

**REVIEW AND
SYNTHESIS****Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions**

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Abstract

Invasion biologists often suggest that phenotypic plasticity plays an important role in successful plant invasions. Assuming that plasticity enhances ecological niche breadth and therefore confers a fitness advantage, recent studies have posed two main hypotheses: (1) invasive species are more plastic than non-invasive or native ones; (2) populations in the introduced range of an invasive species have evolved greater plasticity than populations in the native range. These two hypotheses largely reflect the disparate interests of ecologists and evolutionary biologists. Because these sciences are typically interested in different temporal and spatial scales, we describe what is required to assess phenotypic plasticity at different levels. We explore the inevitable tradeoffs of experiments conducted at the genotype vs. species level, outline components of experimental design required to identify plasticity at different levels, and review some examples from the recent literature. Moreover, we suggest that a successful invader may benefit from plasticity as either (1) a Jack-of-all-trades, better able to maintain fitness in unfavourable environments; (2) a Master-of-some, better able to increase fitness in favourable environments; or (3) a Jack-and-master that combines some level of both abilities. This new framework can be applied when testing both ecological or evolutionary oriented hypotheses, and therefore promises to bridge the gap between the two perspectives.

Keywords

Adaptive evolution, adaptive phenotypic plasticity, ecological genetics, experimental design, fitness homeostasis, general-purpose genotype, genetic assimilation, genotype-environment interaction, invasiveness, molecular markers.

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INTRODUCTION

The number of plant species moved by humans across biogeographic barriers has increased dramatically in the last two centuries (Vitousek *et al.* 1996; Mack *et al.* 2000). Some of these species become extremely abundant in their new range, and cause major environmental and economic problems (Wilcove *et al.* 1998; Pimentel *et al.* 2000). Although interest in preventing and controlling such biological invasions has led to an explosion of scientific studies over the past decades, satisfactory explanations of differential introduction success remain elusive. One mechanism that has been frequently suggested in the context of plant invasions (Baker 1965; Rice & Mack 1991; Sexton *et al.* 2002; Sultan 2004), but has been infrequently investigated empirically, is phenotypic plasticity, the property of a

genotype to express different phenotypes in different environments (Bradshaw 1965; Schlichting 1986; Scheiner 1993; Pigliucci 2001, 2005).

Results from phenotypic plasticity studies indicate that plasticity could play an important role in invasions. In particular, many studies argue that plasticity enhances ecological niche breadth because plastic responses allow organisms to express advantageous phenotypes in a broader range of environments (Bradshaw 1965; Van Valen 1965; Whitlock 1996; Sultan *et al.* 1998a,b; Donohue *et al.* 2001; Sultan 2001; Richards *et al.* 2005). Recent studies also suggest that the evolution of plasticity in response to a set of environments may be beneficial in novel sites after colonization or migration (Agrawal 2001; Donohue *et al.* 2001, 2005; Etterson 2004; Yeh & Price 2004).

Invasion biologists refer to phenotypic plasticity in two distinct ways when attempting to explain plant invasions. Based on the arguments above – either explicitly or implicitly – they have posed two main hypotheses: (1) Invasive species may be more plastic than non-invasive or native ones (e.g. Marshall & Jain 1968; Williams *et al.* 1995; Durand & Goldstein 2001; McDowell 2002). This idea dates back to the ‘general-purpose genotype’ of Baker (1965), who suggested plasticity as one characteristic of an ‘ideal weed’. (2) Populations in the introduced range of an invasive species may evolve greater plasticity than populations in the native range (e.g. Kaufman & Smouse 2001; Sexton *et al.* 2002; Parker *et al.* 2003). If genetic variation for plasticity exists in introduced populations, and genotypes with more plasticity have a fitness advantage in the novel environment, this will cause evolution of increased plasticity. Generally, rapid evolutionary change appears to be common in invasive species (Brown & Marshall 1981; Thompson 1998; Mooney & Cleland 2001; Sakai *et al.* 2001; Lee 2002; Bossdorf *et al.* 2005), and rapid evolution of plasticity could play an important role in explaining their success. Clearly, these two hypotheses reflect to some extent the disparate interests of ecologists and evolutionary biologists.

Whether one is interested in cross-species comparisons or microevolution, there are two primary scenarios which describe how a different reaction norm might contribute to invasion success: (1) a Jack-of-all-trades situation, where through the plasticity of morphological or physiological traits, the invader is better able to maintain fitness in a variety of environments; (2) a Master-of-some situation, in which the plasticity of morphological or physiological traits allows the invader to take advantage of favourable environments; in addition, an invader might be (3) a Jack-and-master that combines some of both of these abilities. While each of these scenarios has been repeatedly mentioned in the literature, it is often not clear to which one invasion biologists are referring when they claim that some species or populations are ‘more plastic’ than others. However, it is important to make this distinction explicitly because each scenario makes different predictions about the shape of the reaction norms of invaders, relative to that of the respective controls.

In this review, we summarize the hypotheses about how plasticity might contribute to the success of invasive plants, and we outline what is necessary to test these hypotheses. We note that greater phenotypic plasticity is one of many possible hypotheses about the causes of invasion success in plants. The aim of this paper is not to advocate plasticity as *the* explanation for invasions, but to summarize existing ideas and discuss their conceptual and methodological basis as well as the evidence necessary to test them. To illustrate the different approaches, we use some examples from the recent literature on plasticity in invasives. However, our

review is by no means meant to be exhaustive. We briefly review the literature, evaluate the experimental evidence, and identify some promising questions for future research. Moreover, the concept of phenotypic plasticity has often been used imprecisely, and sometimes incorrectly, in this context. Therefore, clarification of some conceptual and methodological issues is needed before we can explore the role of plasticity in plant invasions.

THE CONCEPT OF PHENOTYPIC PLASTICITY

All the conceptual and empirical progress of the last decades notwithstanding, it is still common to encounter basic misconceptions about plasticity whenever the topic comes up for discussion. One such misconception is to view plasticity as an ‘alternative’ to genetic variation (see Macdonald & Chinnappa 1989; Pigliucci 2001). Plasticity is a trait – a property of a genotype – which can be visualized graphically as a pattern of expression in different environments (called a reaction norm). Like other traits, plasticity is subject to evolution by natural selection. Therefore, this dichotomy makes little sense.

Phenotypic plasticity refers to the potential of specific traits of a genotype to respond to different environments. This property can affect the performance and reproductive success of individual organisms, which in turn will impact the make-up of the next generation and thus contribute to evolution by natural selection. Because phenotypic plasticity is a property of specific *traits* in specific environments, it is incorrect to think of an organism or genotype *as a whole* as being more or less ‘plastic’ than others. A given genotype may be plastic for a certain trait in a certain set of environments, but not plastic for other traits in the same set of environments, or for the same trait in a different set of environments (Bradshaw 1965; Sultan 1995; Pigliucci 2001).

A special case that causes much confusion is the plasticity of fitness vs. non-fitness traits. Plasticity of morphological and physiological traits is unlikely to have any effect on invasiveness unless that plasticity contributes to fitness (Fig. 1). Natural selection will generally act to maintain high levels of fitness across environments. We can visualize a fitness reaction norm across environments and refer to changes in fitness across environments as ‘plasticity in fitness’. The resulting most favourable reaction norm for fitness, may be invariable or flat (fitness homeostasis; Hoffmann & Parsons 1991; Rejmánek 2000). Often, this type of flat fitness reaction norm may be achieved through plasticity in underlying morphological or physiological traits that influence fitness (Bradshaw 1965; Sultan 1995; e.g. Sultan *et al.* 1998b). In an effort to address this confusion, Fig. 1 illustrates the relationship between fitness traits and other morphological and physiological traits. In this figure,

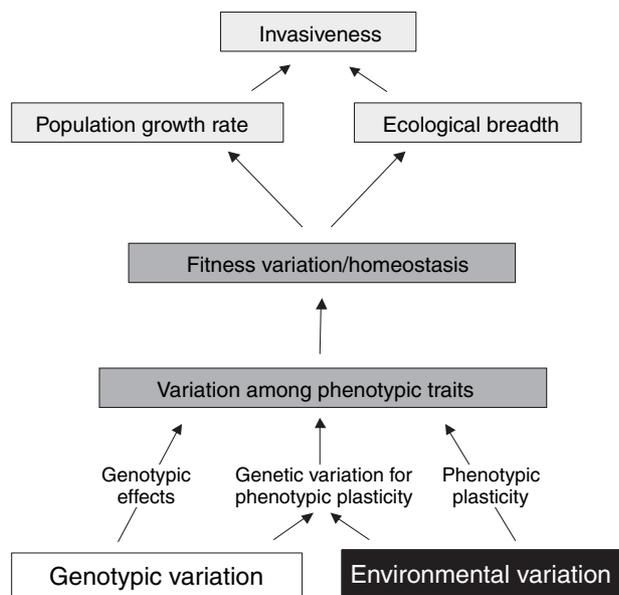


Figure 1 Overview of the relationships between environmental, genetic, phenotypic and fitness variation.

we attempt to make clear that plasticity of morphological and physiological traits is not only distinct from plasticity in fitness traits, but potentially may contribute to or control plasticity in fitness. Thus, there is no contradiction between observing plasticity for a specific morphological or physiological trait and lack of plasticity for a fitness component. In fact, this may be an indication that the observed plasticity in the underlying morphological or physiological trait is advantageous and possibly the result of natural selection (Bradshaw 1965; Sultan 1987, 1995; Pigliucci 2001).

Although the ability to respond to environmental variation is often beneficial, phenotypic plasticity, just like any other aspect of the phenotype, cannot automatically be assumed to be adaptive. It is adaptive plasticity, however, that is of particular importance for ecological and evolutionary studies. Clear cases of adaptive plasticity have been demonstrated (e.g. responses to shade in plants; Dudley & Schmitt 1996; Schmitt *et al.* 1999), while in other cases plasticity is non-adaptive (e.g. where induced responses in plants result in greater damage; Karban & Myers 1989). In cases where it is well established that plasticity in functional traits enhances survival and reproduction, this plasticity is considered adaptive (e.g. Sultan 1987, 1995; Pigliucci 2001; Griffith & Sultan 2005). A rigorous demonstration of adaptive plasticity requires establishing the same elements necessary for demonstrating that any trait is the result of evolution by natural selection: it must be heritable, there must be variation for it, and that variation must be related to fitness. This requires the use of several tools from the

conceptual and empirical arsenal of ecology and evolutionary biology, including common garden experiments, selection studies and the comparative phylogenetic method (see Dudley & Schmitt 1996; Schmitt *et al.* 1999; Sultan 2000; van Kleunen & Fischer 2005; Pigliucci 2005), and is thus a non-trivial task.

Determining the plasticity of target traits can be accomplished in several ways, from laboratory, greenhouse or garden experiments to reciprocal transplant experiments in the field (Pigliucci 2001). The minimum requirements are the ability to control environmental conditions and some level of variation and replication of the genetic material. Typically, researchers conduct factorial experiments that include the environmental treatments as fixed factors and the genetic components as random factors. A trait is considered plastic if the test (e.g. in an ANOVA) for the effect of an environmental factor on that trait is statistically significant. Genetic variation for plasticity in a trait is indicated by a significant statistical interaction between genetic origin and the environmental factor. Ideally, because plasticity in a trait is defined as the property of a genotype, experiments should be conducted by using clonal replicates. However, such clonal replicates are not available for many species, and it is therefore common procedure to study reaction norms of full sibs or half sibs.

Ecological studies on the role of plasticity in invasives often focus on phenotypic variation between populations or species in different environments and thus may include estimates of plasticity at the level of populations or species. Merely showing that there are phenotypic differences on average among a group of plants grown in different environments is not adequate to demonstrate or quantify plasticity. If plasticity is measured by comparing the average values for a trait across different genotypes grown in each environment, such higher-level estimates confound plasticity with components of genetic variation. Nevertheless, examination of species-level plasticity can be informative in a comparative framework as long as one interprets these data appropriately.

The disparity in plasticity estimates between evolutionary studies at the genotype level and ecological studies at the population or species level is related to what Levins (1966) described as the dilemma of model building in ecology: there is no way to be precise, realistic and general all at once. When evolutionary biologists study plasticity, they are interested in the genetic basis of plasticity, its potential and limits to evolve. Hence they aim for precision, while paying less attention to the realism of their experimental set-ups. The situation is reversed with ecologists, who sacrifice some precision in favour of a more realistic evaluation of the role of plasticity in natural populations and communities. In both cases, however, generality can be achieved by a comparative framework of study. Interesting and important

questions about the role of plasticity in natural populations can only be addressed by comparing plastic responses across genotypes, populations, or species. In contrast, because plasticity is a ubiquitous phenomenon (Bradshaw 1965; Pigliucci 2001), the frequently posed question ‘Is species (or genotype) X plastic with regard to environmental factor Y?’ asked in a non-comparative framework provides little biological insight. If we study the plasticity of one genotype in a controlled environment (neither realistic nor general), or of one species in an ecological study (neither precise nor general), then we merely document the existence of plasticity. Instead, we need to elucidate the degree to which invasive genotypes or species differ from non-invasive ones in their trait plasticity.

Plasticity may contribute to plant invasions in two ways: First, plasticity in ecologically important traits is thought to generally promote invasiveness (e.g. Baker 1965; Gerlach & Rice 2003). Second, plasticity in these ecologically important traits may evolve rapidly in introduced species and thereby contribute to spread and invasion success after a lag time (e.g. Agrawal 2001; Sexton *et al.* 2002). The first hypothesis is usually addressed with cross-species comparisons, the second with ecological genetic and quantitative genetic approaches. In the following, we will examine these two approaches in greater detail, including the specific hypotheses and experimental set-ups involved, and we will review and discuss some of the current empirical evidence in support of them.

IS THERE A RELATIONSHIP BETWEEN PLASTICITY AND INVASIVENESS?

Many of the fundamental ideas about the role of phenotypic plasticity in promoting invasiveness were presented over 40 years ago in Herbert Baker’s seminal paper on the characteristics of weeds (Baker 1965). Baker not only

anticipated some of the misconceptions about plasticity by making the important distinction between the plasticity of fitness and non-fitness traits, as discussed earlier (Fig. 1), he also recognized that there are two aspects to the response of fitness traits to environmental variation that might contribute to the success of an invader: (1) the ability to maintain fitness across a broad range of environments, a characteristic clearly related to the concepts of a ‘general purpose genotype’ (Baker 1965) and of fitness homeostasis (Hoffmann & Parsons 1991; Rejmánek 2000); and (2) the ability to increase fitness in favourable environments (see for example, Sultan 2001). The first characteristic stresses the importance of robustness under unfavourable conditions, the second stresses opportunism under favourable conditions. Both characteristics, if they contribute to invasion success, lead to specific, testable predictions about the shape of the fitness reaction norm of an invader, relative to that of other, less successful species. The specific morphological and physiological traits that contribute to these patterns of fitness response can also be evaluated in this context. If robust fitness is the key to success, then we expect a Jack-of-all-trades situation, where plasticity in morphological and physiological traits allows the fitness of the invader to remain relatively constant across environments, in contrast to less effective invaders which perform poorly in certain environments (Fig. 2a). In contrast, if the success of an invader is due to its ability to rapidly take advantage of available resources, then we expect a different pattern of reaction norms where, relative to other species, the invader shows a greater fitness response to favourable conditions (Fig. 2b). To contrast this with the Jack-of-all-trades, we call this the Master-of-some scenario. Since these two scenarios tend to be concerned with opposite ends of the resource gradient, they are not mutually exclusive. By tying the two abilities together we can envision the fitness reaction norm of Baker’s ideal weed,

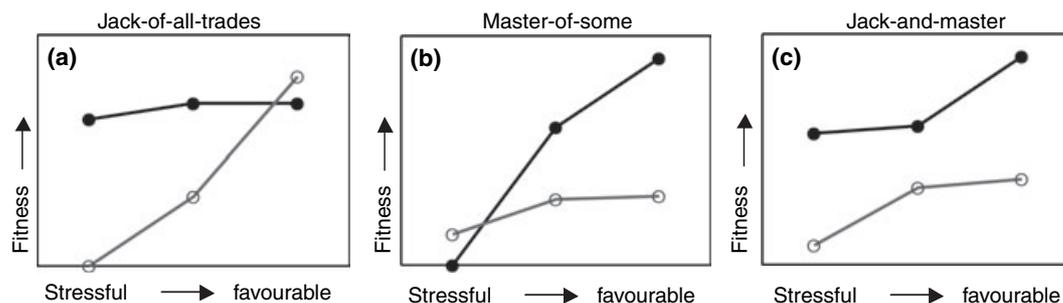


Figure 2 Expectations for fitness plasticity of invasive (black line) vs. non-invasive (grey line) genotypes/populations/species must qualitatively resemble one (or both) of two patterns: (a) invasives have more robust fitness in the face of stressful environmental conditions, possibly conferring greater ecological breadth (Jack-of-all-trades); or (b) invasives are better able to respond with increased fitness in favourable conditions, possibly allowing for higher population densities under favourable conditions (Master-of-some); (c) it is also conceivable to envision a fitness norm-of-reaction that has characteristics of both robustness and responsiveness (Jack-and-master).

a Jack-and-master that exhibits a relatively insensitive (non-plastic) fitness response to harsh conditions, yet is flexible (plastic) enough to exploit favourable environments and increase its fitness (Fig. 2c).

The scenarios outlined above can be tested through greenhouse or field common garden experiments that measure the plasticity of invasive species relative to a control group of native species or other, non-invasive, introduced species. If the fitness response of invasives across environments is consistently different than the fitness response of natives across environments, this will be indicated by a significant statistical interaction between environmental treatment and plant status (native vs. non-native, invasive vs. non-invasive). Comparing the different species' reaction norms will allow us to discriminate between the different scenarios (Fig. 2): if the fitness responses of invaders have smaller slopes or are less variable across environments, and this results in the invasives having higher fitness in unfavourable environments, then we have a Jack-of-all-trades situation. If the invasives have steeper slopes or are more variable across environments, and this results in higher fitness in favourable environments, this suggests a Master-of-some scenario. In the simplest case of only two experimental treatment levels (almost all published studies), we cannot easily differentiate between the Master-of-some and the third scenario, Jack-and-master. To do so may require at least three treatments along a resource gradient.

It is worth pointing out that plasticity of different fitness traits in response to a particular environmental gradient may resemble different scenarios (e.g. seed number may be robust across a phosphorus gradient while seed size is opportunistic). Conversely, one fitness trait may conform to different scenarios when examined under different kinds of environmental gradients (e.g. seed number may be robust across a phosphorus gradient and opportunistic across a nitrogen gradient). The framework described above relates to how fitness of invasives and control groups varies across one or a few environmental axes. Because we are not considering the variety of habitat types where the species might be found in the field, there is no necessary equivalence between any of the described scenarios (i.e. Jack-of-all-trades, Master-of-some, Jack-and-master) and the ecological concepts of generalists vs. specialists. The relationships between the utilitarian framework we present here and the broader issue of how plasticity contributes to the evolutionary differentiation of niche-space or life-history strategies are interesting, but beyond the scope of this paper.

The choice of the control group is a critical step in comparative experiments, because different comparisons will answer slightly different ecological questions. Many previous studies on the plasticity of invaders (see Table 1 for an overview) have made comparisons between invasive

and native species (e.g. Williams & Black 1994; Pattison *et al.* 1998; Milberg *et al.* 1999; Schweitzer & Larson 1999; Gleason & Ares 2004; Wilson *et al.* 2004; Brock *et al.* 2005; Leishman & Thomson 2005) and thereby addressed the general role of plasticity in the superiority of invasives over their new neighbours. Naturally, because a species native to one area may be invasive in another one, the results of these studies, and the conclusions drawn about the role of plasticity in invasion success, are always specific to the particular geographic area considered. For instance, Leishman & Thomson (2005) compared the response to water and nutrient manipulations of seven native and 10 exotic species of an Australian bushland community. The invasive exotics consistently showed the greatest biomass increase after nutrient addition, suggesting that the success of the invasives may be due to a superior opportunistic (Master-of-some) response to favourable conditions.

To reduce the confounding of ecological differences with those attributable to phylogeny (Harvey 1996; Hamilton *et al.* 2005), some of the previous studies (see Table 1) made comparisons only between related species. An elegant example is the study of Milberg *et al.* (1999) who grew five exotic and five native annual Asteraceae at 10 different nutrient levels. There was a strong statistical interaction between nutrient levels and invasiveness: invasive species generally showed greater biomass increase at high nutrient levels than native species, which suggested a Master-of-some superiority of invasives. The authors also tested for a Jack-of-all-trades pattern across environments and found no differences between native and invasive species in this respect.

The experiments described above used native species as controls when investigating the plasticity of invasive species. However, some studies have taken a different approach and compared invasive species to other, non-invasive exotics (e.g. Gerlach & Rice 2003; Burns 2004; Hastwell & Panetta 2005; N.Z. Muth, unpublished data). Clearly, this approach is more appropriate for asking questions about the role of plasticity in determining relative invasion success. For instance, N.Z. Muth (unpublished data) compared the fitness responses of five invasive and four non-invasive Asteraceae to variation in phosphorus and water availability (Fig. 3). He found that the reaction norms of invasive and non-invasive species differed, but the specific pattern depended on the genus: while invasive *Centaurea* species showed a Jack-of-all-trades pattern, the response of a different fitness variable in invasive *Crepis* species resembled a Master-of-some pattern when compared with non-invasive congeners. In another recent study, Hastwell & Panetta (2005) investigated the response to nutrients of 10 congeneric pairs of exotic species where one species was invasive and the other non-invasive. There was no evidence for a general trend of invasive exotics having a

Table 1 Studies that address the role of phenotypic plasticity in plant invasions by comparing exotic species with unrelated or related native species, or other exotic but non-invasive species, or by comparing invasive and native populations of an exotic species. These were controlled experiments in a common garden or greenhouse that included a manipulation of abiotic factors and a statistical test for differences in plasticity between the respective groups.

Plastic response to?	Number of life forms compared	Variables measured	Results for fitness traits	References
<i>Invasive exotic vs. unrelated native species</i>				
Water	1/1 (Grasses)	Biomass, photosynthesis, water potential	No pattern	Williams & Black (1994)
Light	5/4 (Various)	Growth, photosynthesis	No fitness measured	Pattison <i>et al.</i> (1998)
Light	1/1 (Trees)	Growth, nutrient content, photosynthesis	(+) Carbohydrate mass (Master-of-some)	Gleason & Ares (2004)
Nutrients, water	10/7 (Various)	Biomass, nutrient contents, survival	(+) Survival (Master-of-some)	Leishman & Thomson (2005)
<i>Invasive exotic vs. related native species</i>				
Nutrients	5/5 (Herbs)	Biomass, survival	(+) Biomass (Master-of-some)	Milberg <i>et al.</i> (1999)
Climbing support	1/1 (Vines)	Biomass, morphology, photosynthesis	(+) Biomass (Jack-and-master)	Schweitzer & Larson (1999)
Water	1/1 (Herbs)	Biomass, nutrient contents, photosynthesis	(+) Biomass (Jack-and-master)	Wilson <i>et al.</i> (2004)
Light	1/1 (Herbs)	Dispersal, morphology, phenology	No pattern	Brock <i>et al.</i> (2005)
<i>Invasive exotic vs. non-invasive exotic species</i>				
Gap size	1/2 (Herbs)	Biomass, reproduction	(+) Number of inflorescences (Jack-and-master) and biomass (Master-of-some)	Gerlach & Rice (2003)
Nutrients, water	3/3 (Herbs)	Biomass, growth	No pattern	Burns (2004)
Nutrients	12/12 (Grasses, herbs)	Biomass, survival	No pattern	Hastwell & Panetta (2005)
Nutrients, water	5/4 (Herbs)	Biomass, morphology, phenology, fitness	(+) Inflorescence width (Jack-of-all-trades) and number of inflorescences (Master-of-some)	N.Z. Muth, unpublished data
<i>Invasive vs. native populations of exotic species</i>				
Water, pH	4/3 (Tree)	Biomass, growth	(+) Biomass (Master-of-some)	Kaufman & Smouse (2001)
Light	4/4 (Shrub)	Biomass, growth, photosynthesis	No pattern	DeWalt <i>et al.</i> (2004)
Light	8/8 (Herbs)	Biomass, morphology	No pattern	O. Bossdorf <i>et al.</i> , unpublished data

Sample size = numbers of invasive/native species or populations compared.

+, Invasive species/populations more plastic than native species/populations.

No pattern = fitness plasticity of native and invasive species/populations does not differ.

different response to nutrient addition than non-invasive exotics.

Overall, most published studies that have compared the plasticity of invasive species to that of native species or other, non-invasive exotics, support the hypothesis that invaders generally are more plastic for traits affecting fitness in response to ecologically relevant environments. Generally, studies reported higher levels of plasticity in physiological and morphological traits in the invasives, while no study reported the opposite (Table 1). We also attempt-

ed, where possible, to recast the results of these papers in the terms of the introduced framework. In so doing, we found evidence suggesting the existence of Jack-of-all-trades, Master-of-some, and Jack-and-master (Table 1), although many studies did not measure fitness and therefore cannot be assigned to one of the three strategies. A few studies reviewed here find evidence for more than one of our plasticity strategies acting concurrently (Gerlach & Rice 2003, N.Z. Muth, unpublished data). However, further evaluation of the prevalence and magnitude of these

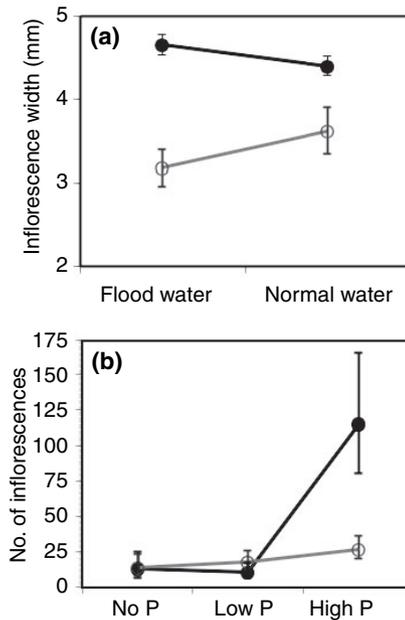


Figure 3 (a) Average fitness response (inflorescence width) of two invasive (black line) and two non-invasive (grey line) *Centaurea* species to variation in water availability resembles a Jack-of-all-trades. (b) Average fitness response (number of inflorescences) of two invasive (black line) and two non-invasive (grey line) *Crepis* species to variation in Phosphorus availability resembles a Master-of-some.

plasticity responses would require an appropriate quantitative synthesis of the results, which is beyond the scope of this study.

IS THERE EVIDENCE FOR THE EVOLUTION OF PLASTICITY DURING INVASIONS?

Ecological studies, such as the ones described above, cannot determine whether an advantageous reaction norm of an invasive plant species was present already in its native range, or whether it evolved in the introduced range. Adaptive evolutionary change can be very rapid, and this might be particularly important in biological invasions, which often involve drastic changes in selection regimes (Brown & Marshall 1981; Thompson 1998; Mooney & Cleland 2001; Reznick & Ghalambor 2001; Sakai *et al.* 2001; Lee 2002). Many of the species that become invasive do so after a lag time (Kowarik 1995; Williamson 1996; Mack *et al.* 2000), perhaps after evolutionary adjustments have taken place. While there is now increasing evidence for genetic change in invasive plants in terms of growth, competitive ability, and herbivore defence (e.g. Blossey & Nötzold 1995; Daehler & Strong 1997; Callaway & Aschehoug 2000; Siemann & Rogers 2001; Bossdorf *et al.* 2004a,b), phenotypic plasticity has received much less attention in this context. To the

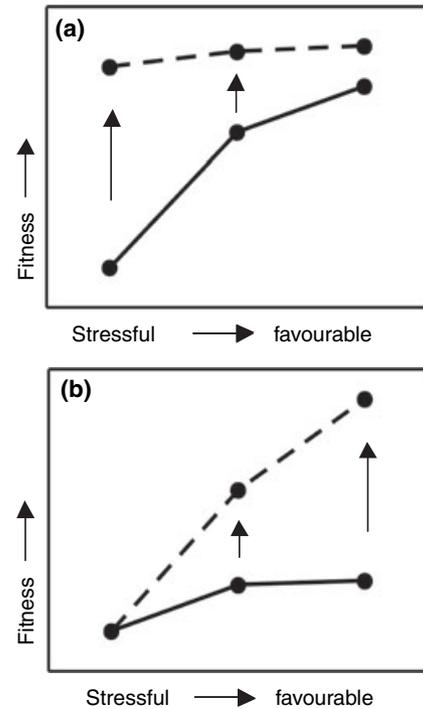


Figure 4 As evolution of the introduced population may occur at any stage of the introduction pathway, trait plasticity to various environments may be significantly altered from initial states (solid line) to some descendant condition (dashed line). Specifically, natural selection may be expected to shift the evolution of fitness plasticity towards: (a) decreased fitness plasticity (increased 'fitness homeostasis') to stressful conditions; and/or (b) increased fitness plasticity towards responding positively to favourable conditions. These possibilities would hold for any population, introduced or otherwise.

extent to which the environment of the invaded range is likely to differ from the native, plasticity may be advantageous and thus selected for, at least initially. If certain norms of reaction confer a fitness advantage in novel environments, then plasticity will evolve in invasive populations. Here, again, we can conceive of three major scenarios: (1) evolution of greater robustness, i.e. of a flatter Jack-of-all-trades fitness reaction norm (Fig. 4a); (2) evolution of greater opportunism, i.e. of a more pronounced Master-of-some fitness reaction norm with a steeper slope (Fig. 4b); or (3) a combination of the two, i.e. a Jack-and-Master. Which of these scenarios is more likely depends on the nature of the particular invasion studied.

The experimental approaches needed to test these evolutionary predictions are similar to those for more strictly ecological studies, with the difference that one would not compare the environmental responses of different species, but those of different genetic origins of the same invasive species in a common environment. Often, these

genetic origins are not exact genetic replicates but some kind of siblings (e.g. seed families) or even populations. One way to investigate evolutionary change in the plasticity of invaders is to compare random samples of genotypes or populations from the native and introduced ranges and test for a continental origin-by-environment interaction (e.g. in an ANOVA). Because multiple introductions seem to be frequent in invasive plants (Bossdorf *et al.* 2005), such random samples are the best solution if the invasion history of a species is not known. There are only a few published studies that have used this approach (Table 1). Kaufman & Smouse (2001) compared the growth of native Australian and introduced US populations of the invasive tree *Melaleuca quinquenervia* at different water and pH levels. There was some indication that invasive populations were more plastic in response to variation in pH. In another recent study, DeWalt *et al.* (2004) compared plasticity in growth and photosynthesis to shading in native vs. introduced populations of the invasive tropical shrub *Clidemia hirta* and found no evidence for evolution of plasticity in invasive populations. A similar shading experiment with garlic mustard (*Alliaria petiolata*) found no overall difference in plasticity of biomass or morphology between native European and invasive US populations, in spite of significant genetic variation for plasticity in these traits within and among populations (Fig. 5; O. Bossdorf, unpublished data).

There are other ways to test for evolution of plasticity in invaders. If the invasion history of a species is well known, studying a sequence of older to more recently introduced populations might reveal evolution of plasticity through time

(Barrett & Shore 1989; Daehler & Strong 1997). Alternatively, if there has been a single introduction, the invasive populations could be compared with the known founder population. An important tool in this context is a survey of neutral genetic markers, not only because they will help elucidate pathways of introduction (e.g. Novak & Mack 1993; DeWalt & Hamrick 2004; Durka *et al.* 2005; Williams *et al.* 2005), but also because they inform about other genetic processes that may contribute to genetic change in the introduced range, such as founder effects (Brown & Marshall 1981; Barrett & Husband 1990) and inter- or intraspecific hybridization (Ellstrand & Schierenbeck 2000). However, we know of no published study that, based on information from molecular markers, tested for evolution of plasticity specifically within the introduced range. A number of studies have investigated variation for plasticity among different populations from the introduced range (e.g. Rice & Mack 1991; Williams *et al.* 1995; Sexton *et al.* 2002; Parker *et al.* 2003), but without reference to a particular invasion history. These studies usually demonstrate that the invasive species of interest had a broad ecological range and that there was genetic variation for plasticity, i.e. potential for evolutionary change, in the introduced range. However, without comparisons to native populations of the same species or native species from the invaded habitat it is not possible to draw conclusions about the role of plasticity in a particular invasion.

An additional complication in assessing the potential role of phenotypic plasticity in invasions could carry broad implications for our understanding of the invasion process in general. In the arguments above, we have generally

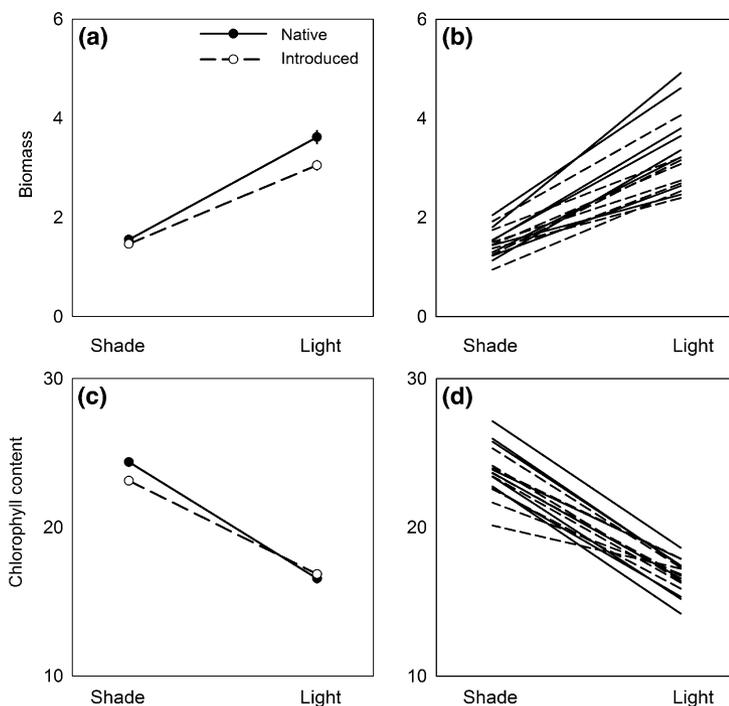


Figure 5 Plasticity to shading in native vs. introduced populations of garlic mustard (*Alliaria petiolata*). Displayed are the continental (+1 SE; a,c) and population (b,d) averages of plants grown at 15% (Shade) or 85% (Light) photosynthetically active radiation for 10 weeks.

assumed that if plasticity is beneficial, it will remain so. However, it is possible that plasticity is beneficial only in an initial stage of an invasion (see e.g. the conceptual model by Sexton *et al.* 2002), but selected against at a later stage due to costs of plasticity (van Tienderen 1991; DeWitt *et al.* 1998). Thus, while plasticity may be a bridge into a novel environment, it may be eventually lost through genetic assimilation of a fitter, less plastic genotype (Waddington 1942; see recent reviews by Pigliucci & Murren 2003; West-Eberhard 2003). Genetic assimilation refers to a mechanism of evolutionary change that turns a plastic response into a genetically invariant one through continued selection for stable expression of the trait under new environmental conditions (Waddington 1942, 1961; see Pigliucci & Murren 2003; West-Eberhard 2003).

Genetic assimilation has particular relevance for plant invasions because invasive species are exposed to novel environmental conditions that may elicit novel phenotypes through phenotypic plasticity. If the novel phenotype increases the organism's fitness in the invaded habitat, it is selected for. The continued process of fine-tuning of the phenotype by selection in the new environment and lack of exposure to the original environment may result in the novel phenotype being stably expressed in the invaded habitat. Plasticity in the trait may be progressively reduced either by a random accumulation of non-lethal mutations, or because of active selection to reduce plasticity, if it is costly. Over time, those individuals that can exhibit the novel phenotype will survive, even if they do not have the same degree of plasticity for that trait that allowed for the initial individuals to accommodate the novel conditions. Although induced defences do not necessarily serve as a bridge into a novel environment, they may serve as a relevant example of this process. Induced defences are a type of plasticity that may be eventually lost because it is less beneficial if invasive plants are released from their specialized herbivores (Keane & Crawley 2002; Mitchell & Power 2003). To our knowledge, no one has attempted to address this possibility, for instance by measuring plasticity and its costs across a chronological sequence of invasive populations.

TESTING FOR THE ROLE OF PLASTICITY IN INVASIONS: SOME RECOMMENDATIONS

It is important to stress again that phenotypic plasticity is a common phenomenon (Sultan 2000; Pigliucci 2001; Schlichting 2002), therefore ecological insight into the role of plasticity in invasions will be gained only if (a) the plasticity in morphological and physiological traits is related to fitness; and (b) the plastic response in invaders is measured relative to that of non-invasive species or genotypes. Experiments without adequate comparisons

simply document the (unsurprising) existence of plasticity or genetic variation for plasticity.

To test the hypothesis that plasticity in ecological traits contributes to invasiveness, and therefore that invasive species will exhibit greater plasticity in major morphological and physiological traits, a study should ideally compare multiple species, in an appropriate environmental context, with appropriate native or non-invasive exotic species that serve as controls. Because of a potential confounding between ecological differences and phylogenetic effects (Harvey 1996; Hamilton *et al.* 2005), the value of such multi-species comparisons is greatly strengthened if they are made between relatives (see Table 1 for examples). Furthermore, although ecological studies will maximize generality across species by sacrificing precision at the genotype level, the choice of genetic material should be representative for each of the species. To understand the overall generality and importance of phenotypic plasticity in biological invasions, many more such studies will have to be done, and the results combined using appropriate methods for quantitative research synthesis, such as meta-analysis (Gurevitch & Hedges 1999; Gurevitch *et al.* 2001).

While ecological studies sacrifice precision, evolutionary studies sacrifice generality to gain the precision required to address the hypothesis that invasive species may have evolved higher levels of phenotypic plasticity in their introduced range. The crucial issue here is having sufficient replication at the population level. If the invasion history of a species is unknown – which is often the case (Bossdorf *et al.* 2005), or there have been multiple introductions, then comparisons should be made between random samples of native and introduced populations. Because effect sizes (i.e. microevolutionary changes) are often small in such studies, and at the same time there is often considerable population variation, comparisons of fewer than 10 native and introduced populations will frequently lack the statistical power to detect genetic differences between the native and introduced range.

Evolutionary changes in invaders not only depend on novel selection regimes, but also on the initial genetic material. Ideally, therefore, one should first use neutral markers to clarify the pathways of introduction for an invasive species before deciding upon which native and introduced populations to compare. Moreover, when making predictions about the evolution of plasticity in invasive plant populations, genetic assimilation, the evolutionary loss of plasticity after successful colonization of a novel environment, should be taken into account as an alternative scenario.

Decisions about which morphological, physiological and fitness traits as well as environmental treatments to focus on will always have to be tailored to the specific study system. Biological knowledge will inform which sets of

environmental parameters are likely to be the most relevant ones regarding the role of plasticity in a particular invasion. The selective environment of the invaded habitat is likely to vary from that of the native habitat, and identifying those differences will inform decisions about which environmental treatments and traits may be relevant. For example, garlic mustard (*Alliaria petiolata*) is often reported to be more frequently occurring in forest understories in its invasive North American range than in its native European range (e.g. Nuzzo 2000). This led O. Bossdorf (unpublished data) to hypothesize that invasive populations may have evolved trait responses, which maintain fitness across a broader range of light conditions, which he could investigate in a controlled greenhouse experiment (Fig. 5).

Finally, in either ecological or evolutionary studies, demonstrating that invasive species are more plastic than native ones, or that invasive populations are genetically differentiated from native populations, does not automatically prove that these differences are a prime cause of invasion success. To do the latter in ecological studies, one would have to demonstrate in additional ecological experiments the relative importance of trait or fitness plasticity to invasion success compared with other ecological traits and mechanisms. A pivotal step in evolutionary studies would be to use reciprocal transplant and selection studies to show that increased plasticity in the invasive is in fact adaptive in natural populations.

CONCLUSIONS AND FUTURE DIRECTIONS

Baker (1965) presents two different ideas about how the reaction norm of an invader may contribute to invasion success. First, invasive species or populations may be better able to maintain fitness under harsh conditions, i.e. they may have a flatter fitness reaction norm due to plasticity in underlying morphological or physiological traits. We call this the Jack-of-all-trades scenario. Second, invasive species or populations may have morphological or physiological trait plasticity that allows for a greater ability to increase fitness in favourable environments, i.e. a steeper and higher fitness reaction norm. We call this the Master-of-some scenario. Furthermore, as fitness norms of reaction may contain elements of both robustness and opportunism, a third scenario, that of Jack-and-master, is also possible. Unfortunately, since Baker (1965), these two concepts have been poorly connected. While some previous studies of invasive species have framed their analyses around expectations of robustness (e.g. Williams & Black 1994; Schweitzer & Larson 1999; Brock *et al.* 2005) and others have looked for opportunistic responses (e.g. Burns 2004; Hastwell & Panetta 2005; Leishman & Thomson 2005), only a handful of studies have expressly discussed the potential for *both*

robustness and opportunism (Pattison *et al.* 1998; Milberg *et al.* 1999; Gerlach & Rice 2003). Clearly, this should be done more often in the future.

Assuming that morphological and physiological trait plasticity ultimately confers a fitness advantage, invasion biologists have posed two main hypotheses: (1) on average, invasive species may have more trait plasticity than non-invasive or native ones; (2) populations in the introduced range of an invasive species may have evolved greater plasticity than populations in the native range. Obviously, these two hypotheses reflect the disparate interests of ecologists and evolutionary biologists. Testing the first hypothesis requires multi-species ecological experiments, whereas testing the latter requires input from ecological genetics. Inevitably, the two approaches differ in the precision of their plasticity estimates. However, with a rigorous experimental design and a careful evaluation of the results, both can be of great value. Many of the studies that have previously addressed the role of plasticity in invasions have reported increased levels of plasticity in invasive species or invasive populations. However, because the overall evidence is still very limited, it seems too early to draw any general conclusions from these results.

Another reason why previous results should be summarized with caution is that there is likely a bias towards publishing positive results. There are a number of additional studies that tested for differences in plasticity between native and introduced populations without emphasizing this component of their results (e.g. van Kleunen & Schmid 2003; Leger & Rice 2003; Vila *et al.* 2003; Blair & Wolfe 2004; Bossdorf *et al.* 2004a). All of these studies manipulated at least one environmental factor and provided a statistical test for the interaction between this factor and continent of origin. Interestingly, most of these studies report no differences in plasticity (no $G \times E$) but do not explicitly discuss the importance of this finding.

While previous research on plasticity in invasive species has often addressed either the ecological *or* the evolutionary aspect of the invader, the two need not be separated. On the contrary, a melding of the two approaches should prove highly fruitful. Adding a species-level comparison with the quantitative genetic approach would bring a much needed comparative perspective to evolutionary ecological studies. Or, from a different point of view, incorporating replicate populations into ecological studies would provide an estimate of within-species variation, and thus an assessment of how representative the observed species differences are. A rare example of this approach is the recent work by Sonia Sultan and her co-workers on phenotypic plasticity in four closely related exotic *Polygonum* species (Sultan *et al.* 1998a,b; Bell & Sultan 1999; Sultan 2001). By carefully designed greenhouse studies of genotypes replicated across controlled environments, Sultan found that the degree of plasticity in

ecologically important morphological and physiological traits were indeed correlated with the breadth of each species' ecological distribution in the field. One of these species, *Polygonum cespitosum* (*Persicaria cespitosa*, Ronse Decraene & Akeroyd 1988; Lamb Frye & Kron 2003) is becoming aggressive in the Northeastern USA and is now considered a 'potential invader' K. Barringer, Brooklyn Botanical Gardens, personal communication). Although these studies were not conducted with the immediate purpose of investigating potential invasion success, Sultan (2001) expressly described *P. cespitosum* as able 'to both maintain fitness in resource-poor environments and opportunistically maximize fitness in favourable conditions', i.e. as a Jack-and-master.

The goal of invasive species research is to increase our understanding of invasion success, and hence our ability to predict invasions. We suggest that the melding of higher-level population and community ecological questions with the rigorous methods of ecological and quantitative genetics will be an important step in this direction. It will allow us to explore questions with far greater precision, realism and generality than either field has been able to accomplish on its own, and eventually to paint a more accurate and relevant picture of the nature of plant invasions.

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