasion context, it is particularly important to distinguish between these components because they could characterize different invasion stages: while traits related to competitive effect may be important for outcompeting

native plants at the establishment phase of invasion, competitive response is likely to be important at later stages when it enables stable persistence. To date, however, this distinction has been applied in only a few studies that have examined the predictions of the EICA hypothesis (Suding *et al.*, 2004; Ridenour *et al.*, 2008; He *et al.*, 2009). Furthermore, these previous experimental setups did not provide an independent evaluation of competitive effect versus response.

Another key element that should be considered when studying the predictions of the EICA hypothesis is the choice of neighbour species. Ideally, evolutionary changes in competitive ability of invasive plants should be examined using heterospecifics that co-occur naturally with the invasive species. However, to provide unbiased evaluation of such competitive ability, this interspecific approach requires neighbours that are similar to the invasive species in size, life form and phenology and that occur with it in both ranges (Bossdorf *et al.*, 2004; Vilà and Weiner, 2004). Unfortunately, only a few studies were able to use an appropriate competitor (Blair and Wolfe, 2004; Barney *et al.*, 2009; He *et al.*, 2009; Dostal, 2011), and no study to date has used a competitor that occurs in both ranges, making a direct comparison of competitive ability between ranges difficult. In an attempt to overcome these limitations, another approach has been applied in a few studies, where conspecifics from the native and invasive ranges were used as competing neighbours (Leger and Rice, 2003; Bossdorf *et al.*, 2004; Zou *et al.*, 2008). Although this intraspecific approach avoids the problem of choosing an appropriate neighbour (Bossdorf *et al.*, 2005), it cannot fully test the EICA hypothesis because native and invasive plants rarely co-occur in nature. A possible way of addressing the limitations of each approach is to use both intra- and interspecific competition, but this has been rarely applied so far (Barney *et al.*, 2009).

Here, the prediction of evolutionarily increased competitive ability was examined in the invasive plant *Lythrum salicaria*, which is native to Europe and highly invasive in North America (Thompson *et al.*, 1987). In a previous study we have shown that invasive-range *L. salicaria* plants exhibit increased growth rate and biomass allocation (Joshi and Tielbörger, 2012) while other studies have shown that they outcompete their native neighbour species (Mal *et al.*, 1997; Hager, 2004; Flanagan *et al.*, 2010; Hovick *et al.*, 2011), but no study has examined genetic differentiation in their competitive ability.

Several key aspects still seldom applied in the study of invasive plants were addressed in a set of common-garden experiments, including a careful distinction between competitive effect and response, under both intra- and interspecific competition. As a neighbour species for the interspecific competition experiment we used *Urtica dioica*, which provides several advantages over previous studies when comparing the competitive ability of invasive and native *L. salicaria*. First, *U. dioica* co-occurs in high densities with *L. salicaria* in both its native and its invasive range (Wolin and MacKeigan, 2005). Second, it is a tall perennial herb, known to be highly competitive and to dominate many plant communities (Taylor, 2009), thus rendering it a highly appropriate competitor to the vigorous *L. salicaria*.

The following questions were addressed in this study: (1) under competition-free conditions, do invasive *L. salicaria* plants exhibit greater growth compared with their native

conspecifics? (2) do invasive plants exhibit greater competitive ability? (3) do potential origin-dependent differences in competitive ability depend on the competition setting (i.e. competitive effect versus response)? (4) do these origin-dependent differences in competitive ability depend on neighbour identity (i.e. intra- versus interspecific competition)?

MATERIALS AND METHODS

Study species

Lythrum salicaria is a herbaceous perennial plant. It was introduced to eastern North America in the early 19th century (Thompson *et al.*, 1987) and has become highly invasive in North American wetland habitats, where it often forms large monospecific stands (Thompson *et al.*, 1987), which have been shown to prevent the growth and establishment of local species and suppress their colonization (Mal *et al.*, 1997; Hager, 2004; Flanagan *et al.*, 2010; Hovick *et al.*, 2011). Genetic evidence supports parallel introductions of this species (Houghton-Thompson *et al.*, 2005; Chun *et al.*, 2009), but rapid evolution in the introduced range rather than the introduction of preadapted populations (Colautti and Barrett, 2013).

Urtica dioica (Urticaceae) is a tall dioecious perennial herb. It is native to and widely distributed in Europe, Asia, North America and northern Africa, where it inhabits riparian and open areas (Taylor, 2009). *Urtica dioica* naturally co-occurs with *L. salicaria* in both its invasive and native ranges (Wolin and MacKeigan, 2005), and has been classified as a classical competitor (C) species in Grime's (1977) model of plant strategy types.

Plant sources and seed handling

Seeds of *L. salicaria* were collected in summer 2006 from four native and four introduced populations in Germany (two from the northeast of Germany and two from the southwest) and the USA, respectively (Table 1). In the invasive range, the sampled populations were chosen so as to depict a range of invasion history, as two were from New Jersey, representing the eastern-most and oldest invasion range of *L. salicaria* in the USA, and two from Iowa, representing a much younger invasion range (Chun *et al.*, 2009). *Urtica dioica* seeds were collected from three

TABLE 1. Sources of native and invasive populations of *Lythrum salicaria* used in the experiments, as well as of *Urtica dioica*

Origin	Population (code)	Latitude	Longitude
Native	Golm (GO)	48°52'N	8°98'E
	Grube (GR)	48°32'N	9°01'E
	Hagelloch (HA)*	52°43'N	12°97'E
	Unterjesingen (UN)*	52°40'N	12°97'E
	Tübingen (TU)*	48°31'N	9°03'E
Invasive	Boone Forks, Iowa (BF)	40°51'N	79°55'W
	Manly, Iowa (MA)	41°25'N	74°80'W
	Beaver Run, New Jersey (BR)	42°17'N	93°56'W
	Hainesville county, New Jersey (HV)	43°16'N	93°07'W

*Source populations of both *U. dioica* and *L. salicaria*.

#Source populations of only *U. dioica*.

populations in Germany in summer 2007 (Table 1). Seeds of both species were sampled from ~20 randomly selected mother plants per population and bagged separately for each mother plant. As *L. salicaria* is an obligate outcrosser (Agren and Ericson, 1996) and *U. dioica* is dioecious (Taylor, 2009), seeds within maternal families of both species were essentially half-sibs. All seeds were cold-stratified during winter at Tübingen University.

Intraspecific competition experiments

In May 2007, *L. salicaria* seeds were germinated in 2-L pots filled with standard potting soil (Topferde, Einheitserde, Kreuztal, Germany), following which they were transplanted into 18-L experimental pots. Our overall aim was to evaluate the performance of conspecific invasive and native plants in a competitive situation. In total we had eight populations [4×2 origins: native (German); invasive (USA)], with each population represented by five maternal genotypes. In competition pots (containing two plants per pot) we used a full factorial design to include all 36 possible combinations of populations (Fig. 1). These were directly compared with individuals in control pots (no neighbour; one plant per pot) containing their maternally related individuals. This experimental design resulted in a total of 400 individuals (8 populations $\times$ 5 maternal genotypes $\times$ 10 replicates per genotype) planted in 220 pots [5 replicated pots $\times$ (8 control pots + 36 competition pots)] (Fig. 1).

Following transplant, the pots were placed in a common garden at Tübingen University (48°32'N, 9°02'E). As *L. salicaria* grows

in wetland habitats, the pots were constantly waterlogged, with one 20-g application of a slow-release fertilizer (Osmocote 18–10–11 NPK; Scotts, Geldermalsen, The Netherlands). Preliminary experiments showed that the use of an insecticide has potential side effects on the performance of *L. salicaria*. Moreover, with concurrent studies we found a 50 % reduction in herbivore attack in the common garden compared with natural habitats, which reduced leaf damage to only 5 % at the common garden (R. Wegerer, Plant Ecology Group, University of Tübingen, Germany, unpubl. data). An insecticide was therefore not applied in this experiment as well as in the following interspecific experiment.

Interspecific competition experiment

In May 2008, seeds of *L. salicaria* from five maternal genotypes per population, as well as seeds of *U. dioica* from five maternal genotypes chosen randomly from the three populations, were germinated as described above for the intraspecific competition experiment. Seedlings from each maternal genotype were then transplanted into 18-L pots filled with the same standard potting soil and randomly assigned to one of the following four treatments: *L. salicaria* control with a single plant per pot; *U. dioica* control with a single plant per pot; competitive response, with *L. salicaria* as a single target plant surrounded by three *U. dioica* neighbours; competitive effect, with *U. dioica* as a single target plant surrounded by three *L. salicaria* neighbours. For the *U. dioica* control treatment, five pots were used in total, one per full treatment combination, and each corresponded to its maternal half-sib in the competitive-effect treatment. This experimental design resulted in a total of 125 pots [2 *L. salicaria* origins (native, invasive) $\times$ 3 competition treatments (*L. salicaria* control, competitive response and competitive effect) $\times$ 20 maternal genotypes + 5 *U. dioica* controls].

As in the intraspecific competition experiment, the pots were placed in the common garden at Tübingen University, where they were constantly waterlogged and 20 g of a slow-release fertilizer was applied.

Response variables

Plant performance in the two experiments was quantified with above-ground biomass and seed output per individual plant as the response variables. In both experiments, above-ground biomass of control and target plants was harvested following seed ripening at the end of October and measured after oven-drying at 60 °C for 24 h. Prior to that, total seed number of *L. salicaria* was estimated as [mean number of seeds per capsule (derived from a total of three capsules from apical, middle and basal stalks) $\times$ mean number of capsules per flowering stalk (derived from six randomly chosen stalks) $\times$ total number of stalks]. For *U. dioica*, which is a dioecious plant, seed output could not be estimated as many individuals were androecious and performance was thus quantified only with above-ground biomass.

Competitive effect and response were estimated using the relative interaction index (RII) (Armas *et al.*, 2004), which calculates the relative change in the performance of a target individual with neighbours ($P_{w/}$) compared with that under control conditions without neighbours ($P_{w/o}$) [$RII = (P_{w/} - P_{w/o}) / (P_{w/} + P_{w/o})$]. RII values range from -1 to +1, where negative and positive

FIG. 1. Layout of the intraspecific competition experiment, with *Lythrum salicaria* from native and invasive populations. Depicted are all plant pair combinations used per pot, containing two plants from populations of the same origin (intra-origin competition) or from different origins (inter-origin competition), as well as single-plant (control) pots. All combinations were replicated ($n = 5$), giving a total of 220 pots.

values indicate suppressive and facilitative effects in the response variable, respectively. In both the intra- and interspecific competition experiments, calculations were carried out between control ($P_{w/o}$) and competition pots (P_w) which contained individuals of the same maternal family. In both experiments competitive response was measured using the identity of the target [i.e. the measured plant (P_w)], whereas competitive effect is given by the identity of the neighbour. For the intraspecific competition experiment, both individuals in the competition pots acted as either target or neighbour, whereas in the interspecific competition experiment the central plant always acted as the target (P_w), with the identities of *L. salicaria* targets giving the competitive response when surrounded by *U. dioica* and the identities of *L. salicaria* neighbours giving competitive effect when surrounding *U. dioica*.

Data analyses

For both experiments, differences in performance (biomass and seed output) between invasive and native plants with or without neighbours were examined using linear mixed models (LMMs), with data square-root-transformed to match model assumptions. For the interspecific competitive response, origin and competition were used as fixed factors and populations as random intercepts nested within origin. For the intraspecific competition experiment as well as for the competitive effect in the interspecific experiment, the competition factor with and without neighbours was unbalanced, and therefore the data were analysed separately to determine the origin effect in the no-competition treatment (intraspecific – random intercepts for populations within origin) and competition treatments (intraspecific – crossed random intercepts for populations within target origin and populations within neighbour origin and pot; and interspecific – random intercepts for populations within neighbour origin).

For the intraspecific competition experiments, origin differences in RII values were examined using LMMs, with competitive response (target origin) and competitive effect (neighbour origin) as fixed factors using the crossed random intercepts for populations within target origin and populations within neighbour origin and pot. For the interspecific competition experiment, origin differences in RII values were analysed separately for competitive response and effect using LMMs, with origin as a fixed factor and populations as random intercepts nested within origin. All statistical analyses were performed using the lmer function in package lme4 (Bates, 2012) of R version 2.15 (R Development Core Team 2012), employing a likelihood ratio test to assess factor significance (χ^2 test; d.f. = 1).

RESULTS

Intraspecific competition experiment

Invasive *L. salicaria* plants exhibited greater performance compared with their native conspecifics under competition-free conditions in both biomass (LMM: $\chi^2 = 12.580$, $P < 0.001$; Fig. 2A) and seed production (LMM: $\chi^2 = 9.849$, $P < 0.01$; Fig. 2B), as well as under intraspecific competition in both biomass (LMM: $\chi^2 = 11.72$, $P < 0.001$; Fig. 2A) and seed production (LMM: $\chi^2 = 7.32$, $P < 0.01$; Fig. 2B). However, this

FIG. 2. Intraspecific experiment. Growth and reproductive measures (mean $\pm$ s.e. per individual) of *Lythrum salicaria* from native and invasive origin when grown alone (no neighbour) or under competition with native or invasive neighbours. For (A and B), from left to right: $n = (20,20)$, $(100,80)$, $(80,100)$.

greater performance did not translate into any overall origin-related differences in competitive ability, i.e. when grown under intraspecific competition there were no significant differences in biomass (LMM: $\chi^2 = 2.86$) or seed production (LMM: $\chi^2 = 0.07$) values in relation to neighbour origin, and no significant interactions between target origin and neighbour origin (LMM: biomass, $\chi^2 = 3.58$; seed, $\chi^2 = 0.36$). In addition, for statistical models run on RII values, all origin-level effects and their interactions were non-significant, using either target origin response to or neighbour origin effect on conspecifics (Table 2; Fig. 3).

Interspecific competition experiment

Matching the results from the intraspecific competition, the interspecific competition experiment revealed greater overall performance of invasive compared with native *L. salicaria* in both biomass (LMM: $\chi^2 = 13.159$; $P < 0.01$; Fig. 4A) and seed production (LMM: $\chi^2 = 9.66$; $P < 0.01$; Fig. 4B), in both the absence and presence of *U. dioica* competitors.

However, unlike the intraspecific competition results, the greater performance of invasive plants did correspond here with their reduced response to competition. This is revealed both in the interaction between neighbour and origin effects on above-ground biomass (LMM: $\chi^2 = 4.575$; $P < 0.05$; Fig. 4A) and in the RII competitive response in both biomass and seed production (Table 3; Fig. 5A, B). Similarly, invasive *L. salicaria*

exerted a greater competitive effect on the biomass production of *U. dioica* compared with their native conspecifics, as revealed in both the neighbour origin effect on *U. dioica* biomass (LMM:

TABLE 2. LMM results for the intraspecific competition experiment, showing the lack of effects of target origin (competitive response) and neighbour origin (competitive effect) of *Lythrum salicaria* when grown with conspecifics. Competitive ability was estimated with the relative interaction index (RII) and population effects were accounted for in the statistical model (see Materials and methods)

(A) Fixed effects	Above-ground biomass (g)	Seed number
Target origin (competitive response)	0.2183	3.5466
Neighbour origin (competitive effect)	3.2291	0.0420
Target origin × neighbour origin	2.6209	0.0357
(B) Error variance		
Pot intercept ($n = 180$)	0	0.0030
Target population intercept ($n = 8$)	0	0.0120
Neighbour population intercept ($n = 8$)	0.0005	0.0003
Residual	0.0525	0.1424

Values are χ^2 (d.f. = 1; $P > 0.05$); total $N = 360$.

$\chi^2 = 4.338$; $P < 0.05$; Fig. 4C) and in the RII competitive effect on biomass and seed production (Table 3; Fig. 5C).

DISCUSSION

The invasive success of plants has been attributed to the purported evolution of increased competitive ability in the introduced range (Blossey and Nötzold, 1995). In this study, we examined this prediction for the invasive plant *L. salicaria* using both intra- and interspecific competition settings and separating competitive effect and response. Our results suggest that inferences of genetically determined increase in competitive ability of invasive plants could depend highly on the choice of competition setting and neighbouring plants. In particular, we show that under interspecific competition invasive *L. salicaria* exhibited greater competitive ability compared with their native conspecifics, but that this divergence was not apparent under intraspecific competition with native or invasive plants.

In the interspecific competition experiment, the competitive dominance of invasive *L. salicaria* plants was evident in their greater ability both to suppress *U. dioica* plants (competitive effect) and to tolerate their impact (competitive response). Superiority in both components of competition might indicate that *L. salicaria*'s invasiveness could be fuelled by its ability to outcompete native plants, and thus successfully establish at

FIG. 3. Intraspecific experiment. Competitive responses and effects of *Lythrum salicaria* from native and invasive populations. Values represent individual per population means $\pm$ s.e. of response to both invasive and native neighbours (A, B) and effect on both native and invasive target plants (C, D) estimated for both growth and reproductive measures with the relative interaction index (RII). Population sources are presented in Table 1. Additional statistical analyses are presented in Table 2. For all populations $n = 45$.

FIG. 4. Interspecific experiment. Growth and reproductive measures (mean $\pm$ s.e.) of *Lythrum salicaria* from native and invasive origin when grown alone (no neighbour) or under competition with *Urtica dioica* (A, B), and growth of *U. dioica* when grown alone or under competition with native or invasive *L. salicaria* (C). From left to right (A, B): $n = (19, 20), (20, 20)$; (C) $n = 5, 19, 20$.

the initial stages of invasion, as well as to persist following establishment. Previous experiments with invasive *L. salicaria* reveal similar results of a strong competitive effect on co-occurring species (Hager, 2004; Hovick et al., 2011), although Hager (2004) found the plants not to be as superior in their competitive response. However, these studies were limited to *L. salicaria*

TABLE 3. LMM results for interspecific competition experiments, showing the effects of *Lythrum salicaria*'s origin on its competitive response, and for the effect of *L. salicaria* origin on its competitive effect under competition with *Urtica dioica*. Competitive response and effect were estimated in separate sub-experiments with the relative interaction index (RII). In all cases random population intercepts were included in the statistical models (see Materials and methods) but accounted for 0 % of the total variation

	Above-ground biomass (g)	Seed number
Competitive response	6.154*	4.54*
Competitive effect	4.546*	–

Values are χ^2 (d.f. = 1; * $P < 0.05$).

from the invaded range and thus provide limited inference regarding the possible evolution of competitive ability in this species. Here, we could demonstrate that invasive *L. salicaria* plants exhibit greater competitive response and effect compared with their native conspecifics in both seed production and vegetative growth, implying genetic diversion in these traits following introduction. While our interspecific setting indicates that invasive *L. salicaria* plants might have evolved into ‘super-competitors’, their greater competitive ability was less apparent under intraspecific competition. Differences in the results of these experiments could have stemmed from their different designs, i.e. the greater neighbour density in the interspecific experiment may have exerted greater competitive impact. However, contrary to these expected density-dependent effects, the competitive response values were much lower in the less dense intraspecific experiment, suggesting that competition here was stronger and therefore that *L. salicaria* might be a stronger overall competitor than *U. dioica*. To some extent this supports the commonly proposed idea that intraspecific interactions should be more intense than interspecific interactions due to greater similarities in the resource requirements of conspecifics (MacArthur and Levins, 1967; Farrer and Goldberg, 2011). Whilst we would not conclude that intra- is stronger than interspecific competition in all cases, our findings do suggest that in our case the greater similarity between conspecifics may have an additional impact on their interactions than mere size-related depletion of resources. Other components, such as plant–soil feedbacks, which have been shown to be more negative under intra- compared with interspecific competition (Kulmatiski et al., 2008), or requirements for specific nutrients could be overriding some of the size-related elements for this highly competitive species, making the responses in origin more similar.

Bossdorf et al. (2004) suggested that the use of conspecific competitors offers an advantage when comparing invasive and native genotypes as it avoids the problem of choosing neighbour species from either range. However, our results indicate that this approach could be misleading; had we examined only intraspecific competition, we would have inferred no evolutionary change in the competitive ability of invasive *L. salicaria*. Interestingly, the few studies that found a decrease in the competitive ability of invasive genotypes were also performed with conspecific neighbours, and a new ‘evolution of reduced competitive ability hypothesis’ has been generated from these findings (van Kleunen and Schmid, 2003; Bossdorf et al., 2004). We suggest that our

FIG. 5. Interspecific experiment. Competitive responses and effect of *Lythrum salicaria* from native and invasive populations. Values represent per population means $\pm$ s.e. of *L. salicaria*'s competitive response (A, B) and effect on *U. dioica* (C) estimated for both growth and reproductive measures with the relative interaction index (RII). Population sources are presented in Table 1. Additional statistical analyses are presented in Table 3. For (A–C) $n = 5$ per population except $n = 4$ for population UN in (C).

interspecific competition results might provide a more factual evaluation of the competitive ability of invasive *L. salicaria*, particularly as *U. dioica* co-occurs in both its native and invasive ranges, where it is one of its most vigorous competitors. Accordingly, despite its merits in terms of experimental design, the use of conspecific neighbours should be considered with care when estimating the competitive ability of invasive plants, especially as invasive and native plants do not co-occur in nature.

A possible caveat of our study is that competitive interactions were examined with co-occurring individuals from only the native range rather than from both. This implies that the greater tolerance of *U. dioica* to competition with native compared with invasive *L. salicaria* might be due to their common evolutionary history (Aarssen and Turkington, 1985; Ehlers and Thompson, 2004; Lankau, 2012) rather than to the evolution of increased competitive ability. However, such co-evolution between neighbouring plants has commonly been shown to be mediated by toxic effects on plants (Callaway and Ridenour, 2004) or soil communities (Lankau, 2012). As *L. salicaria* plants possess no such effects (Nakai et al., 2010; Scharfy et al., 2011) it seems unlikely that such interactions govern the interspecific pattern observed in this study. Nonetheless, while our study goes further than most in terms of determining the competitive ability of an invasive species, an even more comprehensive test could be garnered with the inclusion of *U. dioica* from both ranges, preferably with additional species as well.

In conclusion, our interspecific results demonstrate that introduced populations of *L. salicaria* express a genetically inherent increased competitive ability, which encompasses both strong negative effects on neighbours and the ability to withstand displacement. Combined with our previous findings of a decrease in the resistance of invasive *L. salicaria* to native-range herbivores (Joshi and Tielbörger, 2012), these results provide compelling evidence for the EICA hypothesis within *L. salicaria*, showing that release from enemies may induce an evolutionary shift in resource allocation from traits related to herbivory

resistance to those of competitive ability. To date, we know of only a few studies that provide support for both predictions of the EICA hypothesis (Beaton et al., 2011; Huang et al., 2012). However, the fact that this trend was not apparent under intraspecific competition suggests that these interactions might be species-specific and that our ability to test these predictions may be best served by both an appropriate choice, and preferably multiple numbers, of neighbouring species.

ACKNOWLEDGEMENTS

We thank Ortrun Ebinger for her technical help. We also thank Mick Hanley and two anonymous reviewers for valuable comments on a previous version of this manuscript. This work was supported by the German Research Foundation to K.T. (DFG; TI-338/8–1) and to M.G. (DFG; GR-4325/1–1) and by a fellowship of the Minerva Foundation to M.G.

LITERATURE CITED

- Aarssen LW, Turkington R. 1985. Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *Journal of Ecology* 73: 605–614.
- Agren J, Ericson L. 1996. Population structure and morph-specific fitness differences in tristylous *Lythrum salicaria*. *Evolution* 50: 126–139.
- Alba C, Bowers MD, Hufbauer R. 2012. Combining optimal defense theory and the evolutionary dilemma model to refine predictions regarding plant invasion. *Ecology* 93: 1912–1921.
- Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85: 2682–2686.
- Barney JN, Whitlow TH, DiTommaso A. 2009. Evolution of an invasive phenotype: shift to belowground dominance and enhanced competitive ability in the introduced range. *Plant Ecology* 202: 275–284.
- Bates DM, Maechler M, Bolker B. 2012. lme4: linear mixed-effects models using Eigen and R package version 0.999–0. <http://CRAN.R-project.org/package=lme4>.
- Beaton LL, Van Zandt PA, Esselman EJ, Knight TM. 2011. Comparison of the herbivore defense and competitive ability of ancestral and modern genotypes of an invasive plant, *Lespedeza cuneata*. *Oikos* 120: 1413–1419.

- Blair AC, Wolfe LM. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. *Ecology* **85**: 3035–3042.
- Blossey B, Nötzold R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* **83**: 887–889.
- Bossdorf O, Prati D, Auge H, Schmid B. 2004. Reduced competitive ability in an invasive plant. *Ecology Letters* **7**: 346–353.
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* **144**: 1–11.
- Cahill JF, Kembel SW, Gustafson DJ. 2005. Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. *Journal of Ecology* **93**: 958–967.
- Callaway RM, Ridenour WM. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* **2**: 436–443.
- Chun YJ, Nason JD, Moloney KA. 2009. Comparison of quantitative and molecular genetic variation of native vs. invasive populations of purple loosestrife (*Lythrum salicaria* L., Lythraceae). *Molecular Ecology* **18**: 3020–3035.
- Colautti RI, Barrett SCH. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* **342**: 364–366.
- Doorduyn LJ, Vrieling K. 2011. A review of the phytochemical support for the shifting defence hypothesis. *Phytochemistry Reviews* **10**: 99–106.
- Dostal P. 2011. Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *American Naturalist* **177**: 655–667.
- Drenovsky RE, Grewell BJ, D'Antonio CM, et al. 2012. A functional trait perspective on plant invasion. *Annals of Botany* **110**: 141–153.
- Ehlers BK, Thompson J. 2004. Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia* **141**: 511–518.
- Farrer EC, Goldberg DE. 2011. Patterns and mechanisms of conspecific and heterospecific interactions in a dry perennial grassland. *Journal of Ecology* **99**: 265–276.
- Felker-Quinn E, Schweitzer JA, Bailey JK. 2013. Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and Evolution* **3**: 739–751.
- Flanagan RJ, Mitchell RJ, Karron JD. 2010. Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia* **164**: 445–454.
- Franks SJ, Pratt PD, Dray FA, Simms EL. 2008. Selection on herbivory resistance and growth rate in an invasive plant. *American Naturalist* **171**: 678–691.
- Goldberg DE, Fleetwood L. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* **75**: 1131–1143.
- Goldberg DE, Landa K. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* **79**: 1013–1030.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**: 1169–1194.
- Hager HA. 2004. Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia* **139**: 140–149.
- Hanley ME. 2012. Seedling defoliation, plant growth and flowering potential in native- and invasive-range *Plantago lanceolata* populations. *Weed Research* **52**: 252–259.
- He WM, Feng YL, Ridenour WM, et al. 2009. Novel weapons and invasion: biogeographic differences in the competitive effects of *Centaurea maculosa* and its root exudate (+/-)-catechin. *Oecologia* **159**: 803–815.
- Houghton-Thompson J, Prince HH, Smith JJ, Hancock JF. 2005. Evidence of hybridization between *Lythrum salicaria* (purple loosestrife) and *L. alatum* (winged loosestrife) in North America. *Annals of Botany* **96**: 877–885.
- Hovick SM, Bunker DE, Peterson CJ, Carson WP. 2011. Purple loosestrife suppresses plant species colonization far more than broad-leaved cattail: experimental evidence with plant community implications. *Journal of Ecology* **99**: 225–234.
- Huang W, Siemann E, Wheeler GS, Zou JW, Carrillo J, Ding JQ. 2010. Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *Journal of Ecology* **98**: 1157–1167.
- Huang W, Carrillo J, Ding JQ, Siemann E. 2012. Interactive effects of herbivory and competition intensity determine invasive plant performance. *Oecologia* **170**: 373–382.
- Joshi S, Tielbörger K. 2012. Response to enemies in the invasive plant *Lythrum salicaria* is genetically determined. *Annals of Botany* **110**: 1403–1410.
- Keddy PA, Twolanstrutt L, Wisheu IC. 1994. Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? *Journal of Ecology* **82**: 635–643.
- van Kleunen M, Schmid B. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* **84**: 2816–2823.
- van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* **13**: 235–245.
- Kulmatiski A, Beard KH, Stevens JR, Cobbold SM. 2008. Plant-soil feedbacks: a meta-analytical review. *Ecology Letters* **11**: 980–992.
- Lankau RA. 2012. Coevolution between invasive and native plants driven by chemical competition and soil biota. *Proceedings of the National Academy of Sciences of the USA* **109**: 11240–11245.
- Leger EA, Rice KJ. 2003. Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* **6**: 257–264.
- MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**: 377–385.
- Mal TK, LovettDoust J, LovettDoust L. 1997. Time-dependent competitive displacement of *Typha angustifolia* by *Lythrum salicaria*. *Oikos* **79**: 26–33.
- Maron JL, Vila M, Arnason J. 2004. Loss of enemy resistance among introduced populations of St. John's wort (*Hypericum perforatum*). *Ecology* **85**: 3243–3253.
- Müller-Schärer H, Schaffner U, Steinger T. 2004. Evolution in invasive plants: implications for biological control. *Trends in Ecology and Evolution* **19**: 417–422.
- Nakai S, Zou G, Okuda T, et al. 2010. Anti-cyanobacterial allelopathic effects of plants used for artificial floating islands. *Allelopathy Journal* **26**: 113–121.
- Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ. 2008. Adaptive evolution in invasive species. *Trends in Plant Science* **13**: 288–294.
- R Development Core Team. 2012. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Ridenour WM, Vivanco JM, Feng YL, Horiuchi J, Callaway RM. 2008. No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs* **78**: 369–386.
- Sakai AK, Allendorf FW, Holt JS, et al. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**: 305–332.
- Scharfy D, Funk A, Venterink HO, Gusewell S. 2011. Invasive forbs differ functionally from native graminoids, but are similar to native forbs. *New Phytologist* **189**: 818–828.
- Suding KN, LeJeune KD, Seastedt TR. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* **141**: 526–535.
- Taylor K. 2009. Biological flora of the British Isles: *Urtica dioica* L. *Journal of Ecology* **97**: 1436–1458.
- Thompson DQ, Stuckey RL, Thompson EB. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. US Fish and Wildlife Service. <http://www.npwrc.usgs.gov/resource/plants/loosstrf/index.htm>.
- Vilà M, Gomez A, Maron JL. 2003. Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. *Oecologia* **137**: 211–215.
- Vilà M, Weiner J. 2004. Are invasive plant species better competitors than native plant species? evidence from pair-wise experiments. *Oikos* **105**: 229–238.
- Wang Y, Carrillo J, Siemann E, et al. 2013. Specificity of extrafloral nectar induction by herbivores differs among native and invasive populations of tallow tree. *Annals of Botany* **112**: 751–756.
- Wolfin JA, MacKeigan P. 2005. Human influence past and present – relationship of nutrient and hydrologic conditions to urban wetland macrophyte distribution. *Ohio Journal of Science* **105**: 125–132.
- Zou JW, Rogers WE, Siemann E. 2008. Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. *Biological Invasions* **10**: 291–302.