Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a meta-analysis

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Phenotypic plasticity is commonly considered as a trait associated with invasiveness in alien plants because it may enhance the ability of plants to occupy a wide range of environments. Although the evidence of greater phenotypic plasticity in invasive plants is considerable, it is not yet conclusive. We used a meta-analysis approach to evaluate whether invasive plant species show greater phenotypic plasticity than their native or non-invasive counterparts. The outcome of such interspecific comparisons may be biased when phylogenetic relatedness is not taken into account. Consequently, species pairs belonged to the same genus, tribe or family. The meta-analysis included 93 records from 35 studies reporting plastic responses to light, nutrients, water, CO_2, herbivory and support availability. Contrary to what is often assumed, overall, phenotypic plasticity was similar between invasive plants and native or non-invasive closely related species. The same result was found when separate analyses were conducted for trait plasticity to nutrients, light and water availability. Thus, invasive plant species and their native or non-invasive counterparts are equally capable of displaying functional responses to environmental heterogeneity. The colonization of a wide range of environments by invasive plants could be due to their capacity to undergo adaptive ecotypic differentiation rather than to their ability to display plastic responses. Alternatively, phenotypic plasticity might play a role in plant invasion, but only during the initial phases, when tolerance of the novel environment is essential for plant survival. Afterwards, once alien plants are identified as invaders, the magnitude of phenotypic plasticity might be reduced after selection of the optimum phenotypes in each habitat. The identification of plant traits that consistently predict invasiveness might be a futile task because different traits favor invasiveness in different environments. Approaches at the local scale, focusing on the ecology of specific invasive plants, could be more fruitful than global macro-analyses.

Invasive plant species are able to spread over considerable spatial scales, successfully colonizing a number of habitats (Richardson et al. 2000). Because of their large impact on ecological communities (Mooney and Cleland 2001, Levine et al. 2003), it is deemed of great importance to identify the mechanisms, traits or external factors that contribute to successful invasion by alien plant species (Lake and Leishman 2004, Burns 2006, Pyšek and Richardson 2007). This understanding of the invasion process may possibly lead to accurate predictions of the occurrence or characteristics of future plant invasions (Kolar and Lodge 2001, Richardson and Pyšek 2006).

Since the seminal work by Baker (1965) several studies have addressed whether particular plant traits are positively associated with the likelihood of becoming an invasive species (Gray 1986, Rejmánek and Richardson 1996, Reichard and Hamilton 1997, Goodwin et al. 1999, Pyšek and Richardson 2007, van Kleunen et al. 2010a, b). It has been commonly considered that phenotypic plasticity, broadly defined as the capacity of an organism to modify its phenotypic expression in response to environmental changes (West-Eberhard 2003), could be a mechanism facilitating plant invasion success (Gray 1986, Williams et al. 1995, Daehler 2003, Richards et al. 2006, Funk 2008). Phenotypic plasticity may

be an adaptive feature for plants (Sultan 1995), and this is verified when changes in phenotypic expression of functional traits in response to a particular environment enhance plant fitness (Pigliucci 2001, chapter 7). Plasticity may thus increase ecological breadth of invasive species, allowing them to express advantageous phenotypes in a broader range of environments (Richardson and Pyšek 2006, Richards et al. 2006). Consequently, it has been hypothesized that invasive plant species should express greater phenotypic plasticity than co-occurring native or non-invasive plants in response to environmental factors that are relevant for plant distribution and abundance (Richards et al. 2006).

Importantly, the outcome of comparisons between invasive and native or non-invasive plants may be biased when such tests do not take into account the phylogenetic relatedness of the species (Burns 2006, Richards et al. 2006, Funk 2008). Because phylogenetically close species share a common evolutionary history, they are more likely to show similar traits (Harvey et al. 1995). Consequently, consistent differences in trait plasticity found in comparisons between closely related invasives and non-invasive or native species may be ascribed to the invasive nature of the study species with some confidence (Muth and Pigliucci 2006). In contrast, when invasive species are compared with distantly

related – and hence markedly different – counterparts, hypothetical differences in trait plasticity may be equally explained by several traits other than the invasive feature (Muth and Pigliucci 2006). For instance, it has been shown that root morphological plasticity to soil nutrient heterogeneity is significantly greater in dicots than in monocots (Kembel and Cahill 2005).

The evidence of greater phenotypic plasticity in invasive plant species is not yet conclusive (Richards et al. 2006, Matesanz et al. 2010). While many studies have found higher trait plasticity in invasives, there is some empirical evidence indicating that, at least for some functional traits, invasive plants show no greater plasticity than their native or non-invasive counterparts (González and Gianoli 2004, Brock et al. 2005, Burns 2006, Funk 2008). To draw general conclusions about the relationship between phenotypic plasticity and alien plant invasion, results of different independent studies must be combined using methods that permit a statistical synthesis of them (Gurevitch and Hedges 2001, Richards et al. 2006). Meta-analysis techniques provide more objective appraisals of the available evidence than descriptive reviews, and they are especially helpful to discern patterns in disciplines where empirical results seldom converge, as is the case for ecology (Arnqvist and Wooster 1995, Gurevitch et al. 2000, Koricheva et al. 2004). In the present study, using a meta-analysis approach, we combined the results of published studies on phenotypic plasticity of plants to several environmental factors to test whether invasive species show greater trait plasticity than their native or non-invasive counterparts. First, we conducted a global categorical meta-analysis including studies reporting plastic responses to light, water, nutrients, herbivory, CO_2, and support availability (in the case of vines). Second, to detect possible particular trends masked by the results of the global meta-analysis, we separately conducted meta-analyses of plastic responses to shading, drought and increased availability of nutrients, because these were the environmental factors with the largest sample sizes. In all cases the two contrasted categories were invasive species and closely related native or non-invasive species. In addition, to get a more comprehensive view of the phenotypic plasticity vs invasiveness issue, we used the dataset to test whether plasticity patterns between those two categories differed according to growth form (herbs, trees/shrubs, vines) and plant class (monocots vs dicots).

Methods

Studies addressing phenotypic plasticity in invasive vs native or non-invasive plant species were found using a number of search terms in the Web of Science (ISI), checking the reference lists of the articles so obtained, and from known review articles in the topic. In addition, we considered data from articles that did not intend to compare plasticity levels but were suitable to test our hypothesis. The latter were found in the Web of Science (ISI) entering as search terms the main response variables and major environmental factors included in the analysis (below).

In the invasion ecology literature, a number of terms are used to define similar concepts, and misuse and confusion of terms also occur (Richardson et al. 2000). For the purpose of this meta-analysis, we classified plant species into the general categories of 'native' (a native species that is not invasive in the study area or elsewhere), 'invasive' (an introduced species that is invasive in the study area), or 'non-invasive' (an introduced species that is not invasive in the study area or elsewhere, and that is closely related to an invasive species). This was done following the authors' criteria and descriptions in each article. For instance, we did not filter out studies lacking a detailed distinction between invasive and naturalized species (see Richardson et al. 2000 for concept discussion). In a few cases where the studies referred to the plant species just as 'alien' or 'introduced' we conducted a bibliographical search and categorized them as invasive if they were considered a widespread or noxious weed. A more strict approach to the nomenclature issue would have significantly limited the sample size for this study. Although different definitions and criteria for considering a plant species as invasive coexist in the group of included studies, we consider that it should not generate a bias for hypothesis testing.

Although the original idea was to separately evaluate the plasticity of physiological, morphological and life history traits, in the group of articles complying with all the requisites (below) there were very few studies including plasticity of physiological traits or life history traits. We thus decided to analyze all traits together. The specific requirements for including data from an article in the meta-analysis were as follows. 1) The study included interspecific comparisons between invasive and native or non-invasive closely related species, i.e. species belonging to the same genus, tribe or family. 2) There was an experimental manipulation of environmental factors. To obtain the effect size from the data (below), we designated the control and experimental groups. This considered the customary approaches to study plastic responses of plants to particular factors. As a control group we considered treatments of high light, high water availability, low nutrients, low CO_2 levels, no herbivory, and no available support (for vines). Therefore, our experimental groups were shade, water shortage, high nutrients, high CO_2 levels, herbivory, and available support. Although it would have been interesting to discriminate between plant responses to limiting and non-limiting nutrients, in most cases the authors did not inform whether the tested nutrient was a limiting nutrient for the study species. Furthermore, several studies applied nutrient formulas instead of single nutrients, thus making the distinction between limiting and non-limiting conditions less certain. 3) The experiments were conducted in a common environment (greenhouse or common garden) using genotype replicates sensu lato (clone, genetic family, cultivar, population or species; Pigliucci 2001). 4) The study reported phenotypic plasticity of morphological or physiological traits. When several plant traits were measured, we chose a priori those traits that the literature more often reports as involved in functional responses to particular environmental factors. Thus, we selected root/shoot ratio and root biomass in response to soil moisture, root/shoot ratio and total plant biomass in response to nutrient availability, and specific leaf area (SLA) and leaf area ratio (LAR) in response to light intensity. When both traits were included in a single study, trait choice was random. When none of those traits were included, we chose plant characters related to them, such as biomass allocation traits. For articles evaluating plastic

responses to environmental factors other than water, nutrients or light, we selected the most relevant plant trait according to the authors. For each article, only one trait per species per factor was included in the meta-analysis in order to comply with the required statistical independence of data (Gurevitch and Hedges 2001). This was done because including several traits from a single study would artificially inflate the degrees of freedom of the analysis in the likely event that plant traits were correlated. The fact that the criteria for trait selection within articles were defined beforehand allowed us to undertake a non-biased approach. 5) Means, sample sizes, and standard deviations – or other measure of variation that allowed its calculation – were reported for both control and experimental groups. For those studies in which this information was missing, we contacted the authors and requested the data. Some studies displayed the information in graphs. To use these data, graphs were scanned, digitally enlarged and then analyzed with SigmaScan Pro. We excluded studies that quantified phenotypic plasticity using only plasticity indices. 6) More than one data point was obtained from a single article when the study included several species or several factors. To choose the pair of species to be compared, we checked their phylogeny and selected those that were more closely related and/or shared growth form.

Meta-analysis was conducted using the MetaWin 2.0 software (Rosenberg et al. 2000). We fitted random-effects models to categorical data (mixed-effects model; Gurevitch and Hedges 2001). Mixed-effects models assume that studies within a category share a common mean effect but that, in addition to sampling error, there is also random variation among studies in a category (Gurevitch and Hedges 2001). The two contrasted categories were invasive species and closely related native or non-invasive species. The latter two categories were merged for the main analysis to increase its statistical power and because both contrasts (invasive vs native; invasive vs non-invasive) point to the same question: whether invasiveness is associated with plasticity. Nevertheless, we also conducted separate analyses for the two contrasts to test whether the overall trend of results was verified in each of them. The main hypothesis, greater plasticity in invasive species, was tested by comparing the effect size (an estimate of the magnitude of plasticity, below) between data sets from invasive species vs their native and non-invasive counterparts. In addition to this global meta-analysis including plastic responses to all factors (light, water, nutrients, herbivory, CO_2, and support availability), we separately carried out meta-analyses of plastic responses to shading, drought and increased availability of nutrients because these were the environmental factors with the largest samples sizes. This was done to detect possible particular trends masked by the results of the global meta-analysis. Likewise, we also conducted separate analyses of the main contrast, i.e. invasive species vs native or non-invasive species, according to growth form (herbs, trees/shrubs, vines) and plant class (monocots, dicots).

To estimate the effect size of each study, we chose the log response ratio (L) because it quantifies proportionate changes between experimental and control groups, thus minimizing plant size influences (Hedges et al. 1999, Hawkes and Sullivan 2001). The effect size was calculated as $L = \ln(\overline{X}_{ex}) - \ln(\overline{X}_{co})$. Where $\overline{X}$ represents the sample mean and the subscripts 'ex' and 'co' refer to experimental

and control conditions, respectively. The weighted mean of L is computed considering the pooled study variance (Rosenberg et al. 2000). Because of the sorting of treatments and traits described above, mean effect sizes were considered significant, i.e. overall plasticity was verified, when L was positive and bias-corrected bootstrap 95% confidence intervals (Adams et al. 1997, Gurevitch and Hedges 2001) did not overlap zero (Hawkes and Sullivan 2001). More related to hypothesis testing, if those 95% confidence intervals around mean effect sizes corresponding to invasive species and native or non-invasive species did not overlap, then these categories were considered to differ in plasticity. We further tested this hypothesis of between-category heterogeneity in the global meta-analysis by inspecting the p-values associated with the Q_B statistic, which can be tested against a χ^2 distribution (Gurevitch and Hedges 2001).

The fact that we also included articles that did not intend to compare plasticity levels reduced the possibility of a bias in estimating effect sizes due to the likely underrepresentation of studies finding non-significant results or rejecting the hypothesis of interest (Palmer 1999, Koricheva et al. 2004). Furthermore, because we only chose one of several response traits for a given factor included in each study, and that the focus traits were mostly selected a priori, it is very likely that our sample included non-biased effect sizes.

Results

We found 35 studies suitable to be included in the meta-analysis according to our criteria. This group included 17 studies that did not aim at comparing plasticity levels between species explicitly. The full data set comprised 93 independent cases of comparisons of phenotypic plasticity between invasive plant species and their native or non-invasive closely related counterparts (80 cases of invasives vs natives; 13 cases of invasives vs non-invasives). A total of 81 cases (87%) reported plastic responses to variation in light, water or nutrients (Table 1). Forty cases (43%) were within-genus comparisons and eight cases (9%) were contribal genera comparisons, i.e. comparisons of genera belonging to the same tribe.

Graphical results indicate that mean effect sizes corresponding to invasive plant species and native or non-invasive species were very similar in the full data set (95% confidence intervals showed considerable overlap; Fig. 1). Statistical results confirmed the pattern of similar trait plasticity between categories (invasive vs native or non-invasive species) for the global meta-analysis ($Q_B = 0.164$, p > 0.68). Likewise, when both contrasts (invasive vs native; invasive vs non-invasive) were analyzed separately the overall trend of results was verified in each of them (invasive vs native, $Q_B = 0.127$, p > 0.72; invasive vs non-invasive, $Q_B = 0.084$, p > 0.77). The main outcome of the meta-analysis did not result from contrasting patterns for the different environmental factors; results of the comparisons were nearly identical for studies addressing plastic responses to light, water or nutrients (Fig. 2). All of these groups exhibited significant phenotypic plasticity (CI around mean effect sizes did not overlap zero; Fig. 2) and plasticity to light was greater than plasticity to water (Fig. 2) both for invasive plants

Table 1. Characteristics of studies included in the meta-analysis. The table shows the selected trait in each study, the type of comparison carried out by the study (between invasive and native species, INV & NAT, or between invasive and non-invasive species, INV & NON), the family of the species compared, the taxonomic category shared by the species pair, the growth form of the species compared, and the ecological factor considered in the evaluation of phenotypic plasticity. A full article list is given in Appendix 1.

Article	Trait	Comparison	Family	Shared taxon	Growth form	Factor
Ashton and Lerdau 2008	Shoot/Root ratio	INV & NAT	Caprifoliaceae	Genus	Climber	Herbivory
Ashton and Lerdau 2008	Shoot/Root ratio	INV & NAT	Celastraceae	Genus	Climber	Herbivory
Ashton and Lerdau 2008	Shoot/Root ratio	INV & NAT	Vitaceae	Subfamily	Climber	Herbivory
Bakker and Wilson 2001	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Water
Baruch and Bilbao 1999	Total leaf area	INV & NAT	Poaceae	Tribe	Herbaceous	Herbivory
Bilbao and Medina 1990	Root/Shoot ratio	INV & NAT	Poaceae	Subfamily	Herbaceous	Nutrients
Black et al. 1994	Root length	INV & NAT	Poaceae	Tribe	Herbaceous	Nutrients
Brock and Galen 2005	Specific leaf area	INV & NAT	Asteraceae	Genus	Herbaceous	Water
Burns 2006	Total biomass	INV & NON	Commelinaceae	Genus	Herbaceous	Nutrients
Burns 2006	Total biomass	INV & NON	Commelinaceae	Genus	Herbaceous	Nutrients
Burns 2006	Total biomass	INV & NON	Commelinaceae	Genus	Herbaceous	Nutrients
Burns 2006	Total biomass	INV & NON	Commelinaceae	Genus	Herbaceous	Nutrients
Burns 2006	Total biomass	INV & NON	Commelinaceae	Genus	Herbaceous	Nutrients
Burns 2006	Root/Shoot ratio	INV & NON	Commelinaceae	Genus	Herbaceous	Water
Burns 2006	Root/Shoot ratio	INV & NON	Commelinaceae	Genus	Herbaceous	Water
Burns 2006	Root/Shoot ratio	INV & NON	Commelinaceae	Genus	Herbaceous	Water
Burns 2006	Root/Shoot ratio	INV & NON	Commelinaceae	Genus	Herbaceous	Water
Burns 2006	Root/Shoot ratio	INV & NON	Commelinaceae	Genus	Herbaceous	Water
Drenovsky et al. 2008	Root biomass	INV & NAT	Asteraceae	Family	Herbaceous	Nutrients
Drenovsky et al. 2008	Root biomass	INV & NAT	Asteraceae	Family	Herbaceous	Nutrients
Feng et al. 2007	Specific leaf area	INV & NON	Asteraceae	Subfamily	Herbaceous	Light
Funk 2008	Leaf area ratio	INV & NAT	Poaceae	Subtribe	Herbaceous	Light
Funk 2008	Leaf area ratio	INV & NAT	Myrtaceae	Subfamily	Herbaceous	Light
Funk 2008	Leaf area ratio	INV & NAT	Fabaceae	Subfamily	Tree	Light
Funk 2008	Leaf area ratio	INV & NAT	Rosaceae	Genus	Tree	Light
Funk 2008	Leaf area ratio	INV & NAT	Poaceae	Family	Shrub	Light
Geng et al. 2006	Root biomass	INV & NAT	Amaranthaceae	Genus	Herbaceous	Water
Godoy 2009	Specific leaf area	INV & NAT	Malvaceae	Family	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Fabaceae	Family	Tree and shrub	Light
Godoy 2009	Specific leaf area	INV & NAT	Asteraceae	Genus	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Poaceae	Family	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Asteraceae	Subfamily	Tree	Light
Godoy 2009	Specific leaf area	INV & NAT	Poaceae	Family	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Solanaceae	Genus	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Myrtaceae	Subfamily	Tree and shrub	Light
Godoy 2009	Specific leaf area	INV & NAT	Fabaceae	Subfamily	Tree	Light
Godoy 2009	Specific leaf area	INV & NAT	Solanaceae	Family	Shrub	Light
Godoy 2009	Specific leaf area	INV & NAT	Onagraceae	Subfamily	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Oxalidaceae	Genus	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Pinaceae	Genus	Tree	Light
Godoy 2009	Specific leaf area	INV & NAT	Anacardiaceae	Family	Tree and shrub	Light
Godoy 2009	Specific leaf area	INV & NAT	Solanaceae	Subfamily	Herbaceous	Light
Godoy 2009	Specific leaf area	INV & NAT	Fabaceae	Family	Tree and shrub	Light
Godoy 2009	Specific leaf area	INV & NAT	Ulmaceae	Genus	Tree	Light
Godoy 2009	Root/Shoot ratio	INV & NAT	Malvaceae	Family	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Fabaceae	Family	Tree and shrub	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Asteraceae	Genus	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Asteraceae	Subfamily	Tree	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Solanaceae	Genus	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Myrtaceae	Subfamily	Tree and shrub	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Fabaceae	Subfamily	Tree	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Solanaceae	Family	Shrub	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Onagraceae	Subfamily	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Oxalidaceae	Genus	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Pinaceae	Genus	Tree	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Anacardiaceae	Family	Tree and shub	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Solanaceae	Subfamily	Herbaceous	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Fabaceae	Family	Tree and shrub	Nutrients
Godoy 2009	Root/Shoot ratio	INV & NAT	Ulmaceae	Genus	Tree	Nutrients
Goergen and Daehler 2001	Root/Shoot ratio	INV & NAT	Poaceae	Subfamily	Herbaceous	Water

(Continued)

Table 1. (*Continued*)

Article	Trait	Comparison	Family	Shared taxon	Growth form	Factor
González and Gianoli 2004	Specific leaf area	INV & NAT	Convolvulaceae	Genus	Climber	Light
James et al. 2009	Root length	INV & NAT	Asteraceae	Family	Herbaceous	Nutrients
James et al. 2009	Root length	INV & NAT	Asteraceae	Family	Herbaceous	Nutrients
Kercher and Zedler 2004	Shoot/Root ratio	INV & NON	Poaceae	Tribe	Herbaceous	Flooding
Kolb et al. 2002	Shoot biomass	INV & NAT	Poaceae	Tribe	Herbaceous	Nutrients
Kolb et al. 2002	Root biomass	INV & NAT	Poaceae	Tribe	Herbaceous	Water
Kolb and Alpert 2003	Root/Shoot ratio	INV & NAT	Poaceae	Genus	Herbaceous	Nutrients
Leicht and Silander 2006	Specific leaf area	INV & NAT	Celastreaceae	Genus	Climber	Light
Lowe et al. 2003	Total biomass	INV & NAT	Poaceae	Family	Herbaceous	Nutrients
Miller and Zedler 2003	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Flooding
Pattison et al. 1998	Leaf area ratio	INV & NAT	Asteraceae	Genus	Herbaceous	Light
Pfeifer-Meister et al. 2008	Total biomass	INV & NAT	Poaceae	Family	Herbaceous	Nutrients
Pfeifer-Meister et al. 2008	Total biomass	INV & NAT	Poaceae	Family	Herbaceous	Nutrients
Pfeifer-Meister et al. 2008	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Water
Pfeifer-Meister et al. 2008	Root/Shoot ratio	INV & NAT	Poaceae	Family	Herbaceous	Water
Powell and Knight 2009	Above biomass	INV & NAT	Asteraceae	Genus	Herbaceous	Nutrients
Sans et al. 2004	Total biomass	INV & NAT	Asteraceae	Genus	Herbaceous	Nutrients
Sasek and Strain 1991	Total biomass	INV & NAT	Caprifoliaceae	Genus	Climber	CO_2
Schierenbeck et al. 1994	Shoot/Root ratio	INV & NAT	Caprifoliaceae	Genus	Climber	Herbivory
Schumacher et al. 2009	RGR leaf	INV & NON	Myrtaceae	Genus	Tree	Light
Schweitzer and Larson 1999	Internode lenght	INV & NAT	Caprifoliaceae	Genus	Climber	Support availability
Simoes and Baruch 1991	Water use efficiency	INV & NAT	Poaceae	Tribe	Herbaceous	Water
Simoes and Baruch 1991	Leaf elongation	INV & NAT	Poaceae	Tribe	Climber	Herbivory
Song et al. 2009	Total biomass	INV & NAT	Asteraceae	Genus	Climber	CO_2
Song et al. 2009	Total biomass	INV & NAT	Convolvulaceae	Genus	Herbaceous	CO_2
Thomsen et al. 2006	Root/Shoot ratio	INV & NAT	Poaceae	Genus	Herbaceous	Nutrients
Thomsen et al. 2006	Root/Shoot ratio	INV & NAT	Poaceae	Tribe	Herbaceous	Nutrients
Thomsen et al. 2006	Root/Shoot ratio	INV & NAT	Poaceae	Subfamily	Herbaceous	Nutrients
Williams and Black 1994	Root biomass	INV & NAT	Poaceae	Subfamily	Herbaceous	Water
Wilson et al. 2004	Root biomass	INV & NAT	Acanthaceae	Genus	Herbaceous	Water
Zheng et al. 2009	Specific leaf area	INV & NAT	Asteraceae	Genus	Herbaceous	Light

($Q_B = 7.936$, $p < 0.05$) and native or non-invasive plant species ($Q_B = 9.582$, $p < 0.01$).

The main result, i.e. no difference in plasticity associated with invasive status, was consistently found when the analysis was conducted separately for the included growth forms: herbs ($Q_B < 0.001$, $p > 0.99$; n = 61), trees/shrubs ($Q_B = 1.005$, $p > 0.31$; n = 21), and vines ($Q_B = 0.002$, $p > 0.96$; n = 11). Overall, all plant categories taken together, the three growth forms did not differ in phenotypic plasticity ($Q_B = 4.582$, $p > 0.10$). There was a non-significant trend for herbaceous species to show greater plasticity than woody species and climbing plants (data not shown). With regard to plant class, no differences in plasticity between invasive and native or non-invasive species were found when the analysis was performed singly for monocots ($Q_B = 0.003$, $p > 0.31$; n = 28) and dicots ($Q_B = 0.247$, $p > 0.61$; n = 65). Overall, monocots and dicots showed similar levels of phenotypic plasticity ($Q_B = 1.211$, $p > 0.27$).

We compared effect sizes by category of phylogenetic relatedness (tribe, genus, sub-family, family). We found no significant differences ($Q_B = 3.233$, $p > 0.27$), which indicates that the phylogenetic correction was homogeneous and hence it did not introduce confounding effects in the analysis. Finally, because a significant proportion of the data was obtained from Godoy (2009) (Table 1) and it could introduce a bias in the outcome of the meta-analysis, we ran all the analyses with and without considering these data. It

was then verified that the main results did not change when Godoy's data were excluded (overall plasticity: $Q_B = 0.144$, $p > 0.70$; plasticity to light: $Q_B = 0.372$, $p > 0.54$; plasticity to nutrients: $Q_B = 0.109$, $p > 0.74$; the contrast of plasticity to water was the same because Godoy's study did not include this factor).

Discussion

In a classical work, Baker (1965) proposed that plasticity should be one of the plant traits associated with weediness (colonizing potential). Ever since Baker, several other studies have considered that phenotypic plasticity could be a mechanism enhancing plant invasion (Gray 1986, Williams et al. 1995, Daehler 2003, Richards et al. 2006, Richardson and Pyšek 2006, Funk 2008). Contrary to what is often assumed, results of the present meta-analysis indicate that invasive plant species and their native or non-invasive counterparts show similar levels of phenotypic plasticity, i.e. they are equally capable of displaying functional responses to environmental heterogeneity. This pattern held when the main question was addressed in several subsets, grouped by abiotic factor eliciting the phenotypic response, plant growth form, or plant class. Interestingly, a recent meta-analysis concluded that invasive alien species had higher values of performance-related traits than non-invasive species
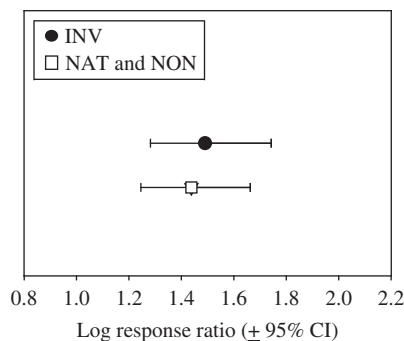
Figure 1. Mean effect size (log response ratio ± bias-corrected bootstrap 95% CI) of phenotypic plasticity of invasive versus native or non-invasive plant species in response to different factors: light, water, nutrients, herbivory, CO_2, and support availability (n = 93 records).

(van Kleunen et al. 2010a). Therefore, it seems that the greater performance typical of invasive plant species relies more on constitutive advantages, probably evolved in the colonized range (below), than on greater flexibility of phenotypic expression.

Our results agree with the arguably most ambitious experimental comparison of plasticity between invasive and native plant species conducted so far (Godoy 2009). In a common garden experiment, Godoy (2009) compared a number of morphological and physiological responses to two gradients of light and nutrient availability in 20 invasive–native confamilial pairs and found similar levels of phenotypic plasticity in both groups. In contrast, a review by Daehler (2003) concluded that invaders are more plastic than natives. However, it was a vote-counting review with a small simple size (12 studies) and, more important, it did not account for phylogeny. The latter may bias the invasive vs native comparison because phylogenetic relatedness may covary with phenotypic trait expression and phenotypic plasticity (Kembel and Cahill 2005, Muth and Pigliucci 2006, Richards et al. 2006, Funk 2008). Burns (2006) found differences between invasive and non-invasive Commelinaceae species in SLA and growth rate using paired
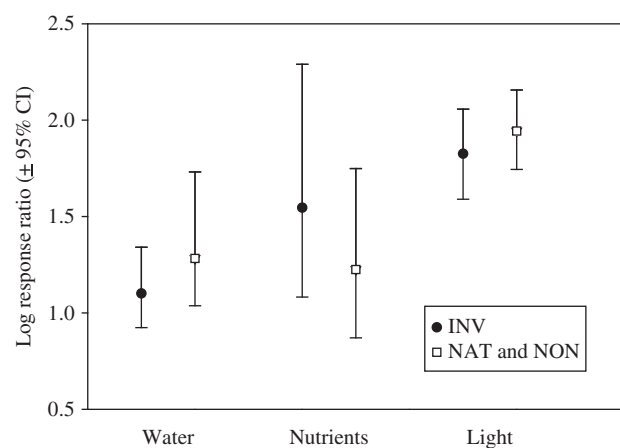

Figure 2. Mean effect size (log response ratio ± bias-corrected bootstrap 95% CI) of phenotypic plasticity of invasive versus native or non-invasive plant species in response to experimental treatments of water (n = 15), nutrients (n = 38), and light (n = 28 records).

analyses – according to relatedness – but these differences were not detected in unpaired analyses. After comparing several traits in invasive and non-invasive plant species in a meta-analysis, van Kleunen et al. (2010a) concluded that analyses that do not account for phylogeny might either fail to detect or spuriously detect traits associated with invasiveness, which in their case were shoot allocation and leaf physiology, respectively. Likewise, in a meta-analysis comparing the effects of alien and native neighbour plant species on visitation to native co-flowering species, Morales and Traveset (2009) found that results of a phylogenetically controlled analysis were only partially consistent with those of a conventional analysis.

Darwin's naturalization hypothesis, which posits that exotic species are more likely to successfully invade an ecological community if they are not closely related to the native flora, has received mixed empirical support (Diez et al. 2008, Proches et al. 2008). Based on this hypothesis, it could be suggested that, by selecting closely related pairs to test for differences in plasticity between invasive and native or non-invasive species, our study dismissed aggressive species that presumably could have expressed significant levels of plasticity. We stress that, regardless of the existence of an association between phylogenetic relatedness and probability of successful invasion, to adequately test whether phenotypic plasticity is linked with invasiveness, the study must control for phylogeny. Thus, even if it is shown that distantly related alien plant species are not only successful invaders but also more plastic than closely related alien species, we could not certainly ascribe their success to phylogenetic distance or phenotypic plasticity.

Ecotypic differentiation, a process by which a population is genetically differentiated in traits that are functional for a given habitat (Turesson 1922), is an alternative (but non-exclusive) mechanism that plants may use to cope with environmental heterogeneity (Bradshaw and Hardwick 1989). Although alien plants experience genetic bottlenecks during founding events, repeated introductions may ameliorate genetic diversity loss, thus allowing invasive plants to undergo adaptive population differentiation (Dlugosch and Parker 2008). There is evidence from invasive plants that plasticity prevails over genetic differentiation at explaining species spread (Williams and Black 1993, Parker et al. 2003, Geng et al. 2007, Loomis and Fishman 2009, Ross et al. 2009) but, in general, both mechanisms can contribute to the invasive potential of alien plants (Sexton et al. 2002, Richardson and Pyšek 2006, Caño et al. 2008, Godoy et al. 2011). In view of the results of the present meta-analysis, it might be hypothesized that the successful colonization of a wide range of environments by invasive plants, rather than explained by their ability to display plastic responses, could be due to a greater capacity to undergo ecotypic differentiation as compared to native species. Thus, the ample ecological breadth commonly observed in invasive plant species could result from a series of locally adapted ecotypes (Rice and Mack 1991, Mooney and Cleland 2001, Dawson et al. 2007, Lavergne and Molofsky 2007).

An alternative explanation to the main results obtained could be that phenotypic plasticity does play a role in plant invasion, but only during the initial phases, wherein tolerance of the novel environment is essential for plant survival.

Afterwards, the novel phenotype resulting from trait plasticity becomes genetically fixed following directional selection on the optimum phenotype in the novel habitat (introduced range) (Sexton et al. 2002), and the magnitude of phenotypic plasticity might be reduced because of plasticity costs. This process is known as genetic assimilation (Pigliucci et al. 2006, Crispo 2007). Because almost all invasion ecology studies are conducted when plant species have already attained the invasive status, i.e. far beyond the initial stages of the invasion process, it might be hypothesized that the occurrence of genetic assimilation caused our analysis to fail in detecting differences in trait plasticity between the subject groups. It has earlier been considered that genetic assimilation could be relevant for the process of plant invasions, and that it should be taken into account as a likely scenario regarding the evolution of plasticity in invasive plant populations (Richards et al. 2006). The genetic assimilation hypothesis, particularly its prediction regarding the selection of the optimum phenotype in the introduced range, is consistent with the above discussed finding of superiority in performance traits in invasive plant species (van Kleunen et al. 2010a).

In contrast to an earlier report on root plasticity (Kembel and Cahill 2005), we found no differences in phenotypic plasticity between monocots and dicots. Likewise, comparable levels of phenotypic plasticity were shown in herbs, trees/shrubs, and vines despite their differences in ecological niches, mechanical attributes and life-history traits (Rowe and Speck 2005). Thus, similar magnitudes of plasticity are found across plant classes, plant growth forms, and invasive status. It seems that the often documented patterns of variation in phenotypic plasticity within species matching theoretical expectations (reviewed by Matesanz et al. 2010) do not find a counterpart at the macroevolutionary level.

Results reported in the current study challenge the notion that the magnitude of phenotypic plasticity is a good indicator of the potential of alien plant species to become invasives. It has proven difficult to identify traits that consistently predict invasiveness because different traits favor invasiveness in different habitats (Alpert et al. 2000, Burns 2006). Results of earlier studies may be interpreted as suggesting that 'the quest for the holy trait' regarding alien plant invasiveness might be futile. Thus, results in Daehler (2003) show that alien invasive plants do not consistently outperform co-occurring native species in terms of growth rate, competitive ability (but see Vilà and Weiner 2004) or fecundity, the outcome being contingent on growing conditions. The latter has been also shown for carbon capture strategies of Australian plant species (Leishman et al. 2010). A review by Pyšek and Richardson (2007) found comparative studies showing that invasiveness was positively associated with clonality, extended flowering period, and dispersal by animals; but they also found studies showing a negative association between those features and alien plant invasiveness. Moreover, it has been suggested that differences in invasiveness between closely related species are better explained as the result of complex trait interactions and specific introduction histories (Muth and Pigliucci 2006), and even that serendipity may be an important factor in successful invasions (Gray 1986). In view of such limited generality of results, it seems that – in the context of alien plant management – approaches at the local scale, focusing on the ecology of specific invasive plant species, could be more fruitful than macro-analyses at the global scale.

Forty-five years after Baker first proposed plasticity as an invasiveness trait, the evidence seems to indicate that invasive plants are not more plastic than natives or non-invaders. However, there is still room for testing this hypothesis on earlier stages of the invasion process, thus indirectly evaluating to what extent genetic assimilation has eroded formerly greater levels of phenotypic plasticity in invasive plants. In addition, because plant invasion ecology and phenotypic plasticity are extremely active research fields, in the short-term there will be enough data to refine the approach conducted herein and test for distinct patterns associated with plasticity of physiological, morphological and life history traits. Furthermore, larger data sets will also allow for an explicit adaptive approach to alien plant plasticity, thus testing to what extent phenotypic plasticity underlies fitness gains or fitness homeostasis in benign and stressful environments, respectively, as compared to closely related native or non-invasive plant species.

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