

# Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments

C. K. GHALAMBOR\*†, J. K. MCKAY‡, S. P. CARROLL§ and D. N. REZNICK¶

\*Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA, ‡Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA, §Department of Entomology, Center for Population Biology, University of California-Davis, Davis, CA 95616, USA, ¶Department of Biology, University of California-Riverside, Riverside, CA 92521, USA

## Summary

1. The role of phenotypic plasticity in evolution has historically been a contentious issue because of debate over whether plasticity shields genotypes from selection or generates novel opportunities for selection to act. Because plasticity encompasses diverse adaptive and non-adaptive responses to environmental variation, no single conceptual framework adequately predicts the diverse roles of plasticity in evolutionary change.
2. Different types of phenotypic plasticity can uniquely contribute to adaptive evolution when populations are faced with new or altered environments. Adaptive plasticity should promote establishment and persistence in a new environment, but depending on how close the plastic response is to the new favoured phenotypic optimum dictates whether directional selection will cause adaptive divergence between populations. Further, non-adaptive plasticity in response to stressful environments can result in a mean phenotypic response being further away from the favoured optimum or alternatively increase the variance around the mean due to the expression of cryptic genetic variation. The expression of cryptic genetic variation can facilitate adaptive evolution if by chance it results in a fitter phenotype.
3. We conclude that adaptive plasticity that places populations close enough to a new phenotypic optimum for directional selection to act is the only plasticity that predictably enhances fitness and is most likely to facilitate adaptive evolution on ecological time-scales in new environments. However, this type of plasticity is likely to be the product of past selection on variation that may have been initially non-adaptive.
4. We end with suggestions on how future empirical studies can be designed to better test the importance of different kinds of plasticity to adaptive evolution.

*Key-words:* phenotypic plasticity, contemporary adaptation, genotype × environment interaction, adaptive divergence, genetic assimilation

*Functional Ecology* (2007) **21**, 394–407  
doi: 10.1111/j.1365-2435.2007.01283.x

## Introduction

A traditional perspective in evolutionary biology is of genes 'leading', and phenotypes 'following' in the process of adaptive evolution. Evolution is by definition a change in allele frequencies and therefore sufficient heritable genetic variation must exist for evolution by natural selection to occur. Accordingly, the conventional perspective on adaptive evolution focuses almost exclu-

sively on the role of allelic substitution or quantitative genetic variation (Pigliucci & Murren 2003; Schlichting 2004). As a consequence, selection that acts on non-heritable phenotypic variation in a population is often regarded as selection that does not produce an evolutionary response (e.g. Endler 1986, pp. 12–15), and has been historically dismissed as unimportant in adaptive evolution (e.g. Wright 1931; Simpson 1953; Williams 1966). Within this context, environmentally induced variation has been thought to constrain or slow the rate of adaptive evolution by shielding the genotype from the effects of selection (e.g. Grant 1977; Falconer 1981; Levin 1988).

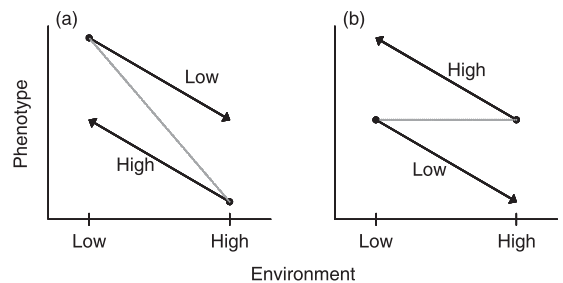
An alternative perspective on adaptive evolution argues that phenotypic variation, even when environmentally induced and not under strict genetic control, plays an important role in creating the conditions that result in an adaptive genetic response (i.e. ‘genes as followers’ West-Eberhard 2003). This suggests that environmentally induced non-heritable variation such as phenotypic plasticity or learning is initially established in a population, and later becomes genetically ‘assimilated’ such that the environmental stimulus previously required to produce the trait is no longer required (Baldwin 1896; Waddington 1942, 1952, 1953, 1956, 1959; Schmalhausen 1949). From this perspective, plasticity may facilitate or even speed up the process of adaptive evolution (reviewed in Robinson & Dukas 1999; Pigliucci & Murren 2003; Price, Qvarnstrom & Irwin 2003; West-Eberhard 2003; Schlichting 2004; Badyaev 2005).

In this paper we examine the role of phenotypic plasticity in adaptive evolution by contrasting different types of plasticity (adaptive vs non-adaptive) and how each may facilitate or constrain the process of adaptive evolution in new environments. In recent years the topic of phenotypic plasticity and evolution has been the subject of extensive review in both books (Schlichting & Pigliucci 1998; Pigliucci 2001; West-Eberhard 2003; DeWitt & Scheiner 2004) and review articles (e.g. Thompson 1991; Sultan 1995; DeWitt, Sih & Wilson 1998; Robinson & Dukas 1999; Pigliucci & Murren 2003; Price *et al.* 2003; Schlichting 2004; Badyaev 2005; de Jong 2005; Grether 2005; van Kleunen & Fischer 2005). We primarily focus our efforts on the role of plasticity that is likely to play in the initial stages of a population becoming established in a new environment and the consequence of this plasticity for adaptive evolution. We take this approach because: (i) most cases of contemporary adaptation have occurred within the ecological framework of colonization of new environments (e.g. Reznick & Ghalambor 2001), (ii) a body of theoretical and empirical work has focused on this perspective (e.g. Price *et al.* 2003; Parsons & Robinson 2006), and (iii) the lessons learned have direct application to understand the processes that occur in biological invasions (e.g. Sexton, McKay & Sala 2002; Lambrinos 2004; Dybdahl & Kane 2005; Richards *et al.* 2006; Strauss, Lau & Carroll 2006). We begin with a brief overview of plasticity and definitions of important terms. Next, we review the various conceptual arguments as to why plasticity exists and is maintained in populations. Given that plasticity exists, we next explore the various ways by which adaptive and non-adaptive plasticity can facilitate or constrain adaptive genetic differentiation in new environments. We briefly review some relevant theoretical and empirical studies that provide insight into the role of plasticity in evolution and comment on the kinds of data future studies should emphasize. Our paper does not review the role of other types of environmentally induced variation in facilitating adaptive evolution, such as maternal effects (Räsänen

& Kruuk 2007) and epigenetic inheritance (e.g. True, Berlin & Lindquist 2004).

#### BACKGROUND: WHAT IS PLASTICITY AND WHY HAS IT EVOLVED?

Phenotypic plasticity is the phenomenon of a genotype producing different phenotypes in response to different environmental conditions and is a ubiquitous aspect of organisms (Travis 1994; West-Eberhard 2003). Phenotypic plasticity is a property of an individual or genotype that may be adaptive, maladaptive or neutral with regard to an individual’s fitness. The particular way an individual’s (or genotype’s) phenotype varies across environments can be described as a reaction norm (Woltereck 1909). Reaction norms for continuously distributed traits, such as many physiological, morphological and life-history traits are typically visualized as a line or curve on a plot of the environmental value vs the phenotypic value (Fig. 1). Alternatively, the reaction norm may be visualized as discrete character states



**Fig. 1.** Example scenarios of adaptive and non-adaptive reaction norms in response to colonization of new environments. (see also van Tienderen 1991, 1997) Phenotypic values in the native site are indicated with filled circles. Arrows represent the phenotype that genotype would express if introduced into the new environment. Solid lines depict the reaction norm for this two-state environment. An all-purpose genotype that produces the perfect phenotype in both environments is shown as a dashed line. Panel a – Here two ecotypes (solid lines) have the same degree of plasticity (i.e. similar slope of the reaction norm), but have divergent phenotypes when each is measured in their native habitat. When measured in a common garden (either Low or High), they are still different, but the plastic response reduces the difference between the ecotypes. If the phenotype expressed by each ecotype in its native habitat is optimal, then the plasticity would play a beneficial role in colonizing the new habitat because the plastic response is in the same direction as what is favoured by directional selection. Because the all purpose genotype (dashed line) is capable of producing an optimal phenotype regardless of environment, stabilizing selection should constrain genetic differentiation. Panel b – Here the two ecotypes also have the same degree of plasticity, and if each is measured in their native habitat, they have the same phenotype. However, if measured in a common garden they are clearly diverged. Assuming the native phenotype is optimal, the observed plasticity would likely hinder colonization and subsequent genetic differentiation of the other environment because each ecotype is unable to produce the favoured phenotype. In contrast, the all purpose genotype is canalized and able to produce the same phenotype regardless of the environment (a situation where a lack of plasticity would favour colonization).

(e.g. Falconer 1990), such as in the case of developmental polymorphisms or polyphenisms. Variation among genotypes in how they respond across environments is referred to as a genotype  $\times$  environment ( $G \times E$ ) interaction (e.g. Fry 1992) and this can be visualized by plotting the reaction norms of multiple genotypes.  $G \times E$  interactions are thus the property of populations or groups of genotypes (Falconer 1990; Thompson 1991; Via *et al.* 1995). Evidence suggests that plasticity has evolved and can be visualized as a change in the slope of the reaction norm between the ancestral and derived population or species (e.g. Doughty 1995; Gotthard & Nylin 1995), and has been empirically shown to occur in nature between ecotypes and species subject to different selection pressures (e.g. Cook & Johnson 1968; Carroll & Corneli 1999; Pigliucci, Cammell & Schmitt 1999; Morey & Reznick 2000; Haugen & Vøllestad 2000; Ghalambor & Martin 2002). The evolution of plasticity may therefore occur independently of, or jointly with, changes in the mean trait value. While this point has been the subject of past debate, from an evolutionary genetics perspective it is most convenient to think of the mean trait value and its reaction norm as separate traits (e.g. Via & Lande 1985; Scheiner 1993, Via *et al.* 1995; de Jong 2005). For example, selection can change the  $y$ -intercept of the reaction norm without changing the slope and vice versa (de Jong 2005).

Why be plastic? It has long been recognized that adaptive plasticity may be advantageous when it allows a genotype to have a broader tolerance to environmental conditions and hence higher fitness across multiple environments (e.g. Bradshaw 1965; Baker 1974; Sultan 1987, 1995; Schlichting & Pigliucci 1998; Pigliucci 2001). Theoretical models for the evolution of adaptive phenotypic plasticity predict that given genetic variation, selection will favour adaptive plasticity when: (i) populations are exposed to variable environments, (ii) environments produce reliable cues, (iii) selection favours different phenotypes in each environment, and (iv) no single phenotype exhibits superior fitness across all environments (e.g. Bradshaw 1965; Levins 1968; Via & Lande 1985; Lively 1986; Gomulkiewicz & Kirkpatrick 1992; Moran 1992). However, the generality of these predictions is sensitive to how fitness costs for the maintenance and/or production of plasticity are expressed (e.g. van Tienderen 1991, 1997; Moran 1992; DeWitt *et al.* 1998; Reylea 2002; Ernande & Dieckman 2004) and the degree of gene flow between populations distributed among different environments (e.g. Scheiner 1993; de Jong & Behera 2002; Sultan & Spencer 2002). Theoretical and empirical studies agree that selection on plasticity can result in phenotypic adaptation to different environmental conditions, yet the question as to whether plasticity acts to facilitate adaptive evolution remains a more contentious issue. Part of the reason for a lack of consensus is that while much attention has been given to case studies of adaptive plasticity, many if not most cases of environmentally induced variation

appear to be non-adaptive (e.g. de Jong 2005; van Kleunen & Fisher 2005), making it less obvious how such non-heritable variation should facilitate adaptive differentiation of populations. Additionally, few if any empirical examples have convincingly demonstrated that plasticity, whether it was adaptive or not, has played an integral initial role in adaptive differentiation of natural populations (de Jong 2005). Such concerns are particularly relevant when there is a need for a high degree of developmental homeostasis, and genotypes need to be sufficiently buffered against environmental variability in order to produce specific phenotypes (i.e. the degree of canalization, see also Fig. 1b). How selection should act on the developmental tension between the need to be buffered from the environment *vs* the ability to track and adaptively respond to environmental differences was discussed early on by Waddington (1942) and Schmalhausen (1949), but progress in understanding the evolutionary outcomes of these processes has been plagued by confusion and a lack of empirical research (Pigliucci 2001).

One reason for a lack of consensus on the role of plasticity in evolution is that plasticity encompasses a variety of different responses. Here, we outline and review the evolutionary implications of different kinds of adaptive and non-adaptive plasticity in new environments. We argue that different kinds of plasticity influence the likelihood and rate of adaptation, depending on how the mean and variance of plastic responses change in the new environment.

#### THE ROLE OF PLASTICITY IN NEW ENVIRONMENTS

The question of whether plasticity is adaptive is dependent upon the environment in which it is expressed. For the purposes of this article, we are concerned with two environments: the current environment and a new one that the population must adapt to. A new environment can be defined by a change in the current environment or by the invasion of a new habitat. *By definition any plasticity that allows individuals to have higher fitness in the new environment than it would were it not plastic will be beneficial.* However, this does not mean that the reaction norm for a given trait was necessarily shaped by natural selection (i.e. be an adaptation in itself; Gotthard & Nylin 1995). Thus, it is necessary to specify the impact different kinds of plasticity might have in the face of directional selection. Below, we explore these ideas by considering general scenarios where a newly established population experiences selection for a new adaptive peak (following the framework of Price *et al.* 2003).

#### *Adaptive reaction norms: perfect vs incomplete responses*

Extinction is a likely fate for a population that experiences an abrupt or strong episode of directional selection

when moving into a new environment (Haldane 1957; Gomulkiewicz & Holt 1995; Lande 1998). Adaptive phenotypic plasticity has long been suspected of playing a critical role in the ability of a species to first tolerate, then adapt to such episodes (e.g. Baldwin 1896; Baker 1974; Robinson & Dukas 1999; Pigliucci 2001; Schlichting 2004). Here we define adaptive plasticity simply as a reaction norm that results in the production of a phenotype that is in the same direction as the optimal value favoured by selection in the new environment (Fig. 1a, see also Conover & Schultz 1995; van Tienderen 1997; Trussell & Etter 2001). Adaptive plasticity thus satisfies the crucial first step in adaptation to new environments; reducing the cost of directional selection (e.g. Haldane 1957) and allowing enough time for a population to become established where standing genetic variation in combination with mutation and/or recombination among individuals can provide a range of heritable phenotypes to respond to local selection pressures (reviewed in Pigliucci 2001). Such plasticity therefore not only reduces the probability of extinction in new environments, but also allows populations to more easily move from one adaptive peak to another (Robinson & Dukas 1999; Pigliucci & Murren 2003; Price *et al.* 2003; West-Eberhard 2003; Schlichting 2004; Amarillo-Suarez & Fox 2006).

A second step of adaptation to new environments via adaptive plasticity can be the conversion of non-heritable environmentally induced variation to heritable variation, a scenario that remains controversial despite theoretical and empirical arguments dating back over a century (e.g. Baldwin 1896; Waddington 1942, 1952, 1953, 1956, 1959; Schmalhausen 1949). The process by which non-heritable environmentally induced variation leads to adaptive heritable variation is often referred to as the Baldwin Effect or more commonly as genetic assimilation (e.g. Waddington 1942, 1952, 1953; Simpson 1953; Robinson & Dukas 1999; Pigliucci & Murren 2003; Price *et al.* 2003; West-Eberhard 2003; Schlichting 2004). Specifically, genetic assimilation is when traits that were originally environmentally induced become (by the process of directional selection) genetically determined and canalized (a loss of plasticity or a flat reaction norm). West-Eberhard (2003) advocates a less restrictive term *genetic accommodation*, which does not necessarily lead to a loss in plasticity. This process can be illustrated with a hypothetical example following West-Eberhard's framework with her general terminology in italics and parentheses as follows: (i) Assume a population of a brightly coloured fish that typically occurs in low predation lakes. (ii) Within the population there is genetic variation for predator-induced phenotypic plasticity in cryptic colouration (*an environmentally induced phenotypic variant as opposed to one determined by a mutation – the origin of the trait*). (iii) A predator colonizes the lake and many individuals exhibit adaptive plasticity for cryptic colouration and other behaviours that collectively allow for a higher probability of survival compared to individuals that lack plasticity

(*phenotypic accommodation by individual phenotypes*). (iv) Within this selective environment, only those individuals capable of producing the plastic response survive and reproduce (*the recurrence of the environmental stimulus leads to a subpopulation of individuals that always express the induced phenotype and facilitates its spread in the population*). (v) Directional selection favouring the most cryptic individuals in the population leads to allelic substitutions in the regulatory pathway that controls colour patterns and the loss of individuals capable of expressing bright colour (*genetic accommodation*). (vi) The establishment of a population that is genetically differentiated from its ancestral state and either constitutively produces cryptic colouration (i.e. canalization) or has become more plastic in response to the presence of the predator (i.e. the slope of the reaction norm has become steeper). Waddington's (1953) experiments on the genetic assimilation of the loss of cross-veins in *Drosophila* wings in response to heat shock followed an analogous scenario in the laboratory. West-Eberhard (2003) has championed this view as a potentially common or perhaps the predominant way by which adaptive evolution occurs (see also Pigliucci & Murren 2003). A key to this argument, and to Waddington's results, is that while the plasticity is environmentally induced, there must still be underlying genetic variation in inducibility and expression (see also de Jong 2005). It is this underlying variation that provides the basis for adaptation. Indeed, while a variety of models confirm that adaptive plasticity may facilitate adaptive evolution (e.g. Hinton & Nowlan 1987; Behera & Nanjundiah 2004; Ancel 1999), others have shown how plasticity slows the rate of evolution (e.g. Behera & Nanjundiah 1995; Ancel 2000, Huey, Hertz & Sinervo 2003). Below we contrast when adaptive plasticity is likely to slow or speed up the rate of adaptation.

The rate of adaptation to new environments is likely to differ depending on how close the plastic phenotype is to the optimum favoured in the new environment (Price *et al.* 2003). When adaptive plasticity produces a near perfect match with the optimal phenotype in the new environment (the all purpose genotype in Fig. 1a), the population should experience stabilizing selection with no subsequent genetic differentiation between populations unless there is a substantial fitness cost to plasticity (e.g. Price *et al.* 2003). In other words, adaptive plasticity should slow or constrain adaptive genetic differentiation between populations. The introduced C4 grass *Pennisetum setaceum* (fountaingrass) in Hawaii may be a case where adaptive plasticity is so good it has prevented adaptive evolution. Fountaingrass is native to North Africa and the Middle East and was introduced as an ornamental into Hawaii over 100 years ago, where it spread rapidly in arid zones (Wagner, Herbst & Sohmer 1990). On the island of Hawaii, fountaingrass colonizes disturbed sites and can become dominant within communities ranging from sea level to almost 3000-m altitude (Wagner *et al.* 1990). Williams, Mack

& Black (1995) investigated whether populations from coastal dry grasslands, mid-altitude shrubland and subalpine dry forest sites were genetically differentiated from each other. These sites experience large differences in the seasonal pattern of precipitation and temperature declines markedly with increasing altitude such that coastal sites never experience frost, whereas winter night time frost is common at the subalpine sites (Williams *et al.* 1995). Individuals from these sites exhibit dramatic differences in morphology, physiology and reproductive strategies that result in locally adaptive, and phenotypically distinct populations (Williams *et al.* 1995). However, despite very different phenotypes and selective environments, reciprocal transplant experiments reveal little genetic differentiation for most physiological and morphological characters between these populations (Williams *et al.* 1995). One interpretation of these results is that adaptive plasticity results in such a good match with the environment when there is no opportunity for directional selection to act and hence no evolution. Alternatively, because fountaingrass may have been founded by a small population, there may not be sufficient genetic variation in these populations for selection to act on (Williams *et al.* 1995). However, a non-significant trend for resident populations at each site to have higher fitness, and for some local adaptation of traits between populations, suggests the potential for genetic differentiation exists (Williams *et al.* 1995). Other examples of adaptive plasticity producing near perfect responses to different environments and constraining genetic differentiation have been documented in a variety of systems (e.g. Dudley & Schmitt 1996; Mittelbach, Osenberg & Wainwright 1999; Lorenzon, Clobert & Massot 2001).

Adaptive plasticity may also result in an incomplete response relative to the new optimum, meaning that the change in the mean trait value is in the same direction favoured by selection in the new environment, but below the new adaptive peak (Fig. 1a). In such cases, the new population will be subjected to directional selection on extreme phenotypes and the potential for adaptation should be facilitated (reviewed in Price *et al.* 2003). Because environments are typically heterogeneous in space and time, incomplete adaptive plasticity is likely to be the most common form of adaptive plasticity. The evolution of offspring size in Trinidadian guppies (*Poecilia reticulata*) is an example in which incomplete adaptive plasticity may have served as a bridge to evolved adaptation. Guppies are often found in either downstream sites where they co-occur with many predators or in headwater streams where these predators are excluded by waterfalls and rapids (Endler 1978). These low predation headwater streams also tend to have lower light levels and lower primary productivity than high predation streams, which in combination with higher densities of guppies results in greater food limitation (Reznick, Butler & Rodd 2001). Selection is thought to favour larger offspring under such competitive conditions (Bashey 2006). Guppies from low pre-

dition environments produce fewer and larger offspring than their counterparts from high predation environments (Reznick, Rodd & Cardenas 1996; Bashey 2006). While these size differences can be shown to have a genetic basis (Reznick 1982; Reznick & Bryga 1996), there is also considerable plasticity in offspring size; female guppies that are reared on low food rations or that experience variation in food availability produce offspring that are 15%–20% larger than those that are kept on constant, high food rations (Reznick & Yang 1993). Thus, the plastic response in offspring size is in the same direction favoured by selection in the low predation environments. Larger offspring in response to lower food availability appear adaptive, because larger offspring have a competitive advantage when food availability is low but not when it is high (Bashey 2006). Genetic analyses suggest that low predation populations have independently originated from downstream high predation regions (e.g. Crispo *et al.* 2006). Such a repeated pattern of colonization means that guppies would regularly experience a reduction in food availability as they move upstream and hence experience selection for increased offspring size. Their ability to produce larger offspring in response to low food availability represents an adaptive plastic response that would increase the probability that they could successfully invade these environments, while their genetic capacity to produce larger offspring is likely to represent an adaptation that follows such invasions. Significant genetic changes in offspring size were recorded after 11 years (approximately 16 generations) after transplanting guppies from a high to a low predation environment (Reznick & Bryga 1987; Reznick, Bryga & Endler 1990; Reznick *et al.* 1997). Thus, plasticity in offspring size does not appear to retard adaptive evolution in guppies, and may even facilitate adaptation to low predation environments, since it will result in females producing larger offspring as soon as they become established in low predation environments, more than a decade before there is detectable evolution in the trait. Other examples of incomplete adaptive plastic responses with respect to the optimum phenotype known to evolve have been documented in various systems (e.g. Day, Pritchard & Schluter 1994; Chapman, Frieston & Shinn 2000; Trussell 2000; Losos *et al.* 2000; Donohue *et al.* 2000; Yeh & Price 2004).

#### *Non-adaptive reaction norms: environmental heterogeneity and stress*

In contrast to new environments that are reasonably similar to native or ancestral ones, new environments that fall outside the range of conditions typically experienced by populations are often studied from the perspective of 'environmental stress' (e.g. Bradshaw & Hardwick 1989; Bijlsma & Loeschcke 1997; Hoffman & Parsons 1997; Badyaev 2005). Here we define stress as new environments that lie outside the range of preferred conditions and impose a challenge to an

organism's ability to maintain homeostasis and proper function. New environments that are stressful will thus pose a twofold challenge to newly established populations: (i) maintaining homeostasis and proper development, and (ii) responding to strong directional selection (e.g. Waddington 1941; Bradshaw & Hardwick 1989). The solution to the first challenge lies in the ability of organisms to buffer themselves against these stresses so that proper development and function can still occur (e.g. Waddington 1953; Scharloo 1991), whereas the solution to the second challenge is dependent on the relationship between stress-induced phenotypic and genetic variation, and the prevailing selection pressure (e.g. Rutherford & Lindquist 1998; Badyaev 2005). In such cases, canalization (i.e. a lack of plasticity) for the most basic physiological and developmental processes to properly function is the best hope for increasing the likelihood of persistence in the new environment. Stressful environments thus illustrate the challenge or trade-off of having a genotype capable of producing the same target (canalized) phenotype under different environments *vs* a genotype having the ability to produce many potentially adaptive phenotypes in different environments (i.e. plasticity).

Non-adaptive plasticity in response to stress may reflect a fundamental breakdown during development or disruption of physiological function because of changes in temperature, pH or moisture that fall outside of the range historically experienced. By non-adaptive we mean that compared to the ancestral phenotype, the environmentally induced phenotype in the new environment has on average reduced fitness or is further away from the new adaptive peak (Fig. 1B). This type of non-adaptive plasticity represents a fundamentally different kind of environmentally induced effect compared to situations where past selection on the reaction norm allows for adaptive plasticity, and better matching of the phenotype and the environment. It is perhaps the most common form of plasticity to environmental heterogeneity, arising as a 'passive' consequence to environmental stress (e.g. Dorn, Pyle & Schmitt 2000; Grether 2005; van Kleunen & Fisher 2005).

In such cases, the slope of the reaction norm is such that the optimal phenotype in the new environment is not produced and the plastic response is usually a non-adaptive shift in the mean trait value away from the new optimum (Fig. 1b). Here a lack of plasticity or canalized response, that allows organisms to produce the same phenotype regardless of environment results in the best strategy (Fig. 1b). For example, plants may fail to grow to an optimal height and produce few seeds when occupying a microenvironment that is lacking moisture and/or essential minerals (e.g. van Kleunen & Fisher 2005). Grether (2005) argues that this kind of non-adaptive plasticity is likely to underlie a form of cryptic evolution because it results in strong directional selection that makes populations in different environments similar to one another as is observed under 'countergradient variation' (e.g. Conover & Schultz 1995;

Carroll *et al.* 2001; Trussell & Etter 2001). Grether (2005) refers to this process as 'genetic compensation' to distinguish it from genetic assimilation because selection results in evolutionary changes that serve to re-establish the phenotype because the same optima are favoured in both the new and the ancestral environments.

The anadromous Sockeye salmon and non-anadromous lake-bound Kokanee are genetically distinct forms of Pacific salmon (*Oncorhynchus nerka*) that provide a good example of how environmental stress acting through a limiting resource results initially in non-adaptive plasticity and ultimately in cryptic adaptive evolution (Craig & Foote 2001; Craig, Foote & Wood 2005). Kokanee populations appear to have evolved repeatedly from anadromous Sockeye individuals that failed to return to the ocean (called 'residuals'). Kokanee therefore tend to be more closely related to Sockeye inhabiting the same lakes for breeding, than to (phenotypically similar) Kokanee in other lakes (e.g. Foote, Wood & Withler 1989; Taylor, Foote & Wood 1996; Wood & Foote 1996). Both Sockeye and Kokanee turn from silver to bright red when they mature and move into streams to spawn, whereas residual Sockeye are distinguished by their olive green skin at maturity (Craig & Foote 2001; Craig *et al.* 2005). The bright red colouration is produced through the acquisition of dietary carotenoids; however, despite Sockeye and Kokanee exhibiting identical red colouration, carotenoid availability is much lower in lakes than it is in the oceans (Craig & Foote 2001). By crossing Sockeye and Kokanee, and measuring their offspring under common environmental conditions, Craig & Foote (2001) found that Kokanee are three times more efficient in acquiring and depositing carotenoids in their flesh than Sockeye. In addition, mate choice trials revealed a strong preference in Sockeye for red colouration over green, suggesting that the evolution from green colouration (residuals) to red colouration (Kokanee) is driven by sexual selection (Craig & Foote 2001). These results argue for a compelling case of genetic differentiation via a series of events: (i) ancestral Sockeye colonize freshwater lakes via residuals, (ii) residuals initially fail to produce the desired phenotype due to resource limitation, and (iii) directional selection leads to the evolution of greater efficiency in the use of dietary carotenoids and the return of the ancestral or favoured phenotype. Grether (2005) reviews other examples of evolutionary change via a similar process.

Another perspective on non-adaptive plasticity and adaptive evolution considers the role stressful environments play in increasing the expression of genetic and phenotypic variance (e.g. Hoffmann & Parsons 1997; Hoffmann & Merilä 1999). In contrast to the previously discussed types of plasticity that act primarily on the mean value of a trait, stressful environments that fall far outside the range historically encountered can break down genetic buffering mechanisms, and in turn increase the variance associated with different traits (e.g. Rutherford 2000, 2003). This type of stress-induced

plasticity is thought to reveal cryptic genetic variation which results in an increase in the genotypic and phenotypic variance that is 'hidden' or unexpressed under normal environmental conditions (e.g. Rutherford & Lindquist 1998; Rutherford 2000, 2003; Ruden *et al.* 2003; see also Schlichting 2004). In other words, under typical environmental conditions most individuals in a population will exhibit similar patterns of plasticity (low variance), whereas under stressful environments individuals diverge in their response (high variance). An important aspect of this perspective is that most of the stress induced variants are likely to be quickly eliminated by selection in the new stressful environment because they exhibit deleterious phenotypes. Indeed, studies that have used environmental stress to express cryptic genetic variation produce phenotypes that would be unlikely to survive and reproduce under most natural condition (Rutherford & Lindquist 1998; Queitsch, Sangster & Lindquist 2002). However, if by chance a small number of genotypes exhibit a beneficial plastic response that either allows a subset of individuals to persist long enough to survive and reproduce in the new environment for directional selection to act (see above) or is passed on via a maternal or epigenetic effect, adaptive evolution may occur (Rutherford 2000, 2003).

An often cited example documenting the interplay between stress, plasticity, and the potential for adaptive evolution via the increased expression of genetic and phenotypic variation are the heat shock proteins (HSPs), specifically Hsp90 (e.g. Rutherford & Lindquist 1998; Rutherford 2000, 2003; Queitsch *et al.* 2002). HSPs are families of enzymes and chaperones that are mobilized in large numbers by cells under temperature stress to assist in the correct folding of proteins (Rutherford 2000, 2003). In addition to its increased expression in response to elevated temperatures, Hsp90 also interacts in diverse signalling networks and is intimately involved in several developmental pathways (Rutherford & Lindquist 1998; Queitsch *et al.* 2002). These diverse functions place Hsp90 in the unique position of not only buffering organisms from external temperature stress, but also preventing the expression of genetic variants which accumulate but are not expressed, such that different genotypes reliably produce the same phenotype across a range of environments (Rutherford 2003). The buffering capacity of Hsp90 has been revealed in complimentary studies in *Drosophila* (Rutherford & Lindquist 1998) and *Arabidopsis* (Queitsch *et al.* 2002) which show that reduced Hsp90 function, whether due to mutation, chemical impairment or changes in temperature, results in significant increases in phenotypic variation due to the expression of previously cryptic genetic differences. While much of this cryptic variation would surely be deleterious under natural conditions, some of the Hsp90 controlled variation could possibly be advantageous under particular environmental conditions and result in an adaptive response (Queitsch *et al.* 2002). The 'hopeful monsters' associated with the release of cryptic genetic variation

have been argued to provide a potential mechanism by which stressful environmental change may create the conditions for rapid adaptation through the release of novel variation that selection can act on (Rutherford & Lindquist 1998; Rutherford 2000, 2003; Queitsch *et al.* 2002). Badyaev (2005) reviews other examples where stress induced variation may have facilitated adaptive evolution.

#### *The mosaic nature of plasticity and evolution in new environments*

We have described how different types of plasticity in individual traits can lead to adaptive evolution. However, within any given individual, a new selective environment is likely to induce a variety of responses in different traits (e.g. Williams *et al.* 1995; Parsons & Robinson 2006). Thus, individuals are likely to be made up of both canalized traits that do not respond to novel environmental stimuli as well as traits that differ in the type of plasticity they exhibit (adaptive and non-adaptive), resulting in individuals that represent a mosaic of traits. What is the consequence of this mosaic nature in creating individual variation and its resultant importance to population persistence and adaptive evolution to new environments? To answer this question, we need to know more about: (i) whether suites of plastic and non-plastic traits respond independently or in an integrated manner to environmental change, and (ii) if and how the potential for adaptation is influenced by either of these scenarios. Only a few studies have been designed to consider such questions (e.g. Parsons & Robinson 2006), but in the case of the Soapberry bug (*Jadera haematoloma*) where reaction norms of seven traits were compared between recently ancestral and derived populations, the answer suggests a lack of integration. Floridian Soapberry bugs adopted an introduced plant as a food source in about 1960, a colonization event that caused selection on host-based performance reaction norms over the next tens of generations, and resulted in distinctive 'host races' (Carroll, Dingle & Klassen 1997; Carroll, Klassen & Dingle 1998). In the laboratory, bugs of each type were reared on seeds of each host to simultaneously compare reaction norms for beak length, body size, survivorship, development time, fecundity and other traits. Not unexpectedly, the response of certain traits was strongly correlated, such as larger-bodied individuals normally having longer beaks and larger eggs. In contrast however, the direction and magnitude of mean trait responses to being reared on alternate host were not closely correlated. For example, adults from the native host plant were substantially smaller-bodied when reared on the exotic host, but their beak length did not differ and was instead canalized. Most interestingly, in the reciprocal comparison with the derived race, that canalization is lost, and body and beak values responded with similar diminution when rearing was on the native host (Carroll *et al.* 1997). Thus, even among these recently diverged host races,

the patterns of plastic and canalized responses can vary for the same traits.

The mosaic nature of the responses is further illustrated when the reaction norms of different traits are examined. For example, reduced survivorship and development rate of the native-host race reared on the new host reveals the evolutionary path via which countergradient selection has had to overcome stress induced plasticity in order to return the traits in the derived population to their former (ancestral) values (e.g. Carroll *et al.* 1997). In contrast, in other traits, including beak length, the pattern of plasticity on the new host plant is adaptive and in the same direction favoured by selection, suggesting a facilitating role of plasticity in moving the population closer to a new adaptive peak (Carroll *et al.* 1997). Thus, new maladapted and adaptive reaction norms may simultaneously be generated as a pleiotropic effect, but in other traits (e.g. egg size) the slope and magnitude of environmental effects may also remain the same.

The differentiation between Soapberry bug host races is substantial, and adaptive evolution was likely facilitated by the presence of an abundant new resource and the absence of competitors which permitted unfettered evolutionary 'experimentation' in a growing population (Reznick & Ghalambor 2001). Yet the complex mosaic of interacting plastic and non-plastic traits in response to directional selection that has produced the derived race shows that the bugs are altered far beyond what a superficial assessment of current phenotypic differences would suggest, given that some of the original values are now re-established. These results also suggest that adaptive plasticity in at least some traits may play an important role in population persistence to new environments and allowing time for directional selection to act on other traits that exhibit non-adaptive plasticity or are canalized. Such a perspective is consistent with long held ideas that adaptive plasticity in behaviour may help in population persistence to new environments and in turn facilitate evolutionary divergence in morphological or physiological traits (e.g. Losos, Schoener & Spiller 2004, but see Huey *et al.* 2003). Other currently diversifying populations provide an opportunity to examine the levels of genetic divergence, integrated plastic responses, and the interaction of relative degrees of plasticity and intensities of selection (Parsons & Robinson 2006; S.P. Carroll & C.W. Fox, unpublished).

### Synthesis and discussion

While never fully woven into the fabric of the Neo-Darwinian synthesis, phenotypic plasticity has had a long history of study across a wide range of biological disciplines, most notably developmental biology, ecological genetics, behavioural and evolutionary ecology (reviewed in West-Eberhard 2003). Here we have argued that this legacy supports the argument that phenotypic plasticity in response to new environments does not

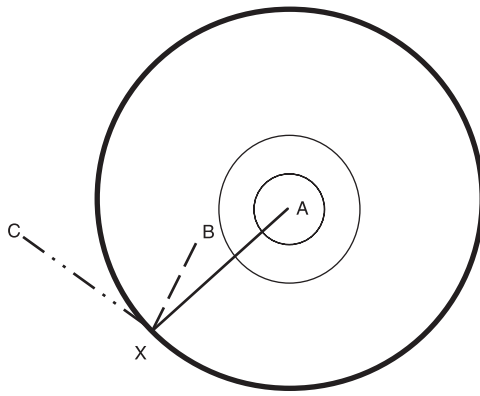
preclude evolutionary change, however, the route and speed by which plasticity can lead to adaptive genetic differentiation depends in part on the type of plasticity being considered. Distinguishing between different types of plasticity is an important first step in understanding the consequences of environmentally induced variation in evolutionary change. Here we: (i) attempt to synthesize different views on plasticity and its contribution to adaptive evolution on ecological time-scales, (ii) show how adaptive plasticity may arise from initially non-adaptive responses to these environments, and (iii) provide a conceptual framework for future research examining the role plasticity might play in contemporary adaptation.

### PLASTICITY AND ADAPTATION ON ECOLOGICAL TIME-SCALES

The first hurdle of adapting to new environments is the ability to persist in the face of directional selection, followed by the second hurdle of exhibiting an adaptive evolutionary response to selection. Phenotypic plasticity encompasses a wide range of adaptive and non-adaptive responses to heterogeneous environments, yet too often the term plasticity is used in a general context that obscures different kinds of environmentally induced variation, with different consequences for the likelihood of persistence and adaptation to new environments. We distinguish between four types of plasticity that are likely to have very different consequences for evolution on ecological time-scales and can be summarized in a two-dimensional phenotypic landscape (Fig. 2). What interests us here is whether or not it can be argued that any of these forms of plasticity enhance an organism's probability of surviving an episode of directional selection and facilitate adaptation at the population level. We distinguish between two types of adaptive plasticity that differ in the degree to which the mean phenotype tracks the environment. First, when adaptive plasticity produces a mean phenotype that is a close match to what is favoured by selection in the new environment, the derived population is most likely to persist, but unlikely to evolve because the population will be subjected to stabilizing, as opposed to directional selection (Fig. 2 response *A*). Second, when adaptive plasticity produces a mean phenotype that is closer to the optimum favoured by selection, but incomplete (i.e. still short of the optimal response), the derived population will likely persist, but still be far enough away from the favoured optimum to be subjected to directional selection (Fig. 2 response *B*). This second, and perhaps more common, form of adaptive plasticity is likely to result in the most rapid adaptive genetic differentiation between populations because of the reduced likelihood of extinction in combination with moderate directional selection on extreme phenotypes (see review in Price *et al.* 2003).

We also distinguish between two types of non-adaptive plasticity that differ primarily in how the environment alters the mean *vs* the variance of a trait. First, when





**Fig. 2.** The role of plasticity in allowing colonization and subsequent adaptation to new habitats can be illustrated using Fisher's geometric model of adaptation. In this figure the thick outer circle represents the  $n$ -dimensional phenotype of the ancestral population,  $X$ . The optimal phenotype for the new environment is at the centre of the circle. Shown are three types of phenotypic plasticity.  $A$ , represents a genotype with perfect adaptive plasticity, the new environment causes individual phenotypes to change in exactly the correct vector in  $N$ -dimensional phenotypic space.  $B$  represents a genotype in which the plasticity is also adaptive, but incomplete, placing individuals outside the optimum. In genotype  $C$ , the plasticity is non-adaptive and moves individuals further away from optimal phenotype. Finally, in the case of extreme stress, increased variance may produce responses in all directions (random vectors not shown), most of which are expected to be maladaptive but some by chance may be adaptive in the new environment.

plasticity results in the mean phenotype being further away from the new optimum relative to the ancestral phenotype, the derived population is less likely to persist in the new environment and plasticity becomes an impediment that selection must overcome (Fig. 2 response  $C$ ). Here, the combination of plasticity that is not beneficial in increasing the likelihood of persistence in the new environment and strong directional selection are in theory most likely to result in extinction. However, at least one empirical study suggests that adaptive differentiation between populations has occurred relatively rapidly in the face of initially non-adaptive plasticity (e.g. Carroll *et al.* 1997). Second, when environmental stress increases the variance around the mean phenotype via the expression of cryptic genetic variation, the beneficial effects of plasticity in facilitating the establishment of a new population or the opportunity for adaptation to the new environment is dependent on the chance occurrence of an adaptive variant appearing (Fig. 2). Successful establishment and subsequent adaptation under this scenario is completely dependent on the probability that somewhere among the genetic variation normally suppressed in a population resides a beneficial mutation that is captured by selection.

Our distinction between different types of plasticity suggests that no single conceptual framework can easily be applied to encompass these diverse forms of environmentally induced variation. However, in the context of adaptation to new environments it is clear

that adaptive plasticity is most likely to reduce the probability of extinction by facilitating the move from one adaptive peak to another (Robinson & Dukas 1999; Pigliucci & Murrern 2003; Price *et al.* 2003; West-Eberhard 2003; Schlichting 2004; Amarillo-Saurez & Fox 2006). This may be especially important in cases where an invading population is comprised of a small number of individuals that have undergone a severe genetic bottleneck, and are dependent on adaptive plasticity to survive during the initial phases of invasion (Sexton *et al.* 2002; Lambrinos 2004; Dybdahl & Kane 2005; Richards *et al.* 2006; Strauss *et al.* 2006). In this sense, plasticity is not in itself an evolutionary mechanism on a par with natural selection (de Jong 2005), but rather provides the first step in the adaptive walk otherwise dependent on new mutation, as described in the geometric models of Fisher (1930) and Orr (1998). Instead of waiting for a rare, non-deleterious mutation along the correct  $n$ -dimensional vector of selection (e.g. Fisher 1930; Kimura 1983; Orr 1998), plasticity can allow a lineage to cross an adaptive valley, and move closer to the optimum phenotype in the new environment.

Empirical studies of adaptive evolution reveal that adaptations to new environments rarely involve single traits, but rather suites of traits that respond to diverse selection pressures (Reznick & Ghalambor 2001). At the whole organism level, new environments are likely to result in a combination of adaptive and non-adaptive plasticity in a suite of traits, but the consequences of such responses for evolution on ecological time-scales remains largely unexplored territory. To date, empirical studies looking at multivariate phenotypes suggest the potential for integrative (Parsons & Robinson 2006) and non-integrative responses (Carroll *et al.* 1997) to play some role in plasticity leading to adaptive evolution. We feel that identifying different types of plasticity and viewing individuals as being made up of a mosaic of traits is an important starting point in reconciling different viewpoints on the relative importance of plasticity to adaptive evolution.

#### THE GHOST OF SELECTION PAST AND ADAPTIVE PLASTICITY IN NEW ENVIRONMENTS

We have argued that adaptive plasticity enhances the probability of persistence in a new environment and can facilitate adaptive genetic differentiation when directional selection acts on extreme phenotypes (Price *et al.* 2003), but it is less obvious what the origins of this plasticity are and why variation in plasticity persists. The most parsimonious explanation is that past selection shapes the reaction norm, and as long as fitness costs to maintaining a plastic response are not large, adaptive plasticity should persist in a population (e.g. Sultan 1995). This was empirically demonstrated by Cook & Johnson (1968) in their study of leaf development in populations of *Ranunculus flammula* that

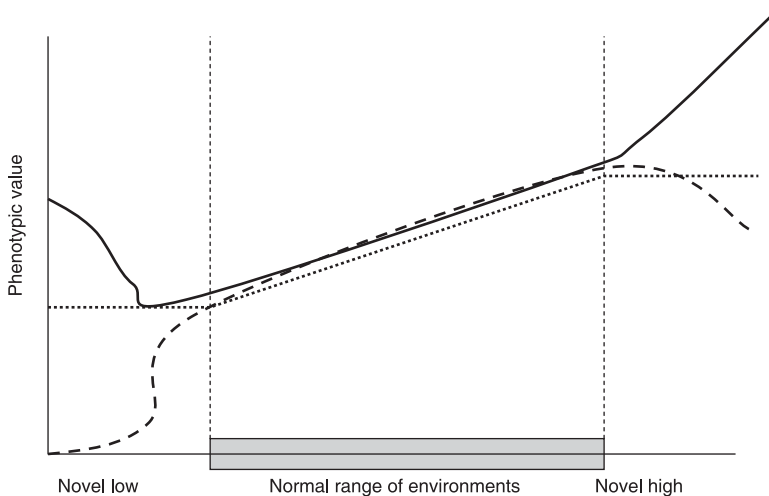
experience both aquatic and terrestrial conditions. Populations that experience persistent aquatic or terrestrial conditions are more specialized and exhibit less adaptive plasticity in leaf development when reared in the opposite environment, whereas populations that regularly experience both aquatic and terrestrial conditions exhibit the greatest adaptive plasticity in leaf development (Cook & Johnson 1968). Thus, an important attribute distinguishing adaptive from non-adaptive plasticity is that it is an adaptation to past and/or current selection, rather than being a serendipitous response to environmental variation.

One conceptual framework for understanding the origins of adaptive reaction norms is to visualize how natural selection acts on neutral genetic variation in the reaction norm. Populations appear to have abundant genetic variation for phenotypic plasticity, although it is only under certain environments that this cryptic genetic variation is expressed (Rutherford 2000). In other words, the reason that stressful environments generate a greater variation in phenotypes is because outside the range of ‘non-stressful’ ancestral environments there is no opportunity for selection to act on the reaction norm, which in turn allows for the accumulation of genetic variation that is effectively neutral (Rutherford 2000). If we think of the reaction norm metaphorically as a piece of string, selection should act to keep the string taught and at an angle or shape that is adaptive across current and historical environments (Fig. 3). In contrast, new environments that fall outside the range of current and past selection result in regions of the reaction norm that have never or rarely experienced the effects of stabilizing selection, thus releasing ten-

sion on the string and allowing it to move more freely (Fig. 3). This release of cryptic genetic variation should be manifest as a significant  $G \times E$  effect only in the stressful environments, whereas only environmental effects will be significant in non-stressful environments (Fig. 3). Adaptive change in the reaction norm across a wider range of environments will therefore occur when an adaptive variant is captured by the process of natural selection and the ‘tension’ on the string is extended into the new environment (Fig. 3). A comparison of reaction norms of derived populations living in extreme environments relative to ancestral ones may provide insight into the prospect that such events have commonly occurred in the past (e.g. Haugen & Vøllestad 2000).

#### FUTURE RESEARCH IDEAS

We have reviewed and outlined different routes by which adaptive and non-adaptive plasticity may facilitate evolution on ecological time-scales, however, no study to date has actually provided empirical evidence for a major role of plasticity in facilitating adaptive evolution in natural populations. A lack of evidence may reflect a failure in past research programmes to specifically design studies that evaluate processes such as genetic assimilation (e.g. Pigliucci & Murren 2003) or simply suggests that plasticity is unimportant (e.g. de Jong 2005). We argue that in theory both adaptive and non-adaptive plasticity can facilitate adaptive differentiation of populations, albeit through different means. Recognizing the different means by which plasticity can contribute to adaptive evolution is a critical starting point for designing empirical studies that explicitly test for these processes. We envision two general approaches to testing the role of plasticity in adaptation: (i) selection/introduction experiments in nature, and (ii) comparisons of contemporary reaction norms in ancestral *vs* derived population sets. For the experimental method, the more direct approach is to conduct selection experiments in nature and follow populations over time (Reznick & Ghalambor 2005). A straightforward design would be to replicate planned introductions of individuals into new environments. Such selection experiments in nature have the benefit of providing an opportunity to measure the patterns of plasticity and the rate at which populations become genetically differentiated from each other (Reznick & Ghalambor 2005). In addition, by conducting these experiments in nature, plasticity can be evaluated in a context where the fitness trade-offs associated with plasticity can be realized. To date, the only study that has used such an approach to explicitly study plasticity and evolution is work carried out by Losos and colleagues (1997, 2000, 2001, 2004). For example, Losos *et al.* (2000) have found that plasticity in hindlimb length in response to different substrates leads to the production of beneficial phenotypes appropriate to particular environments; adaptive plasticity in this case foreshadows adaptive changes that evolve over longer periods of time.



**Fig. 3.** Depicts three genotypes that have the same reaction norms within the range of environments they experience. All three genotypes coexist in the same population, and experience the same variable environment, for example, temperature. Selection maintains the ability of these three genotypes to respond appropriately (adaptive plasticity) to the range of environments that they experience. However, since these genotypes have never been exposed to the novel environments on the high and low end, this part of the reaction norm evolves neutrally and accumulates cryptic genetic variation. This part of the reaction norm is not adaptive or even relevant for the current environment, but since the genotypes differ in this part of the reaction norm, by chance one of them could be pre-adapted for a novel environment.

Similarly, behavioural changes (a type of adaptive plasticity) in response to predatory lizard introductions, appear to not only bring lizard populations within the realm of a new adaptive peak, but also appear to facilitate evolutionary change in the direction expected based on patterns of habitat use and co-existence observed in lizard communities on other islands (Losos *et al.* 2004). Whether these initial patterns of plasticity will be observed to evolve over a contemporary time-scale remain to be seen, however, at least the conditions for future investigation have been established.

A second approach to studying plasticity and evolution is to compare the reaction norms of known ancestral and derived populations that occupy different environments (as described in Carroll *et al.* 1997, 1998; Parsons & Robinson 2006). Reciprocal transplant experiments that measure plasticity in the native and introduced environments can provide insights into the initial patterns of plasticity (ancestral type reared in novel environment) and how that plasticity has evolved (derived type in native environment). Introduced species are good candidates for this approach because in many cases the ancestral and derived populations are known and the rate of adaptation can be inferred if the approximate time of establishment is known. While, a more indirect measure, such comparisons are potentially readily available for a wide range of species.

Under both approaches, it is important that suites of fitness related traits be measured, and attention be paid to the subset of individuals that persist and flourish in the new environments (Carroll *et al.* 1997). If an identifiable subset of individuals that possess a particularly favourable combination of plastic traits are found to be the successful colonizers of new environments, such evidence could show an important role of plasticity in facilitating adaptation. One area where such an approach can be applied and has practical application is in understanding the mechanisms that result in the spread of invasive species. For example, many introduced species persist as small populations for various periods of time before undergoing rapid population growth and range expansion (e.g. Lambrinos 2004). Despite scepticism regarding the role of plasticity in invasions (Lee 2002), it would be interesting to know whether the period of persistence is made possible by plasticity, and that evolutionary changes in the reaction norm allow for adaptation and expansion. At the very least, integrating an explicit role for plasticity in studies of invasive species has the advantage of bringing ecological and evolutionary processes into a common framework (Lambrinos 2004; Richards *et al.* 2006).

### Conclusion

A traditional perspective that phenotypic plasticity shields the genotype from selection and constrains adaptive evolution is not inevitable. Instead, plasticity encompasses a diversity of environmentally induced responses leading to different potential evolutionary outcomes.

### Acknowledgements

This manuscript was improved by comments from Chuck Fox, Andrew Hendry, two anonymous reviewers and C. del Agua. We appreciate the patience of the editors with our attempts to reach a consensus on the diversity of views regarding the evolutionary role of phenotypic plasticity. We want to acknowledge and credit Stephen Tonsor for the idea of reaction norms as strings. C.G. and D.R. were supported by the U.S. National Science Foundation (IBN-0111023). J.M. was supported by the U.S. National Science Foundation (DEB 0618302) and the Colorado Agricultural Experiment Station. S.C. was supported by his own devices.

### References

- Amarillo-Suarez, A.R. & Fox, C.W. (2006) Population differences in host use by a seed beetle: local adaptation, phenotypic plasticity and maternal effects. *Oecologia* **150**, 247–258.
- Ancel, L.W. (1999) A quantitative model of the Simpson–Baldwin effect. *Journal of Theoretical Biology* **196**, 197–209.
- Ancel, L.W. (2000) Undermining the Baldwin expediting effect: does phenotypic plasticity accelerate evolution. *Theoretical Population Biology* **58**, 307–319.
- Badyaev, A.V. (2005) Role of stress in evolution: from individual adaptability to evolutionary adaptation. *Variation: A Central Concept in Biology* (eds B. Hallgrímsson & B.K. Hall), pp. 277–302. Elsevier Academic Press, London.
- Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics* **5**, 1–24.
- Baldwin, J.M. (1896) A new factor in evolution. *American Naturalist* **30**, 441–451; 536–553.
- Bashey, F. (2006) Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* **60**, 348–361.
- Behera, N. & Nanjundiah, V. (1995) An investigation into the role of phenotypic plasticity in evolution. *Journal of Theoretical Biology* **172**, 225–234.
- Behera, N. & Nanjundiah, V. (2004) Phenotypic plasticity can potentiate rapid evolutionary change. *Journal of Theoretical Biology* **226**, 177–184.
- Bijlsma, R. & Loeschcke, V. (ed.) 1997 *Environmental Stress, Adaptation and Evolution*. Birkhauser Press, Basel.
- Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.
- Bradshaw, A.D. & Hardwick, K. (1989) Evolution and stress-genotypic and phenotypic components. *Biological Journal of the Linnean Society* **37**, 137–155.
- Carroll, S.B. & Corneli, P.S. (1999) The evolution of behavioral norms of reaction as problem in ecological genetics. *Geographic Variation in Behavior* (eds S. Foster & J. Endler), pp. 53–68. Oxford University Press, Oxford.
- Carroll, S.P., Dingle, H., Famula, T.R. & Fox, C.W. (2001) Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica* **112–113**, 257–272.
- Carroll, S.P., Dingle, H. & Klassen, S.P. (1997) Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution* **51**, 1182–1188.
- Carroll, S.P., Klassen, S.P. & Dingle, H. (1998) Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evolutionary Ecology* **12**, 955–968.
- Chapman, L.J., Frieston, G. & Shinn, J. (2000) Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecology Letters* **3**, 387–393.

- Conover, D.O. & Schultz, E.T. (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution* **10**, 248–252.
- Cook, S.A. & Johnson, M.P. (1968) Adaptation to heterogeneous environments. I. Variation in heterophylly in *Ranunculus flammula* L. *Evolution* **22**, 496–516.
- Craig, J.K. & Foote, C.J. (2001) Countergradient variation and secondary sexual color: phenotypic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* **55**, 380–391.
- Craig, J.K., Foote, C.J. & Wood, C.C. (2005) Countergradient variation in carotenoid use between sympatric morphs of sockeye salmon (*Oncorhynchus nerka*) exposes nonanadromous hybrids in the wild by their mismatched spawning colour. *Biological Journal of the Linnean Society* **84**, 287–305.
- Crispo, E., Bentzen, P., Reznick, D.N., Kinnison, M.T. & Hendry, A.P. (2006) The relative influence of natural selection and geography on gene flow in guppies. *Molecular Ecology* **15**, 49–62.
- Day, T., Pritchard, J. & Schluter, D. (1994) A comparison of two sticklebacks. *Evolution* **48**, 1723–1734.
- de Jong, G. (2005) Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytologist* **166**, 101–118.
- de Jong, G. & Behera, N. (2002) The influence of life-history differences on the evolution of reaction norms. *Evolutionary Ecology Research* **4**, 1–25.
- DeWitt, T.J. & Scheiner, S.M. (2004) *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford University Press, Oxford.
- DeWitt, T.J., Sih, A. & Wilson, D.S. (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13**, 77–81.
- Donohue, K., Messiqua, D., Pyle, E.H., Heschel, M.S. & Schmitt, J. (2000) Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. *Evolution* **54**, 1956–1968.
- Dorn, L.A., Pyle, E.H. & Schmitt, J. (2000) Plasticity to light cues and resources in *Arabidopsis thaliana*: testing for adaptive value and costs. *Evolution* **54**, 1982–1994.
- Doughty, P. (1995) Testing the ecological correlates of phenotypic plasticity within a phylogenetic framework. *Acta Oecologia* **16**, 519–524.
- Dudley, S.A. & Schmitt, J. (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist* **147**, 445–465.
- Dybdahl, M.F. & Kane, S.L. (2005) Adaptation vs. phenotypic plasticity in the success of a clonal invader. *Ecology* **86**, 1592–1601.
- Endler, J.A. (1978) A predator's view of animal color patterns. *Evolutionary Biology* **11**, 319–364.
- Endler, J.A. (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton.
- Ernande, B. & Dieckmann, U. (2004) The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. *Journal of Evolutionary Biology* **17**, 613–628.
- Falconer, D.S. (1981) *Introduction to Quantitative Genetics*. Longmans, New York.
- Falconer, D.S. (1990) Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. *Genetical Research* **56**, 57–70.
- Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Foote, C.J., Wood, C.C. & Withler, R.E. (1989) Biochemical genetic comparison of sockeye salmon and kokanee, the anadromous and nonanadromous forms of *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 149–158.
- Fry, J.D. (1992) The mixed-model analysis of variance applied to quantitative genetics: biological meaning of the parameters. *Evolution* **46**, 540–550.
- Ghalambor, C.K. & Martin, T.E. (2002) Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* **13**, 101–108.
- Gomulkiewicz, R. & Holt, R.D. (1995) When does evolution by natural selection prevent extinction. *Evolution* **49**, 201–207.
- Gomulkiewicz, R. & Kirkpatrick, M. (1992) Quantitative genetics and the evolution of reaction norms. *Evolution* **46**, 390–411.
- Gotthard, K. & Nylin, S. (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life-history. *Oikos* **74**, 3–17.
- Grant, V. (1977) *Organismic Evolution*. Freeman, San Francisco.
- Grether, G.F. (2005) Environmental change, phenotypic plasticity, and genetic compensation. *American Naturalist* **166**, E115–E123.
- Haldane, J.B.S. (1957) The cost of natural selection. *Journal of Genetics* **55**, 511–524.
- Haugen, T.O. & Vøllestad, L.A. (2000) Population differences in early life-history traits in grayling. *Journal of Evolutionary Biology* **13**, 897–905.
- Hinton, G.E. & Nowlan, S.J. (1987) How learning can guide evolution. *Complex Systems* **1**, 497–502.
- Hoffmann, A.A. & Parsons, P.A. (1997) *Extreme Environmental Change and Evolution*. Cambridge University Press, Cambridge.
- Hoffmann, A.A. & Merilä, J. (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution* **14**, 96–101.
- Huey, R.B., Hertz, P. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *American Naturalist* **161**, 357–366.
- Kimura, M. (1983) *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge.
- Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology* **85**, 2061–2070.
- Lande, R. (1998) Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches on Population Ecology* **40**, 259–269.
- Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* **17**, 386–391.
- Levin, D.A. (1988) Local differentiation and the breeding structure of plant populations. *Plant Evolutionary Biology* (eds L.D. Gottlieb & S.K. Jain), pp. 305–329. Chapman & Hall, New York.
- Levins, R. (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton.
- Lively, C.M. (1986) Canalization versus developmental conversion in a spatially-variable environment. *American Naturalist* **128**, 561–572.
- Lorenzon, P., Clobert, J. & Massot, M. (2001) The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. *Evolution* **55**, 392–404.
- Losos, J.B., Creer, D.A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., Haskell, N., Taylor, P. & Etlings, J. (2000) Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* **54**, 301–305.
- Losos, J.B., Schoener, T.W. & Spiller, D.A. (2004) Predator-induced behavior shifts and natural selection in field-experimental lizard populations. *Nature* **432**, 505–508.
- Losos, J.B., Schoener, T.W., Warheit, K.I. & Creer, D. (2001) Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards. *Genetica* **112–113**, 399–415.
- Losos, J.B., Warheit, K.I. & Schoener, T.W. (1997) Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* **387**, 70–73.

- Mittelbach, G.C., Osenberg, C.W. & Wainwright, P.C. (1999) Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? *Evolutionary Ecology Research* **1**, 111–128.
- Moran, N. (1992) The evolutionary maintenance of alternative phenotypes. *American Naturalist* **139**, 971–989.
- Morey, S. & Reznick, D. (2000) A comparative analysis of plasticity in larval development in three species of spadefoot toads. *Ecology* **81**, 1736–1749.
- Orr, H.A. (1998) The population genetics of adaptation: the distribution of factors fixed during adaptive evolution. *Evolution* **52**, 935–949.
- Parsons, K.J. & Robinson, B.W. (2006) Replicated evolution of integrated plastic responses during early adaptive divergence. *Evolution* **60**, 801–813.
- Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Johns Hopkins University Press, Baltimore.
- Pigliucci, M., Cammell, K. & Schmitt, J. (1999) Evolution of phenotypic plasticity a comparative approach in the phylogenetic neighbourhood of *Arabidopsis thaliana*. *Journal of Evolutionary Biology* **12**, 779–791.
- Pigliucci, M. & Murren, C.J. (2003) Genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? *Evolution* **57**, 1455–1464.
- Price, T.D., Qvarnstrom, A. & Irwin, D.E. (2003) The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London, Series B* **270**, 1433–1440.
- Queitsch, C., Sangster, T.A. & Lindquist, S. (2002) Hsp90 as a capacitor of phenotypic variation. *Nature* **417**, 618–624.
- Reylea, R.A. (2002) Costs of phenotypic plasticity. *American Naturalist* **159**, 272–282.
- Reznick, D. (1982) The impact of predation on life-history evolution in Trinidadian guppies: genetic basis of life-history patterns. *Evolution* **36**, 1236–1250.
- Reznick, D., Butler, M.J. & Rodd, H. (2001) Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *American Naturalist* **157**, 126–140.
- Reznick, D. & Yang, A.P. (1993) The influence of fluctuating resources on life history patterns of allocation and plasticity in female guppies. *Ecology* **74**, 2011–2019.
- Reznick, D.N. & Bryga, H. (1987) Life-history evolution in guppies (*Poecilia reticulata*). 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41**, 1370–1385.
- Reznick, D.N. & Bryga, H. (1996) Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae) 4. Genetic basis of parallelism in life histories. *American Naturalist* **147**, 339–359.
- Reznick, D.N., Bryga, H. & Endler, J.A. (1990) Experimentally induced life history evolution in a natural population. *Nature* **346**, 357–359.
- Reznick, D.N. & Ghalambor, C.K. (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112–113**, 183–198.
- Reznick, D.N. & Ghalambor, C.K. (2005) Selection in nature: experimental manipulations of natural populations. *Integrative and Comparative Biology* **45**, 456–462.
- Reznick, D.N., Rodd, F.H. & Cardenas, M. (1996) Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae) 4. Parallelism in life history phenotypes. *American Naturalist* **147**, 319–338.
- Reznick, D.N., Shaw, F.H., Rodd, F.H. & Shaw, R.G. (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275**, 1934–1937.
- Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., & Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* **9**, 981–993.
- Robinson, B.W. & Dukas, R. (1999) The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives. *Oikos* **85**, 582–589.
- Ruden, D.M., Garfinkel, M.D., Sollars, V.E. & Lu, X. (2003) Waddington's widge: Hsp90 and the inheritance of acquired characters. *Seminars in Cell & Developmental Biology* **14**, 301–310.
- Rutherford, S.L. (2000) From genotype to phenotype: buffering mechanisms and the storage of genetic information. *BioEssays* **22**, 1095–1105.
- Rutherford, S.L. (2003) Between genotype and phenotype: protein chaperones and evolvability. *Nature Review Genetics* **4**, 263–274.
- Rutherford, S.L. & Lindquist, S. (1998) Hsp90 as a capacitor for morphological evolution. *Nature* **396**, 336–343.
- Scharloo, W. (1991) Canalization: genetic and developmental aspects. *Annual Review of Ecology and Systematics* **22**, 65–93.
- Scheiner, S.M. (1993) Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* **24**, 35–68.
- Schlichting, C.D. (2004) The role of phenotypic plasticity in diversification. *Phenotypic Plasticity: Functional and Conceptual Approaches* (eds T.J. DeWitt & S.M. Scheiner), pp. 191–200. Oxford University Press, Oxford.
- Schlichting, C.D. & Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland.
- Schmalhausen, I.I. (1949) *Factors of Evolution*. Blakiston, Philadelphia.
- Sexton, J.P., McKay, J.K., & Sala, A. (2002) Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecological Applications* **12**, 1652–1660.
- Simpson, G.G. (1953) The Baldwin effect. *Evolution* **7**, 110–117.
- Strauss, S.Y., Lau, J.A. & Carroll, S.P. (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities. *Ecology Letters* **9**, 354–371.
- Sultan, S.E. (1987) Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* **21**, 127–178.
- Sultan, S.E. (1995) Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica* **44**, 363–383.
- Sultan, S.E. & Spencer, H.G. (2002) Metapopulation structure favors plasticity over local adaptation. *American Naturalist* **160**, 271–283.
- Taylor, E.B., Foote, C.J. & Wood, C.C. (1996) Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*) *Evolution* **50**, 401–416.
- Thompson, J.D. (1991) Phenotypic plasticity as a component of evolutionary change. *Trends in Ecology and Evolution* **6**, 246–249.
- Travis, J. (1994) Evaluating the adaptive role of morphological plasticity. *Ecological Morphology* (eds P.C. Wainwright & S.M. Reilly), pp. 99–122. University of Chicago Press, Chicago.
- True, H.L., Berlin, I. & Lindquist, S.L. (2004) Epigenetic regulation of translation reveals hidden genetic variation to produce complex traits. *Nature* **431**, 184–187.
- Trussell, G.C. (2000) Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. *Evolutionary Ecology Research* **2**, 803–822.
- Trussell, G.C. & Etter, R.J. (2001) Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. *Genetica* **112–113**, 321–327.
- van Kleunen, M. & Fischer, M. (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **165**, 49–60.
- van Tienderen, P.H. (1991) Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* **45**, 1317–1331.
- van Tienderen, P.H. (1997) Generalists, specialists, and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution* **51**, 1372–1380.
- Via, S., Gomulkiewicz, R., DeJong, G., Scheiner, S.M., Schlichting, C.D. & VanTienderen, P.H. (1995) Adaptive

- phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution* **10**, 212–217.
- Via, S. & Lande, R. (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**, 505–522.
- Waddington, C.H. (1941) Evolution of developmental systems. *Nature* **147**, 198–110.
- Waddington, C.H. (1942) Canalization of development and the inheritance of acquired characters. *Nature* **150**, 563–565.
- Waddington, C.H. (1952). Selection of the genetic basis for an acquired character. *Nature* **169**, 278.
- Waddington, C.H. (1953) Genetic assimilation of an acquired character. *Evolution* **7**, 118–126.
- Waddington, C.H. (1956) Genetics assimilation of the bithorax phenotype. *Evolution* **10**, 1–13.
- Waddington, C.H. (1959) Canalization of development and genetic assimilation of acquired characters. *Nature* **183**, 1654–1655.
- Wagner, W.L., Herbst, D.R. & Sohmer, S.H. (1990) *Manual of the Flowering Plants of Hawaii*. University of Hawaii Press, Honolulu.
- West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*. Oxford University Press, New York.
- Williams, D.G., Mack, R.N. & Black, R.A. (1995) Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* **76**, 1569–1580.
- Williams, G.C. (1966) *Adaptation and Natural Selection*. Princeton University Press, Princeton.
- Woltereck, R. (1909) Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterscheide by Daphniden. *Verhandlungender Deutschen Zoologischen Gesellschaft* **19**, 110–192.
- Wood, C.C. & Foote, C.J. (1996) Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*) *Evolution* **50**, 1265–1279.
- Wright, S. (1931) Evolution in Mendelian populations. *Genetics* **16**, 97–159.
- Yeh, P.J. & Price, T.D. (2004) Adaptive phenotypic plasticity and successful colonization of a novel environment. *American Naturalist* **164**, 531–542.

Received 12 September 2006; accepted 5 April 2007

Editor: Andrew Hendry