

Research review

Evolutionary responses of native plant species to invasive plants: a review

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Summary

Strong competition from invasive plant species often leads to declines in abundances and may, in certain cases, cause localized extinctions of native plant species. Nevertheless, studies have shown that certain populations of native plant species can co-exist with invasive plant species, suggesting the possibility of adaptive evolutionary responses of those populations to the invasive plants. Empirical inference of evolutionary responses of the native plant species to invasive plants has involved experiments comparing two conspecific groups of native plants for differences in expression of growth/reproductive traits: populations that have experienced competition from the invasive plant species (i.e. experienced natives) versus populations with no known history of interactions with the invasive plant species (i.e. naïve natives). Here, I employ a meta-analysis to obtain a general pattern of inferred evolutionary responses of native plant species from 53 such studies. In general, the experienced natives had significantly higher growth/reproductive performances than naïve natives, when grown with or without competition from invasive plants. While the current results indicate that certain populations of native plant species could potentially adapt evolutionarily to invasive plant species, the ecological and evolutionary mechanisms that probably underlie such evolutionary responses remain unexplored and should be the focus of future studies.

Introduction

Invasive plant species can dramatically alter the structure and dynamics of native plant communities and the functioning of ecosystems (D'Antonio & Meyerson, 2002; Levine *et al.*, 2003; Vilá *et al.*, 2011). Understanding patterns of interactions between invasive and native plant species and the mechanisms underlying such interactions is key to predicting the broader impacts of invasive plants, and to mitigating or managing their negative effects (Levine *et al.*, 2003; Vilá *et al.*, 2011). Competitive interactions between invasive plant species and native plant species are one of the mechanisms underlying the impacts of invasive plants in terrestrial ecosystems (Levine *et al.*, 2003). Strong competition from invasive plants often leads to declines in the abundances and dominance, and, in certain cases, to localized extinctions of native plant species (D'Antonio & Meyerson, 2002; Callaway *et al.*, 2005; Sax *et al.*, 2007). Nevertheless, numerous studies have reported that, within the invaded ecosystems, certain populations of native plant species

(hereafter called 'remnant natives' *sensu* Leger & Espeland, 2010) can co-occur with invasive plant species despite the strong competition exerted by the invasive plants (Mealor *et al.*, 2004; Callaway *et al.*, 2005; Lesica & Atthowe, 2007; Mealor & Hild, 2007; Leger, 2008; Ferrero-Serrano *et al.*, 2011; Goergen *et al.*, 2011; Dostál *et al.*, 2012). It has been hypothesized that strong competition from invasive plants acts as a selective agent, eliminating native plant genotypes that cannot resist/tolerate the strong competition, resulting in an accumulation of native plant genotypes that can resist/tolerate the strong competition within the populations of remnant natives (Strauss *et al.*, 2006; Leger & Espeland, 2010). Genetic variation in traits that confer resistance/tolerance to strong competition from invasive plant species may enable native plant species to adapt evolutionarily to the invasive plant species (Strauss *et al.*, 2006).

An insight into evolutionary responses of native plant species to invasive plant species can be gained from common environment (glasshouse or field) experiments that compare two groups of native

plants for phenotypic expressions of growth/reproductive traits: native plants collected from remnant native source populations (hereafter referred to as experienced natives) versus conspecific native plants collected from adjacent source populations with no known history of interactions with the invasive plant species (hereafter referred to as naïve natives (Strauss *et al.*, 2006; Rowe & Leger, 2011)). The basic assumption in this kind of experiment is that the experienced natives have undergone natural selection imposed by strong competition from the invasive plants, and hence should have higher fitness than naïve natives when both groups of native plants are grown in the presence of invasive plant species (Strauss *et al.*, 2006; Leger & Espeland, 2010; Rowe & Leger, 2011). The higher fitness of experienced natives (as indicated by their higher growth/reproductive output) in the presence of invasive plants could be a result of their evolved higher tolerance to and/or ability to compete against invasive plant species (Strauss *et al.*, 2006; Leger & Espeland, 2010; Rowe & Leger, 2011). Significantly higher growth of the experienced natives even in the absence of invasive plants could also indicate evolved higher competitive ability (Keddy *et al.*, 2002).

Increasing numbers of papers report on the results of experiments undertaken to infer evolutionary responses of native plant species to invasive plant species (e.g. Callaway *et al.*, 2005; Lau, 2006; Lesica & Atthowe, 2007; Meador & Hild, 2007; Leger, 2008; Ferrero-Serrano *et al.*, 2011; Goergen *et al.*, 2011; Rowe & Leger, 2011; Dostál *et al.*, 2012). However, the present lack of a broad-scale synthesis of those results limits our ability to generalize and predict under what ecological conditions the native plant species might adapt to the invasive plant species. In the present brief review, a quantitative approach, a meta-analysis, was employed to obtain a general pattern of inferred evolutionary responses of native plant species to invasive plant species. A meta-analysis uses formal statistical techniques that enable exploration of the heterogeneity that characterizes ecological experiments, summary of the data accruing from those experiments, and identification of broad-scale patterns across diverse species and environmental gradients (Hedges *et al.*, 1999; Rosenberg *et al.*, 2000). The following question was addressed in the present review: do experienced natives express higher mean values of growth/reproductive traits than naïve natives when both groups of plants are grown under common environmental conditions? The review also attempted to identify areas for future research that will advance our understanding of the ecological and evolutionary mechanisms that may influence evolutionary responses of native plant species to invasive plant species.

Materials and Methods

Relevant peer-reviewed publications were identified from electronic databases (ISI Web of Science, Scopus, Elsevier and Blackwell-Synergy) using various search term combinations (e.g. (invasive plant OR invader plant OR exotic plant OR alien plant OR invasive weed) AND (natural selection* OR evolutionary response* native plant resistance* native plant tolerance* native plant adaptation*)). Additionally, reference list checks were performed on the relevant publications so obtained. Some data were

obtained directly from the corresponding authors. Publications were considered relevant only if they reported on factorial experiments in which experienced and naïve native plants had been compared for phenotypic expression of growth/reproductive traits in common environmental conditions (glasshouse or field) either in competition with invasive plant species or without competition.

To prepare data for the meta-analysis, a meta-data set was assembled using the following data extracted from figures, tables, or texts: mean trait values and associated standard deviations (or other measure of variation that allowed their calculation), and sample sizes (n). When various growth parameters (e.g. total plant biomass, plant height, number of tillers, and basal area) had been quantified for the same experimental units, an average value was computed for all those parameters (using effect sizes computed for each parameter) and treated as one mean response value per study. Some papers reported on several experiments testing evolutionary responses of several native plant species to a single invasive plant species. In such experiments, every test of a native plant species against an invasive plant species was deemed an independent study. In addition, certain native plant–invasive plant tests had been conducted across environmental gradients (e.g. light, nutrients, and herbivory). Such experiments were also deemed independent studies. An effect size was computed for each independent study. An effect size refers to the mean responses measured in the treatment group relative to the mean responses measured in the control group (Gurevitch & Hedges, 2001). In the present context, the treatment group comprised the experienced native plants, while the control group comprised the naïve native plants. The effect size metric used was the log response ratio ($\log_e R$), which is considered to be ecologically more relevant than other metrics (Hedges *et al.*, 1999). A log response ratio ($\log_e R$) and the associated variance (v_i) were calculated for each study in the meta-data set (for the native plants grown alone or with competition) according to the equations of Rosenberg *et al.* (2000). The log response ratio, $\log_e R = \log_e \left(\frac{\bar{X}^E}{\bar{X}^C} \right)$, where, in the present context, \bar{X}^E is the mean growth/reproductive output of experienced natives, and \bar{X}^C is the mean growth/reproductive output for naïve natives.

To understand the overall mean effect of previous exposure of native plants to invasive plants on phenotypic expression of growth/reproductive traits by native plants (i.e. compare performances of experienced natives versus naïve natives), a meta-analysis was performed using the effect sizes computed above. An overall effect size was considered significant when its 95% confidence interval (CI) did not overlap with 1 in the back-transformed response ratio. Here, a back-transformed response ratio greater than 1 indicates that the experienced natives expressed higher levels of growth/reproductive traits than the naïve natives. In contrast, naïve natives expressed significantly higher growth/reproductive traits than experienced natives when the back-transformed response ratio was less than 1. A test of homogeneity of effect sizes across all studies was performed in the global meta-analysis of all data combined, as well as in categorical meta-analyses. This was done by inspecting the P -values associated with a Q statistic, which is tested against a chi-squared distribution (Gurevitch & Hedges, 2001). For this, total

heterogeneity (Q_{total}) and heterogeneity between groups (Q_{between}) were computed. A significant Q value ($P < 0.05$) indicates that variance among effect sizes was greater than expected by sampling error (Rosenberg *et al.*, 2000; Borenstein *et al.*, 2010). A target plant may express phenotypic traits differently when grown alone versus when grown with another plant (Armas *et al.*, 2004). At the same time, micro-environmental variations in the field might cause the effect sizes to differ between field experiments and glasshouse experiments (Morris *et al.*, 2007). Thus, using the same data set as above, two separate categorical meta-analyses were performed to test whether the experienced natives differed from the naïve natives in phenotypic expression of growth/reproductive traits when the plants were grown: (1) with competition or without competition from the invasive plant species; and (2) in glasshouse versus field conditions. In the categorical meta-analyses, mean effect sizes were considered similar when their CIs overlapped. Data were analysed using random-effects models that are suitable for ecological data synthesis, allowing the resulting conclusions to be generalized to a broader array of situations (Rosenberg *et al.*, 2000; Borenstein *et al.*, 2010).

Meta-analyses can be faced with a problem of publication bias, that is, the tendency to publish only significant results (Rosenthal, 1979). To test for a possibility of publication bias affecting the present meta-data set, fail-safe numbers were calculated. Fail-safe numbers are the number of nonsignificant, unpublished and/or missing studies that would be added to a meta-analysis data set before the results of the meta-analysis become nonsignificant (Rosenberg *et al.*, 2000). If the effect size is expected to vary across studies, use of the fail-safe number is a suitable method for testing for publication bias (Gurevitch & Hedges, 1999). Hence, fail-safe

numbers were calculated in the present analysis using Rosenthal's method (Rosenthal, 1979). A fail-safe number needs to be at least $5n + 10$ for one to be confident of results, where n is equal to the number of studies included in the meta-data set (Rosenthal, 1979). All the analyses were performed using METAWIN Version 2 (Rosenberg *et al.*, 2000).

Results

A total of 53 independent studies reported in 14 peer-reviewed journal articles and one manuscript under revision met the selection criteria (Table 1). In total, 20 different native plant species had been tested against 10 distinct invasive plants species (Table 1). Out of the 53 studies, 41 were those in which experienced and naïve native plants had been grown in competition with invasive plant species, while in the remaining 12 studies, experienced and naïve native plants had been grown without competition from invasive plant species. With respect to the common environmental conditions, 31 studies had been conducted in a glasshouse, while the remaining 22 studies had been conducted in the field (Table 1). In the global meta-analysis of all studies, experienced natives had higher mean phenotypic expression of growth/reproductive traits than naïve natives (mean response ratio = 1.21; 95% CI 1.12–1.30). There was significant variation in effect sizes among the 53 studies combined ($Q_{\text{total}} = 70.54$; $df = 52$; $P = 0.044$). For the two categorical meta-analyses, the mean phenotypic expression of growth/reproductive traits by experienced natives was higher than that by naïve natives regardless of competition treatment (mean response ratio with competition = 1.21 (95% CI 1.09–1.34) versus mean response ratio with no competition = 1.20 (95% CI 1.06–1.37)) or

Table 1 Studies included in the meta-analysis comparing phenotypic expression of growth/reproductive traits by experienced and naïve natives

Reference	Native species	Invasive species	Habitat type	Number of studies	Response ratio
Bergum <i>et al.</i> (2012) ^G	<i>Sporobolus airoides</i>	<i>Acroptilon repens</i>	Rangeland	2	> 1
Cipollini & Hurley (2009) ^G	<i>Impatiens capensis</i>	<i>Alliaria petiolata</i>	Ns	1	> 1
Callaway <i>et al.</i> (2005) ^G	<i>Festuca idahoensis</i> ; <i>Pseudoroegneria spicata</i> ; <i>Stipa occidentalis</i> ; <i>Koeleria cristata</i> ; <i>Poa sandbergii</i>	<i>Centaurea maculosa</i>	Grassland	10	> 1
Dostál <i>et al.</i> (2012) ^F	<i>Impatiens noli-tangere</i>	<i>Impatiens parviflora</i>	Woodland and forest	6	> 1
Ferrero-Serrano <i>et al.</i> (2010) ^G	<i>S. airoides</i> ; <i>Hesperostipa comata</i>	<i>Cirsium arvense</i>	Rangeland	2	> 1
Goergen <i>et al.</i> (2011) ^G	<i>Achnatherum thurberianum</i> ; <i>Elymus multisetus</i> ; <i>Poa secunda</i> ; <i>Achnatherum hymenoides</i> ; <i>Hesperostipa comata</i>	<i>Bromus tectorum</i>	Sagebrush steppe	5	< 1
Leger (2008) ^G	<i>Elymus multisetus</i>	<i>B. tectorum</i>	Grassland	5	< 1
Lau (2006) ^F	<i>Lotus wrangelianus</i>	<i>Medicago polymorpha</i>	Sagebrush steppe	8	> 1
Mealor & Hild (2007) ^F	<i>Hesperostipa comata</i> ; <i>S. airoides</i>	<i>A. repens</i>	Rangeland	1	> 1
Rowe & Leger (2010) ^G	<i>E. multisetus</i>	<i>B. tectorum</i>	Sagebrush steppe	4	< 1
Sebade <i>et al.</i> (2012) ^F	<i>S. airoides</i>	<i>Rhaponticum repens</i>	Rangeland	1	> 1
Lesica & Atthowe (2007) ^F	<i>Agropyron spicatum</i>	<i>C. maculosa</i>	Grassland	2	< 1
S. Y. Strauss <i>et al.</i> (unpublished) ^G	<i>Achillea millefolium</i>	<i>Holcus lanatus</i>	Coastal prairie	2	> 1
Jensen & Ehlers (2010) ^G	<i>Agrostis capillaris</i> ; <i>Campanula rotundifolia</i>	<i>Thymus pulegioides</i>	Dry grassland	1	> 1
Grøndahl & Ehlers (2008) ^G	<i>A. millefolium</i>	<i>T. pulegioides</i>	Dry grassland	6	> 1

A response ratio (back-transformed) > 1 indicates that the experienced natives expressed higher levels of growth/reproductive traits than the naïve natives, while a response ratio < 1 indicates higher growth/reproductive traits for naïve natives. Superscripts indicate the common environment where the experiments were conducted (G, glasshouse; F, field). Habitat type refers to ecosystems where invasive plant species interacted with the native plant species (Ns, habitat type not specified in the reference).

common environmental conditions (mean response ratio for glasshouse = 1.17 (95% CI 1.07–1.28) versus mean response ratio for field = 1.32 (95% CI 1.14–1.53)). Hence, the phenotypic expression of growth/reproductive traits by the experienced and naïve natives was not influenced significantly by the type of competition ($Q_{\text{between}} = 2.10$; $P = 0.147$) or common garden environment ($Q_{\text{between}} = 0.001$; $P = 0.97$).

The fail-safe number for the global meta-analysis was 307. For the categorical meta-analyses, the fail-safe numbers were 299.8 in the test for the effects of plant neighbour treatment (competition versus no competition), and 322.4 in the test for the effect of common environmental growth conditions (field versus glasshouse). All these three fail-safe numbers were larger than a threshold of 275 (i.e. $53 \times 5 + 10$); hence it is safe to conclude that these results are not affected by publication bias.

Discussion

The present results show that, generally, experienced natives express higher levels of growth/reproductive traits than naïve natives. That this pattern holds true regardless of whether the two groups of native plants were grown with or without competition from the invasive plant species or in glasshouse or field conditions is noteworthy. While these results support the hypothesis that native plant species can respond evolutionarily to invasion by exotic plant species (Callaway *et al.*, 2005; Strauss *et al.*, 2006; Leger & Espeland, 2010; Rowe & Leger, 2011), the logical next step will be to identify the ecological processes (i.e. mechanisms) and genetic changes underlying such evolutionary responses by the native plant species, as well as the adaptive value (i.e. fitness consequences) of such genetic changes.

What ecological processes are likely to underlie evolutionary responses of native plant species? How do they influence the evolutionary responses?

Besides impacting on the fitness of native plants through direct competitive effects, invasive plant species can significantly impact on the native plant fitness indirectly through allelopathy, altered interactions between native plants and their above-ground/below-ground natural enemies (herbivores and pathogens) or mutualists (e.g. pollinators and mycorrhizas), and alteration of ecosystem processes such as nutrient cycles, water cycles, and fire regimes (for reviews see Levine *et al.*, 2003; Morales & Traveset, 2009; Leger & Espeland, 2010; Van der Putten *et al.*, 2013). However, there is still no empirical demonstration of how any of those processes can influence evolutionary responses of native plant species.

When can native plant species adapt evolutionarily to selection imposed by invasive plant species?

Adaptive evolution of native plant species in response to selection imposed by invasive plant species can occur only when certain criteria for Darwinian natural selection are met (Strauss *et al.*, 2006; Leger & Espeland, 2010). First, populations of the native plant species must possess heritable genetic variations in

traits that confer fitness, with some genotypes in the population being fitter than others in the face of selection pressure. Secondly, the selection pressures exerted by the invasive plant must be sufficiently strong and consistent and affect the fitness of the native plants (Strauss *et al.*, 2006; Leger & Espeland, 2010). A lack of genetic variability in traits upon which the selection pressure acts could lead to local extinction of the native plant populations (Strauss *et al.*, 2006; Leger & Espeland, 2010). The phenotypic traits of native plant species upon which natural selection acts may be underpinned by standing (i.e. pre-existing) genetic variation, recombinations or new mutations within the native plant populations (Strauss *et al.*, 2006; Leger & Espeland, 2010). Other factors that may influence the capacity of native plant populations to adapt evolutionarily include population sizes and growth rates, and gene flow between/among invaded and uninvaded populations of the native plant species (for comprehensive reviews, see Strauss *et al.*, 2006; Leger & Espeland, 2010). Having empirical insights into these population genetics and demographic processes will be key to an understanding of the adaptive evolutionary responses of native plant species to invasion by exotic plant species.

Genetic versus nongenetic basis for differences in phenotypic trait expression between experienced and naïve natives

Thus far, there is little molecular genetic evidence for evolutionary responses of native plant species to invasion by exotic plant species. Only a study by Meador *et al.* (2004) has attempted to decipher molecular genetic differences between experienced natives and naïve natives. Using a neutral genetic marker, they showed that individuals of four native grass species collected from habitats invaded by *Acroptilon repens* and *Cardaria draba* were differentiated from their conspecifics collected from adjacent uninvaded habitats. This study provides a useful framework upon which to build and expand. With advances in the use of molecular tools, we may gain insights into, for example, what parts of the genomes of native plant species are specifically targeted by natural selection imposed by invasive plant species.

A fundamental question in evolutionary ecology is to what extent variation in ecologically relevant traits is heritable, because heritability determines the potential for evolutionary adaptation to altered ecological conditions (Hoffmann & Sgro, 2011). Variations in phenotypic trait expression among offspring upon which natural selection acts are determined by factors that are inherited from parents via two pathways: genetic material inherited in a Mendelian fashion, and a nongenetic inheritance of environmental influence (Bossdorf *et al.*, 2008; Bonduriansky & Day, 2009). Genetic inheritance refers to the effect on an offspring phenotype caused by DNA sequences transmitted from parents to the offspring (Bonduriansky & Day, 2009). In contrast, nongenetic inheritance of environmental influence refers to any effect on offspring phenotypes caused by the transmission of factors other than DNA sequences (i.e. epigenetic, cytoplasmic, or somatic factors) from parents to offspring (Bossdorf *et al.*, 2008; Bonduriansky & Day, 2009). Nongenetic inheritance of these factors does not involve modification of germline DNA

sequence by the environment (Bonduriansky & Day, 2009). Examples of nongenetic environmental influence include parents providing offspring with: nutrients (Latzel *et al.*, 2009), induced defence against herbivores (Agrawal *et al.*, 1999), and symbionts such as endophytes (Afkhami & Rudgers, 2008). Empirical evidence has shown that the stability of traits inherited in a nongenetic fashion can attenuate after only a few offspring generations (Afkhami & Rudgers, 2008). To date, only one study has tested for trans-generational stability of phenotypic traits expressed by offspring of the experienced and naïve native parental plants. Bergum *et al.* (2012) found that the level of phenotypic trait expression changed from the first to the second offspring generations in *Sporobolus airoides*. Nevertheless, studies that tease apart the influence of inherited environmental effects from those of inherited genetic effects on phenotypic trait expression by offspring of experienced and naïve native plants are still lacking. To discriminate between the relative roles of inherited genetic and inherited nongenetic effects, it is desirable to conduct experiments similar to that by Bergum *et al.* (2012), which span multiple generations.

Effects of herbivores on evolutionary responses by native plants

Herbivores can drive the evolution of competitive interactions between plants (Agrawal *et al.*, 2012). This can occur when herbivore attacks on a host plant species drive the evolution of anti-herbivore defence strategies that in turn influence competitive interactions between the host plant and other plant neighbours (Agrawal *et al.*, 2012). An empirical example of how herbivory can drive changes in the genotype frequency of a given host plant species, and hence competitive interactions between that host plant species and another plant species, comes from a study by Agrawal *et al.* (2012). Agrawal *et al.* (2012) used a 5-yr factorial field experiment in which 18 different genotypes of a native plant species (*Oenothera biennis*) were either exposed to ambient levels of insect damage or protected from the insects. Then they tracked changes in the frequency of occurrence of each *O. biennis* genotype over time. At the end of the experiment, they found that one genotype was entirely extirpated, while others were severely diminished in frequency in plots that were exposed to natural levels of herbivory. What is more, they found that exclusion of the herbivore selected for *O. biennis* genotypes that had low anti-herbivore resistance and a high ability to compete against another plant species, *Taraxacum officinale*. Current understanding of the effects of herbivores on evolutionary responses of native plants to competition from invasive plants is based on inferred evidence. Through manipulative field experiments, Lau (2006) inferred an insect herbivore (*Hypera brunneipennis*)-mediated evolutionary adaptation of a native plant species, *Lotus wrangelianus*, to competition from an invasive plant species, *Medicago polymorpha*. In the absence of the insect herbivore and under competition from the invasive plant, experienced *L. wrangelianus* had higher seed production than naïve *L. wrangelianus*, suggesting that insect herbivores can foil evolutionary adaptation of native plant species to

competition from invasive plant species (Lau, 2006). Empirical demonstrations of herbivore-mediated evolution of native plant species in response to competition from exotic plant species will require factorial experiments in which the presence of herbivores and invasive plant species is manipulated, and populations of the native plant species are allowed to evolve for multiple generations.

Role of habitat quality on evolutionary responses by native plants

Habitat quality – the level of light, moisture, temperature and nutrients under which plants grow – may influence the evolutionary responses of native plant species to invasion by exotic plant species (Leger & Espeland, 2010). It is widely accepted that native plant species use limited growth resources more efficiently than invasive plant species, which should confer the native plant species with a higher ability to compete against the invasive plant species in resource-poor habitats (Funk & Vitousek, 2007 and references therein). Nevertheless, field studies have shown that invasive plant species can also have higher resource use efficiency than resident native plant species in conditions of low resource availability (Funk & Vitousek, 2007 and references therein). Hence, the strength of competitive interactions between invasive and native plants that may result in evolutionary responses of the native species may be context-dependent, varying with both habitat productivity and the inherent traits of the invasive and native plants under consideration (Funk & Vitousek, 2007; Leger & Espeland, 2010). Thus far, only one study has tested the effects of habitat quality on evolutionary responses by native plant species. Dostál *et al.* (2012) manipulated levels of light and nutrient availability to infer evolutionary responses of *Impatiens noli-tangere* to an invasive plant species, *Impatiens parviflora*. Experienced *I. noli-tangere* produced higher root biomass than naïve *I. noli-tangere* under conditions of high nutrients and light availability (Dostál *et al.*, 2012). However, the experienced and naïve *I. noli-tangere* produced a similar amount of root biomass under low light and nutrient conditions (Dostál *et al.*, 2012).

Effects of experienced natives on population density of invasive plant species

The hypothesized ability of experienced natives to resist/tolerate strong competition from invasive plant species has led to suggestions that seeds/plant material from the experienced natives should be preferentially used to restore invaded ecosystems (Rice & Emery, 2003; Leger, 2008; Goergen *et al.*, 2011; Dostál *et al.*, 2012). Because reducing population densities of invasive plants is one of the principal aims of restoration of ecosystems invaded by exotic plant species (Bakker & Wilson, 2004), it then becomes interesting to ask whether use of experienced native plants in restoration can significantly reduce population growth rates and densities of invasive plants. Results from future experiments aiming to resolve this question may offer insight into whether adaptive evolution by native plant species can reduce impacts of the invasive plant species.

Variability in effect sizes

Despite the overall higher phenotypic expression of growth/reproductive traits by the experienced natives relative to the naïve natives, there was variability not only in the magnitude but also in the direction of effect sizes among individual studies (Table 1). For example, experienced *Sporobolus airoides* had much higher phenotypic expression of traits that confer resistance/tolerance to an invasive plant, *Cirsium arvense*, than naïve *S. airoides* in a rangeland habitat (Ferrero-Serrano *et al.*, 2011). In contrast, naïve *Achnatherum hymenoides* and *Hesperostipa comata* had higher resistance against invasive *Bromus tectorum* than their experienced conspecifics in a sagebrush steppe habitat (Goergen *et al.*, 2011). This underscores the importance of performing studies similar to those presently reviewed that cut across broad taxonomic groups within a broad range of habitats in order to capture the variability in evolutionary responses by native plant species.

Conclusions

The present results support the hypothesis that native plant species can respond evolutionarily to selection pressures exerted by invasive plant species. However, as discussed, the ecological and evolutionary mechanisms that are likely to underlie the evolutionary responses of native plant species still remain unexplored empirically, and this review will hopefully motivate further research to fill these gaps. An empirical understanding of evolutionary responses of native plant species to selection imposed by invasive plant species, and whether such responses are adaptive, will require studies that employ an integral approach: the combined use of field-based selection experiments along biotic and abiotic gradients, population genetic analyses, and molecular evolution studies.

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References

Afkhami ME, Rudgers JA. 2008. Natural history note: symbiosis lost: imperfect vertical transmission of fungal endophytes in grasses. *The American Naturalist* 172: 405–416.

Agrawal AA, Hastings AP, Johnson MTJ, Maron JL, Salminen JP. 2012. Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science* 338: 113–116.

Agrawal AA, Laforsch C, Tollrian R. 1999. Transgenerational induction of defences in animals and plants. *Nature* 401: 60–63.

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85: 2682–2686.

Bakker JD, Wilson SD. 2004. Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology* 41: 1058–1064.

Bergum EK, Hild AL, Meador BA. 2012. Phenotypes of two generations of *Sporobolus airoides* seedlings derived from *Acroptilon repens*-invaded and non-invaded grass populations. *Restoration Ecology* 20: 227–233.

Bonduriansky R, Day T. 2009. Nongenetic inheritance and its evolutionary implications. *Annual Review of Ecology Evolution and Systematics* 40: 103–125.

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR. 2010. A basic introduction to fixed-effect and random-effects models for meta-analysis. *Research Synthesis Methods* 1: 97–111.

Bosdorf O, Richards CL, Pigliucci M. 2008. Epigenetics for ecologists. *Ecology Letters* 11: 106–115.

Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology* 93: 576–583.

Cipollini KA, Hurley SL. 2008. Variation in resistance of experienced and naïve seedlings of Jewelweed (*Impatiens capensis*) to invasive garlic mustard (*Alliaria petiolata*). *Ohio Journal of Science* 108: 47–49.

D'Antonio CM, Meyerson LA. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10: 703–713.

Dostál P, Weiser M, Koubek T. 2012. Native jewelweed, but not other native species, displays post-invasion trait divergence. *Oikos* 121: 1849–1859.

Ferrero-Serrano A, Hild A, Meador B. 2010. Can invasive species enhance competitive ability and restoration potential in native grass populations? *Restoration Ecology* 19: 545–551.

Ferrero-Serrano A, Hild AL, Meador BA. 2011. Can invasive species enhance competitive ability and restoration potential in native grass populations? *Restoration Ecology* 19: 545–551.

Funk JL, Vitousek PM. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446: 1079–1081.

Goergen EM, Leger EA, Espeland EK. 2011. Native perennial grasses show evolutionary response to *Bromus tectorum* (Cheatgrass) invasion. *PLoS ONE* 6: e18145.

Grøndahl E, Ehlers BK. 2008. Local adaptation to biotic factors: reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. *Journal of Ecology* 96: 981–992.

Gurevitch J, Hedges LV. 1999. Statistical issues in conducting ecological meta-analyses. *Ecology* 80: 1142–1149.

Gurevitch J, Hedges LV. 2001. Meta-analysis: combining the results of independent experiments. In: Scheiner SM, Gurevitch J, eds. *Design and analysis of ecological experiments*. New York, NY, USA: Oxford University Press, 347–369.

Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80: 1150–1156.

Hoffmann AA, Sgro CM. 2011. Climate change and evolutionary adaptation. *Nature* 470: 479–485.

Jensen CG, Ehlers BK. 2010. Genetic variation for sensitivity to a thyme monoterpene in associated plant species. *Oecologia* 162: 1017–1025.

Keddy PA, Neilsen K, Weiher E, Lawson R. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13: 5–16.

Latzel V, Hájek T, Klimešová J, Gómez S. 2009. Nutrients and disturbance history in two *Plantago* species: maternal effects as a clue for observed dichotomy between resprouting and seeding strategies. *Oikos* 118: 1669–1678.

Lau JA. 2006. Evolutionary response of native plants to novel community members. *Evolution* 60: 56–63.

Leger EA. 2008. The adaptive value of remnant native plants in invaded communities: an example from the great basin. *Ecological Applications* 18: 1226–1235.

Leger EA, Espeland EK. 2010. Coevolution between native and invasive plant competitors: implications for invasive species management. *Evolutionary Applications* 3: 169–178.

Lesica P, Atthowe HE. 2007. Identifying weed-resistant bluebunch wheatgrass for restoration in western Montana. *Ecological Restoration* 25: 191–198.

Levine J, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 775–781.

Meador BA, Hild AL. 2007. Post-invasion evolution of native plant populations: a test of biological resilience. *Oikos* 116: 1493–1500.

- Mealor BA, Hild AL, Shaw NL. 2004. Native plant community composition and genetic diversity associated with long-term weed invasions. *Western North American Naturalist* 64: 503–513.
- Morales CL, Traveset A. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters* 12: 716–728.
- Morris WF, Hufbauer RA, Agrawal AA, Bever JD, Borowicz VA, Gilbert GS, Maron JL, Mitchell CE, Parker IM, Power AG *et al.* 2007. Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. *Ecology* 88: 1021–1029.
- Rice KJ, Emery NC. 2003. Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* 1: 469–478.
- Rosenberg MS, Adams D, Gurevitch J. 2000. *MetaWin: statistical software for meta-analysis, version 2*. Sunderland, MA, USA: Sinauer Associates, Inc.
- Rosenthal R. 1979. The file drawer problem and tolerance for null results. *Psychological Bulletin* 86: 638–641.
- Rowe CLJ, Leger EA. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* 4: 485–498.
- Rowe CLJ, Leger EA. 2010. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* 4: 485–498.
- Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM *et al.* 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution* 22: 466–471.
- Sebade BM, Hild AL, Mealor BA. 2012. Native grasses collected from invasions demonstrate invasion resistance. *Ecological Restoration* 30: 209–217.
- Strauss SY, Lau JA, Carroll SP. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 9: 357–374.
- Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA *et al.* 2013. Plant-soil feedbacks: the past, the present and future challenges. *Journal of Ecology* 101: 265–276.
- Vilá M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.



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