REVIEW AND SYNTHESIS

Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis

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Abstract

Do invasive plant species have greater phenotypic plasticity than non-invasive species? And, if so, how does this affect their fitness relative to native, non-invasive species? What role might this play in plant invasions? To answer these long-standing questions, we conducted a meta-analysis using data from 75 invasive/non-invasive species pairs. Our analysis shows that invasive species demonstrate significantly higher phenotypic plasticity than non-invasive species. To examine the adaptive benefit of this plasticity, we plotted fitness proxies against measures of plasticity in several growth, morphological and physiological traits to test whether greater plasticity is associated with an improvement in estimated fitness. Invasive species were nearly always more plastic in their response to greater resource availability than non-invasives but this plasticity was only sometimes associated with a fitness benefit. Intriguingly, non-invasive species maintained greater fitness homoeostasis when comparing growth between low and average resource availability. Our finding that invasive species are more plastic in a variety of traits but that non-invasive species respond just as well, if not better, when resources are limiting, has interesting implications for predicting responses to global change.

Keywords

Adaptive, alien, climate change, environmental gradient, indigenous, resource, weed.

Ecology Letters (2011) **14**: 419–431

INTRODUCTION

Phenotypic plasticity is defined as the change in phenotypic expression of a genotype in response to environmental factors (Bradshaw 1965; Schlichting 1986) and has been shown to have significant evolutionary consequences (Schlichting 2004; Murren *et al.* 2005). Plasticity is adaptive if the phenotypes produced in response to a change in the environment result in higher average fitness across both environments than either fixed phenotype would (van Kleunen & Fisher 2005).

The idea that high phenotypic plasticity has contributed to the success of invasive plants was proposed almost half a century ago (see Baker 1965). The theory makes intuitive sense because it is based on several plausible assumptions. First, an invasive plant usually arrives in a new area with few individuals (and generally relatively low genetic diversity) and faces an environment that differs from that in which it evolved. High levels of phenotypic plasticity should enable a colonizing species to cope with, and become established, under these novel conditions (Schlichting & Levin 1986). Indeed, ecological breadth has been shown to be positively correlated with plasticity in some species (Sultan 2001; but see Pohlman *et al.* 2005). Second, the ability to take advantage of environmental fluctuations through adaptive phenotypic plasticity is likely to affect not only a plant's ability to become established in a new environment but also its ability to outcompete the existing vegetation, i.e. its success as an invader (Murray *et al.* 2002; van Kleunen & Richardson 2007).

In a manner analogous to the novel environmental conditions that are experienced upon invasion of a new habitat, increasing temperatures, higher CO_2 levels and associated climate changes over recent decades have introduced novel environmental conditions. This might favour more phenotypically plastic species (see Chown *et al.* 2007) and result in an increased competitive ability of invasive plants over co-occurring native, non-invasive species (Dukes 2007).

Many studies have suggested that invasive species have higher levels of phenotypic plasticity, but direct empirical tests of this theory are less common (Hulme 2008) and previous reviews have not achieved quantitative conclusions (see Daehler 2003; Richards *et al.* 2006). Richards *et al.* (2006) drew on Baker (1965) to pose three testable scenarios regarding the importance of phenotypic plasticity in plant invasions and the role of plasticity in maintaining fitness across different environments (Fig. 1). These are that relative to a non-invasive species, an invasive species might be a:

(a) 'Master-of-some' if phenotypic plasticity in response to more favourable conditions enables a larger increase in fitness.

(b) 'Jack-of-all-trades' if phenotypic plasticity in response to stressful conditions enables greater fitness homoeostasis (i.e. a smaller decline in fitness).

(c) 'Jack-and-master', when characteristics of (a) and (b) are combined such that phenotypic plasticity in response to more favourable environments enables greater fitness, and plasticity in response to more stressful conditions permits a smaller decline in fitness (i.e. greater fitness homoeostasis).

It is now possible to gather sufficient data to empirically test the proposed scenarios about the relationship between adaptive phenotypic plasticity (Fig. 1) and biological invasion. The power of the 'Jack-of-all-trades' and 'Master-of-some' scenarios is that they provide guidelines about the expected relationship between plant traits and fitness proxies (Box 1). Comparing the relationship between the degree of trait plasticity and the change in fitness proxies of the invasive plant with that of a co-occurring non-invasive plant in response to a given shift in resource availability enables us to quantify the relative importance of plasticity in providing invasive species with a competitive advantage over non-invasive species.
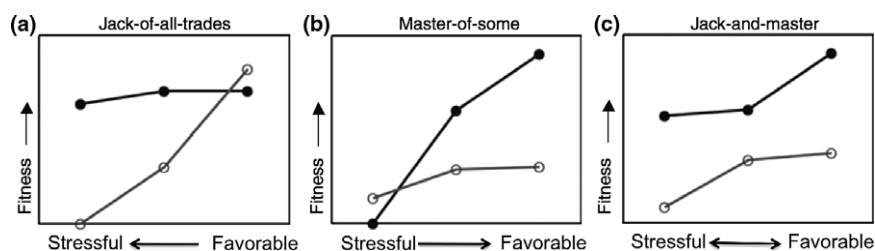
Figure 1 Black lines represent invasive species, grey lines represent non-invasive species. (a) Invasive species have more robust fitness in the face of stressful environmental conditions (Jack-of-all-trades), (b) invasives are better able to respond with increased fitness in favourable conditions (Master-of-some) and (c) fitness norm-of-reaction of invasives has characteristics of both robustness and responsiveness (Jack-and-master). Adapted from Richards *et al.* (2006) with permission.
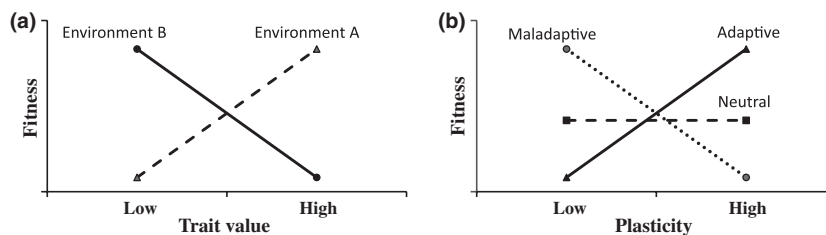

Figure 2 Two methods for assessing the adaptive value of plasticity. In method (a), fitness is plotted against different values of a phenotypic trait of interest for multiple environments. Plasticity in the trait has the potential to be adaptive if different trait values confer the highest fitness in each environment. Alternatively, adaptive plasticity may be assessed by regressing the fitness of an organism against its average plasticity in a trait of interest as in (b). [Adapted from Nicotra *et al.* (2010) and van Kleunen & Fisher (2005) with permission].

Box 1 Plasticity and fitness

As J.B.S. Haldane once noted: 'Fitness is a bugger' (Hunt & Hodgson 2010). To determine whether a plastic response is adaptive a researcher must regress plasticity in the focal trait against some estimate of fitness. This is difficult, because fitness is almost impossible to measure directly (e.g. Head *et al.* 2005; Hunt & Hodgson 2010). Thus, to explore the relationship between trait plasticity and fitness we must make a distinction between those aspects of the phenotype that are considered to be components of, or proxies for, fitness and other traits where the relationship with fitness is less clear (see Fig. 2). Ideally, measuring fitness requires a demographic approach whereby one tracks a population over multiple generations to monitor the rate of increase in a trait or the relative number of descendents derived from each organism in the original generation. Sometimes researchers use lifetime reproductive output as a measure of fitness; although even this is flawed as it fails to account for potential variation in the reproductive value of offspring (e.g. Head *et al.* 2005). In most cases, however, logistic constraints force researchers to rely on various fitness indices or proxies as a measure of fitness, e.g. traits closely related to size or fecundity (see table 4.3 in Hunt & Hodgson 2010). Researchers then assume that these components of fitness are positively correlated with net fitness; where net fitness is the relative ability of an individual (or population) to survive, reproduce and propagate genes in a given environment. This is a compromise, but it is a basic reality that is common to almost all studies of selection.

Selection will always act to maximize fitness in a given environment, thus plasticity in net fitness is unlikely to be adaptive (Scheiner 1993; Sih 2004). Plasticity in individual components of fitness (e.g. biomass, seed weight, etc.), however, can be under direct selection and can elevate average net fitness across environments (see Weiner 2004) because the relative contribution of different fitness components to net fitness often varies across environments. For example, low fecundity in 1 year for a perennial plant might reflect diversion of resources to survival or vegetative growth that ultimately boosts lifetime fitness (Sih 2004). Another example might be lower seed production in many species in response to water stresses (Freeman *et al.* 1981). In an agricultural setting, Sadras *et al.* (2009) found that wheat lines that had greater plasticity in yield (where yield is measure of fitness for agriculture crops) in response to water availability had higher average yields across years than genotypes that did not show phenotypic plasticity in yield across conditions. Similarly, Scheiner (1993) reported selection for different rates of reproductive output in different native environments due to a trade-off between reproduction and survival.

In this study, we examined plasticity in a broad range of traits for our overall plasticity analysis. However, when explicitly testing the Jack-of-all-trades and Master-of-some hypotheses we had to distinguish between measures that were reasonable proxies or components of fitness (fitness proxies) and those growth, morphological and physiological traits that we were testing for adaptive plasticity. For simplicity's sake, we describe morphological, physiological and growth traits as 'focus traits' for our effect size estimates and consider their plasticity relative to our fitness proxies. We recognize that these distinctions are not clear-cut, and often studies of plasticity do not identify a measure of fitness against which the adaptive value of a plastic trait response can be tested. We therefore stress the importance in future studies of carefully choosing to measure explicit and meaningful components of fitness to better evaluate the adaptive value of plasticity in other traits.
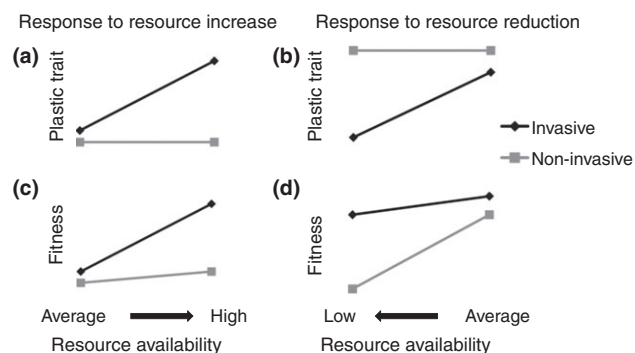
Response to resource increase   Response to resource reduction

Figure 3 Theoretical relationships between trait values and resource availability and the corresponding fitness outcomes for non-invasive and invasive species. In both the increase-in-resources (a, c) and decrease-in-resources (b, d) scenarios, the invasive species responds more plastically to the change in resource availability than the non-invasive species does (a, b) and this is associated with higher average fitness (c, d).

Hypotheses

In this study, we conducted a meta-analysis to synthesize the published literature and test three specific hypotheses regarding the role of phenotypic plasticity in plant invasions:

(1) that invasive species show greater phenotypic plasticity across various growth, morphological, physiological and fitness traits compared with co-occurring non-invasive species (tested using the 'Overall plasticity analysis');
(2) that increased plasticity in growth, morphological and physiological traits is correlated with *higher fitness gains* in invasives compared with non-invasives when plasticity is measured as the difference between a *high resource supply* environment and average conditions (tested using the plasticity and fitness analysis; Fig. 3);
(3) that increased plasticity in growth, morphological and physiological traits is correlated with *lower fitness losses* in invasives compared with non-invasives when *low resource supply* environment and average conditions (also tested using the plasticity and fitness analysis; Fig. 3).

METHODS

Data selection

We conducted a literature search on Web of Science and Cab Abstracts for the terms [invas* or nonnat* or non-nat* or alien* or weed or nonindig* or non-indig*] and [nat* or indig* or endemic]. All published records up until 30 May 2009 were searched. We limited results to the topics of plant science and weeds. In addition, a cited literature search on Richards *et al.* (2006) was conducted in Web of Science to the same date. Studies were then individually assessed and retained if the following conditions were met:

(1) The study included at least one non-invasive and one invasive species. Native species were all presumed to be non-invasive and hereafter are referred to under the general title 'non-invasive'. The authors' definitions of invasive were accepted in all cases as they did not vary greatly and generally related to nationally agreed criteria.
(2) Both the invasive and non-invasive species had each to be grown in at least two standardized conditions that differed in resource availabilities.

(3) Data could be obtained for the mean values, standard deviations and sample sizes for measurement of focal traits for both the invasive and non-invasive species in two or more conditions.

The Database

Suitable data were available from 46 studies, measuring 362 individual traits across 150 species that were assigned into 75 species pairs (see Appendix S1). Within a given study, one or more pairs consisting of an invasive and non-invasive species were generated to maximize the phylogenetic relatedness within pairs. It was not possible to pair species across studies because the environmental conditions that were manipulated, and the traits that were measured differed greatly among studies. The pairing of species allowed us to investigate *differences* in plasticity between species that can more readily be attributed to invasiveness status because we have partially removed variation in phenotypic plasticity that is due to systematic differences among studies (e.g. methodology, exact levels of treatments). A database of all species pairs was created.

To construct the database of all species pairs, we first categorized the growing conditions into eight 'resource treatment' types based on analysis of the most common types used in the available studies. These were manipulation of: (1) nutrients (including different elements, e.g. nitrogen, phosphorous, etc.), (2) light, (3) water, (4) competition or density, (5) disturbance, (6) CO_2 enrichment, (7) presence/absence of climbing substrate and (8) presence/absence of soil biota and/or mycorrhiza. Second, we categorized the response traits for plasticity measures into 11 categories: (1) water use efficiency (WUE), (2) photosynthetic rate, (3) biomass, (4) relative growth rate, (5 and 6) tissue nitrogen or phosphorous content, (7) root biomass, (8) shoot length, (9) specific leaf area (SLA), (10) root to shoot ratio (R:S) and (11) nitrogen use efficiency (NUE). Third, we noted the extent of phylogenetic relatedness between the pair of non-invasive and invasive species, which we defined as: (1) congeners, (2) confamilial or (3) less closely related. Fourth, we noted whether the growth form of the invasive was: (1) herb, (2) grass, (3) shrub or (4) tree or (5) vine. And fifth, we divided the invaded habitat into eight types: (1) grassland, (2) forest, (3) scrub-, shrub- or heath-land, (4) tropical forest, (5) wetland, (6) desert, (7) tree-shrub mix and (8) disturbed land or agriculture.

As described above, if we had data on trait plasticity for more than one invasive and one non-invasive species in a given study, species were paired to provide the closest phylogenetic matches between the invasive and non-invasive species. In each study, a species was only represented in a single species pair. Of the 46 available studies, five had two species pairs and eight had more than two species pairs. We treated species pairs as independent data points for the purposes of most analyses. In so doing, we make the reasonable assumption that there is no systematic variation among studies in the likelihood that they will report greater plasticity in invasive than non-invasive species. Biologically, this assumption is well justified because plants of different species were grown separately and were not in competition. The only exception is seven field-based studies in which natural competition occurred.

Likewise, when two or more types of environmental manipulations were imposed on the same species pair, we calculated separate effect sizes for each resource treatment. Of the 46 studies, 14 studies measured responses to two treatments and 10 studies to more than two treatments. Finally, we calculated separate effect sizes for each

response trait for each species pair for each treatment type. Thirteen studies recorded two response traits per species pair per treatment and 23 recorded three or more response traits.

Plasticity was not explicitly measured or specifically reported in the majority of the studies used in our meta-analysis as the traits were originally measured for other purposes. This has the advantage of avoiding any publication bias directly associated with our main hypothesis (i.e. towards only publishing positive results). This should reduce any associated 'file drawer' problems (Rosenthal 1979). It does not, however, avoid the issue of a 'research bias' whereby data are more often collected from certain species (Gurevitch & Hedges 1999). For example, the available species pairs might over-represent commercially important invasive species (although inspection of our species list does not support this claim) or be biased towards species which are more easily grown in greenhouse experiments (e.g. short-lived herbs and grasses). As with most research fields, these caveats about the availability of data in the current literature should inform interpretation of our meta-analyses (Jennions *et al.* in press).

The available studies rarely used clones or full-siblings, so genotypes *per se* were imperfectly replicated across experimental environments. Phenotypic difference between treatments could therefore be due to both genetic differences in plants assigned to each treatment and phenotypic plasticity. If, however, plants from a given population (or species) express consistently different pheno-types in the different environments, phenotypic plasticity can still be analysed. Clearly, the resultant plasticity estimates will have greater uncertainty than those based on measurement of replicated genotypes (see Funk 2008). On the other hand, however, the use of only a few genotypes could result in a poor sample of the available mean level of plasticity within a species if there are moderate to high levels of genotypic variation in phenotypic plasticity within a species. Perhaps most importantly, however, there are no obvious bias in how individual plants were assigned to growing treatments (i.e. no propensity to assign certain genotypes to specific treatments), so there should be no systematic bias in the resultant measure of the difference in plasticity.

Data analysis

Calculation of effect size for plasticity and general analysis

A commonly used effect size is Hedges' *d* (i.e. *J*-corrected Hedges' *g sensu* Rosenberg *et al.* 2000). This is the difference between two mean values divided by an estimate of their pooled standard deviation, using *J* to correct for any bias due to low sample size (equations in Rosenberg *et al.* 2000). We first calculated Hedges' *d* for a specific trait and specific treatment for each species. In other words, how much did the measured trait differ between the two environmental treatments when expressed in the unitless measure of standard deviations? We used the *absolute* value of Hedges' *d* as our measure of the plasticity for a given species (hereafter we refer to |*d*| which is a species' effect size for plasticity, as '*P*'). We calculated the absolute difference in means rather than the difference in any one direction (e.g. *P* = high resource mean − low resource mean) for two reasons. First, because an adaptive trait change in a given environment could require either an increase or a decrease in trait value. For some environmental changes there might even be multiple adaptive response strategies such that a shift in some traits may potentially be adaptive in either direction (e.g. fast growth in response to a drought to reach reproductive maturity quickly or slower growth to prolong lifespan). Second, Hypothesis 1 is

simply whether invasive species are more plastic than non-invasive species. As such it is essential, by definition, to compare the absolute change in phenotype between invasive and non-invasive species. We calculated *P* using the mean and standard deviation for each treatment extracted from summary tables, figures (using Graphclick; Arizona Software, 2008) or by contacting the author directly.

Next, to test whether invasive species have higher phenotypic plasticity than non-invasive species we calculated an effect size for the difference in plasticity between a pair of invasive (*i*) and non-invasive (*n*) species ($P_{diff} = P_i - P_n$). The effect size we used to calculate the difference in plasticity for each focal trait differs from the type that the reader might be familiar with because it is the *difference* between two effect sizes, rather than the difference in means from two populations (Hedge's *d* – used for our estimate of P_i and P_n – are examples of the latter; Borenstein *et al.* 2009). An example of the type of effect size we used is Cohen's *q* which is the difference between two effects size that are Fisher Z_r transformations of correlation coefficients. The variance of the difference between two uncorrelated effect sizes (e.g. our P_{diff}) is simply the sum of their variance (see Borenstein *et al.* 2009, p. 228). If the value of $P_{diff} > 0$ it indicates that the invasive species showed a greater degree of phenotypic plasticity (i.e. P_i, the absolute change in phenotypic means between the two treatments) than the non-invasive species.

We calculated the mean value of P_{diff} in Metawin 2.0 using a random effects model. Given modest to low sample sizes when data were subdivided to consider specific treatment types or focal traits we used the nonparametric, bias-corrected, bootstrapped 95% confidence interval to assess the significance of results. If the confidence interval for P_{diff} excluded zero, we consider the effect to be significant at the 0.05 level. For the overall plasticity analysis, we tested whether invasive species display higher average phenotypic plasticity than non-invasives (Hypothesis 1) by calculating the mean value of P_{diff} for all available traits and assessing whether it was significantly greater than zero. We also calculated the total heterogeneity (Q_T) in effect sizes. Although the probability test associated with Q_T is not relevant for a random effects model, it helps highlight which models might benefit from the inclusion of moderator variables that could account for variation in P_{diff}. We assessed the significance of five moderator factors: response trait type, treatment type, growth form, invaded habitat type and level of relatedness using the test statistic $Q_{between}$ (Q_b) with the associated *P*-value as a guide (for details, see Gurevitch *et al.* 2001; Borenstein *et al.* 2009).

Correction for possible non-independence of effect sizes

Some species pairs contributed two or more effects sizes (P_{diff}) because more than one trait was measured and/or more than one treatment applied to the same pair. We therefore pooled effect sizes where possible to reduce the potential non-independence. The extent to which we could pool effect sizes varied with the moderator variable (trait, treatment type, relatedness of invasive and non-invasive, invaded habitat type and growth form). To assess the influence of trait type we were unable to pool the effect sizes and thus used the individual species pair trait responses (hereafter referred to as 'individual traits' analysis; Fig. 4a). For the assessment of the effect of treatment on the relative plasticity of invasive and non-invasive species, we pooled traits within treatments for each species pair (hereafter referred to as the 'treatment mean' analysis; Fig. 4b). For the remaining moderator variable categories (growth form, invaded habitat type and relatedness of the invasive and non-invasive), we
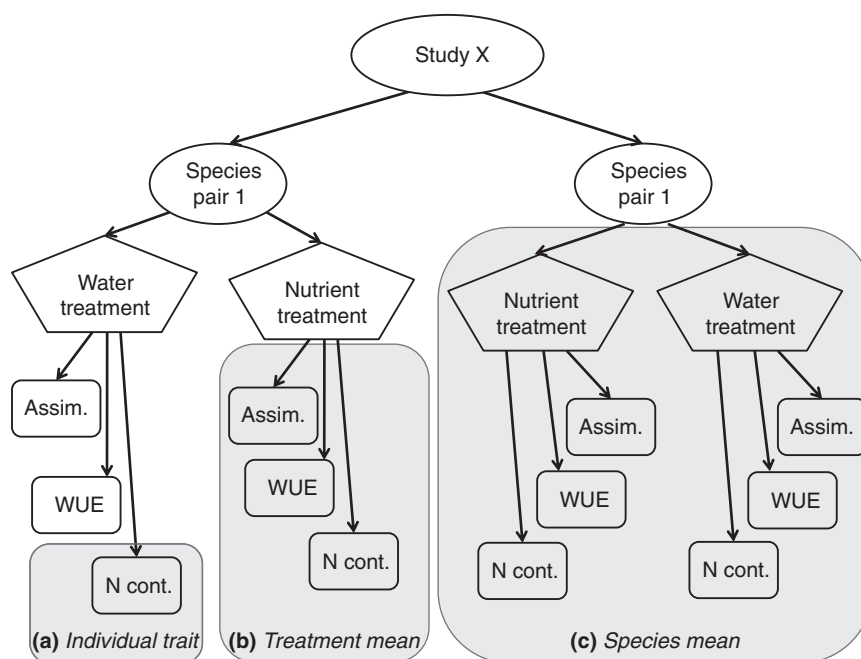
Figure 4 Hypothetical example of the hierarchical approach used to analyse the difference in plasticity between invasive and non-invasive species (P_{diff}). The individual trait (a) was used to assess the effect of trait on P_{diff}, the treatment mean (e.g. in Study X there would be 12 individual traits); the treatment mean (b) was used to assess the effect of treatment type on P_{diff} (e.g. in study X there would be four treatment means); and the species mean (c) was used to assess the effects of invaded habitat type, growth form and relatedness of the invasive and native species in the species pair on P_{diff} (e.g. in study X there would be two species means).

calculated a single composite effect size for each species pair by pooling effect sizes across traits and treatments (hereafter referred to as the 'species mean' analysis; Fig. 4c).

Although we assume, based on how plants were grown, that estimates of the species mean for different species pairs are independent when measured in the same study, we did conduct a sensitivity analysis to test this assumption. To do so, we repeatedly calculated the mean value of P_{diff} after randomly selecting a single P_{diff} estimate from each of 46 studies (hereafter this analysis is referred to as 'random trait' analysis). We then ran 50 iterations of the randomization process to calculate the 95% confidence interval for the mean. Additional iterations were unnecessary due to the small range in the resultant estimates of the mean for P_{diff}.

We compared the summary statistics for P_{diff} for all four analysis types: individual traits, treatment means, species means and random trait. The outcome was qualitatively very similar (see Results). This justifies retention of an analysis based on P_{diff} of the individual traits because presenting trait-specific results is more biologically informative. It should be noted that the use of a composite effect size to remove non-independence between P_{diff} estimates requires the assumption that the estimates are all measuring the 'same' general property of interest. So, for example, a difference in plasticity between an invasive and non-invasive species of the same magnitude is treated as equivalent estimate of plasticity regardless of whether the trait is photosynthetic rate or biomass. Although this might seem unwarranted it is consistent with there being no *a priori* reason to weight some traits as more important than others and the main conceptual task being quantification of overall phenotypic plasticity.

To calculate the pooled mean effect sizes discussed above (species mean and treatment mean), we first calculated the weighted mean for P_{diff} for each species using the appropriate set of P_{diff} estimates.

We used a standard fixed effects model so that it was also possible to calculate the variance of P_{diff} taking into account any correlation between effect sizes (Mengersen *et al.* in press). For the variance of this mean, we calculated the variance of the mean of X_i effects each with a variance of V_i and V_{ij} where V_i and V_{ij} represent the covariance between X_i and X_j, and r_{ij} represents the correlation between X_i and X_j (only one combination of a given pairing is required) as:

$$V_{mean} = \left(\sum_{i=1}^{m} V_i + 2 \sum_{i,j} V_{ij} \right) / m^2$$

$$= \left(\sum_{i=1}^{m} V_i + 2 \sum_{i,j} (r_{ij} \sqrt{V_i} \sqrt{V_j}) \right) / m^2$$

(modified from Borenstein *et al.* 2009, p. 228).

If the variance differed between effect size estimates, we multiplied each V_i in the first sum by (W_i / W_{mean}) and each term in the second sum by ($W_{i*}W_j$)/$W_i W_{j\ mean}$ (i.e. give greater weighting to estimates from traits with lower variances) ($W_i = 1/V$). The correlation between different traits is usually unknown, so we calculated two values where we either set $r = 0$ (i.e. assumes each trait provides a fully independent estimate of phenotypic plasticity for the species pair in question) or $r = 1$. This acts as a form of sensitivity analysis bracketing the upper and lower boundaries. For calculation of means and standard deviations and confidence intervals, we report only the results of $r = 1$ as this is the more statistically conservative measure.

The role of the five categorical moderators (trait, treatment type, relatedness of the invasive and non-invasive species, invaded habitat type and growth form of the invasive) that might account for variation in effect sizes was investigated by calculating Q_B. The *P*-values for

Q_B were Bonferroni adjusted for these five tests so that $P_{critical} = 0.05/5 = 0.01$.

Plasticity and fitness analysis

We tested hypotheses 2 and 3 by assessing the relationship between phenotypic plasticity in growth, morphological and physiological traits (hereafter referred to as focus traits) and our fitness proxies. Each study was examined individually to determine whether it included any measures that could be used as fitness proxies. We considered variables directly related to fecundity (number of seeds or flowers, reproductive biomass, germination rates of second generation), survival and biomass to be indicators of fitness. Total biomass was used as a fitness proxy because greater vegetative size is often associated with higher reproductive output (Weiner *et al.* 2009). The final set of focus traits used to assess plasticity for the plasticity and fitness analysis were: WUE, tissue nitrogen content, tissue phosphorous content, shoot length, SLA, R:S and NUE.

The available data meant that the original hypotheses of Richards *et al.* (2006) had to be simplified. We substituted 'resource availability' for an environmental gradient progressing from stressful to favourable. In many cases, data were only available for two levels of resource availability, whereas the hypotheses originally proposed by Richards *et al.* (2006) require data from at least three points along an environmental gradient. Resource levels were used to distinguish environments rather than the categories: 'favourable' and 'stressful', as the former can be objectively defined and are independent of the species-specific responses (e.g. high light could, depending on the species, be either favourable or stressful). As described below, comparisons were dependent upon both species responding in the same direction to the change in resource availability.

When a study compared average to high resource availability the situation was classified as a Master-of-some scenario (Hypothesis 2). If a study compared low and average resource availability the situation was classified as a Jack-of-all-trades scenario (Hypothesis 3). The original hypotheses included a third strategy of 'Jack-and-master' that we were unable to test because it requires at least three points along a resource gradient and there are very few such studies available that met our initial conditions for inclusion in the database.

'Average' conditions were based on information provided in the original paper. Interpretation was relatively simple for field-based and common garden studies as meteorological data were usually available to demonstrate which year represented average conditions for climatic treatments. For field nutrient, competition and other treatments representative sites were used and similar sites modified for the elevated and/or reduced resource treatments. For glasshouse studies we were more reliant on the author's interpretations. For example, average conditions for water or nutrient treatments in glasshouses often required authors to decide what soil moisture availability or nutrient level represented average field conditions. For nutrients this often involved fertilizer being added to obtain similar nitrogen/phosphorous levels to field soils although many authors used actual field collected soil. When such soil was unmodified we assumed this represented the 'average' condition. In general the definition of average conditions was explicitly specified in the methods sections of the papers. If it was not possible to determine 'average' conditions, the studies were omitted from the plasticity and fitness analysis.

We calculated Hedges' *d* for each species for each fitness proxy as the difference between the average and altered resource treatment (i.e. either higher *minus* average or lower *minus* average). An effect size for each fitness proxy (P_{diff_fit}) for the species pair was then calculated as the difference in the value of Hedges' *d* between the paired species (i.e. invasive *minus* non-invasive species). P_{diff_fit} is a measure of the extent to which invasive and non-invasive species differed in the fitness change that occurs following an environmental change. If $P_{diff\_fit} > 0$ then the invasive species had a larger fitness gain in response to an *increase* in resources than the non-invasive species *or* a smaller reduction in fitness in response to a *reduction* in resources. We only calculated P_{diff_fit} for a species pair if both species responded in the same direction to the change in resource availability. This ensured that the favourable environment was the same for both species enabling a meaningful comparison of P_{diff_fit}. Furthermore, this approach ensures that a resource increase is synonymous with a shift to a favourable environment, and a resource decrease to a shift to a stressful environment.

For the analysis of responses to an increase in resources, we had P_{diff_focus} estimates from 36 studies of 59 species pairs representing 182 species pair trait combinations. Data to calculate P_{diff_fit} were available from 24 studies representing 34 species pairs and 45 different species pair fitness trait combinations. For the analysis of a response to a decrease in resources, we had P_{diff_focus} estimates from 22 studies of 26 species pairs representing 86 different species pair trait combinations. Data for P_{diff_fit} were available from 13 studies representing 16 species pairs and 18 response traits. As with the overall plasticity analysis we analysed data using the individual traits as well as the species means for P_{diff_focus} and P_{diff_fit}.

Separate scatter plots of P_{diff_fit} on P_{diff_focus} were generated for each resource scenario using those species pairs for which both P_{diff_focus} and P_{diff_fit} could be calculated. This analysis used lower level trait estimates rather than species pair means to ensure a sufficient sample size ($n = 52$ and 24 to test hypotheses 2 and 3 respectively). For Hypotheses 2 and 3 to be supported the majority of the data should fall in the upper right quadrant of the correlation graph. This is consistent with the invasive species showing greater plasticity ($P_{diff\_focus} > 0$) coupled with the appropriate fitness response (i.e. $P_{diff\_fit} > 0$ so either a bigger increase in fitness in response to added resources or smaller decrease in fitness in responses to a decline in resources for invasive than non-invasive species).

RESULTS

Overall plasticity analysis

The summary effect size for the analysis using the individual traits, treatment means, species means and random trait analysis all yielded highly concordant results. In all cases, there was a significantly positive mean for P_{diff} indicating that invasive species have greater phenotypic plasticity. The estimated mean ranged from $P_{diff} = 0.42$–0.67 standard deviations (Table 1). Using multiple data points from some studies therefore did not have a strong effect on the estimated mean.

Invasive species had greater phenotypic plasticity for all 11 traits (Table 1). Furthermore, the 95% bootstrap confidence intervals indicated that the effect size was significantly positive for five traits: WUE, biomass, root biomass, R:S ratio and NUE, and only marginally non-significant for photosynthesis ($P \approx 0.05$; Fig. 5; Table 1). The magnitude of the difference in phenotypic plasticity between invasives and non-invasive species did not depend on which of the 11 response traits was measured ($Q_B = 3.13$, d.f. = 10, $P = 0.978$).

Table 1 Results of the meta-analysis comparing plasticity of invasive species to non-invasive species

Analysis	d.f.	Mean effect size	Bootstrap CI
Individual trait	361	0.668	0.417 to 0.895*
Treatment mean	138	0.509	0.272 to 0.749*
Species mean	74	0.548	0.322 to 0.768*
Random trait	49	0.686	0.446 to 0.927*
Trait			
Biomass	91	0.629	0.145 to 1.318*
N content	31	0.742	−0.054 to 1.606
NUE	16	1.004	0.392 to 1.701*
P content	10	0.343	−0.142 to 0.847
Photosynthesis	26	0.830	−0.007 to 1.729
Root biomass	39	0.760	0.214 to 1.334*
RGR	21	0.976	−0.014 to 2.176
Root:shoot	61	0.601	0.090 to 1.123*
Shoot length	26	0.131	−0.617 to 0.832
SLA	12	0.480	−0.290 to 1.713
WUE	18	0.488	0.080 to 1.049*

NUE, nitrogen use efficiency; RGR, relative growth rate; SLA, specific leaf area; WUE, water use efficiency.

*Mean is statistically significant at 0.05 level.

The effect sizes are reported for four different methods of analysis: using the individual trait data for each treatment and species pair (individual trait), combining trait data within treatments for each species pair (treatment mean) and combining trait data to all treatments within species pairs (species mean). Data are also reported for a randomization test where one trait from each study was randomly selected for each of 50 iterations (random trait). The data for each of the traits for the individual trait analysis are also provided.

The effect of treatment type was examined using the treatment means (excluding treatments with fewer than five effect size estimates). Treatment explained a reasonable amount of the heterogeneity in effect sizes ($Q_B = 10.97$, d.f. $= 3$, $P = 0.012$), and was only marginally non-significant if multiple testing was taken into account ($P_{critical} = 0.01$). The mean effect size was positive for all four treatments, and significantly so for light and water (Table 2), meaning the greater overall P_{diff} was not biased by certain treatment types but rather invasive species were more able to respond plastically to a suite of environmental changes.

Finally, using the species means we tested whether P_{diff} estimates differed depending on the plant growth form, invaded habitat type or the level of relatedness between the invasive and non-invasive species. None of these three moderators explained a significant portion of the heterogeneity in effect sizes (Growth form: $Q_B = 1.84$, d.f. $= 4$, $P = 0.765$; Habitat: $Q_B = 5.77$, d.f. $= 4$, $P = 0.217$ and Relatedness: $Q_B = 2.02$, d.f. $= 2$, $P = 0.363$) (Table 3).

In sum, irrespective of how the data were subdivided or the level of analyses used to estimate the mean effect size, the consistent conclusion was that invasive species show greater phenotypic plasticity ($P_{diff\_fit} = 0.4$–0.7) than non-invasive species. Hypothesis 1 was therefore supported.

Plasticity and fitness analysis

Response to an increase in resources

The subset of data available to test the response to an increase in resources (Hypothesis 2) was consistent with the finding that invasive species are more plastic in focus traits than non-invasive species (mean $P_{diff\_focus} > 0$; Table 4). The 'Master of some' hypothesis
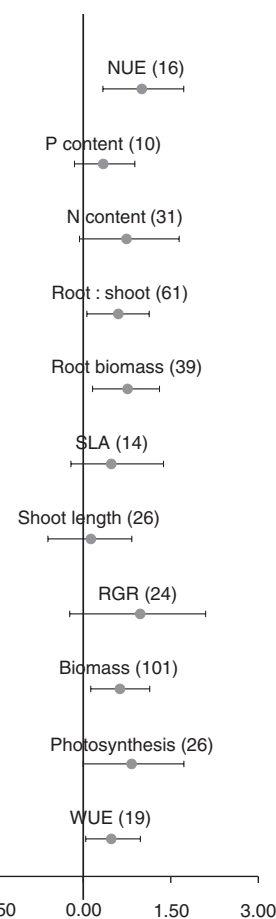

Figure 5 The mean difference in plasticity between invasive and non-invasive species for 11 traits using effect sizes for individual trait with separate effect sizes for each resource treatment. A positive mean effect size indicates that the invasive species has greater average plasticity than the non-invasive species. The bars represent 95% confidence intervals. The number of effect sizes used to calculate the mean is shown in parentheses.

Table 2 Results of the overall plasticity meta-analysis comparing plasticity in invasive species to non-invasive species using mean effect sizes per treatment of each species pair within a study (treatment mean)

Treatment	d.f.	Mean effect size	Bootstrap CI
Competition	24	0.185	−0.434 to 0.689
Light	22	1.285	0.747 to 1.888*
Nutrient	50	0.300	−0.085 to 0.694
Water	11	0.833	0.074 to 1.666*

*Mean is statistically significant at 0.05 level.

predicts that higher plasticity in invasive species is associated with a greater increase in fitness in response to an increase in resources (Hypothesis 2). This should result in the majority of data being in the upper right quadrant of the scatter plot. In our analyses, however, the greater plasticity of invasives did not correlate with greater improvements in fitness. There was a weak trend (i.e. $P_{diff\_fit} > 0$) but invasive species did not display a significantly higher average gain in fitness than non-invasive species (Table 4). Even if the analysis is confined to the 57% of cases where the invasive species showed greater plasticity (i.e. $P_{diff\_focus} > 0$), these are almost evenly divided into those where

Table 3 Results of the overall plasticity meta-analysis comparing plasticity in invasive species to non-invasive species using mean effect sizes of each species pair within a study (species mean)

Category	d.f.	Mean effect size	Bootstrap CI
By invasive species growth form			
Grass	22	0.397	0.057 to 0.735*
Herb	34	0.649	0.302 to 1.055*
Shrub	4	0.356	−0.386 to 1.084
Tree	4	0.477	−0.176 to 0.968
Vine	6	0.912	−0.127 to 2.014
By habitat			
Disturbed land	9	0.459	0.223 to 0.824*
Forest	30	0.762	0.248 to 1.231*
Grassland	17	0.428	−0.053 to 0.934
Scrub/heath	11	0.188	−0.194 to 0.643
Wetland	4	1.133	0.161 to 1.945*
By species pair level of relatedness			
Genus	17	0.755	0.284 to 1.262*
Family	23	0.361	0.060 to 0.584*
Less-related	32	0.582	0.241 to 0.944*

Summary effect sizes are provided for the following categorical explanatory variables: growth form, invaded habitat type and level of relatedness between the invasive and non-invasive species.
*Mean is statistically significant at 0.05 level.

Table 4 Results of the plasticity and fitness meta-analysis comparing invasive species to non-invasive species using species means (mean effect sizes of species pairs within each study)

Treatment type	Trait type	d.f.	Mean effect size	Bootstrap CI
Resource increase	Focus traits	58	0.414	0.151 to 0.701*
	Fitness proxies	33	0.474	−0.237 to 1.279
Resource decrease	Focus traits	21	0.387	−0.021 to 0.828
	Fitness proxies	15	−4.177	−9.986 to −1.052*

*Mean is statistically significant at 0.05 level.

P_{diff_fit} is above and below zero (Fig. 6a). The Master-of-some hypothesis was therefore not supported.

Responses to a decrease in resources

The Jack-of-all-trades hypothesis predicts that invasive species show both higher plasticity in focus traits and a smaller decline in fitness in response to a reduction in resources (Hypothesis 3). This should result in most data being in the upper right quadrant of the correlation graph. Again, the subset of data used to test the response to a decrease in resources agrees with the wider pattern that invasive species are more plastic than non-invasive species. The mean estimate of P_{diff_focus} was only slightly lower than that from the full dataset, although it was marginally non-significant ($P \approx 0.06$, probably due to the modest sample size; Table 4). In contrast, the mean value of P_{diff_fit} was significantly *less* than zero, indicating that invasive species had a significantly *larger* decline in fitness than non-invasive species when resources were reduced (Table 4). This can be interpreted as meaning that non-invasive species show greater fitness homoeostasis. Even if the analysis is confined to the 63% of cases where the invasive species showed greater plasticity, in most cases P_{diff_fit} is still less than zero (Fig. 6b). We can therefore actively refute the Jack-of-all-trades hypothesis.
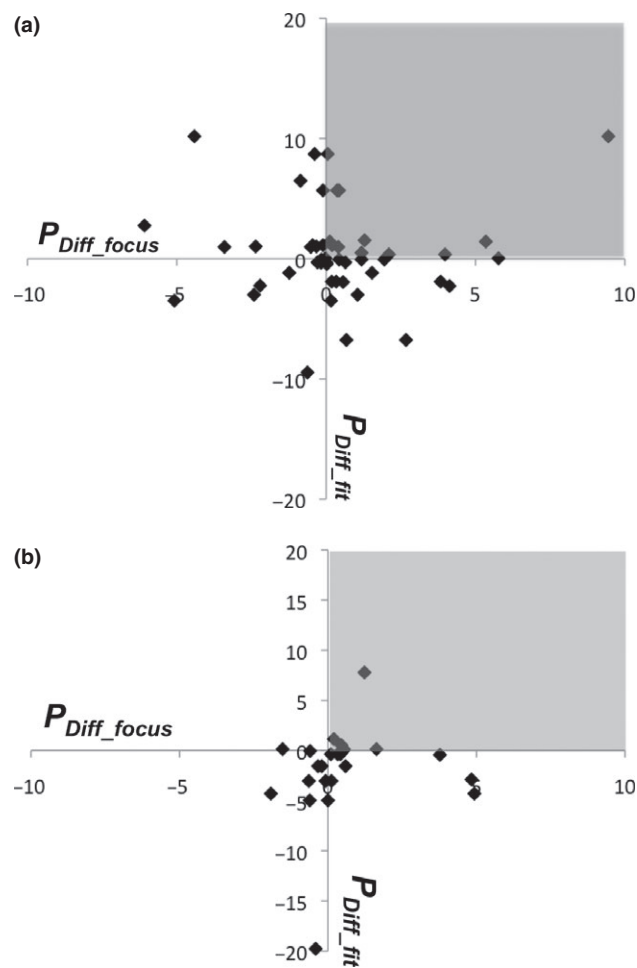
Figure 6 The relationship between P_{diff_focus} (relative plasticity of invasive vs. non-invasive species) and P_{diff_fit} (relative change in fitness of invasive vs. non-invasive species) in response to (a) increases in resources (Master-of-some) and (b) decreases in resource availability (Jack-of-all-trades). Positive P_{diff_focus} values indicate the invasive species is more plastic and positive P_{diff_fit} values indicate the invasive species has a better fitness response to a change in resources. The shaded quadrant is where points are expected to cluster if the Master-of-some and Jack-of-all-trades hypotheses are supported.

DISCUSSION

Our results indicate that invasive species do show greater phenotypic plasticity than non-invasive species. Perhaps surprisingly, this conclusion is not dependent on the type of response trait measured or the level of relatedness between invasive and non-invasive species. The higher plasticity of invasive species only sometimes resulted in their showing a greater gain in fitness than non-invasive species in response to a resource increase. In contrast, non-invasive species were more likely than invasive species to show an adaptive fitness response – that of fitness homoeostasis – in response to a decrease in resources.

Overall plasticity

Our meta-analysis strongly supports the general claim that invasive species are more phenotypically plastic than co-occurring non-invasive species across a wide range of growth, morphological, physiological and fitness related traits across several different types of environmental variation (Fig. 5). This result is concordant with the argument

that pioneering plants and plants that colonize new sites have inherently higher phenotypic plasticity than later settlers (Bazzaz 1979, 1996). The degree of phylogenetic relatedness between matched pairs of invasive and non-invasive species did not significantly affect our estimate of the effect of invasiveness on plasticity (Table 3). The most tightly controlled analysis is based on studies where species were paired at the genus level, and this produced the largest effect size estimate. The higher observed plasticity of invasive species is therefore not due to a taxonomic bias with invasive species being preferentially derived from clades with a tendency to show greater phenotypic plasticity than those from which non-invasive species were sampled.

When traits were assessed separately, invasive species had significantly higher phenotypic plasticity than non-invasive species for 6 of 11 traits, and the trend was in the same direction for all 11 traits (Fig. 5; Table 1). This is an interesting result given that it is generally argued that phenotypic plasticity is trait specific (Givnish 2002). Superficially this finding may suggest that the use of a composite measure of phenotypic plasticity (e.g. the species means used here) or a single trait can provide an effective indicator of relative differences in plasticity. We urge caution in extending this result, however, as it is likely to be dependent on the traits chosen being relevant to the specific nature of the investigation (e.g. treatment imposed, experiment set-up and species).

Plasticity and fitness analysis

It is difficult to draw conclusions about the adaptive significance of phenotypic plasticity, especially with respect to its role in successful plant invasions, unless the fitness consequences of phenotypic changes are measured (Richards *et al.* 2006; Nicotra & Davidson 2010). To this end, we tested the hypotheses of Richards *et al.* (2006) and Baker (1965) that greater plasticity provides a fitness advantage to invasive species in response to environmental changes. We found that despite invasive species generally showing greater phenotypic plasticity in focus traits when resource availability increased (a substitute for the Master-of-some scenario) this higher plasticity did not correlate with greater fitness gains.

When resources shifted from average to lower levels (the Jack-of-all-trades scenario), invasive species were still more plastic than non-invasive species ($P \approx 0.06$) but they rarely showed greater fitness homoeostasis than non-invasive species as predicted by the Jack-of-all-trades hypothesis. In fact, non-invasive species were significantly *more* likely to demonstrate fitness homoeostasis indicating the generally superior relative response of non-invasive species to poorer conditions. This is a surprising result, but provides a message of hope for restoration efforts and future scenarios under climate change. Of course, this presupposes that the absolute fitness (i.e. population growth rate) of invasive and non-invasive species is fairly similar under average conditions (because effect sizes measure the change in fitness relative to that under average conditions).

Greater fitness homoeostasis by non-invasive species under more stressful conditions where resources are limited is in line with Grime (1979)'s 'stress tolerator' plants. However, the C-S-R strategy (Grime 1979) is generally interpreted as suggesting that plants with a 'stress-tolerator' phenotype will be characterized by relatively low levels of phenotypic plasticity. Indeed, the notion that plants are unable to allocate resources to change their phenotype in response to an environmental change when resources availability is, on average, low is common in the plasticity literature (e.g. see deWitt *et al.* 1998).

However, Funk (2008) reported high phenotypic plasticity in both native, non-invasive and invasive plants from environments which on average are resource limited, likewise, our plasticity values were of a similar magnitude for the response to an increase as for the response to a decrease in resources for both the invasive and non-invasive species.

Data considerations

Although our results do not support the hypothesis that greater plasticity confers a fitness advantage to invasives, there are some caveats about our assessment of the relationship between plasticity in focus traits and fitness. First, in most studies, plants were grown in individual pots in the absence of competition. Second, we considered only the relative change in trait values, with no correction for any difference in mean trait values between invasive and non-invasive species. A recent meta-analysis of several of the traits measured in our meta-analysis found that, on average, invasive species showed higher mean values than pair-matched non-invasive native species (van Kleunen *et al.* 2009). For example, invasive species were larger and had higher SLA values. These larger trait values could mean that even when the relative fitness response to resource change is smaller in response to a resource increase (or the decline is greater in response to a resource decrease) for the invasive species compared with the non-invasive species, the average net fitness of the invasive might still be higher. It seems plausible that the combination of higher means and greater plasticity in many traits for invasive species could confer a significant fitness advantage when competing for resources (particularly when they are non-limiting), but that in the absence of competition this advantage is minimal.

We can identify two further constraints that limit our current ability to fully test the hypothesis which future research could alleviate. First, we did not exclude traits based on any *a priori* judgements (e.g. mechanistic models of plant function) about whether they were likely to display adaptive plasticity to a specific resource treatment. It is unlikely that plasticity in all traits is adaptive, and it has been suggested that the majority of phenotypic plasticity is actually selectively neutral (van Kleunen & Fisher 2005). Neutral plasticity can arise from environmental constraints that limit trait expression (Scheiner 1993) but do not affect fitness, or from linkage with other traits. Such linkage of traits is unimportant if the change in the linked trait is also adaptive but can complicate matters if it is not. Inclusion of all measured traits, even if they actually display neutral plasticity, was however, appropriate in both our overall plasticity analysis and our plasticity and fitness analyses to avoid introducing potential bias. In addition, the available data are limited so reducing the number of traits examined would have resulted in tests with very low statistical power. Future studies should therefore focus on measuring plasticity in traits that are assumed to have a strong effect on fitness, which ideally should be empirically tested.

Second, fitness proxies in our analysis were related to biomass or fecundity-related measures. Only 15% of studies provided any information on reproductive output or performance of the second generation (see Appendix S1). The paucity of accurate measures of fitness is a widespread problem in most areas of evolutionary ecology (review: Hunt & Hodgson 2010). Baker (1965, 1974) actually proposed that higher plasticity confers an advantage to invasive species over non-invasive species through seed production (larger increases in production in response to favourable conditions and

lower relative decreases under more stressful conditions). It was not possible to directly assess Baker's 1965 proposal as very few studies measured seed production. Such an enquiry would be valuable, however, given the importance of propagule pressure in many invasion processes (Burke & Grime 1996; Davis *et al.* 2000; Brown & Peet 2003; Lockwood *et al.* 2005).

In addition to methodological constraints, the results of our fitness and plasticity analyses might be partially explained by the theory that higher plasticity evolves in populations of an invasive species after colonization of the novel habitat rather than being a characteristic that preselects species as potential invaders (see Bossdorf *et al.* 2005; Richards *et al.* 2006 and references within). It is usually proposed that the evolutionary response would be very rapid and occur during the establishment stage (Richards *et al.* 2006). It is possible, however, that evolution of higher phenotypic plasticity could occur at a more moderate pace, or that higher plasticity evolves rapidly but that selection against traits that display maladaptive plasticity takes longer. This could explain why non-invasive species showed less plasticity but the plasticity that was expressed was more often associated with a smaller decline in fitness (i.e. non-invasives had a greater proportion of adaptive plasticity) compared to invasive species in response to a reduction in resources (Fig. 5a,b). The invasion histories of all the species used in this analysis are unknown but such information could enable analyses of the relationships between an invasive species' residency time, and the proportion of phenotypic plasticity in key traits that are an adaptive response to changes in resource availability. In addition, direct comparisons of phenotypic plasticity in invasive species between their native and introduced ranges could help to resolve how often there is evolution of adaptive plasticity post-colonization by invasive species.

Implications under climate change

The results of the fitness and plasticity analyses have important implications for predicting how invasive and non-invasive species might respond to projected climate changes and rising CO_2. It has been suggested that adaptive phenotypic plasticity confers greater tolerance to changing conditions (Ghalambor *et al.* 2007), either by enabling species to tolerate new environments and persist long enough to adapt, or by directly facilitating evolution through genetic assimilation (Waddington 1953; West-Eberhard 2005). Indeed, recent studies on arthropods (Chown *et al.* 2007) and birds (Charmantier *et al.* 2008) suggest that higher phenotypic plasticity is advantageous in tolerating novel conditions associated with climate change. As demonstrated in Fig. 6, however, showing greater plasticity did not always elevate relative fitness.

Some environmental changes, such as higher CO_2, lead to increased resource availability. Our analyses suggest that invasive species were marginally more likely to respond with adaptive plasticity to such an increase (Fig. 6a). Even if the higher plasticity of invasive species in response to increased resources only resulted in a greater fitness increase than that seen in non-invasive species half of the time, this suggests that we have an increasingly large weed problem on our hands. However, other global climate changes will create more stressful environments (e.g. increased rainfall variability) favouring species that maintain fitness homoeostasis. This ability was more often seen in non-invasive than invasive species (Fig. 6b). Of course, species that exhibit an adaptively plastic response to both favourable conditions and greater environmental stresses should thrive, particularly under

climate change. There is, however, little evidence for species that display such a Jack-and-master phenotype (Richards *et al.* 2006).

Future directions

Plasticity studies in glasshouses and field/common garden studies can yield important and relevant information for management of agricultural and conservation areas, but only if the manipulation of resource conditions is biologically meaningful. Studies are most useful when multiple conditions are selected that represent a range of resource levels that span very favourable to highly stressful resource levels. Ideally the extremes should include levels predicted to be potential future conditions (Hulme 2008; Schlichting 2008). This is particularly important if we are to make inferences about the value of phenotypic plasticity and its effect on species performance under future environmental conditions – due to greater urbanization, climate change or increased carbon dioxide levels (IPCC 2007). Such information would enable better assessment of the hypotheses of Richards *et al.* (2006).

As discussed above, our analyses of how plasticity affects fitness have to be interpreted with caution due to the limited availability of appropriate fitness data. It is major challenge to decide what measurement to use as a proxy for fitness, or whether the same trait instead should be assessed for adaptive plasticity. Without good fitness measures it is impossible to know if phenotypic plasticity in focal traits is adaptive. Future studies should therefore include explicit measures of fitness (albeit in variables based on measures of proxy traits). In the case of annual and short-lived perennial plant species estimates of fitness based on a plant's lifetime fecundity and, if possible, offspring viability would be particularly valuable.

CONCLUSION

Our meta-analysis indicates that invasive species generally have greater phenotypic plasticity than co-occurring non-invasives. This result is consistent across several traits and a range of resource conditions and is robust to the accuracy with which pairs of species are matched based on phylogenetic relatedness. Even so, the extent to which this greater phenotypic range facilitates survival under rapidly changing environmental conditions remains largely unknown. Further, in our dataset non-invasive species, were found to maintain fitness homoeostasis better than invasives under resource limited or stressful conditions.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

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

Appendix S1 Data source and raw data used in the calculation and comparison of phenotypic plasticity in invasive and noninvasive species.

Appendix S2 Complete references of all data sources used in the meta-analyses comparing plasticity of invasive species to non-invasive species.

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