

Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species

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Summary

1. Concerns over the ecological impacts of invasive alien plant species have generated great research interest in understanding the mechanisms that underlie the capacity of such plants to occupy a broad range of habitats. It has been repeatedly suggested that rapid evolution of local adaptation to novel environments may enable invasive plants to occupy a broad range of habitats. However, the classical Darwinian view on evolution by natural selection is that the process is slow and gradual, occurring over thousands of years. Invasive plants typically have a relatively short residence time in their introduced ranges (decades or just a few centuries). Besides the time constraint, founder effects (reduction in population size and genetic diversity) may also limit the capacity of invasive plants to rapidly evolve local adaptation. Thus, invasive plants may be less likely than native plants to evolve local adaptation. Interestingly, however, an expanding body of literature documents the existence of local adaptation in invasive plant species within their exotic ranges.

2. Here, we did a phylogenetically controlled meta-analysis to compare invasive and native plant species for differences in the frequency and magnitude of local adaptation. The meta-analysis was based on different experiments performed in various habitats including grasslands, steppes, deserts, forests, mountains, wetlands and dunes, and used a total of 134 plant species in 52 families. Forty seven of these species (in 24 families) are alien invaders in the region where the studies were undertaken, while the other 91 species (in 38 families) are native.

3. On average, local plants performed better than foreign plants, and invasive plant species expressed local adaptation just as frequently, and at least as strongly as that exhibited by native plant species. An analysis performed while taking into account different plant life-history traits showed that self-incompatible invasive plants exhibited significantly higher frequencies of local adaptation than native plants characterized by the same breeding system.

4. *Synthesis.* The present results support the suggestion that rapid evolution of local adaptation may enable invasive plant species to occupy a broad range of novel habitats.

Key-words: adaptive divergence, biological invasions, colonization, common garden experiment, invasion ecology, local adaptation, local vs. foreign criterion, phenotypic plasticity, pre-adaptation, reciprocal transplant experiment, translocation experiment

Introduction

When spatially separated populations within a plant species experience strongly divergent environmental conditions, natural selection exerted on the plant populations by their respec

tive environments may result in local adaptation (Linhart & Grant 1996; Kawecki & Ebert 2004). A population is deemed to have evolved local adaptation when resident individuals in that population produce phenotypes with higher relative performance than conspecific individuals transplanted from other habitats (Linhart & Grant 1996; Kawecki & Ebert 2004). Although local adaptation is prevalent in wild populations of numerous plant species within their native ranges (Hoeksema & Forde 2008; Leimu & Fischer 2008; Hereford 2009), it is less clear whether local adaptation is common in invasive alien plant species.

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Across the globe, a large number of plant species have been introduced to biogeographic regions where they did not occur before, and encounter a suite of novel biotic and abiotic selective agents (Vitousek *et al.* 1996; Mack *et al.* 2000; Facon *et al.* 2006; van Kleunen *et al.* 2015). A small fraction of the introduced plant species have become invasive wherein they spread over large areas and may outcompete resident native plants, and hence may cause declines in the abundance and dominance of native plants in the invaded habitats (Vitousek *et al.* 1996; Mack *et al.* 2000; D'Antonio & Meyerson 2002). Consequently, the question as to what mechanisms enable invasive plants to thrive in a broad range of environments is of long standing research interest (Parker, Rodriguez & Loik 2003; van Kleunen, Weber & Fischer 2010; van Kleunen *et al.* 2010).

It has been repeatedly suggested that rapid evolution of local adaptation to novel environments may enable invasive plant species to thrive across a broad range of habitats in their introduced ranges (García Ramos & Rodríguez 2002; Lee 2002; Parker, Rodriguez & Loik 2003; Facon *et al.* 2006). However, this suggestion runs counter to the traditional Darwinian view on evolution by natural selection that the process is slow and gradual, often occurring over thousands of years (Darwin 1859; Hendry & Kinnison 1999; Reznick & Ghalambor 2001; Stockwell, Hendry & Kinnison 2003). Unlike native plants with a much longer residence time, invasive plant species typically have a relatively short residence time in their introduced ranges, typically decades or just a few centuries (Pyšek & Jarošík 2005; Hulme 2009; Colautti & Lau 2015). Apart from the time constraint, founder effects (reduction in population size and genetic diversity) may also limit the capacity of invasive plants to rapidly evolve local adaptation. Although little is known about the levels of quantitative genetic variation in the introduced ranges, molecular marker based studies suggest that introduced populations possess lower levels of neutral genetic diversity than conspecific native range populations (Dlugosch & Parker 2008). Given that short residence time and founder effects may constrain adaptive evolution in invasive plants, a frequent default has been to associate invasiveness of alien plants to other mechanisms such as phenotypic plasticity (Baker 1965; Williams, Mack & Black 1995; Lambrinos 2004; Richards *et al.* 2006; Chun *et al.* 2007; Davidson, Jennions & Nicotra 2011). Interestingly, however, an expanding body of literature documents the existence of local adaptation in invasive plant species within their introduced ranges (e.g. Leger & Rice 2007; Ross, Faust & Auge 2008; Leger *et al.* 2009; Godoy *et al.* 2010; Lachmuth, Durka & Schurr 2011; Colautti & Barrett 2013; Kilkenny & Galloway 2013; Grossman & Rice 2014), thus suggesting that local adaptation may be just as important as plasticity in enabling invasive plants to inhabit a broad range of environmental conditions. Therefore, a key question that then arises is how common and how strong is local adaptation among invasive plant species in comparison to native plant species. To address this question, we conducted a meta analysis of published results from experimental studies on local adaptation in invasive and native plant species.

Materials and methods

DATA COMPILATION AND CALCULATION OF EFFECT SIZES

Experimental tests of local adaptation can be undertaken using the 'local vs. foreign' (individuals from a local population have higher performance than conspecific individuals transplanted from other habitats) or 'home vs. away' (the same genotype produces a higher performance in a local habitat than when grown in another habitat) criterion (Kawecki & Ebert 2004). There has been some debate in the literature regarding which of the two criteria above should be diagnostic of local adaptation. Kawecki & Ebert (2004) have argued that a pattern that satisfies the 'local vs. foreign' but not necessarily the 'home vs. away' criterion offers as much support for local adaptation as a pattern that satisfies both criteria. Nevertheless, an experimental design that tests local adaptation through reciprocal transplant of individuals between populations combines both criteria. Therefore, we based our analysis on studies that used the reciprocal transplant design. According to this design, there are, conceptually, three possible outcomes (i.e. reaction norm patterns) (Kawecki & Ebert 2004). These include cases where plants from a local population have higher performance than conspecific plants from a foreign population at: (i) both sites of a reciprocal transplant (POS POS), (ii) only one of two sites of a reciprocal transplant (POS NEG) and (iii) at neither site of a reciprocal transplant (NEG NEG) (Kawecki & Ebert 2004).

We expanded the data set compiled by Leimu & Fischer (2008) by searching electronic databases (Web of science, Scopus, PubMed, and Google scholar) for relevant peer reviewed publications that reported on these types of experiments by use of the key word 'plant' in combination with: 'local adaptation', 'genecology', 'adaptive divergence', 'adaptive differentiation', 'phenotypic variation', 'adaptive evolution', 'reciprocal transplant', 'translocation experiment', 'ecotypic response' or 'adaptation'. The last date for literature search was 10th March 2015, with the search resulting in 6304 hits. References cited in articles found through the electronic literature databases were also searched.

SELECTION OF STUDIES

Titles and abstracts of the resulting papers were then screened to check whether they reported fitness related traits of the experimental plants. Studies that used only molecular markers to test divergence between populations were eliminated. In addition, studies that only reported plant traits conferring adaptation to mutualists (floral symmetry, floral size, pollinator attraction and mycorrhizal colonization), herbivory (level of herbivore damage and seed predation) and pathogen infection (number or percent pathogen infection or resulting plant mortality), without providing fitness measures, were omitted. Thus, a study was included in the meta analysis only if it reported mean scores, standard deviations (or standard errors) and sample sizes of a fitness related trait for the experimental plants. The fitness related traits included in the analysis were: measures of reproductive success (number of flowers, fruits, seeds or seed biomass), plant size (plant biomass, plant height, number of leaves or number of ramets), survival percentage and germination percentage. If some of the required data on these fitness related traits were not reported, we obtained them from the corresponding authors.

Based on these selection criteria, we used a total of 130 publications (128 peer reviewed international scientific papers and two PhD theses) for data extraction. The experiments reported in these 130

publications had been conducted using a total of 134 plant species (in 52 families) in a range of natural habitats (grasslands, steppes, deserts, forests, mountains, wetlands and dunes) or under controlled environmental conditions (in the greenhouse/growth chamber) simulating field conditions. Forty seven of the species (in 24 families) were reported as invasive aliens (i.e. plants that had been introduced from a different continent or to an oceanic island and subsequently increased in abundance over wide geographic areas) in the region of study, while 91 native plant species (in 38 families) were reported as native to the region of study (Table 1). The remaining six species were range expanding plants that are native to a contiguous part of the same continent where the plant material was collected for study, and hence we considered them as non invasive aliens and excluded them from the analyses described below.

CALCULATION OF EFFECT SIZES

We computed effect sizes and the associated variances for each plant population that had been grown in a pairwise reciprocal transplant with other populations (a total of 1776 pairwise population comparisons). The effect size metric used was Hedges' d , which is not biased by small sample sizes (Rosenberg, Adams & Gurevitch 2000). Hedges' d is the weighted average of the mean standardized difference (based on pooled variance measures) between a treatment group and a control group (Rosenberg, Adams & Gurevitch 2000). Hedges' d was computed as: $d = (\bar{X}^E - \bar{X}^C/S)J$, where in the context of the 'local vs. foreign' criterion, \bar{X}^E is the mean fitness related trait for a 'local' plant and \bar{X}^C is the mean fitness related trait for a 'foreign' plant. S is the pooled standard deviation, and J is a weighting factor based on the number of replicates (N) per treatment. Hedges' d is a unitless index whose values range from $-\infty$ to $+\infty$. In the present context, a positive effect size signifies local adaptation.

When effect sizes for several traits were obtained from the same study, we computed a mean effect size (d^*) per individual study. Numerous studies of local adaptation used more than two populations of the same plant species in reciprocal transplant experiments, which resulted in multiple pairwise population comparisons within a study. Thus, to circumvent the problem of pseudoreplication that would arise from running a meta analysis using effect sizes from multiple pairwise population comparisons within a study, we pooled multiple effect sizes within a study. Pooling of effect sizes was undertaken

Table 1. The number of invasive and native plant species (and their life history traits and growth environment) used in the meta analysis. In brackets are the relative proportions of each species expressed as a percentage of the total species count (i.e. 134 species)

Moderator	Invasive	Native
Reproductive system		
Clonal	4 (2.98)	11 (8.21)
Non clonal	43 (32.09)	76 (56.72)
Breeding system		
Self compatible	30 (22.39)	57 (42.53)
Self incompatible	17 (12.69)	30 (22.39)
Life cycle		
Annual	22 (16.42)	25 (18.66)
Perennial	25 (18.66)	62 (46.26)
Growth environment		
Field	22 (16.42)	78 (58.21)
Controlled environment	25 (18.66)	9 (6.71)

with a fixed effects model that estimates the average effect (weighted by inverse variance), and assumes there is a single, true underlying effect per study (Borenstein *et al.* 2009). The effect sizes and associated variances were computed (from 999 iterations) and pooled using METAWIN v2.1 software (Rosenberg, Adams & Gurevitch 2000). We also computed the frequencies of three types of reaction norms (POS POS, POS NEG, and NEG NEG). The pooled effect sizes (and their associated pooled variances) and frequencies of reaction norm patterns were used in the analyses described below.

ANALYSIS

We first performed a general meta analysis using a random effects model to test whether the plants, overall, exhibited local adaptation (indicated by an overall mean effect size significantly greater than zero) regardless of their invasive status. Then to test whether plant invasive status (invasive or native) was associated with the magnitude of local adaptation, we constructed mixed effects multivariate models that assume that differences among studies are not only due to sampling error but also due to true random variation, as is the rule for ecological data (Gurevitch & Hedges 2001). Plant life history traits (i.e. reproductive system, breeding system and longevity) have divergent effects on population genetic structure, and could thereby influence the magnitude and frequency of local adaptation in plants (Barrett, Colautti & Eckert 2008; Leimu & Fischer 2008; Hereford 2010). In addition, experimental condition (i.e. field vs. controlled environment in the greenhouse or growth chamber) may significantly influence the effect size of experimental intervention (Verdú & Traveset 2005). Therefore, we included plant life history traits and experimental condition (established from published literature) as additional moderator variables in the multivariate models. In each model, study was specified as a random factor. Addition of phylogenetic information can have a significant impact on the effect size estimates from meta analysis models (Chamberlain *et al.* 2012). Therefore, we controlled for possible non independence of effect sizes from species with shared evolutionary history by performing a phylogenetically controlled meta analysis. Briefly, we first constructed a super tree using the online tool (<http://www.phylodiversity.net/phyloomatic>), and additional published phylogenies (Bayer & Starr 1998; Bailey *et al.* 2006; Strauss, Webb & Salamin 2006; Beilstein *et al.* 2008) were used to resolve polytomies (see Fig. S1 for phylogenetic relationships among the species). This tree was then imported into the APE package v3.1.1 (Paradis, Claude & Strimmer 2004) in Newick format, and a correlation matrix was obtained using the *vcv* function. This correlation matrix was then incorporated into the multivariate meta analysis models as an additional random factor.

We used likelihood ratio tests to determine the significance of association of the moderator variables (plant invasive status, plant life history traits and experimental condition) and the magnitude of local adaptation by comparing a full model containing all the moderators with a reduced model where a moderator of interest was removed. A similar analytical procedure was used to test whether invasive and native plants differed in the magnitudes of local adaptation across alternative forms of plant life history traits (reproductive system: clonal vs. non clonal, breeding system: self compatible vs. self incompatible and longevity: annual vs. perennial) and different growth environments (field vs. controlled environment). In the latter test, significance of plant invasive status was tested by comparing a model with plant invasive status (full model) with a model containing only the intercept (null model). In each model, pooled effect size per study and the associated pooled variance were specified as dependent

variables. The models were run using the `rma.mv` function in `METAFOR` package v1.9.5 (Viechtbauer 2012).

To test whether the frequency of local adaptation (POS POS), partial local adaptation (POS NEG) and maladaptation (NEG NEG) was significantly associated with plant invasive status, plant life history traits and the growth environment, we ran Bayesian analyses by fitting generalized linear mixed models using Markov chain Monte Carlo (MCMC) techniques with the help of the `MCMCGLMM` package for R (Hadfield 2010). `MCMCGLMM` uses a Markov chain Monte Carlo (MCMC) estimation approach, and accounts for non independence among closely related species by including the phylogenetic relationships among species as a random variable. In our models, the dependent variable (i.e. the frequency of POS POS, POS NEG or NEG NEG) had a binomial error distribution (specified as 'multinomial2' in the family argument) (Hadfield 2010). We ran 1.5×10^6 MCMC iterations, with a burn in period of 500 000 iterations and convergence of the chain tested by means of an autocorrelation statistic. The default priors ($\nu = 0, V = 1$) were used. The effect of moderators (plant invasive status, life history traits and growth environment) was estimated by calculating the 95% credible interval of their posterior distribution and computing the probability that such effect is larger than zero (PMCMC). The proportion of remaining variance explained by a random factor (study) was estimated by calculating the 95% credible interval of its posterior distribution.

For non native plant species, residence time (i.e. time since introduction to a new range) may be an important determinant of the capacity to evolve local adaptation; the longer a species is present in a region, the greater the probability of the species forming large population sizes and high genetic variation necessary for evolution of adaptation to novel ecological conditions (Dietz & Edwards 2006). Hence, using a subset of data containing only invasive plant species, we performed a simple linear regression to test whether the magnitude of local adaptation was positively correlated with the species residence time in the exotic range. We estimated residence time by subtracting the year of first record in the region of study from the year of seed collection (both were extracted from the same sources as the primary data used in the analyses). As a species might have been introduced to a region before the first record has been made, our estimate of residence time is the minimum residence time (e.g. Rejmánek 2000).

In many ecological studies, there can be a bias against publishing negative results (Rosenthal 1979). Thus, we used Rosenberg's fail safe number and a funnel plot to test for a possibility of publication bias affecting the present meta data set. Rosenberg's fail safe number is the number of non significant, unpublished and/or missing studies that would need to be added to a meta data set to change the results of the meta analysis from significant to non significant (Rosenberg, Adams & Gurevitch 2000). A fail safe number needs to be at least $5n + 10$ for results of a meta analysis to be treated as a reliable estimate of the true effects (Rosenthal 1979). For our case, the computed fail safe values had to be larger than a threshold value of 885 (i.e. $5N + 10 = 845$, where N = number of pooled effect sizes in our data set (i.e. $n = 167$) in order for the results to be robust. A funnel plot graphs effect sizes against standard errors, and assumes that studies with the largest sample sizes will have lower standard error, and hence will be near the average effect size, while studies with smaller sample sizes will be spread on both sides of the average effect size (Koricheva, Gurevitch & Mengersen 2013). Variation from this assumption can indicate publication bias (Koricheva, Gurevitch & Mengersen 2013). Positive asymmetry in a funnel plot is typically taken to mean publication bias, in that those studies with positive

effects are published with a greater frequency than those studies with negative effects (Koricheva, Gurevitch & Mengersen 2013). All statistical analyses were performed with R version 3.1.3 (R Development Core Team 2013).

Results

Overall, the meta analysis revealed a general pattern of local adaptation (mean Hedges' $d = 0.133, P < 0.0001$). Across all studies, local plants performed better than conspecific foreign plants at both sites of a pairwise reciprocal transplant in 28% of the cases, while local plants outperformed foreign plants at only one of the two sites of reciprocal transplants (i.e. partial local adaptation) in 52% of the cases. Local plants were outperformed by native plants at both sites of a pairwise reciprocal transplant (i.e. maladaptation) in 20% of the cases. The magnitude (Table 2; Fig. 1) and frequency (Table 3; Fig. 2) of local adaptation were not significantly associated with plant invasive status, plant life history traits or growth environment. The extent of local adaptation at both sites of reciprocal transplant (POS POS) in invasive and native plants was 36% and 24% respectively (Fig. 2a). The extent of partial local adaptation (POS NEG) in invasive and native plants was 45% and 55% respectively (Fig. 2a). Maladaptation (NEG NEG) was detected in 19% and 21% of studies on invasive and native plants respectively (Fig. 2a).

Invasive and native plant species exhibited similar magnitudes of local adaptation across alternative forms of plant life history traits, and when grown in the field or controlled environment (Table 4; Fig. 3). However, self incompatible invasive plants exhibited significantly higher frequencies of local adaptation than native plants characterized by the same breeding system (Table 5; Fig. 4d). Nevertheless, the frequency of local adaptation in invasive and native plants was not significantly associated with reproductive system, life cycle or growth environment (Table 5; Fig. 4). Minimum residence time of invasive plants in their exotic ranges was not significantly associated with the magnitude of local adaptation (Fig. 5). There was no evidence for a publication bias as the computed Rosenberg's weighted fail safe value of 2115 exceeds the minimum threshold value of 845 (also see symmetrical funnel plot presented in Fig. S2). Therefore, the present results are robust estimates of the true local adaptation in the wild populations of invasive and native plant species.

Discussion

Invasive plant species are expected to be less likely than native plants to evolve local adaptation due to the conventional view that adaptations evolve slowly and introduced populations are genetically depauperate as a consequence of founder effects. Contrary to the expectation, results of the present meta analysis show that invasive plant species evolve local adaptation within their exotic ranges just as frequently (or more frequently), and at least as strongly as native plant species. Furthermore, the present results show that minimum

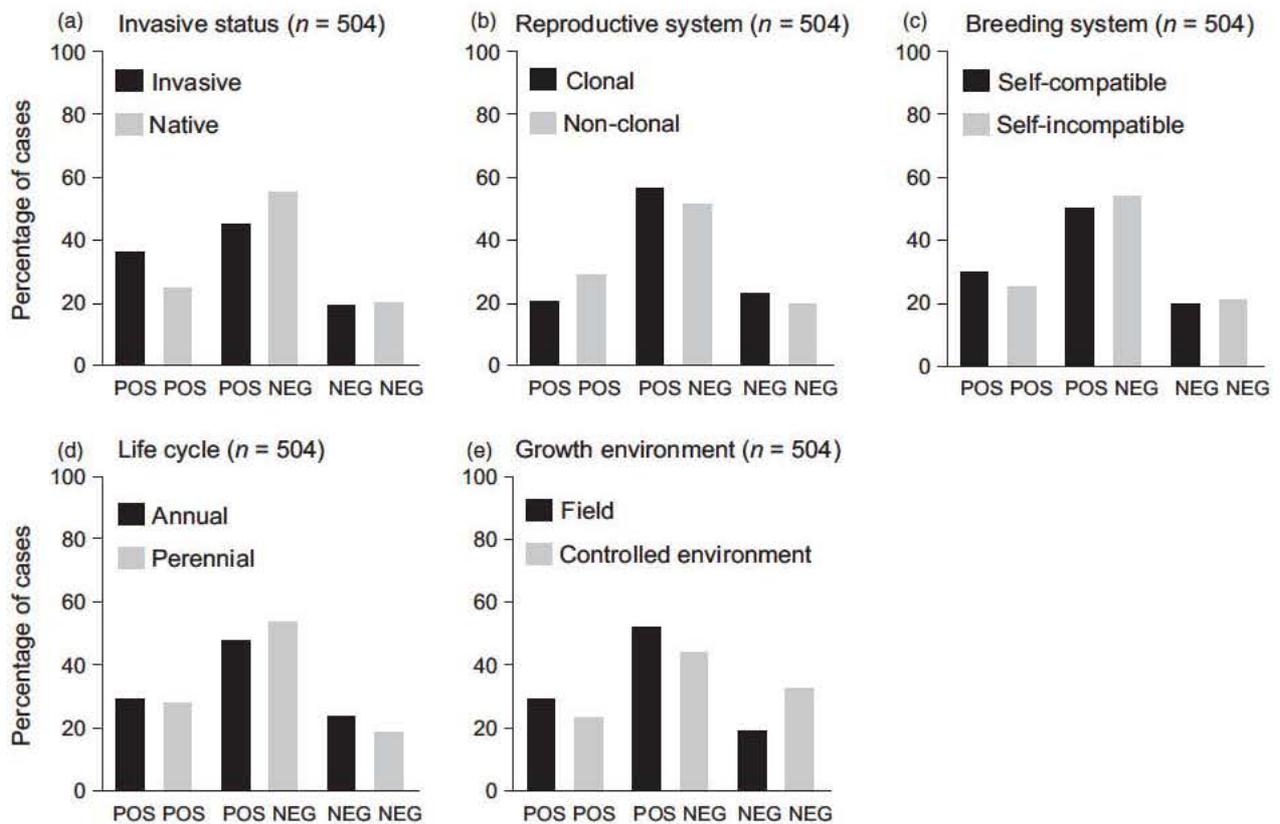


Fig. 2. The percentage of cases of local adaptation at: (i) both sites of reciprocal transplants (POS POS), (ii) only one of two sites of reciprocal transplants (POS NEG), and maladaptation at both sites of reciprocal transplants (NEG NEG) in plants categorized according to: (a) invasive status, (b) reproductive system, (c) breeding system, (d) life cycle and (e) growth environment. The number of cases for each moderator category is given in parentheses.

inbreeding depression (Lande 1988; Frankham 2005). Second, in small populations, loss of genetic variability due to random genetic drift and exposure of accumulated deleterious alleles as a result of inbreeding can diminish the capacity to evolve adaptations (Leimu *et al.* 2006; Willi, van Buskirk & Hoffmann 2006; Bijlsma & Loeschke 2012). Invasive plant species have been shown to have higher population growth rates than native plant species (Ramula *et al.* 2008). Hence, it is likely that the residence times reported here (ranging from 20 to 500 years) were sufficient for the invasive plant species to overcome founder effects through rapid demographic expansions that limited the loss of adaptive alleles by random genetic drift.

Invasive plant species may also overcome genetic constraints to adaptive evolution through multiple introductions (i.e. introductions of diverse genetic lineages from different source populations in the native range) (Ellstrand & Schierenbeck 2000; Lavergne & Molofsky 2007; Roman & Darling 2007; Dlugosch & Parker 2008; Verhoeven *et al.* 2011) or even a single introduction event from a native range source population having high genetic variation (Novak & Mack 1993; Kolbe *et al.* 2004; Uller & Leimu 2011). Multiple introductions can create invasive range populations that are much more genetically diverse than any single source population in the native range of the same plants (Ellstrand & Schierenbeck 2000; Durka *et al.* 2005; Roman & Darling

2007; Dlugosch & Parker 2008; Verhoeven *et al.* 2011; Oduor *et al.* 2015). This can occur through two processes: (i) an increase in the standing levels of quantitative genetic variation through admixing of different populations from the native range (Roman & Darling 2007; van Kleunen, Röckle & Stift 2015; Oduor *et al.* 2015) and (ii) creation of novel genotypes as a result of recombination between diverse genotypes introduced from distinct source populations (Ellstrand & Schierenbeck 2000). In fact, some of the invasive species included in the current meta analysis (e.g. *Bromus tectorum*, *Ambrosia artemisiifolia* and *Phalaris arundinacea*) have been shown to have undergone multiple introductions, and consequently have higher genetic diversity in their invasive range populations relative to conspecific populations from the native range (Novak & Mack 1993; Genton, Shykoff & Giraud 2005; Lavergne & Molofsky 2007). Therefore, local adaptation in invasive plants could also be facilitated by multiple introduction events.

At present, the long held view that founder effects may limit capacity of invasive plants to rapidly evolve adaptations to novel environments has only weak empirical support. Existing empirical evidence based on neutral molecular markers indicates that diversity is only marginally reduced in invasive range populations relative to conspecific native range populations, with an average within population reduction of about 10–20% in both average heterozygosity and allelic

Table 4. Results of Likelihood ratio model comparisons of mixed effects multivariate models to test for differences between invasive and native plants in the magnitude of local adaptation across alternative forms of plant life history traits (reproductive system: clonal vs. non clonal, breeding system: self compatible vs. self incompatible, and life cycle: annual vs. perennial) and different growth environments (field vs. controlled environment)

Moderator	χ^2 (d.f. 1)	<i>P</i>	<i>n</i>
Reproductive system			
Clonal	0.009	0.921	17
Non clonal	0.068	0.794	150
Breeding system			
Self compatible	0.003	0.954	116
Self incompatible	0.008	0.931	51
Life cycle			
Annual	0.022	0.882	62
Perennial	0.006	0.940	105
Growth environment			
Field	0.45	0.504	126
Growth chamber	1.16	0.281	41

Significance of plant invasive status (invasive or native) was tested by comparing a model containing the invasive status as a moderator with a null model containing the intercept only. The χ^2 and corresponding *P* value test for a difference between invasive and native plants. Phylogenetic relatedness among the species was controlled for by including variance covariance matrix of species relatedness in each model as random effects factors. Study was specified as a random factor in each model. The number of pooled effect sizes used in the analysis is indicated by *n*.

richness (Dlugosch & Parker 2008). Even so, the relevance of variation in neutral molecular markers for determining the potential of introduced populations to adapt to novel environments has been persistently questioned (Roman & Darling

2007). Neutral molecular markers likely underestimate variation in fitness related traits that is acted upon by natural selection (Barrett & Richardson 1986; Reed & Frankham 2001; McKay & Latta 2002). This might be because the markers are more sensitive to founder effects than fitness related traits (Lande 1988; Novak & Mack 2005). A rigorous prediction for adaptation to emerge among invasive plant species requires empirical data on within population variation in fitness related traits of introduced populations. However, such data are currently lacking (Colautti & Lau 2015), but this could be an important avenue of future research.

The present finding that local adaptation is a frequent phenomenon in natural populations of both invasive and native plants, although not ubiquitous implies that plant species persistence in different habitats may be explained by additional mechanisms other than local adaptation. Besides local adaptation, phenotypic plasticity is the other major mechanism that has been proposed to explain the ability of plants to inhabit a broad range of environmental conditions (Baker 1965; van Kleunen & Fischer 2005; Richards *et al.* 2010). These two mechanisms, both are paths to maximize fitness in response to environmental heterogeneity and are not mutually exclusive (Nicotra *et al.* 2010; Yampolsky, Schaer & Ebert 2014). Some populations may respond through plasticity, others through evolution and others through some combination of the two (Franks, Weber & Aitken 2014). At present, however, the role of phenotypic plasticity in persistence of invasive plants in novel environments remains unclear as comparisons of plasticity in invasive vs. non invasive alien and native plants are often inconsistent. Davidson, Jennions & Nicotra (2011) found that invasive species showed higher plasticity than non invasive congeners, while Palacio López & Gianoli

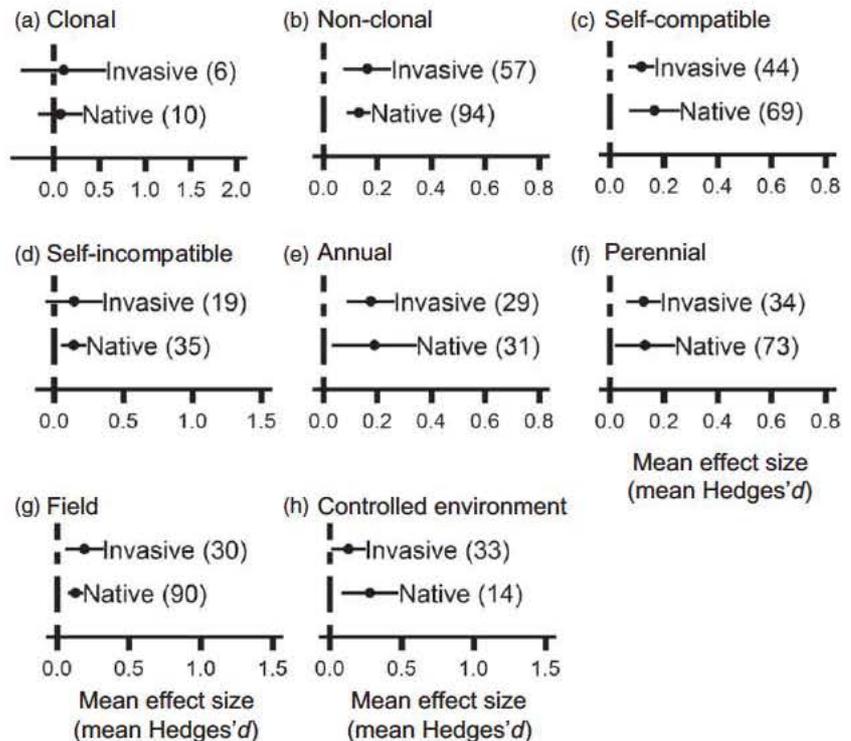


Fig. 3. The magnitude of local adaptation (indicated by mean effect sizes with their 95% confidence intervals) in invasive and native plant species across alternative forms of life history traits (a & b: reproductive system: clonal vs. non clonal; c & d: breeding system: self compatible vs. self incompatible; e & f: life cycle: annual vs. perennial) and g & h: different growth environments (field vs. controlled environment). The number of effect sizes for each moderator category is given in parentheses.

Table 5. Results of memglm testing for a difference between invasive and native plant species in the frequencies of local adaptation at both sites of reciprocal transplants (POS-POS), only one of two sites of reciprocal transplants (POS-NEG), and maladaptation at both sites of reciprocal transplants (NEG-NEG) in respect of alternative forms of plant life-history traits (reproductive system: clonal vs non-clonal; breeding system: self-compatible vs self-incompatible; life cycle: annual vs perennial) and growth environment (field vs controlled environment) Phylogenetic relatedness among the species was controlled for by including variance-covariance matrix of species relatedness in each model as random-effects factors. Study was treated as a random factor. PMCMC tests for a difference between invasive and native plants. A significant factor is marked in bold font

Moderator	POS-POS					NEG-NEG						
	Posterior mean	1-95% CI	u-95% CI	PMCMC	Posterior mean	1-95% CI	u-95% CI	PMCMC	Posterior mean	1-95% CI	u-95% CI	PMCMC
Clonal	-256.30	-1196.30	367.10	0.378	-19.42	-325.01	246.58	0.822	359.66	-339.79	1247.13	0.274
Non-clonal	-15.81	-93.89	61.29	0.624	24.00	-28.45	90.30	0.364	-24.89	-129.50	58.12	0.558
Self-compatible	10.08	-92.43	108.62	0.836	6.90	-67.81	78.56	0.822	-30.36	-170.05	79.88	0.588
Self-incompatible	-147.54	-313.95	9.50	0.036	63.93	-16.38	187.88	0.168	31.01	-121.02	187.45	0.658
Annual	-2.13	-165.50	147.62	0.956	-19.13	-143.01	99.43	0.710	22.92	-124.18	218.81	0.760
Perennial	-45.15	-156.16	56.02	0.326	46.43	-10.90	118.73	0.108	-17.22	-129.27	93.88	0.714
Field	-74.94	-177.68	12.79	0.086	23.43	-44.95	95.05	0.450	39.46	-53.71	146.28	0.334
Controlled environment	328.93	-136.26	966.43	0.166	-97.24	-442.50	248.76	0.558	-223.99	-846.94	209.14	0.370

(2011) and Godoy, Valladares & Pilar (2011) did not find such a difference. Our current data set did not permit a rigorous comparison of invasive and native plants for differences in plastic response because the native and invasive species occurred at different sites. To assess whether a high plasticity is a pre adaptation promoting invasiveness, one would ideally compare plasticities between invasive and non invasive alien species in their native range. van Kleunen *et al.* (2011) compared shade responses between invasive and non invasive alien species in their native European range, and did not find any differences. However, there are still too few such studies to draw general conclusions on the importance of plasticity as a pre adaptation for invasion.

In addition to influencing ecological niche breadth of invasive plants, local adaptation evolving in an invading species could also influence its ecological impact on native communities (e.g. community diversity) and ecosystem processes (e.g. nutrient cycling). However, the extent to which adaptive evolution can influence ecological dynamics in invaded ecosystems remains poorly understood. The available data did not allow us to show causality between occurrence of local adaptation in invasive plant species and their ecological impacts. Of the 47 invasive plant species used to assess occurrence of local adaptation, information on ecological impacts was available for only seven. But even for each of these seven species, local adaptation and ecological impacts had been assessed using different sets of populations. To directly link occurrence of local adaptation in invasive plant species to ecological impacts of the species, experiments are needed that use the same set of invasive populations to simultaneously assess occurrence of local adaptation and ecological impacts on native communities and ecosystem processes.

As most reciprocal transplant studies use seeds that were collected directly in the respective field sites, without one intermittent common garden generation, the observed local adaptation could also have been achieved by transgenerational inheritance mechanisms other than genetic inheritance. For example, differences in maternal seed provisioning can affect the performance of the offspring (Roach & Wulff 1987). Moreover, there is increasing evidence that epigenetic mechanisms, such as DNA methylation, may play a role in the inheritance of traits, and that such processes may be adaptive (Bossdorf, Richards & Pigliucci 2008; Richards, Bossdorf & Pigliucci 2010; Richards, Verhoeven & Bossdorf 2012). For example, it was recently shown that methylation mediated regulation of cold tolerance played a role in the northward spread of the invasive plant *Ageratina adenophora* in China (Xie *et al.* 2015). Although the role of epigenetic mechanisms in local adaptation is still speculative, future studies on local adaptation, both in invasive and in native plants, could seek to separate between the genetic and non genetic processes that underlie local adaptation.

The present finding that the magnitude and frequency of local adaptation were not associated with growth environment suggests that experimental condition (i.e. field vs. controlled environment in the greenhouse or growth chamber) may not influence detection of local adaptation (or lack thereof) in

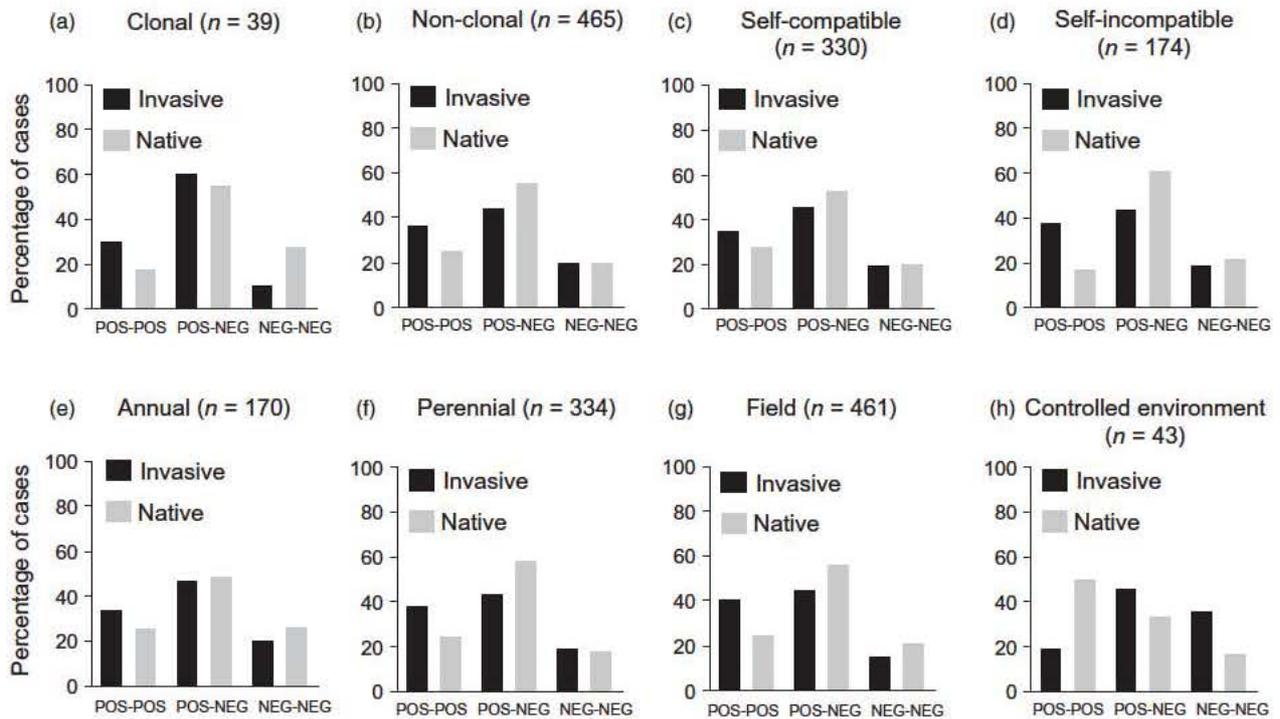


Fig. 4. The percentage of cases of local adaptation at: (i) both sites of reciprocal transplants (POS POS), (ii) only one of two sites of reciprocal transplants (POS NEG), and maladaptation at both sites of reciprocal transplants (NEG NEG) in invasive (black bars) and native (grey bars) plant species across alternative forms of plant life history traits (a & b: reproductive system: clonal vs. non clonal; c & d: breeding system: self compatible vs. self incompatible; e & f: life cycle: annual vs. perennial) and g & h: different growth environments (field vs. controlled environment). The number of cases for each moderator category is given in parentheses.

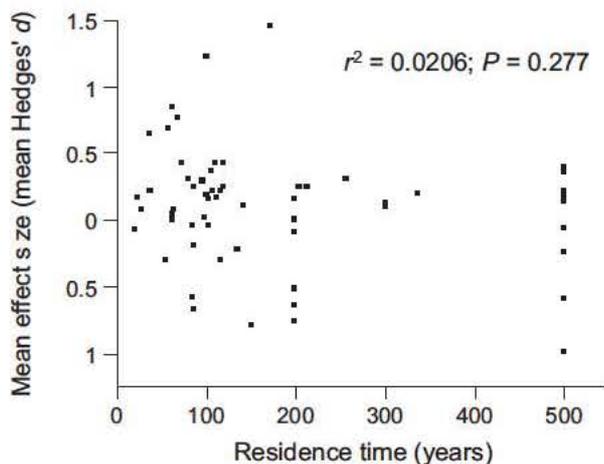


Fig. 5. Correlations between the magnitude of local adaptation and minimum residence time (i.e. time since first record) for 47 exotic invasive plant species. A positive mean Hedges' d value indicates local adaptation while a negative value indicates maladaptation.

plants. Controlled environmental conditions are often favourable to plant growth, with no nutrient or water limitation (Verdú & Traveset 2005). Under natural growth conditions in the field, in contrast, strong fluctuations in the biotic and abiotic factors may strongly influence early plant growth and development. In our data base, however, no single study compared the same set of invasive and native plant species for differences in the expression of local adaptation under field

vs. controlled environmental conditions. Future studies seeking to elucidate the relative significance of field vs. controlled environment in influencing detection of local adaptation (or lack thereof) in invasive vs. native plants should use the same set of invasive and native plants under both field and controlled environmental conditions.

In plants, the alternative forms of life history traits may have divergent effects on genetic variation within populations, and this may in turn influence occurrence of local adaptation in plant populations (Linhart & Grant 1996; Kawecki & Ebert 2004; Leimu & Fischer 2008). For instance, clonal or self compatible reproduction strategies may limit gene flow between populations, hence preserving locally adapted genotypes (Leimu & Fischer 2008). On the other hand, self incompatibility may enhance evolution of local adaptation through an increase in genetic variation within populations (Leimu & Fischer 2008; Hereford 2010). As a short generation time may increase the opportunities for establishment of new genotypes within existing populations, populations of annual plant species may evolve local adaptation much faster than populations of perennial plant species (Linhart & Grant 1996; Jump & Penue las 2005; Hereford 2009). In the present study, however, only self incompatibility was significantly associated with occurrence of local adaptation (Fig. 4d). A previous review of the literature found no correlation between mating system and local adaptation (Hereford 2010). Overall, existing empirical data offer little (or no) support for the idea that occurrence of local adaptation may be associated with plant life history traits.

Many studies seeking to understand the general strategies and traits associated with plant invasion success have often focused on drawing contrasts between invasive alien plant species, non invasive alien plant species and native plant species on the basis of various attributes including: (i) life history traits (reproductive system, breeding system and longevity), (ii) vital rates (survival, growth, and fecundity), (iii) defence related traits, (iv) population growth rates and (v) rates of dispersal (Ramula *et al.* 2008; van Kleunen, Weber & Fischer 2010; van Kleunen *et al.* 2010). However, the current paucity of empirical data on local adaptation in non invasive alien plants (non invasive alien species have no or only few established populations, which makes it difficult to study local adaptation in non invasive alien plants) precludes a rigorous quantitative comparison of occurrence of local adaptation in invasive alien plants vs. non invasive alien plants vs. native plants. Therefore, more experimental tests of local adaptation in alien plants varying in their degree of invasion may help elucidate further the significance of local adaptation as an explanation for the invasion success of alien plant species.

One criticism of the reciprocal transplant approach to the study of local adaptation among introduced populations is that it does not distinguish between the influence of contemporary natural selection vs. stochastic forces (i.e. introduction of pre adapted genotypes from locations in the native range with similar local environmental conditions to those in the introduced range) in shaping population differentiation and local adaptation (Colautti & Lau 2015). At present, however, no study has used molecular markers to trace the native range origins of locally adapted invasive populations. Even so, Colautti & Lau (2015) suggest that at least four unlikely conditions must be met to establish that local adaptation detected among introduced populations occurred through introductions of pre adapted genotypes. Hence, they suggest that local adaptation detected in invasive range populations is most likely the outcome of contemporary natural selection (as opposed to introduction of pre adapted genotypes).

We are likely to make a more robust inference of the role of adaptive evolution or phenotypic plasticity in invasiveness of alien plants by finding consistent differences between invasive range and conspecific native range populations in the occurrence of these processes (Hierro, Maron & Callaway 2005; Colautti, Maron & Barrett 2009). However, the current lack of biogeographical studies that investigate local adaptation or phenotypic plasticity in invasive range vs. conspecific native range populations precludes such an inference, but it is a ripe area for future research.

In conclusion, the present finding that invasive and native plant species did not differ consistently in the extent and frequency of local adaptation challenges the long held views that invasive plant species are less likely than native plant species to evolve local adaptation due to founder effects and the glacially slow process of adaptive evolution. Our results further more support the suggestion that post introduction rapid adaptive evolution may enable invasive plant species to persist and expand their ecological niche breadth in the introduced ranges (García Ramos & Rodríguez 2002; Lee 2002;

Parker, Rodriguez & Loik 2003). Future studies should address the underlying mechanisms and the contribution of local adaptation to the degree of invasiveness.

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Supporting Information

Figure S1. Phylogeny used to conduct phylogenetically independent meta analysis.

Figure S2. Funnel plot (publication bias assessment) showing the relationship between effect size (Hedges' *d*) and standard error.