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Preadapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range?

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ABSTRACT

Aim Species capable of vigorous growth under a wide range of environmental conditions should have a higher chance of becoming invasive after introduction into new regions. High performance across environments can be achieved either by constitutively expressed traits that allow for high resource uptake under different environmental conditions or by adaptive plasticity of traits. Here we test whether invasive and non-invasive species differ in presumably adaptive plasticity.

Location Europe (for native species); the rest of the world and North America in particular (for alien species).

Methods We selected 14 congeneric pairs of European herbaceous species that have all been introduced elsewhere. One species of each pair is highly invasive elsewhere in the world, particularly so in North America, whereas the other species has not become invasive or has spread only to a limited degree. We grew native plant material of the 28 species under shaded and non-shaded conditions in a common garden experiment, and measured biomass production and morphological traits that are frequently related to shade tolerance and avoidance.

Results Invasive species had higher shoot–root ratios, tended to have longer leaf-blades, and produced more biomass than congeneric non-invasive species both under shaded and non-shaded conditions. Plants responded to shading by increasing shoot–root ratios and specific leaf area. Surprisingly, these shade-induced responses, which are widely considered to be adaptive, did not differ between invasive and non-invasive species.

Main conclusions We conclude that high biomass production across different light environments pre-adapts species to become invasive, and that this is not mediated by plasticities of the morphological traits that we measured.

Keywords

Biological invasions, common garden experiment, comparative study, invasive plants, phenotypic plasticity, shade avoidance, shade treatment, tolerance.

INTRODUCTION

The number of species that have been accidentally or intentionally introduced into new regions is enormous, and is still steadily increasing (Hulme *et al.*, 2008). Although only a small proportion of these species establishes naturalized populations, and only a few of these spread in the landscape (i.e. become invasive *sensu* Richardson *et al.*, 2000), they may cause considerable ecological (Vitousek *et al.*, 1997; Ricciardi, 2007) and economical (Pimentel *et al.*, 2005) damage, and decrease phylogenetic uniqueness of regional floras (Winter *et al.*, 2009). Therefore, it is paramount to advance our mechanistic understanding of why some introduced alien species become invasive and others do not (van Kleunen &

Richardson, 2007; Moles *et al.*, 2008; Catford *et al.*, 2009). Clearly, to answer this question, one should compare species with different degrees of invasiveness (Rejmánek, 2000; Muth & Pigliucci, 2006; van Kleunen *et al.*, 2010a).

Based on theory, one would expect that species capable of vigorous growth under a wide range of environmental conditions should be pre-adapted to becoming invasive after introduction into new regions (Baker, 1974; Richards *et al.*, 2006; Theoharides & Dukes, 2007; Hulme, 2008). This is in line with the frequent finding that species with a large geographical or climatic native range – possibly reflecting a large niche breadth – are more likely to be invasive elsewhere (Scott & Panetta, 1993; Goodwin *et al.*, 1999; Prinzing *et al.*, 2002; van Kleunen *et al.*, 2007; Bucharova & van Kleunen, 2009; Pyšek *et al.*, 2009). Moreover, the few experimental studies comparing invasive and non-invasive alien species grown in multiple environments suggest that invasive species are more capable of maintaining high fitness in stressful environments (Muth & Pigliucci, 2007), that invasive species are more capable of taking advantage of benign environments (Burns & Winn, 2006), or both (Sultan, 2001; Richards *et al.*, 2006; Schlaepfer *et al.*, 2010). Thus, although the performance responses are variable, averaged across environments, invasive species appear to perform better than non-invasive ones. However, it is not clear whether this is a general pattern or how such a high performance under different environmental conditions is achieved.

It is implicitly assumed that high performance across different environments is brought about by high phenotypic plasticity of physiological and morphological traits (Baker, 1974; Richards *et al.*, 2006). This should, however, only hold for plastic responses that are adaptive (i.e. increase fitness; Burns & Winn, 2006; Muth & Pigliucci, 2007; Funk, 2008). In contrast, non-adaptive plastic responses should not increase the range of environmental conditions under which a species can outperform others, and might even decrease it when the plastic responses are maladaptive (van Kleunen & Fischer, 2005; Ghalambor *et al.*, 2007). Therefore, it is very important to distinguish between adaptive and non-adaptive plasticity.

For most plastic responses of traits to environmental variation, we still do not know if they are adaptive (van Kleunen & Fischer, 2005). There is, however, wide consensus that plastic responses associated with shade avoidance and tolerance, such as increases in leaf length, specific leaf area and biomass allocation to aboveground parts (i.e. increases in shoot–root ratio) in response to shading constitute adaptive phenotypic plasticity (Dudley & Schmitt, 1996; Schmitt *et al.*, 1999; van Kleunen & Fischer, 2005; Valladares & Niinemets, 2008). Introduced alien plants usually first establish in disturbed habitats, where shading may initially be minimal but increases rapidly over time when more plants establish. Moreover, once alien plants start to spread into (semi-)natural vegetation, they may also experience considerable shading from resident plants. Shade-induced responses could then be particularly beneficial to tolerate the shade or to avoid competition for light, and are thus likely to assist alien species during invasion. Moreover, such plastic responses could assist plants in overtopping neighbours, and consequently reduce their growth through asymmetric competition for light (Weiner & Thomas, 1986; Damgaard & Weiner, 2008). Alternatively, it could be that high performance under different light intensities is provided by certain characteristics (such as high shoot–root ratio) that generally allow for high light interception rather than by plasticity in these traits.

Daehler (2003) reviewed studies that compared phenotypic plasticity between co-occurring invasive alien and native plant species. Most of these studies, and also later ones (e.g. Funk, 2008; Raizada *et al.*, 2009), concluded that invasive species are more plastic than native species. However, it is not always clear whether the plastic responses in these studies actually represent adaptive phenotypic plasticity (but see Funk, 2008 for an exception), and to what extent studies controlled for potential confounding of genotypic effects with environmental effects (i.e. whether they used the same genetic material in each environment; Stearns, 1992). There is some evidence indicating that invasive species have stronger shade-induced responses and take more advantage of high light conditions than do co-occurring native species (Luken *et al.*, 1997; Pattison *et al.*, 1998; Brock *et al.*, 2005). While such invasive alien versus native comparisons might reveal why some invasive species have an advantage over native species, they do not reveal why some alien species become invasive and others do not (Hamilton *et al.*, 2005). This can only be assessed by comparing invasive and non-invasive alien species (Muth & Pigliucci, 2006; van Kleunen *et al.*, 2010a). Such studies are still rare, and mostly restricted to a few species (Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010b), which makes it hard to generalize the results.

The studies that have compared invasive and non-invasive alien species were usually performed in the non-native range of the species with non-native plant material (Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010b) or with a mixture of native and non-native material (Muth & Pigliucci, 2006, 2007). As a consequence, these studies do not indicate whether invasive species possessed the traits that allowed them to invade already in their native range before introduction elsewhere (i.e. whether they were pre-adapted to become invasive) or whether they evolved invasiveness after introduction elsewhere (Schlaepfer *et al.*, 2010). To test specifically for pre-adaptation, studies should be performed with native plant material of a large number of species that differ in their degree of invasiveness elsewhere in the world (van Kleunen *et al.*, 2010a).

We grew 14 congeneric pairs of invasive and non-invasive herbaceous plant species with and without shading in a common garden experiment. All 28 herbaceous species are native to Europe and naturalized in North America, where one species of each pair is invasive while the other is not or is to a lesser degree. In a parallel study, we showed already that the invasive species produce consistently more biomass than the congeneric non-invasive species under different fertilization conditions (Schlaepfer *et al.*, 2010). Here we test whether this is also the case under different light conditions. Moreover, we test whether invasive and non-invasive species differ in, presumably adaptive, shade-induced plasticity of morphological traits. We asked the following specific questions: (1) Do invasive species produce more biomass than non-invasive species in their native range, and is this true under both shaded and non-shaded conditions? (2) Do invasive and non-invasive species differ in morphological traits relevant to light capture? (3) Do invasive species have stronger phenotypic plasticity of these morphological traits than non-invasive species in response to shading?

MATERIALS AND METHODS

Study species and seed collection

We used 14 congeneric pairs of invasive and non-invasive species representing ten families of terrestrial herbaceous plants (see Appendix S1 in the Supporting Information). All 28 species are native to Europe and naturalized in North America. In Europe, most of these species occur in relatively open habitats, such as along road sides and in grasslands. For each congeneric pair, we categorized the species that is most widely naturalized in North America as invasive and the least widely naturalized one as non-invasive. This means that within each congeneric pair, the invasive species occurs in many more US states and Canadian provinces than the non-invasive species (Appendix S1). In addition, most of the invasive species are listed as 'invaders of natural areas' and/or as 'noxious weeds' in North America, and have more references than the non-invasive species in the Global Compendium of Weeds (Randall, 2002) (Appendix S1). The latter indicates that our distinction between invasive and non-invasive species of European origin holds not only for North America but also at a global scale.

For 11 congeneric pairs, both species have the same life form (nine perennial pairs and two biennial pairs), for two pairs (*Dianthus* and *Geranium*) the invasive species is an annual or biennial while the non-invasive species is a perennial, and for one pair (*Campanula*) the reverse was true (Appendix S1). Species that are more widespread in North America were recorded earlier in North American herbaria (Appendix S1; regression of number of US states and Canadian provinces on year since first record: regression coefficient ± SE = 0.41 ± 0.06, $t_{26} = 6.62$, $P < 0.001$, $R^2 = 0.63$). This could suggest that invasive species were introduced earlier than non-invasive species. However, because invasive species are more likely to be collected than non-invasive species – even when they were introduced at the same time – year since first herbarium record might simply reflect invasiveness of the species. For example, based on herbarium records one might conclude that the invasive species *Plantago lanceolata*, *Trifolium repens* and *Verbascum thapsus* were introduced into North America in the late 1800s (Appendix S1), even though these species were already reported to be abundant and widespread in the eastern parts of North America at that time (Gray, 1879). Therefore, we think that it is very likely that invasive species were recorded earlier than non-invasive species because of their difference in invasiveness. Consequently, we did not consider year of first record in the analyses.

For 20 of the 28 species, we collected seeds from four to 16 plants (i.e. seed families) in each of one to three populations in Switzerland or France (i.e. in the native range). Populations were separated by at least 10 km. For the eight remaining species and for six of the species collected in natural populations, we ordered native seeds from two commercial seed suppliers (UFA Samen, BH Gärten & Bio-Suisse, Switzerland; Appendix S1). We cannot exclude the possibility that these seeds were not fully representative for some of the species. However, when comparing invasive and non-invasive species, it is more important that these two groups of species are represented by large numbers of species than that each single species is represented by large numbers of populations. In April 2008, we sowed 25 seeds per seed family or per seed lot provided by a seed supplier in *c.* 4-cm high 1.3-L trays filled with a sand : soil : peat mixture (2:2:1) in an uncontrolled greenhouse (46°55′16.31″ N, 7°30′08.53″ E, 550 m a.s.l., Muri near Bern, Switzerland).

Experimental set-up

In June 2008, we transplanted on average 41 seedlings per species (range = 3–99 due to variable germination success; totalling 1150 seedlings, Appendix S1) individually into 1.2-L pots filled with a sand : soil : peat mixture (2:2:1). Three weeks after transplantation, we moved the pots into the garden next to the greenhouse. We randomly assigned the plants to one of two light treatments. Plants in the shaded treatment were randomly partitioned over ten cages (i.e. subplots; length × width × height = 1.3 × 1.3 × 1.5 m) covered with a green shade cloth (Neeser AG, Reiden, Switzerland) reducing ambient photosynthetically active radiation by 60%, which is in the range of light reductions found in grasslands (Fick, 1972) and forests (Louda *et al.*, 1987). Plants in the non-shaded treatment (i.e. ambient light) were randomly partitioned over ten subplots, each paired to one of the ten shade cages. Thus, we had ten pairs (blocks) of shaded and non-shaded subplots. To avoid confounding effects of light treatments and genetic differences, we randomly assigned plants of each seed family and population or of each seed supplier to each treatment level (i.e. we tried to have the same genetic material represented in each light treatment). We randomized the positions of pots in each subplot (i.e. block-by-treatment combination) every four weeks throughout the experiment. For two of the 14 non-invasive species (*Geranium pratense* and *Trifolium medium*), we did not have plants in the shaded treatment due to low germination success.

Between the end of August and the beginning of November 2008, we harvested above- and belowground biomass of each plant. We harvested each species at the moment of its maximum biomass production. For species that flowered this was at their peak of flowering, and for the other species this was when their first leaves started to senesce. We dried the plant samples at 70 °C for at least 72 h, and weighed them to the nearest mg. At harvest, we also measured the length of the longest leaf blade on each plant. Furthermore, to determine specific leaf area, we measured the combined area of ≥ 10 randomly selected leaves per plant with a leaf-area meter (LI-3100C, LI-Cor Inc., Lincoln, NE, USA) to the nearest mm^2, and divided the area by the dry mass of these leaves. We calculated shoot–root ratio as the aboveground biomass divided by the belowground biomass. We did not measure lengths of leaf petioles or stem internodes, which usually show strong shade-induced responses, because many of the mainly rosette-forming species did not have these structures.

Statistical analyses

We analysed all data with linear mixed models, i.e. models including both fixed and random terms. Because the final data set was unbalanced, we used restricted maximum likelihood (REML) analysis of variance implemented in GENSTAT v. 12.1 (Payne *et al.*, 2008). The data included outliers that were outside the biologically possible range. This was probably because the leaf-area meter was not sensitive enough to measure small and thin leaves accurately, and because some soil sticking to the roots had gone unnoticed. Therefore, we report results based on analyses with all outliers excluded (64–164 of 1150 plants per trait), i.e. we excluded data points beyond a distance of 1.5 times the inter-quartile range (computed as Tukey's hinges) for each combination of variable and main factor (Tukey, 1977). We included light treatment (ambient light, shade), invasiveness status (invasive, non-invasive) and their interaction as fixed terms. Because fixed terms are sequentially fitted in REML analysis of variance, we ran two analyses with reciprocated order of both main factors, and report results for each factor from the analysis in which the other factor was fitted first. To account for possible variation due to different starting dates of the experiment (due to differences in time of germination), duration of the experiment and whether the plant flowered or not, we included these variables at the beginning of the fixed model (Payne *et al.*, 2008). A significant 'light treatment' effect would indicate that species showed on average a plastic response, and a significant 'light treatment × invasiveness status' interaction would indicate that invasive and non-invasive species differ in plasticity. In all tests, we considered an effect significant when $P < 0.05$.

We included block (i.e. pair of shaded and non-shaded subplots) and subplot nested within block as random factors. To account for the hierarchical taxonomic structure of our set of study species, we included plant family, genus nested within plant family, and species nested within genus, and the interactions of plant family, genus and species with light treatment as random terms. Because we did not have seed families for all species, and because for some seed families we had no replicates, we could not include 'seed family' in the model. Although nine of the 28 species in our experiment were represented by single populations, we also included population nested within species in the random model to account for variation within the species with multiple populations. Log transformations of leaf length and specific leaf area, and double-log transformations of total biomass and shoot–root ratio satisfied test assumptions (i.e. normality of residuals and homoscedasticity).

The level of significance of each fixed factor was determined with F-ratio tests and numerically estimated denominator degrees of freedom (Payne *et al.*, 2008). The level of significance of each random term was determined with chi-square tests for changes in deviance after dropping the term in question from the model (Littell *et al.*, 1996). For all analyses, we report the significance of both fixed and random terms of the complete statistical model in Tables 1 and 2, but because only the fixed terms 'light treatment', 'invasiveness' and 'light treatment × invasiveness' were of major biological interest, we focus on these in the results section.

To test whether invasive and non-invasive species differed in overall plasticity of all three morphological traits jointly, we did two further analyses. First, we did a multivariate REML analysis of shoot–root ratio, specific leaf area and leaf-blade length. Second, we tested for differences in plasticity using within-study meta-analysis (e.g. van Zandt, 2007). As effect size (i.e. index of plasticity) for each population or seed supplier of a species, we calculated log-

Table 1 Summary of restricted maximum likelihood (REML) analyses for total biomass of 14 pairs of invasive and non-invasive herbaceous congeners grown at low and high light intensities in a common garden experiment.

Effect	d.f., d.d.f.	F or χ^{2}*	P
Fixed terms			
Start of treatment	1, 206.4	25.73	**< 0.001**
Duration of treatment	1, 23.9	1.73	0.201
Flowering	1, 694.6	40.18	**< 0.001**
Light treatment	1, 11.5	7.60	**0.018**
Invasiveness	1, 11.3	11.46	**0.006**
Light × invasiveness	1, 7.1	0.00	0.971
Random terms			
Block	1	4.54	**0.033**
Subplot (block)	1	0.00	1.000
Family	1	910.55	**< 0.001**
Genus (family)	1	124.32	**< 0.001**
Species (genus)	1	158.33	**< 0.001**
Population (species)	1	10.11	**0.002**
Light × family	1	6.18	**0.013**
Light × genus (family)	1	12.31	**< 0.001**
Light × species (genus)	1	0.58	0.447
Residuals	975		

*Fixed effects were tested with numerical approximations of the F-statistic and denominator degrees of freedom (d.d.f.). Random effects were tested with deviance differences as χ^2-statistic and one degree of freedom (d.f.). Biomass was double-log transformed to satisfy test assumptions. Bold P-values indicate significance levels < 0.05.

Table 2 Summary of restricted maximum likelihood (REML) analyses for morphological traits of 14 pairs of invasive and non-invasive herbaceous congeners grown at low and high light intensities in a common garden experiment.

	Leaf-blade length			Specific leaf area			Shoot–root ratio		
Effect	d.f., d.d.f.	F or χ^{2*}	P	d.f., d.d.f.	F or χ^{2*}	P	d.f., d.d.f.	F or χ^{2*}	P
Fixed terms									
Start of treatment	1, 86.4	1.69	0.197	1, 105.0	3.69	0.057	1, 126.1	0.60	0.440
Duration of treatment	1, 26.3	5.00	**0.034**	1, 25.1	9.20	**0.006**	1, 42.2	13.55	**< 0.001**
Flowering†	–	–	–	–	–	–	1, 857.5	9.10	**0.003**
Light treatment	1, 24.5	1.51	0.230	1, 11.9	27.72	**< 0.001**	1, 17.6	6.62	**0.019**
Invasiveness	1, 12.8	4.67	0.050	1, 12.4	1.48	0.247	1, 17.8	4.66	**0.045**
Light × invasiveness	1, 21.9	0.31	0.583	1, 6.4	2.17	0.188	1, 18.1	0.25	0.620
Random terms									
Block	1	1.48	0.224	1	21.74	**< 0.001**	1	8.26	**0.004**
Subplot (block)	1	2.97	0.085	1	0.00	1.000	1	0.00	1.000
Family	1	1878.20	**< 0.001**	1	626.72	**< 0.001**	1	249.65	**< 0.001**
Genus (family)	1	66.78	**< 0.001**	1	100.76	**< 0.001**	1	137.24	**< 0.001**
Species (genus)	1	311.63	**< 0.001**	1	199.92	**< 0.001**	1	291.74	**< 0.001**
Population (species)	1	41.22	**< 0.001**	1	13.80	**< 0.001**	1	8.06	**0.005**
Light × family	1	0.16	0.687	1	9.76	**0.002**	1	0.67	0.411
Light × genus (family)	1	4.93	**0.026**	1	11.32	**< 0.001**	1	2.67	0.102
Light × species (genus)	1	11.20	**0.001**	1	0.00	0.992	1	3.82	0.051
Residuals	1070			1058			968		

*Fixed effects were tested with numerical approximations of the F-statistic and denominator degrees of freedom (d.d.f.). Random effects were tested with deviance differences as χ^2-statistic and one degree of freedom (d.f.). Shoot–root ratio was double-log transformed and specific leaf area and leaf-blade length were log transformed to satisfy test assumptions.

†The covariate 'flowering' was included in the analyses of shoot–root ratio. Bold P-values indicate significance levels < 0.05.

response ratios (ln R) from the trait means ($\bar{X}$) in each light treatment as

$$\ln R = \ln \frac{\bar{X}_{\text{Shaded}}}{\bar{X}_{\text{Ambient}}}$$

with variance

$$v_{\ln R} = \frac{(s_{\text{Shaded}})^2}{N_{\text{Shaded}}(\bar{X}_{\text{Shaded}})^2} + \frac{(s_{\text{Ambient}})^2}{N_{\text{Ambient}}(\bar{X}_{\text{Ambient}})^2}$$

using MetaWin v. 2 (Rosenberg *et al.*, 2000). Here s is the standard deviation and N is the sample size. Log-response ratios and variances of different populations were pooled for each species per trait. Then we pooled the log-response ratios and variances of the three traits per species. Pooling was done by separate meta-analyses on the subsets of data. Because for some species we did not have data for all three morphological traits, we only included the 11 species pairs with complete plasticity data in this analysis. The pooled mean effect size and the mean variance were used in the final data set.

We tested for differences in log-response ratios between invasive and non-invasive species with linear mixed models using REML implemented in the lme4 package (Bates & Maechler, 2010) of the statistical software R v. 2.11.0 (R Development Core Team, 2010). We controlled for taxonomy by including 'genus' as a random factor. To account for differences in variance among species, we weighted log-response ratios according to the inverse of their variances (Sheu & Suzuki, 2001). For each of the estimated effects of the factor 'invasiveness status', we calculated the 95% confidence interval (CI) from the distribution of effects based on 1000 Monte Carlo simulations implemented in the languageR package (Baayen, 2010).

RESULTS

Biomass production of invasive and non-invasive species

Overall, invasive species produced significantly more biomass than non-invasive species by the end of the growing season (Fig. 1, Table 1). Plants produced significantly more biomass under ambient light than when shaded (Fig. 1, Table 1), and this response to the light treatment did not differ significantly between invasive and non-invasive species (Fig. 1, Table 1). This indicates that invasive species had a higher performance than non-invasive species under both light conditions.

Morphological traits and shade-induced responses of invasive and non-invasive species

Invasive species and non-invasive species did not differ significantly in specific leaf area, but invasive species, on average, tended to have longer leaves and had a significantly higher shoot–root ratio than did non-invasive species (Fig. 2, Table 2). Averaged over all species, leaf-blade length was not significantly affected by shading, but both specific leaf area and shoot–root ratio increased significantly in response to shading

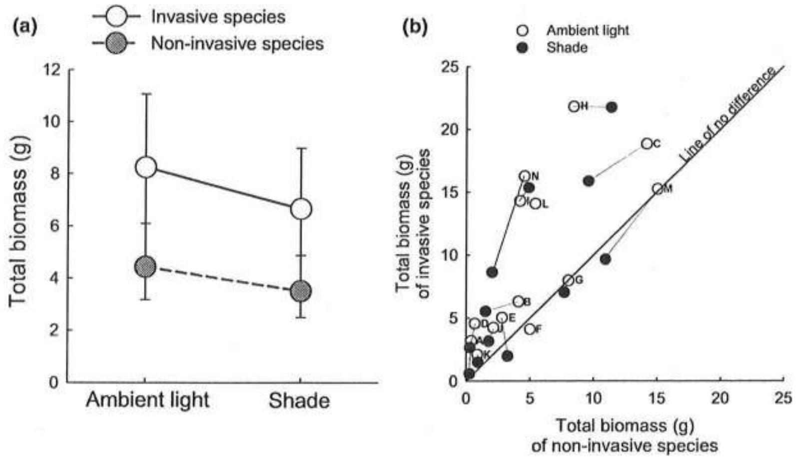

Figure 1 Biomass responses to shading of congeneric invasive and non-invasive herbaceous species. (a) Means and standard errors of total biomass of 14 invasive (open circles) and non-invasive (filled circles) species measured under ambient light and shade. Means and standard errors are back-transformed predicted means and standard errors from linear mixed models. Total biomass was double-log transformed prior to analysis. (b) Mean total biomass of congeneric invasive and non-invasive species grown under ambient light (open circles) and shade (filled circles). Means are back-transformed means of double-log transformed data. Open and filled circles connected by lines belong to the same congeneric species pairs. Points above the line show species-by-treatment combinations in which the biomass of the invasive species was greater than that of the non-invasive species. Slopes of lines connecting the treatments that are > 45 degrees show pairs where plasticity in biomass was greater for the invasive than for the non-invasive congener. The numbers on the right of the open symbols refer to the genus names of the species pairs: ^{A}*Campanula*, ^{B}*Centaurea*, ^{C}*Cirsium*, ^{D}*Dianthus*, ^{E}*Galium*, ^{F}*Geranium*, ^{G}*Lotus*, ^{H}*Malva*, ^{I}*Plantago*, ^{J}*Potentilla*, ^{K}*Silene*, ^{L}*Trifolium*, ^{M}*Verbascum*, ^{N}*Vicia*. Note that for two congeneric species pairs, we did not have plants of the non-invasive species in the shade environment.

(Fig. 2, Table 2). There were no significant interactions between invasiveness status and the light treatment for any of the morphological traits (Fig. 2, Table 2). In a multivariate REML analysis including all three morphological traits, the interaction between invasiveness status and the light treatment was also not significant ($F_{3,95.4} = 0.55$, $P = 0.650$). Similarly, overall shade-induced plasticity, measured as log-response ratios pooled over the three morphological traits, did not differ significantly between invasive and non-invasive species [estimate of 'invasiveness status' effect (95% CI) = 0.027 (−0.022 to 0.071); Fig. 3]. These results indicate that shade-induced plasticity in the measured traits was not different between invasive and non-invasive species.

DISCUSSION

Our experiment on 28 herbaceous species collected in their native European range showed that species that have become invasive in North America and elsewhere in the world produced more biomass, both under low and high light, than congeneric species that have not become invasive (or have become invasive to a lesser degree). While invasive species had on average a higher shoot–root ratio, and tended to have longer leaf-blades than non-invasive species, phenotypic plasticity of morphological traits in response to shading was not higher for invasive than for non-invasive species. This indicates that the high performance of invasive species across different light environments is not mediated by adaptive plasticity of morphological traits, at least not by the ones that we measured.

Biomass production of invasive and non-invasive species

It has frequently been suggested that species with the capacity to maintain high performance in stressful environments (jack-of-all-trades species *sensu* Richards *et al.*, 2006), species with the capacity to take advantage of benign environmental conditions (master-of-some species *sensu* Richards *et al.*, 2006), and particularly species capable of both (jack-and-master species *sensu* Richards *et al.*, 2006) should be more likely to become invasive than species that are not capable of high performance in multiple environments (Baker, 1974; Richards *et al.*, 2006; Theoharides & Dukes, 2007; Hulme, 2008). In line with this hypothesis, most invasive species in our study produced more biomass than non-invasive congeners both under low and high light (i.e. they are jack-of-all-trades species). There were a few pairs for which we did not find differences in biomass production between invasive and non-invasive species. These exceptions might partly reflect that some species categorized as non-invasive may actually have a high invasion potential. When the same species were grown at different levels of nutrient availability, we also found that invasive species produced more biomass than non-invasive species (Schlaepfer *et al.*, 2010). Similarly, database studies have shown that herbaceous and woody species that are large

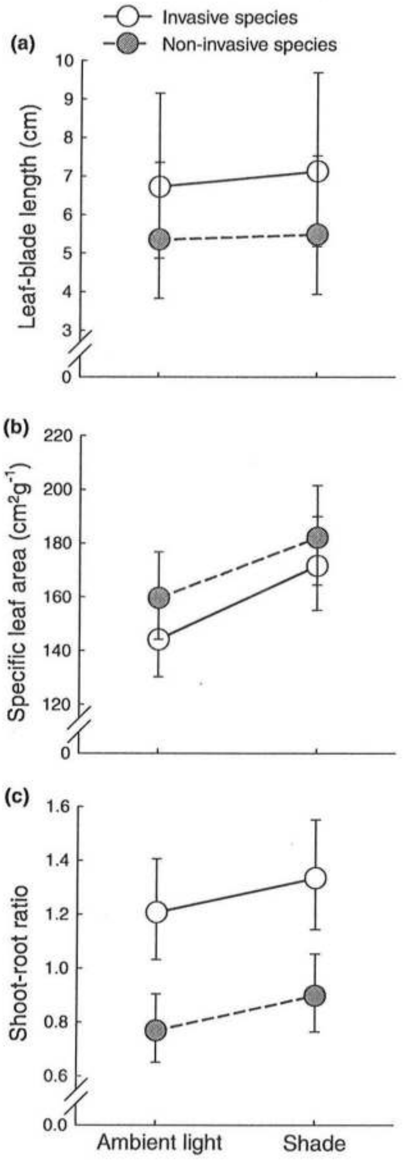

Figure 2 Morphological responses to shading of congeneric invasive and non-invasive herbaceous species. Means and standard errors of (a) leaf-blade length, (b) specific leaf area, and (c) shoot–root ratio of invasive (open circles) and non-invasive (filled circles) species measured under ambient light and shade. Means and standard errors are back-transformed predicted means and standard errors from linear mixed models. Leaf-blade length and specific leaf area were log transformed, and shoot–root ratio was double-log transformed prior to analysis.

in their native range are more likely to become invasive elsewhere than small species (Goodwin *et al.*, 1999; van Kleunen *et al.*, 2007; Bucharova & van Kleunen, 2009; but see Pyšek *et al.*, 2009). Clearly, this indicates that species capable of high biomass production under a wide range of environmental conditions in their native range are likely to be pre-adapted to become invasive elsewhere.

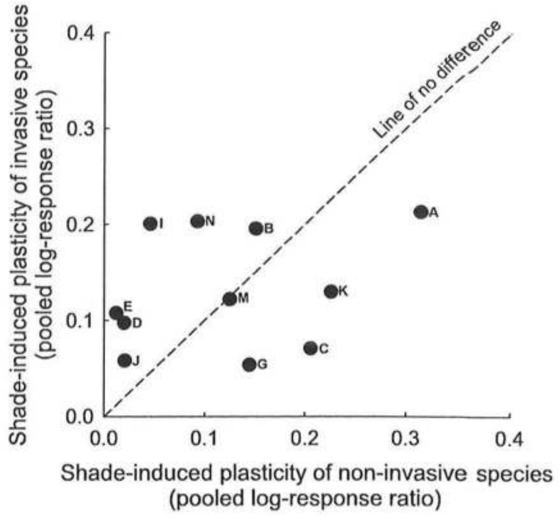

Figure 3 Morphological shade-induced plasticity of congeneric invasive and non-invasive herbaceous species. Plasticity of each species was quantified as pooled log-response ratios calculated from the mean untransformed trait values (shoot–root ratio, specific leaf area and leaf-blade length) of each species in the shaded environment and the unshaded environment. The capital letters on the right of the symbols refer to the genus names of the species pairs (see caption of Fig. 1). Because there were incomplete plasticity data for some traits for some species, there are 11 instead of 14 congeneric species pairs in this graph.

Morphological traits of invasive and non-invasive species

Of the three measured morphological traits, leaf-blade length, specific leaf area and shoot–root ratio, only shoot–root ratio was significantly higher for invasive species than for non-invasive species. Invasive species also tend to have longer leaves than non-invasive species but this was at the border of being statistically significant ($P = 0.050$; Table 2). A recent meta-analysis comparing invasive alien plant species to non-invasive, mostly native, species showed that invasive alien species frequently do not only grow larger but also have higher biomass allocation to shoots than do non-invasive species (van Kleunen *et al.*, 2010b). These results suggest that species with a high shoot–root ratio produce more biomass, and consequently have a higher likelihood to become invasive. Possibly, a high shoot–root ratio could give the invasive species an advantage over native and over non-invasive alien species because competition for light, in contrast to competition for belowground resources, is usually asymmetric – resulting in suppression of smaller plants by larger plants (Weiner & Thomas, 1986; Damgaard & Weiner, 2008).

In our study, invasive and non-invasive species did not differ in specific leaf area. This is surprising, because specific leaf area is frequently positively associated with relative growth rate (Lambers & Poorter, 1992), and because previous studies found that a high specific leaf area is frequently associated with invasive species when compared to native species (Daehler, 2003; Funk, 2008) or when compared to non-invasive alien species in their introduced range (Grotkopp *et al.*, 2002; Hamilton *et al.*, 2005; Burns, 2006; Grotkopp & Rejmánek, 2007). The discrepancy between the results of our study performed in the native range and those of other studies in the introduced range could indicate that invasive plants frequently have evolved high specific leaf area after introduction or that there has been biased introduction of genotypes with high specific leaf areas.

Shade-induced plasticity of invasive and non-invasive species

Averaged over all species in our study, plants increased their shoot–root ratio and specific leaf area in response to shading. However, leaf blades did not elongate in response to shading. It is possible that plants had active leaf-blade-elongation responses to compensate for passive reductions in leaf-blade length due to limited resource availability (i.e. plants actively maintained homeostasis in leaf-blade length; van Kleunen & Fischer, 2005). Alternatively, it could be that leaf-blade elongation is for some species less effective than petiole elongation and/or stem elongation for shade avoidance. However, because many of our study species did not have obvious petioles and stems, we restricted our measurements to leaf blades. Overall, morphological traits of our study species responded to shading in line with the predictions of adaptive plasticity in response to shading (Dudley & Schmitt, 1996; Schmitt *et al.*, 1999; van Kleunen & Fischer, 2005; Valladares & Niinemets, 2008).

Plastic morphological responses to shading are likely to constitute adaptive plasticity, and to result in high performance of plants across different light regimes. Although invasive species had a higher biomass production under both shaded and non-shaded conditions than non-invasive species, invasive species did not have stronger plastic responses to shading than non-invasive species. Ideally, one would test for each species whether shade plasticity in the measured traits is adaptive by means of selection-gradient analysis [i.e. regression of fitness parameters on trait values in each environment separately (e.g. Dudley & Schmitt, 1996) or on plasticity of these traits across environments (e.g. van Kleunen & Fischer, 2001)]. Tests for adaptive plasticity were not possible in our study, because they would require very large sample sizes for each of the species. Therefore, although there is wide consensus that the measured shade-induced responses usually constitute adaptive phenotypic plasticity (Dudley & Schmitt, 1996; Schmitt *et al.*, 1999; van Kleunen & Fischer, 2005; Valladares & Niinemets, 2008), it could be that these responses were not adaptive for some of our study species.

Few studies have tested whether presumably adaptive shade-induced responses differ between invasive and non-invasive alien species. Feng *et al.* (2007) found a higher plasticity of shoot allocation and specific leaf area in two invasive species compared to a related non-invasive alien species, a finding that contrasts with our findings on a larger number of species. Some previous studies grew multiple invasive alien and native species under different light conditions and measured physiological and morphological traits (e.g. Pattison *et al.*, 1998; Funk, 2008). Unfortunately, few of these studies tested explicitly whether invasive alien and native species differ in presumably adaptive plasticity. Funk (2008) compared physiological and morphological plastic shade responses in five confamilial pairs of invasive and native species in Hawai'i, and did not find differences in physiological or morphological shade plasticity. Clearly, we need more multi-species experimental studies that explicitly test for adaptive shade-induced plasticity in invasive and non-invasive species before we can draw general conclusions.

CONCLUSIONS

Our study is among the first experimental studies comparing native plant material of invasive and non-invasive naturalized congeners in their native range (but see van Kleunen & Johnson, 2007; Schlaepfer *et al.*, 2010). Our results indicate that high biomass production across different light environments pre-adapts species to become invasive elsewhere. The higher biomass production of invasive over non-invasive species could be related to differences in biomass allocation and morphology, because invasive species also had higher shoot–root ratios and tended to have longer leaf blades than non-invasive species.

In contrast to theoretical expectations (Baker, 1974; Richards *et al.*, 2006), the high performance of invasive species across different light conditions could not be attributed to high levels of presumably adaptive shade-induced plasticity in the traits that we measured. Possibly, the high environmental tolerance of invasive species is mediated by phenotypic plasticity in morphological traits that we did not measure. It could also be that the high environmental tolerance of invasive species is due to greater plasticity in physiological traits such as chlorophyll content and photosynthesis. We therefore strongly recommend that future studies should also measure physiological traits and additional morphological traits, as has been done in some of the studies comparing invasive to native species (e.g. Pattison *et al.*, 1998; Funk, 2008). Alternatively, it could be that high environmental tolerance is achieved by high values of certain traits, such as leaf-blade length and shoot–root ratio, irrespective of plasticity in these traits.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Congeneric pairs of invasive and non-invasive herbaceous species used in this study.

BIOSKETCH

Our lab works on basic and applied research in a wide spectrum of plant ecological disciplines (http://www.botany.unibe.ch/planteco/index.php). Among our main research topics are functional biodiversity, plant rarity and plant invasiveness.

Author contributions: M.v.K, M.F. and M.G. conceived the ideas, M.G. collected the data, D.R.S. analysed the data, and M.v.K. led the writing.

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