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Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics

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Abstract

Ecology and evolution have long been recognized as reciprocally influencing each other, with recent research emphasizing how such interactions can occur even on very short (contemporary) time scales. Given that these interactions are mediated by organismal *phenotypes*, they can be variously shaped by genetic variation, phenotypic plasticity, or both. I here address 8 key questions relevant to the role of plasticity in eco-evolutionary dynamics. Focusing on empirical evidence, especially from natural populations, I offer the following conclusions. 1) Plasticity is—not surprisingly—sometimes adaptive, sometimes maladaptive, and sometimes neutral. 2) Plasticity has costs and limits but these constraints are highly variable, often weak, and hard to detect. 3) Variable environments favor the evolution of increased trait plasticity, which can then buffer fitness/performance (i.e., tolerance). 4) Plasticity sometimes aids colonization of new environments (Baldwin Effect) and responses to *in situ* environmental change. However, plastic responses are not always necessary or sufficient in these contexts. 5) Plasticity will sometimes promote and sometimes constrain genetic evolution. 6) Plasticity will sometimes help and sometimes hinder ecological speciation but, at present, empirical tests are limited. 7) Plasticity can show considerable evolutionary change in contemporary time, although the rates of this reaction norm evolution are highly variable among taxa and traits. 8) Plasticity appears to have considerable influences on ecological dynamics at the community and ecosystem levels, although many more studies are needed. In summary, plasticity needs to be an integral part of any conceptual framework and empirical investigation of eco-evolutionary dynamics.

Subject areas: Quantitative genetics and Mendelian inheritance
Keywords: adaptation, adaptive divergence, community structure, contemporary evolution, ecosystem function, heritability, population dynamics, rapid evolution.

Eco-evolutionary dynamics is an emerging research field that considers interactions between ecology and evolution as they play out on contemporary time frames. These interactions can take place in either direction (Figure 1). In one direction, ecological change can cause evolutionary change on time frames ranging from only a few to hundreds of generations (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Hendry et al. 2008). In the other direction, evolutionary change on those time scales can have important ecological consequences at the population, community, and ecosystem levels (Thompson 1998; Hairston et al. 2005; Fussmann et al. 2007; Kinnison and Hairston 2007; Pelletier et al. 2009; Schoener 2011). Given that these effects flow in both directions (eco-to-evo and

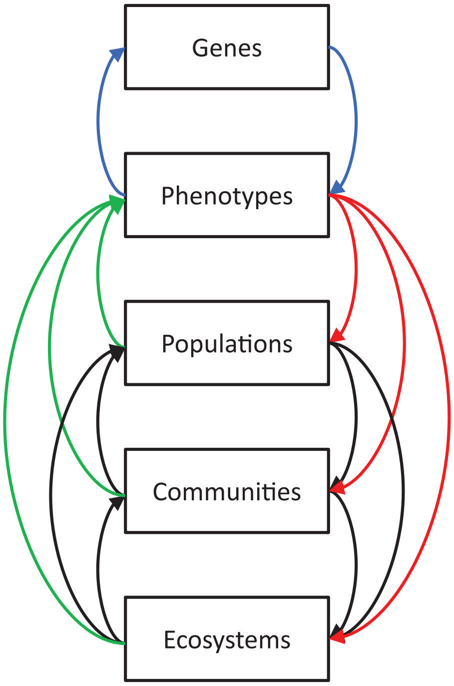

Figure 1. Conceptual diagram outlining the basic elements of eco-evolutionary dynamics. Phenotypic traits in a focal species can influence the population dynamics of that species, which can then influence the structure of the community in which that species is embedded, as well as the functioning of the overall ecosystem. In addition, phenotypic traits in the focal species can directly (i.e., not through population dynamics) influence community structure and ecosystem function. Ecological effects at the population, community, and ecosystems levels can then feedback through plasticity or selection to influence phenotypic traits. These phenotypic changes will be passed on to the next generation to the extent that they are heritable. This figure and caption are the same as in the previously-published companion paper "Key questions in the genetics and genomics of eco-evolutionary dynamics" (Hendry 2013).

evo-to-eco), feedback loops can emerge, and these loops can reinforce or dampen the ecological or evolutionary changes (Post and Palkovacs 2009).

Eco-evolutionary dynamics are driven by interactions between the environment and organismal *phenotypes*. It is typically assumed that these phenotypes have a genetic basis, which has often (but not always) been established for the eco-to-evo pathway. By contrast, a genetic basis for evo-to-eco effects has been confirmed only rarely (Hendry 2013), with a logical alternative being phenotypic plasticity (encompassing developmental plasticity, environmental induction, acclimation, inducible defenses, maternal effects, and epigenetics). In fact, plasticity is expected to be very important in shaping both phenotypic change in response to ecological change and ecological change in response to phenotypic change (see also Miner et al. 2015). These influences need to be incorporated into the developing framework of eco-*evolutionary* dynamics for reasons that I briefly introduce here and detail later. First, the current level of plasticity in a population typically will have evolved as a result of past selection (as opposed to drift), and so plastic changes expressed by individuals have a genetic basis and are often adaptive. In such cases, one can think of plastic changes as a contemporary manifestation of historical genetic change. Second, plasticity can evolve on contemporary time scales, and so phenotypic changes in a population might reflect evolving plasticity. Third, plasticity modifies selection on genotypes, and so influences evolutionary responses to ecological change and ecological responses to evolutionary change. In short, plasticity needs to be an integral part of any general framework for eco-evolutionary dynamics—and the present article is designed to make steps in that direction.

Plasticity has been the focus of considerable interest in recent decades, partly inspired by several key books (Schlichting and Pigliucci 1998; West Eberhard 2003). I obviously cannot cover all of the nuances in a single (admittedly long) article, and so I instead focus on key aspects of plasticity that are necessary for exploring eco-evolutionary dynamics. I specifically address 8 key questions that are much discussed in the literature, attempting to answer them by reference to empirical data—especially from natural (as opposed to laboratory) populations. This article is intended as a complement to a previously published companion article on "Key questions in the genetics and genomics of eco-evolutionary dynamics" (Hendry 2013).

How to Infer Plasticity

By far the most common approach to studying phenotypic plasticity is to implement experimental manipulations under otherwise controlled conditions. Such experiments yield information on the phenotype produced by a given genotype under different conditions, a relationship called the "reaction norm" (Scheiner 1993; Schlichting and Pigliucci 1998). Often, the goal is to compare plasticity between different groups, such as different time periods or species or populations, which can be accomplished by comparing slopes and elevations (or other features when nonlinear) of their reaction norms.

Such experiments work most elegantly for species where inbred lines or clones can be generated because a single genotype can be examined in multiple environments. However, this approach is not possible for many other organisms, where different "genotypes" must instead be represented by different full-sibling families (i.e., different individuals from a given family are split between different conditions) or by unrelated individuals randomly sampled from the different groups (usually different populations). The assumption in these cases is that substantial genetic differences are not present between the individuals from a given family/population exposed to the different conditions. If this assumption is correct, the resulting family/population-level reaction norm should be representative of the average reaction norm of genotypes from those families/populations.

Once average reaction norms are estimated for different groups (e.g., clones, populations, or species), a number of outcomes might emerge—here conceptualized in linear form (the following alternatives correspond to Panels A–F in Figure 1 of Morbey and Hendry 2008). First, environmental conditions might not have a plastic effect on the trait (flat reaction norms) and the groups might not differ genetically (identical reaction norms). Second, environmental conditions might have a plastic effect on the trait (nonflat reaction norms), but the groups might not differ genetically (identical reaction norms). Third, environmental conditions might not have a plastic effect (flat reaction norms), but the 2 groups might differ genetically in trait expression (different elevations). Fourth, environmental conditions might have a plastic effect for which the groups differ genetically (different slopes), with the genetic and plastic influences reinforcing each other (i.e., cogradient: *sensu* Conover and Schlutz 1995). Fifth, environmental conditions might have a plastic effect that differs in direction between the 2 groups (slopes differ in sign). Sixth, environmental conditions might have a plastic effect for which the groups differ genetically, with the genetic and plastic influences this time opposing each other (i.e., countergradient: *sensu* Conover and Schlutz 1995).

A number of considerations attend reaction norms and their estimation (Schlichting and Pigliucci 1998). First, although concepts are most easily envisioned for only 2 environments, reaction norms can be quantified for any number of environments and for continuous environmental variables. Second, although reaction norms are typically represented as linear functions, they can take any shape. Third, reaction norms can be quantified for phenotypes of any sort. Traditional organismal phenotypes include behavior, physiology, color, morphology, life history, and various fitness metrics; but reaction norms also can be evaluated for variables such as gene expression (Swindell et al. 2007; McCairns and Bernatchez 2010) or protein expression (Tomanek 2008; Martínez-Fernández et al. 2010). In addition, phenotypes can be continuous functions of time, such as growth curves, which have been called "function-valued traits" (Kingsolver et al. 2001; Stinchcombe et al. 2012). Fourth, additive genetic (co)variances and heritabilities can be calculated for the slopes and elevations of reaction norms (or other parameters for nonlinear functions), just as for trait values in a single environment. Moreover, one can evaluate plasticity as the genetic variance of the trait in each environment along with the genetic covariance between environments, which also works for function-valued traits (Via and Lande 1985; Via et al. 1995). Fifth, it is sometimes possible to study the specific genes or gene regions underlying some aspects of plasticity (Gutteling et al. 2007), with prime examples being heat shock proteins (Rohner et al. 2013) and DNA methylation patterns (Herrera and Bazaga 2010). Sixth, reaction norms induced by a particular environmental variable likely depend on levels of other environmental variables (G × E becomes G × E × E), and so results will be context-dependent.

The above approaches typically involve experimental manipulations of the environment, but plasticity also can be studied in an observational approach: individuals/populations in nature can be followed through time to quantify the relationship between environmental conditions and trait expression. At the individual level, this approach relies on the same individuals experiencing, and responding to, different environments at different episodes in their life (Nussey et al. 2007). In long-lived birds or mammals, for example, the breeding times of an individual across years can be related to temperature in those years, allowing the estimation of individual-level reaction norms for breeding time in relation to temperature (Nussey et al. 2005; Charmantier et al. 2008; Husby et al. 2010; Porlier et al. 2012). Of course, such analyses focus on traits showing "labile" plasticity that can be adjusted by an individual on an episode-by-episode basis; most obviously various aspects of behavior and physiology. The same approach is often impossible for developmentally plastic traits that then become "fixed", such as many (although not all) aspects of morphology and life history. At the population level, the observational approach relates average trait values to average environmental conditions across years (Phillimore et al. 2010). Although such analyses are extremely common (Parmesan and Yohe 2003), they have severe limitations (Merilä and Hendry 2014). For instance, factors other than plasticity can cause temporal changes, and unmeasured correlated traits or environmental variables might influence observed trends (see also Schlichting and Pigliucci 1998). Fortunately, theory-motivated analytical improvements are being developed (Michel et al. 2014).

Another set of approaches for inferring plasticity seeks to rule out (or partition out) genetic contributions to observed differences, thus leaving plasticity as the default explanation (Merilä and Hendry 2014). First, groups that differ phenotypically in nature can be raised under common-garden conditions to see if those differences vanish, which thus implies plasticity, with a classic example being James (1983). Second, estimates of selection and genetic variation can be used in the breeder's equation or the Robertson–Price Identity to predict the likely contribution of evolution, leaving plasticity as the explanation for any change not explained thereby (Crozier et al. 2011). Third, animal model analyses can measure genetic change based on breeding values and thus, corresponding to the remainder, any plastic contributions (Merilä et al. 2001). Fourth, the Price equation can be used for post hoc partitioning of phenotypic changes into those due to selection versus various forms of plasticity (Ellner et al. 2011). Each of these approaches can be informative but each is also attended by inferential caveats (details in Merilä and Hendry 2014).

Evidence From Nature

I now address key questions surrounding phenotypic plasticity and its role in eco-evolutionary dynamics from the perspective of both causes and consequences. With respect to the causes of plasticity, we need to know how the ecological environment shapes the evolution of plasticity (eco-to-evo-to-pheno). Thus, I will first revisit several key questions that are commonly considered in the literature. 1) To what extent is plasticity adaptive (i.e., increases fitness), as opposed to a nonadaptive or maladaptive response to (for example) stressful conditions? 2) To what extent does plasticity have limits or costs, which will influence selection and potential responses to environmental change? 3) What environmental and organismal characteristics favor the evolution of plasticity? From the perspective of consequence, we need to know how plasticity shapes the evolutionary dynamics of populations and their ecological effects (pheno-to-evo-to-eco). Some of the questions here are classic whereas others are rather new. 4) To what extent does plasticity aid colonization and responses to environmental change—a demographic consequence? 5) Does plasticity constrain or promote genetic evolution and 6) ecological speciation? 7) How fast can plasticity evolve, which is particularly germane given the focus of eco-evolutionary dynamics on short time scales. Finally, I address an emerging question: 8) How might plasticity have community/ecosystem effects?

Most of these questions, which I have intentionally framed in a manner typical of the literature, ultimately prove hard to answer definitively. As a result, my conclusions often resort to a vague "sometimes yes and sometimes no" or "maybe" or "we don't know." While this ambiguity initially might seem unsatisfying, it reflects the empirical reality and it highlights the need for progress, which is ultimately more exciting and interesting than a cut-and-dried "yes" or "no" answer that brooks no debate. As noted by one of the reviewers of this article, ambiguous conclusions and vague answers likely arise when "either the available data is not sufficient to answer, or the questions have been framed in too vague terms that cannot have a general answer". Thus, when I have to be vague or waffle, I will try to distinguish which of these 2 causes is most likely, and then suggest how the ambiguity might be resolved through more research or more refined questions.

Question 1: To What Extent is Plasticity Adaptive?

Some types of plasticity are clearly adaptive, such as immune responses to parasites or behavioral avoidance of predators, whereas other types of plasticity are clearly not adaptive (Grether 2005; Ghalambor et al. 2007). For instance, resource limitation can cause developmental problems that generate phenotypes of no benefit to the organism. Given these alternative possibilities, it is important to not only quantify plasticity but to also evaluate its adaptive significance. One way to do so is through experiments where plastic responses are induced and changes in fitness are monitored. For instance, defensive responses to a particular enemy often decrease vulnerability to that enemy. As a specific example, herbivory on plants decreases following herbivore-induced increases in volatile chemicals (Kessler and Baldwin 2001), setose trichome density (Agrawal 1999), and spine length (Milewski et al. 1991). Similarly, predation decreases following predator-induced increases in body depth in *Carassius carassius* carp (Brönmark and Miner 1992) and shell thickness in *Physa acuta* snails (Auld and Relyea 2011). Plastic responses of this sort are expected to influence population dynamics. As an example, animals that evolved on islands without predators often lack adaptive antipredator behaviors (Cooper et al. 2014), and so suffer major declines when a predator is introduced (Sih et al. 2010).

Even in cases where plasticity is seemingly adaptive, caveats and nuances exist. For instance, defenses induced by exposure to one enemy might be disadvantageous in the presence of a different enemy (DeWitt et al. 2000), and induced defenses can be costly in general. (More generally, the adaptive value of plasticity can be considered in one environment but whether it is adaptive overall requires assessment across multiple environments.) Moreover, the above examples were targeted investigations of specific changes expected *a priori* to be adaptive, whereas more diverse results are obtained when traits are chosen more objectively. For example, Caruso et al. (2006) exposed 2 wildflowers (*Lobelia cardinalis* and *Lobelia siphilitica*) to wet or dry conditions, measured a series of phenotypic traits related to photosynthesis, and used above-ground biomass as a surrogate for fitness. The 2 species showed different levels of plasticity in different traits, and the consequences ran the gamut from adaptive to maladaptive to neutral. As will be considered further in the next question, a series of similar studies have been performed with other organisms and the results are highly variable with respect to the adaptive significance of plasticity (Van Kleunen and Fischer 2005; Auld and Relyea 2011).

Most studies of the adaptive significance of plasticity are conducted under controlled experimental conditions, such as common gardens or mesocosms. Given that these arenas do not include all potential selective forces, the overall adaptive significance of plasticity often remains uncertain. The alternative is to evaluate plasticity and its consequences in natural populations (Nussey et al. 2007). This approach is rarely implemented owing to logistical constraints, but we do have some informative case studies. I would especially like to highlight a contrast between 2 studies of individual plasticity in populations of great tits, one in the Netherlands (Nussey et al. 2005) and one in the United Kingdom (Charmantier et al. 2008). In each case, plasticity was quantified as the extent to which individual birds changed in their breeding date between years as a function of changes in temperature, and this individual plasticity was related to lifetime reproductive success. In the Dutch population, individuals differed dramatically in plasticity, selection favored increased plasticity, and current levels of plasticity were insufficient for fully adaptive responses to climate change (Nussey et al. 2005). Results were opposite in the UK population: individuals did not differ strongly in plasticity, plasticity was not under selection, and the current levels of plasticity were sufficient for fully adaptive responses (Charmantier et al. 2008). More recent work has formally compared these 2 studies and, although some conclusions change, the different populations (and traits) clearly differ dramatically in individual plasticity, its genetic basis, and its adaptive significance (Husby et al. 2010). Dramatic intra-specific variation in these properties is also present on small spatial scales, as demonstrated by work on Blue Tits (*Cyanistes caeruleus*) (Porlier et al. 2012). I will return to estimates of selection on plasticity in Question 2—because they have also been used to infer costs of plasticity.

Conclusion

Plasticity is sometimes adaptive, sometimes maladaptive, and sometimes neutral. This vague answer reflects the vague way in which this question is typically posed. A much more informative question would be: *What are the conditions under which plasticity has the greatest adaptive value?* It seems likely that such conditions occur when traits have different optimal values under different environmental conditions that the population has routinely experienced in the past, particularly when reliable environmental cues allow appropriate and timely plastic changes (Padilla and Adolph 1996; Reed et al. 2010). These expectations will be revisited in Question 3. In addition, some of the vagueness of the answer arises because the adaptive significance of plasticity can be considered in a particular environment (e.g., when exposed to a particular predator) or over the entire life time of the organism. It is critical to make these distinctions in empirical studies and meta-analyses.

Question 2: To What Extent is Plasticity Costly or Limited?

Organisms faced with variable environments might evolve genetically based adaptive divergence or might instead use plasticity to mold phenotypes to current conditions (Or both, including adaptive divergence in plasticity.). In the absence of constraints, plasticity would seem the best of these alternatives because it should be the most immediately responsive to environmental change. Yet adaptive divergence is common (Schluter 2000; Hereford 2009; Hendry 2013), which suggests that plasticity must have constraints in the form of costs or limits (DeWitt et al. 1998; Auld et al. 2010, Murren et al. 2015).

One suggested method for assessing costs of plasticity is to relate fitness in a given environment to trait values in that environment and to plasticity between environments (Van Tienderen 1991; DeWitt 1998; Scheiner and Berrigan 1998). The data are then analyzed in a Lande and Arnold (1983) style multiple regression model, where one predictor is the trait value in an environment and the other predictor is the difference in trait value between environments. The partial regression coefficient for the latter term provides an estimate of the cost of plasticity while controlling for mean trait value. When this coefficient is negative (selection against plasticity), a cost is inferred. When this coefficient is positive (selection for plasticity), a "cost of canalization" (benefit of plasticity) is inferred. Van Buskirk and Steiner (2009) performed a meta-analysis of 27 studies reporting 536 separate selection estimates. Costs of canalization were found to be as common as costs of plasticity, and both types of costs were relatively weak and rarely significant (see also Van Kleunen and Fischer 2005; Auld et al. 2010) (Figure 2). At face value, these results might be taken to mean that costs of plasticity are not strong (see also Auld et al. 2010). In reality, however, these analyses test for selection on plasticity (i.e., Question 1), which will reflect a combination of costs and benefits acting on plasticity across the various environments/

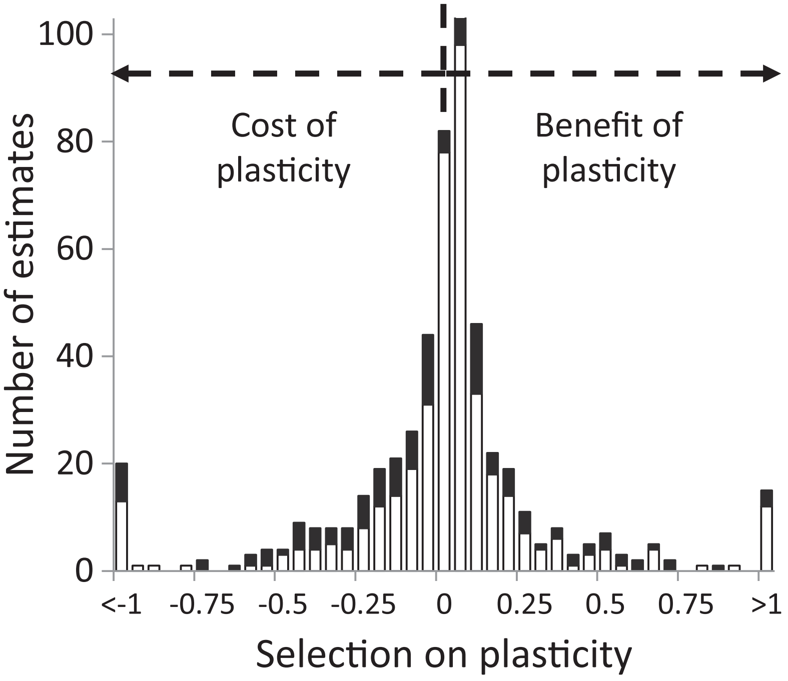

Figure 2. Distribution of estimates of selection on plasticity (540 estimates from 27 studies), with individually significant estimates ($P < 0.05$) shown as the dark portions of bars. These estimates are from standardized multiple regression analyses that also include the mean value of the trait. Negative values imply a net cost of plasticity, whereas positive values imply a net benefit of plasticity (or a cost of canalization). These data are from van Buskirk and Steiner (2009) and were provided by J. van Buskirk.

conditions/contexts experienced during the selection interval. As a result, a lack of selection against plasticity could reflect a combination of strong benefits and strong costs offsetting each other during the selection interval.

Plasticity certainly has limits—both ultimate and proximate. In an ultimate sense, some phenotypic changes will be forever impossible through plasticity, just as some phenotypic changes will be forever impossible through evolution. In a proximate sense, the plasticity currently present within a population is often insufficient for fully adaptive responses to environmental change. For example, although some birds can plastically match their breeding time to appropriate conditions, such as the timing of peak caterpillar abundance, migratory birds cannot breed before they arrive. Migratory timing, which is often genetically based, thus places a limit on what can be achieved through plasticity of breeding time (Both and Visser 2001; Gill et al. 2014). Further examples of limits to plasticity are legion: for instance, current plasticity appears insufficient for responding to climate change in British frogs (Phillimore et al. 2010), a number of birds (Nussey et al. 2005; Gill et al. 2014), and many plants (Willis et al. 2008; Wolkovich et al. 2012; Van Buskirk et al. 2012). What remains uncertain is just how prevalent and important are these limitations (Murren et al. 2015).

Another context for considering limits to plasticity is the idea of behavioral syndromes: suites of "correlated behaviors expressed either within a given behavioral context (e.g., correlations between foraging behaviors in different habitats) or across different contexts (e.g., correlations among feeding, antipredator, mating, aggressive, and dispersal behaviors)" (Sih et al. 2004). The basic idea is that different individuals fall at different positions along behavioral or "personality" axes, which makes it difficult to alter behaviors from one context to another (Sih et al. 2004). For example, selection might favor boldness in the presence of potential mates but shyness in the presence of potential predators (Smith and Blumstein 2007), and yet bold individuals might remain bold in both contexts as a result of limited moment-to-moment flexibility. Such syndromes could have important consequences for a variety of ecological and evolutionary processes (Wolf and Weissing 2012). At present, however, the relative frequency and importance of syndromes in causing maladaptive context-dependent behavior is unknown. Another uncertainty is the extent to which behavioral syndromes reflect hard limits to behavioral plasticity, as opposed to adaptive responses to past selection resulting from, for example, high costs of excessive plasticity. What is known from meta-analyses is that 1) the behavioral repeatability of individuals is highly variable (Bell et al. 2009)—that is, behaviors are sometimes very repeatable and sometimes not (Figure 3), and 2) different personality axes (boldness, exploration, aggression) can influence fitness components (reproductive success and survival) in a variety of ways (Smith and Blumstein 2007).

Costs and limits of plasticity should be context dependent: for example, costs might be strong only when plastic responses are large and environmental conditions are stressful. The first possibility (large responses) was considered by Lind and Johansson (2009) through a comparison of common frog (*Rana temporaria*) populations that showed large versus small plastic changes in developmental timing in response to simulated pond drying. Costs of plasticity were found only in populations that showed the largest plastic responses (see also Merilä et al. 2004). However, it is difficult to separate selection on plasticity from selection on trait values in a given environment if the 2 are correlated such that individuals with the greatest plasticity produce the most extreme traits values (Auld et al. 2010). The second possibility (stressful conditions) was considered in the meta-analysis of van Buskirk and Steiner (2009).

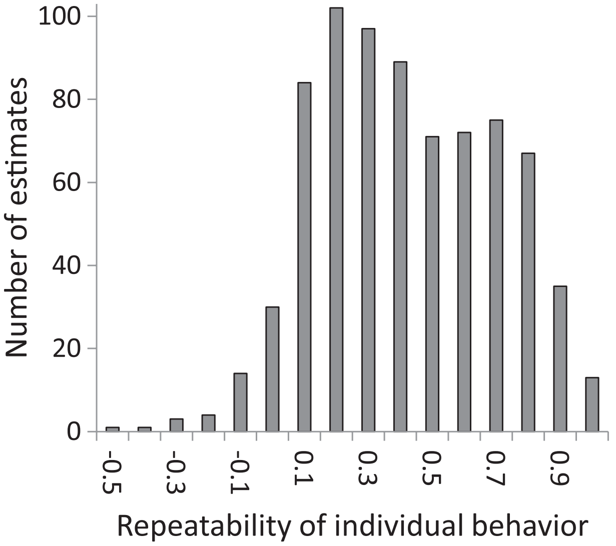

Figure 3. Distribution of 659 repeatability estimates from studies of behavior. Repeatability is the variance in behavior among individuals divided by the sum of the variance among individuals and the variance across repeat measurements within individuals. For improved presentation, one very low repeatability value (–0.95) is not shown. These data are from Bell et al. (2009).

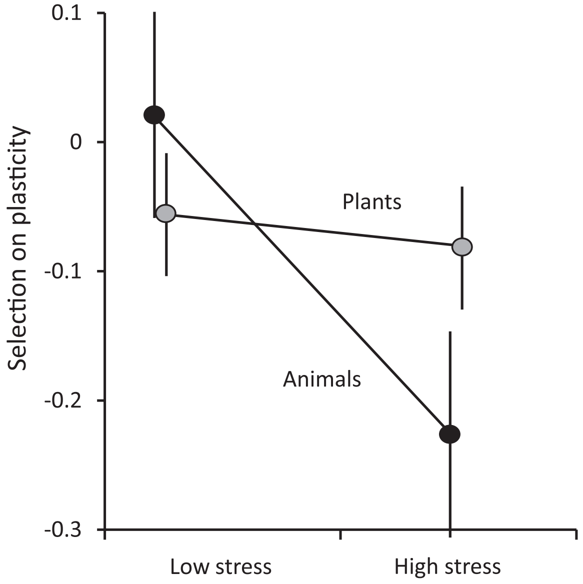

Figure 4. Distribution of estimates of selection on plasticity for plants and animals in low stress or high stress conditions (redrafted from Van Buskirk and Steiner 2009). Shown are means and standard errors from a mixed model controlling for other factors (van Buskirk and Steiner 2009), which is presumably why they don't closely match the raw data in Figure 2. Negative values imply a net cost of plasticity, whereas positive values imply a net benefit of plasticity (or a cost of canalization).

Specifically, costs of plasticity were highest when environmental stress was greatest, at least for animals (Figure 4)—although this result is not universal (Steiner and Van Buskirk 2008). Not surprisingly, then, costs of plasticity depend on properties of organisms, traits, and environments.

Conclusion

Plasticity must have costs and limits but these constraints are highly variable, often weak, and hard to detect. Moreover, it has proven difficult for studies to reliably separate limits, costs, and benefits, all of which might interact and be context-dependent (Auld et al. 2010). A great need exists for more studies that partition the fitness consequences of plasticity between different aspects of an organism's life, such as different ages, environments (e.g., different predators, parasites, diets, and competitors), and fitness components (survival, fecundity, mating success). Such studies could more effectively assess the various context-specific benefits and costs and also how these factors combine to determine overall fitness consequences. It seems likely that costs of plasticity will be highest when plastic changes are greatest, when environmental conditions are stressful, and in rarely experienced environmental conditions (because past selection will have had less opportunity to reduce costs). In addition, it has been suggested that limits to plasticity are most likely in cases of relaxed selection and variable selection intensities (Murren et al. 2015).

Question 3: What Environmental and Organismal Characteristics Favor the Evolution of Plasticity?

Given that the adaptive benefits and costs/limits of plasticity vary among traits, organisms, and environments, the evolution of plasticity should vary at these same levels. For instance, theoretical models have shown that adaptive phenotypic plasticity readily evolves when selective conditions are variable. Some of these models have altered optimal phenotypes/genotypes through time for a single population (Gabriel 2005; Stomp et al. 2008; Svanbäck et al. 2009; Gomez-Mestre and Jovani 2013; Ezard et al. 2014), whereas others have analyzed meta-populations where optimal phenotypes/genotypes vary across space (Levins 1968; Via and Lande 1985; Van Tienderen 1997; Thibert-Plante and Hendry 2011; Scheiner and Holt 2012). These models consistently suggest that greater plasticity is favored when 1) spatial variation is greater, 2) dispersal is higher, 3) temporal variation is greater, 4) environmental cues are more reliable, 5) genetic variation for plasticity is higher, and 6) costs/limits of plasticity are lower. I now summarize studies testing the first 4 of these predictions, with the final 2 being discussed elsewhere in this article.

1. Several empirical studies have tested the prediction that higher plasticity should evolve when environments are more spatially heterogeneous. Lind and Johansson (2007) examined plasticity in common frog populations from 14 islands off the coast of Sweden. Islands with more spatial variation in pond-drying regimes (some ponds dry quickly and others slowly) were found to have frogs with greater plasticity in developmental timing when exposed to simulated drying regimes (water volume changes) (Figure 5). Along the same lines, Baythavong (2011) showed that plasticity for the plant *Erodium cicutarium* was higher in environments with more fine-grained spatial variation. Although a number of other such studies further support the above expectation, too few have been conducted to warrant sweeping generalizations.
2. If spatial variation favors the evolution of plasticity (as above), greater plasticity is expected to evolve under higher dispersal rates, which increase the spatial variation experienced by a given lineage. Lind et al. (2011) used the frog system described just above to suggest (statistical significance was lacking) that phenotypic plasticity was greater when gene flow (based on DNA microsatellites) was higher among islands with different drying regimes. A potential uncertainty in such analyses is ascertaining whether higher gene

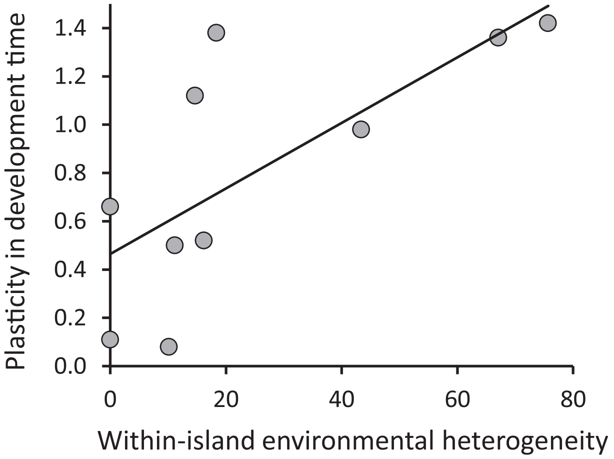

Figure 5. For frogs on recently colonized Swedish islands, within-island heterogeneity of pond drying regimes is correlated (across islands) with the degree of plasticity frogs show in their development time. Plasticity is "mean development time for the offspring of a female under constant water level, minus the development time under the artificial pool drying treatment." Heterogeneity is the coefficient of variance in pool drying on an island. These data are from Lind et al. (2011) and were provided by M. Lind.

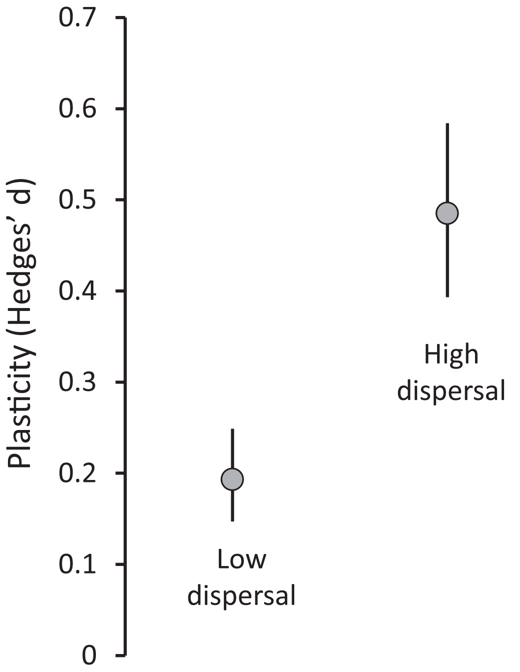

Figure 6. Plasticity in marine invertebrates with low dispersal (nonplanktonic larvae) or high dispersal (planktonic larvae). Shown are means and confidence intervals for the magnitude of plasticity (Hedges' d) based on different experimental treatments in common garden or reciprocal transplant experiments. Shown are calculations based on all data—similar results are obtained in reduced analyses (one study per species). These data are from Hollander (2008).

flow is the cause or the consequence of higher plasticity (Crispo 2008). The role of dispersal was evaluated more generally in a meta-analysis of 258 experiments on plasticity in marine invertebrates (Hollander 2008). In accordance with the expectation, species with low dispersal (nonplanktonic larvae that had "viviparous/ovoviviparous development or direct development from benthic egg masses") showed lower plasticity than did species with high dispersal (planktonic larvae) (Figure 6). The inference is that planktonic species have limited control over the conditions they experience and should therefore evolve higher plasticity, with a recent example being eastern oysters, *Crassostrea virginica* (Eierman and Hare 2015).

3. Several studies inform the expectation that populations experiencing greater temporal variation will evolve greater plasticity. For example, temporal variation in fish predation on *Daphnia* is present in lakes with fish but not in lakes without fish—and plasticity in kairomone-induced phototactic responses of *Daphnia* is correspondingly higher in the former than the latter (De Meester 1996). Interestingly, an opposite result is seen for some traits in Trinidadian guppies, where the population not experiencing the predator shows greater plastic responses to predator cues (Torres-Dowdall et al. 2012)—probably as a result of correlated responses to selection on the mean phenotype. Returning to supportive examples, Gianoli and Gonzalez-Teuber (2005) compared 3 populations of the plant *Convolvulus chilensis* that experience dramatically different inter-annual variation in precipitation and therefore drought stress. Four traits showed plastic responses to simulated drought conditions in the laboratory and, in each case, plasticity was greatest for the population that experienced the greatest temporal variation in nature. However, the adaptive significance of plasticity could be confirmed for only one of the traits: foliar trichome density.
4. Plastic responses should evolve only when an environmental cue provides a reliable and timely indicator of appropriate adaptive phenotypes (Padilla and Adolf 1996; Reed et al. 2010). This topic has been studied extensively in plants that respond to crowding conditions by elongating internodes and accelerating flowering, with the first response helping to escape competition for light and the second response helping to increase reproduction before death. The environmental cues that initiate these responses are overall irradiance and the ratio of red to far red wavelengths, both of which are indicators of vegetation-generated shade. However, the same cues will not reliably indicate local competitive conditions in woodland habitats, where shade is mostly determined by larger trees. As expected, populations from non-woodland habitats show greater responses to light cues than do populations from woodland habitats (Morgan and Smith 1979), and reciprocal transplant experiments in *Impatiens capensis* have confirmed the adaptive significance of these differences (Donohue et al. 2000, 2001). Evidence that plasticity is stronger under more predictive conditions has also been reported for animals (Porlier et al. 2012).

Conclusion

Multiple lines of evidence support the expectation that greater trait plasticity evolves in more variable environments, when environmental cues are more reliable, and when costs are lower. This plasticity can then buffer performance and fitness across a range of environments (Lynch and Gabriel 1987; Chevin et al. 2010; Lande 2014; Resuch 2014). Yet counter-examples exist, such as the maintenance of high plasticity in isolated populations experiencing relatively stable environments (Torres-Dowdall et al. 2012; Wiens et al. 2014) and the failure of generalists to evolve in variable environments in some laboratory experimental evolution studies (Condon et al. 2014). Thus, while the general expectations are often upheld, numerous exceptions point to the importance of additional interacting factors (Angilletta 2009; Condon et al. 2014).

Question 4: To What Extent Does Plasticity Aid Colonization and Responses to Environmental Change?

Large environmental shifts should pose problems for populations because existing phenotypes will not be well suited for the new conditions. In such cases, organisms are expected to shift their phenotypes in an adaptive direction, which might then make the difference between persistence versus extirpation. This "phenotypic rescue" can occur if populations undergo adaptive genetic change ("evolutionary rescue"), if individuals move to more appropriate locations, or if individuals manifest adaptive plasticity ("plastic rescue") (Chevin et al. 2010; Yamamichi et al. 2011; Barrett and Hendry 2012; Gomez-Mestre and Jovani 2013; Kovach-Orr and Fussmann 2013; Ezard et al. 2014). In the present question, I focus on how phenotypic rescue might be achieved through plasticity in 2 contexts: *in situ* environmental disturbance (e.g., climate change) and the introduction of populations to new environments.

The basic idea behind plastic rescue is that individuals evaluate altered conditions and adjust their phenotypes appropriately, which might then increase mean population fitness and thereby enhance persistence and colonization of new environments. This phenomenon has been called the "Baldwin Effect" (Simpson 1953; Price et al. 2003; Ghalambor et al. 2007; Crispo 2007) following its exposition by Baldwin (1896, 1902). Baldwin further suggested that, once adaptive plasticity occurred, genetic change would be expected in the direction of the plastic response. This second step has been termed "genetic accommodation" (West Eberhard 2003; Schlichting and Wund 2014). Waddington (1953, 1961) argued that the specific type of post-plasticity genetic change would be canalization of the trait such that the new phenotypes would no longer require environmental induction, a phenomenon he called "genetic assimilation" (West Eberhard 2003; Crispo 2007; Schlichting and Wund 2014). Spalding (1873) had a similar idea, as described by Price (2008, p. 133). Despite the appeal of these ideas, it has been argued that concrete evidence is lacking (De Jong 2005) and that the opposite sequence (evolution first, then plasticity) is also possible (Scheiner and Holt 2012). Here I will consider evidence for the first part of the idea: plasticity aids persistence, colonization, and invasiveness.

Perhaps the best evidence for the importance of plasticity in responding to environmental change comes from studies of phenological responses to climate warming. Many organisms have advanced the timing of spring life-history events (e.g., flowering, breeding, migration) as temperatures have increased and winters shortened over the past 50 years (Parmesan and Yohe 2003). It is hard to ascertain whether these changes are the result of genetic evolution or phenotypic plasticity (or both), mainly because the common methods for confirming a genetic basis for phenotypic change (e.g., common-garden experiments) are difficult to apply in a temporal (allochronic) context (Gienapp et al. 2008; Merilä and Hendry 2014). That is, it is hard to take genotypes that live at different times and assess them under the same conditions, with the exception being organisms with dormant stages (e.g., seeds or resting eggs: De Meester 1996, Boersma et al. 1998; Cousyn et al. 2001) or when the common garden environment can be exactly duplicated at different times. Without disputing the importance of evolution in at least some phenological changes (Bradshaw et al. 2006; Merilä and Hendry 2014), plasticity also must often be important. For instance, the study of the UK population of great tits (Charmantier et al. 2008; Vedder et al. 2013), suggested that plasticity was entirely sufficient for adaptive responses of reproductive timing to climate change. Similar arguments have been made for other species, including Gotland collared flycatchers, *Ficedula albicollis* (Przybylo et al. 2000). By contrast, phenotypic plasticity seems insufficient for fully adaptive responses to climate change in other instances (see Question 2). The next step should be the transition from trait changes to fitness consequences.

The populations referenced in the above paragraph all persisted in the face of environmental change, and perhaps adaptive plasticity was the reason, although explicit confirmation is not available. A more informative analysis, however, would be to consider the role of plasticity in populations showing alternative demographic responses to climate change. For example, Willis et al. (2008) recorded changes in the flowering time and abundance of plant species over 150 years in "Thoreau's Woods," Concord, MA. In this location, the species that were extirpated were those that showed low plasticity in flowering time in relation to temperature. The implication is that persistence of the remaining species, whose flowering time advanced by an average of 7 days, was at least partly due to plastic rescue. As another example, limits to plasticity in pied flycatchers (*Ficedula hypoleuca*) have prevented sufficient change in breeding time, which has caused population declines (Both and Visser 2001; Both et al. 2006). It thus seems that plasticity will be sufficient for phenotypic rescue in some instances, whereas evolutionary changes will be needed in others (see also Phillimore et al. 2010). With this recognition, plasticity has been increasingly incorporated into population viability and evolutionary rescue models for specific taxa (Baskett et al. 2009; Gienapp et al. 2012; Vedder et al. 2013). The upshot of these analyses is that plasticity, as long as current cues reliably predict appropriate future phenotypes, generally should have a positive effect on population persistence.

When organisms are introduced into new environments, adaptive plasticity might play a key role in colonization, persistence, and invasiveness (Baker 1965; Richards et al. 2006; Hulme 2007). One way to inform this possibility is to compare levels of plasticity in fitness-related traits between invasive and noninvasive species. Early qualitative reviews for plants yielded inconclusive results, with greater plasticity found as commonly for noninvasive species as for invasive species (Bossdorf et al. 2005; Richards et al. 2006). However, a more recent quantitative meta-analysis that examined 75 invasive/noninvasive plant species pairs came down decisively in favor of greater plasticity in invaders (Davidson et al. 2011). A related, but independent, line of inquiry asks whether behavioral plasticity promotes invasion success in animals (Wright et al. 2010). Sol and colleagues (2008, 2012) found that brain size (expected to be correlated with behavioral flexibility) and foraging innovation (a measure of behavioral flexibility) were positively associated with the probability that introduced birds and mammals became invasive. At the same time, however, some species with modest brain sizes become invasive and some species with large brain sizes don't (Figure 7): that is, the variance explained isn't very high. Overall, then, although behavioral plasticity in animals (and trait plasticity in plants) might sometimes aid responses to new environments, it certainly isn't a universal solution.

Conclusion

Plasticity sometimes aids colonization of new environments and responses to in situ environmental change. However, plastic responses aren't always necessary or sufficient in these contexts. In one sense, this qualified answer reflects data deficiency: very few studies have examined the contributions of plasticity to population dynamics in the face of environmental change. In addition, no experimental studies in nature have assessed the role of plasticity in mediating such challenges, such as by assessing the responses of more or less plastic genotypes. (Studies of invasive species often show that invaders are more plastic but cannot confirm that plasticity was a

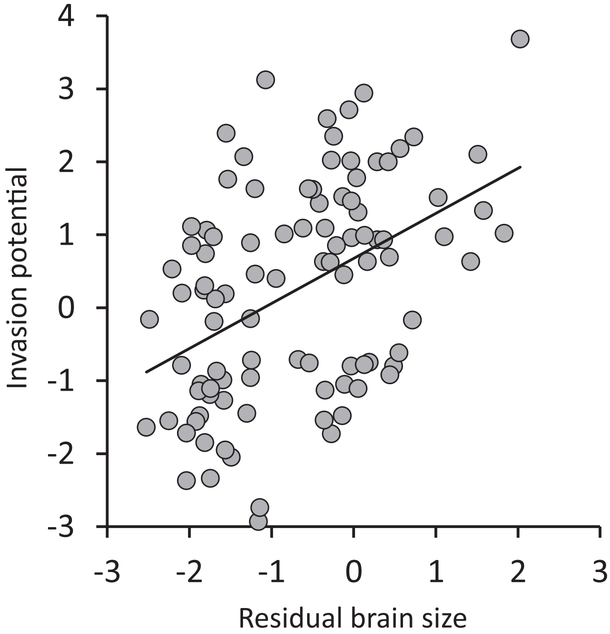

Figure 7. In birds, invasion potential (probability of establishment following introduction) is positively related to residual brain size (brain size corrected for body size). Each point represents a different species and similar results are obtained if phylogeny is controlled through independent contrasts. These data are from Sol et al. (2012) and were provided by D. Sol.

key contributor to the invasion.) However, I expect that the above answer will remain qualified even when more data are gathered. Instead, a more profitable question might be: *Under which conditions is plasticity most likely to aid colonization and in situ rescue?* I suggest that the answer is likely to be when 1) the trait is particularly important for fitness, 2) the new conditions are similar to those previously experienced by a lineage (plasticity is then more likely to have been shaped by past selection), 3) plasticity can accomplish large phenotypic changes, 4) plasticity isn't very costly, and 5) the traits are behavioral or physiological as these should be the most malleable traits on short time scales.

Question 5: Does Plasticity Promote or Constrain Genetic Evolution?

A number of arguments have been advanced for how plasticity might promote or constrain adaptive genetic change. On the constraining side, the main argument is that plasticity shields the genotype from selection, thereby slowing adaptive *genetic* change (Huey and Kingsolver 1993; Linhart and Grant 1996; Ghalambor et al. 2007). This argument applies mainly to *adaptive* plasticity, whereas maladaptive plasticity would be expected to increase selection for adaptive "genetic compensation" (West Eberhard 2003; Grether 2005; Ghalambor et al. 2007). On the promoting side, a common argument is that plasticity allows colonization of, and persistence in, extreme environments (Question 4), which thereby increases selection on that trait or other traits (West Eberhard 2003; Schlichting and Wund 2014). Another suggested positive influence is that plasticity can expose otherwise cryptic genetic variation (not expressed under normal conditions) to selection (West Eberhard 2003; Suzuki and Nijhout 2006; Pfennig et al. 2010; Moczek et al. 2011; Gomez-Mestre and Jovani 2013; Schlichting and Wund 2014). Related to this point, increasing genetic variance in reaction norm slopes is one way in which genetic variation in the trait can be increased in at least some environments, thus aiding trait evolution in those environments. In addition, simulations have suggested that plasticity can alter genetic architecture so as to increase the production of adaptive phenotypes (Fierst 2011). Given that nearly everything seems possible in theory (Paenke et al. 2007), I will here focus on empirical observations relevant to the key ideas.

The phenomenon of counter-gradient variation, where genetic effects are in the opposite direction to plastic effects, provides a nice demonstration of how maladaptive plasticity can promote, indeed necessitate, compensatory adaptive genetic change (Conover and Schultz 1995; Levins 1968; Conover et al. 2009). A well-known example is growth rate in Atlantic silversides, *Menidia menidia*. Northern and southern populations of this fish have similar body sizes in nature despite better growing conditions in the south. When raised in a common garden, however, fish from the northern population grow faster and to a larger size than do fish from the southern population. In this case, plastic effects on growth that result from environmental differences have led to the evolution of compensating genetic differences in intrinsic growth rate (Conover and Present 1990; Present and Conover 1992). The contrasting pattern of cogradient variation, where plastic effects are in the same direction as genetic effects, can imply that plasticity has reduced genetic divergence (Byars et al. 2007). (Of course, initial plasticity could well have allowed the cogradient genetic variation to evolve—as in genetic accommodation.) As both patterns are known to exist in nature, the important question becomes: how common is each? Although a formal meta-analysis has not been conducted, Conover et al. (2009) summarized more than 60 examples of counter-gradient variation, while finding many fewer examples of cogradient variation.

Counter-gradient variation thus provides a particularly obvious situation where plasticity can promote genetic change—because the plasticity is maladaptive and thus imposes selection for genetic compensation. Another such situation occurs when plastic change in one trait necessitates genetic change in other traits: that is, altering one aspect of the phenotype requires compensatory genetic changes in other aspects of the phenotype. As a clear example, the introduction of a predator (curly-tailed lizards, *Leiocephalus carinatus*) caused a prey species (*Anolis sagrei* lizards) to plastically shift their habitat to narrow perches in trees, which imposed selection for shorter legs (Losos et al. 2006). Of course, the opposite effect is also possible: behavioral thermoregulation (plasticity) reduces exposure to extreme temperatures and thereby reduces selection for physiological temperature adaptation (Huey and Kingsolver 1993).

It is much more difficult to ascertain whether *adaptive* plasticity in a trait *promotes* genetic change in the same trait. Some correlative support for this idea comes from studies of ecological speciation, as will be discussed further in Question 6. However, the best evidence would come from experiments showing that populations with greater adaptive plasticity in a trait also show faster adaptive evolution of the same trait. One such experiment has been performed. Schaum and Collins (2014) performed a laboratory experimental evolution study using 16 lineages of *Ostreococcus* (a marine green algae microbe) that initially differed in CO_2-related plasticity for "oxygen evolution rates" (generating oxygen through chemical reaction). During 400 generations of rearing under constant or fluctuating CO_2 conditions, lineages with higher ancestral plasticity showed faster evolution of population growth rates (a measure of fitness). This positive relationship between plasticity and evolution was, as expected, strongest in the treatments with fluctuating CO_2.

Evidence for the converse—plasticity in a trait *constrains* genetic divergence in that trait—also could be generated through the above-suggested experiments. Given their current scarcity, we can start with correlative support from 2 sorts of comparisons—one based on populations and one based on traits. For the first, populations showing greater plasticity in a trait should show lower genetic divergence (among populations) in that trait. For the second, traits showing greater plasticity should show lower genetic divergence. Exemplifying a population-based comparison, Misty Lake and Misty Inlet stickleback (*Gasterosteus aculeatus*) show strong genetic divergence in a number of adaptive traits, whereas Misty Lake and Misty Outlet stickleback show no genetic divergence but rather plastic differences (Sharpe et al. 2008). Of course, cause and effect is here difficult to establish given that high gene flow between the lake and outlet populations (Roesti et al. 2012) could prevent genetic divergence, leaving plasticity as the only recourse (as opposed to plasticity evolving and then limiting genetic divergence). Exemplifying a trait-based comparison, we have the adaptive responses of fish to low dissolved oxygen. In many species, fish from low-oxygen environments have larger gills so as extract more oxygen, and they also have smaller brains due to the resulting limitations on cranial space. Crispo and Chapman (2010) collected populations of the cichlid fish *Pseudocrenilabrus multicolor victoriae* from different oxygen environments in nature and raised their offspring under high and low oxygen conditions in the laboratory. Essentially all of the resulting variation in gill size was plastic, with no apparent genetic differences among populations (Figure 8). By contrast, brain size was less plastic and showed more genetic variation among populations (Figure 8). Similar findings (more plastic traits show lower genetic divergence) emerged in a study of the effects of predators on guppies (Torres-Dowdall et al. 2012).

Although the above observations are consistent with the idea that plasticity constrains genetic divergence, causation is hard to establish and, regardless, too few studies have been conducted to invite generalization. Moreover, the effects of plasticity could be—indeed they are often expected to be—transient during the course of evolution, such as in the case of genetic assimilation. Detecting such effects requires the tracking of genetic and plastic contributions during the course of environmental change or in controlled experiments (e.g., Schaum and Collins 2014).

Conclusion

Plasticity will sometimes promote and sometimes constrain genetic evolution. In this case, my vague answer mostly reflects a vague question: that is, the opposing expectations—and everything in between—should be differentially likely under different conditions. Thus, we here clearly need a better question, such as *Under which conditions does plasticity promote versus constrain genetic evolution?* Some predictions are that promoting effects will be most likely when 1) plasticity enables colonization/persistence where it would not be otherwise possible, 2) plasticity in one trait (e.g., behavioral flexibility that alters resource use) results in altered selection on other traits, 3) selection is on plasticity itself, 4) plasticity exposes otherwise cryptic genetic variation, and 5) plasticity is maladaptive. Although correlative tests of these hypotheses will be useful, particularly informative approaches would be experimental. In particular, more versus less plastic genotypes could be introduced into new environments and subsequent adaptive evolution monitored—as Schaum and Collins (2014) did in the laboratory.

Question 6: Does Plasticity Help or Hinder Ecological Speciation?

The previous question focused on variation within species, whereas the present question considers the same issues with respect to species formation. The debate has crystallized around 2 opposing schools of thought, which I here dichotomize for the sake of argument. (Both perspectives, and various intermediates, are acknowledged in most publications.) The first perspective is an extension of the "Baldwin Effect" described in Question 4. It argues that plasticity facilitates colonization of new environments, or the use of new resources, after which phenotypes are exposed to divergent selection that causes adaptive genetic divergence and hence ecological speciation (Skúlason and Smith 1995; Smith and Skúlason 1996; Robinson and Parsons 2002; West Eberhard 2003; Pfennig et al. 2010). One branch of this argument specifically emphasizes behavioral flexibility that results in the use of new resources, which can then enhance speciation through a process sometimes called "behavioral drive" (Wyles et al. 1983). The opposing school of thought is an extension of an idea from Question 5, arguing that plasticity shields the genotype from selection and thereby reduces genetic divergence and hampers speciation (Price et al. 2003; Ghalambor et al. 2007; Crispo 2008; Svanbäck et al. 2009; Thibert-Plante and Hendry 2011). Behavior also could have constraining effect by allowing organisms to maintain their use of a particular resource even as environments change,

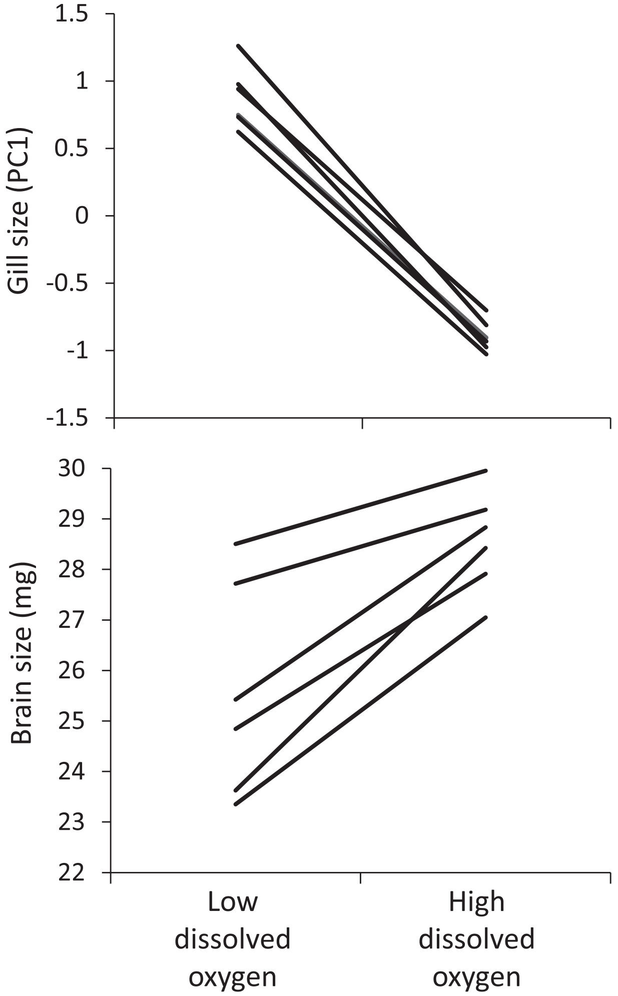

Figure 8. Population-level reaction norms for gill size (PC1 of measurements standardized to a common body size) and brain size (standardized to a common body size) for 6 populations of *Pseudocrenilabrus multicolor victoriae* raised under low and high oxygen conditions in the laboratory. These data are from Crispo and Chapman (2010).

which would reduce divergent selection (Duckworth 2009). I start by summarizing and evaluating 3 empirical observations suggested to indicate that plasticity promotes ecological speciation.

1. Plasticity within species, ideally demonstrated in ancestral forms, is sometimes in the same direction as genetic differences between species. One clear example is trophic morphology in fishes, where "limnetic" versus "benthic" diets cause plastic divergence in trophic morphology in a direction that parallels genetically based divergence between closely-related species (Day et al. 1994; Robinson and Parsons 2002; Adams and Huntingford 2004; Wund et al. 2008). The common inference therefrom is that ancestral plasticity initiated and promoted the subsequent genetic divergence.
2. Character displacement between species is sometimes facilitated by polyphenism (different, discrete phenotypes emerge when the same genotype is exposed to different environments), which can then sharpen reproductive barriers (Pfennig and Pfennig 2009). In spadefoot toads, for example, 2 species (*Spea bombifrons* and *S. multiplicata*) can develop either herbivorous or carnivorous tadpoles: but, when reared together, *S. multiplicata* produces many fewer carnivores than does *S. bombifrons*. In addition, *S. multiplicata* from ponds with more *S. bombifrons* in nature are genetically less likely to produce carnivores in a common-garden environment (Pfennig and Murphy 2002). The common inference therefrom is that selection in sympatry has enhanced ancestral polyphenism and thereby exaggerated species divergence.
3. Plasticity might be greater in taxonomic groups that are more speciose, as a number of studies have shown. Nicolakakis et al. (2003) reported that innovation rate, a proxy for behavioral flexibility, is positively related to the number of species within bird taxa. Sol et al. (2005) showed that relative brain size, which is correlated with behavioral flexibility, is positively related to the number of subspecies in Holarctic passerines. Tebbich et al. (2010) pointed out that the bird group that has diversified most in Galápagos, Darwin's finches, shows very high levels of behavioral flexibility. Pfennig and McGee (2010) used sister group comparisons to show that fish and amphibian lineages that include polyphenic species are more speciose. The common inference from such findings is that plasticity generally promotes diversification, speciation, and adaptive radiation.

Each of the above arguments is *consistent* with idea that plasticity promotes speciation, yet none of them provides strong evidence. One problem is that no meta-analysis has yet quantified the extent to which plasticity within species is in the same direction as divergence between species. Moreover, observed plastic effects within species are often much smaller than observed differences between species, even if they are in the same direction (e.g., Losos et al. 2000). Another limitation of the first 2 types of analysis is that a low-plasticity "control" comparison is not normally considered: that is, speciation might have been even more likely/rapid/dramatic if plasticity wasn't present. Most critically, the identical prediction (plastic and genetic differences are in the same direction) also emerges from arguments that plasticity *constrains* divergence. In the third type of analysis, the level of plasticity is often unknown in the ancestral species. As a result, it is difficult to establish whether plasticity was the cause or the consequence of high diversification.

One process by which plasticity is particularly likely to promote speciation occurs when juveniles imprint on parents, conspecifics, environments, or resources. Such imprinting can lead to assortative mating that allows genetic divergence and the evolution of reproductive barriers. In birds, nestlings sometimes imprint on the songs of their fathers (Price 2008), with male offspring later singing—and female offspring later preferring—similar songs. The result can be mating isolation between groups whose songs have diverged for whatever reason (Price 2008). Remarkably, male and female nestlings of brood-parasitic *Vidua* finches imprint in a similar way on the songs of their host species, which leads to assortative mating between finches parasitizing different hosts (Payne et al. 2000). In insects, larvae sometimes imprint on the plant on which they feed ("conditioning") and then preferentially select those plants during mating and oviposition, thus generating mating isolation between groups using different host plants (Funk et al. 2002). In salmonid fishes, juveniles often imprint on chemical properties of their natal site and then strongly "home" back to that site for reproduction, which reduces gene flow between populations (Hendry et al. 2004). Considering these examples as instances of "positive" imprinting, "negative" imprinting also can reduce gene flow: for example, exposure to heterospecifics can strengthen preferences against them (Price 2008; Delbarco-Trillo et al. 2010). In each of these cases, reproductive isolation depends on individuals being exposed to different environments, with another example being the commensal bacteria in *Drosophila* that influence the chemical signals that drive mating isolation (Sharon et al. 2010).

What of the opposing school of thought—that plasticity retards speciation? Empirical support might be provided through evidence that groups with *lower* plasticity speciate more often, or that the traits determining reproductive isolation between species are not especially plastic (especially in the ancestor). Formal tests of these predictions have not been performed; however, many populations in different environments show strong plastic differences and yet minor—if any—reproductive isolation. Following up on examples from Question 5, gene flow is high between populations where phenotypic divergence has a primarily plastic basis in *Pseudocrenilabrus* from different oxygen environments (Crispo and Chapman 2008) and between the Misty Lake and Outlet stickleback populations (Roesti et al. 2012). Despite such putative examples, the idea that plasticity hampers speciation has not yet been subject to rigorous testing.

Conclusion

Plasticity will sometimes help and sometimes hinder ecological speciation (see also Duckworth 2009). This vague answer reflects both weak data and a vague question, with a better question mirroring those suggested for the above questions: *Under what conditions does plasticity help versus hinder ecological speciation?* With respect to data, current empirical tests are insufficient to allow general conclusions as to how often and when each result is most common. Among the improvements suggested above, the most critical would be controlled experiments that examine progress toward ecological speciation in lineages that are initially more or less plastic. In general, I predict that plasticity is especially likely to have positive effects in the various manifestations of imprinting, when mating cues depend on environmental exposure, and when dispersal occurs after (rather than before) plastic changes occur (Thibert-Plante and Hendry 2011).

Question 7: How Fast Does Plasticity Evolve?

Many studies dichotomize phenotypic change into that caused by genetic change versus that caused by plasticity. In reality, both effects can occur at the same time and can influence each other—as has been described previously. Moreover, plasticity can evolve and such change should have important consequences for population dynamics, including "rescue" (Question 4). It is therefore important to ask how quickly plasticity can evolve and what factors increase or decrease this rate.

A first point is that many studies have documented the evolution of reaction norms on the time scale of decades, with a classic example being the phototactic behaviour of *Daphnia* in response to changing fish predation (De Meester 1996; Boersma et al. 1998; Cousyn et al. 2001). Many other examples exist—and I will here mention 2. The Asian shade annual plant *Polygonum cespitosum* colonized North America in the early 1900s and has recently spread into more open habitats. In the 10 years following this niche expansion, the plant has evolved increased plasticity in root allocation and physiological traits in response to open versus shaded conditions (Sultan et al. 2013). The Asian shore crab *Hemigrapsus sanguineus* was first reported in North America in 1988 and feeds on native marine mussels *Mytilus edulis*. At present, mussels in areas where the crab has invaded (southern New England) show inducible shell thickening in response to waterborne *H. sanguineus* cues, whereas mussels in areas where the crab has not invaded (northern New England) do not (Freeman and Byers 2006). At the same time, however, a number of other studies have documented instances where plasticity did not evolve even on long time scales despite a change in selection pressure. A particularly obvious example is the retention of antipredator behavior long after the predator is no longer present (Lahti et al. 2009). These latter cases likely reflect relaxed selection (the trait is not expressed in the absence of the cue), in which case trait evolution would occur only through the relatively slow processes of drift and mutation.

As always, selected examples can only take us so far and any hope of generality must come from meta-analyses. In one meta-analysis, Crispo et al. (2010) analyzed 20 studies that measured plasticity in 2 or more populations, at least one of which was subject to recent human disturbance and at least one of which was not. The authors calculated rates of change for plasticity in darwins and haldanes, 2 common metrics of rates of change in phenotypic traits (Hendry and Kinnison 1999). Results showed that disturbed plant populations often evolved changes in plasticity and that different taxa and traits showed different responses. Based on a qualitative comparison between Crispo et al. (2010) and Hendry et al. (2008), rates of evolution of plasticity were qualitatively similar to rates of evolution of mean phenotypes.

Conclusion

Plasticity can show considerable evolutionary change on contemporary time scales, although the rates of this evolution are highly variable. These findings confirm theoretical expectations that plasticity can evolve quickly and thereby have important fitness consequences (Thibert-Plante and Hendry 2011; Chevin et al. 2013a). More data is certainly needed and more refined questions would be advantageous, such as: *What types of traits, taxa, and environmental conditions generate the fastest evolution of plasticity?* In this case, the way forward is clear: use laboratory experiments to assess plasticity either in ancestor/descendent pairs (the allochronic approach, *sensu* Hendry and Kinnison 1999 in populations that had a common ancestor at a known time in the recent past (the synchronic approach).

Question 8: How Might Plasticity Have Community/Ecosystem Effects?

To the extent that organismal traits have community/ecosystem effects, plastic changes in traits should alter those effects (Murren et al. 2015; Collins and Gardner 2009; Chevin et al. 2013b; Kovach-Orr and Fussmann 2013). Very few empirical studies have directly assessed this question but a few examples will illustrate the possibilities, starting with community influences and then moving to ecosystem influences.

Many foraging traits of fishes are phenotypically plastic in response to diet. For instance, fish fed on zooplankton diets (as opposed to benthic diets) tend to have longer gill rakers and changes in jaw morphology that increase foraging efficiency on those food items (Day and McPhail 1996). Because these traits have dramatic influences on aquatic prey communities (Harmon et al. 2009; Palkovacs and Post 2009), diet-induced trophic plasticity should influence prey communities (Lundsgaard-Hansen et al. 2014). Such effects have not yet been demonstrated formally in nature but they would be fascinating to explore, not the least because they show a strong chance of feedbacks. That is, plastic changes in traits that influence foraging success on a given food type should reduce the availability of that food type (and induce its evolution) which should then influence further plasticity and selection. Another situation for which plasticity is almost certainly critical for community structure is the relative phenology of interacting species (Both et al. 2009; Phillimore et al. 2012).

Rates of feeding, metabolism, and growth dramatically influence biological stoichiometry, "the balance of energy and multiple chemical elements in living systems", by altering the consumption and excretion of various elements (Elser et al. 2000; Matthews et al. 2011). As a result, plastic changes in these rates could have dramatic effects on the availability and transfer of elements within and between communities and ecosystems. As one example, Schmitz (2013) argued that increasing animal metabolic rates with increasing temperature owing to climate change should cause "phenotypically plastic shifts in animal elemental demand, from nitrogen-rich proteins that support production to carbon-rich soluble carbohydrates that support elevated energy demands." The resulting change in diets should then have important consequences for carbon cycling (Schmitz 2013). As another example, Dalton and Flecker (2015) showed that the presence of dangerous predators (simulated with predator cues in the laboratory) decreased N excretion rates of guppies by 39%, which could have important consequences for this limiting nutrient in their stream ecosystems.

Another likely arena for ecosystem effects of plasticity is for organisms that produce chemical resources that are used by many other organisms, such as plants producing CO_2 or fixing nitrogen. Such effects seem particularly likely given the great plasticity in these processes depending on environmental conditions, such as ambient levels of CO_2 or nitrogen, as well as temperature and humidity. Collins and Gardner (2009) provide a "worked example" of how to calculate the potential contribution of plasticity, evolution, and community change to carbon uptake by marine phytoplankton experiencing elevated CO_2 levels. At present, however, all such applications (for other examples, see Chevin et al. 2013b) are theoretical, hypothetical, or lab-based. Sorely needed are formal assessment in natural systems.

Conclusion

Plasticity likely has considerable influence on ecological dynamics at the community and ecosystem levels, with foraging traits, biological stoichiometry, and chemical production by plants being particularly promising candidates. In addition, any plasticity-induced effect on population dynamics (e.g., plastic rescue) should also have indirect effects on community and ecosystem parameters. At present, however, formal demonstrations of the effects of organismal plasticity on community and ecosystem variables are extremely rare, especially in nature. Thus, the lack of a strong answer here is, at least currently, an issue of data availability.

Conclusions, Significance, and Implications

Plasticity is the prodigal son of evolutionary biology. Ignored for many years owing to a primary focus on the role of natural selection in shaping differences between populations, plasticity has recently returned with a vengeance—perhaps too much so for the liking of some (e.g., de Jong 2005). The reality is that essentially all traits will be influenced by plasticity, although the extent, type, and consequences will be highly variable among traits and taxa. Importantly, evolution and plasticity are not strict alternatives, but rather both contribute to divergence in many instances. Of particular note, many trait differences are likely due to the *evolution of* plastic differences (i.e., divergent reaction norms), which can occur on contemporary time scales. With regard to its evolution, plasticity is often (but not always) adaptive, often (but not always) costly, and often (but not always) an evolved response to spatiotemporal environmental variation. Given these numerous and diverse possibilities, it is not surprising that valid arguments can be raised that plasticity will sometimes promote and sometimes constrain adaptive genetic divergence and speciation. At present, however, the data supporting either alternative is indirect and often unconvincing. We need more data and better questions, as I have suggested throughout.

Given that plasticity will influence traits in nearly every instance, it is also likely to have an important role in shaping the ecological effects of those traits: that is, the evo-to-eco of eco-evolutionary dynamics (see also Miner et al. 2005). For instance, adaptive plasticity will often (but not always) aid the ability of populations to persist in changing environments and to colonize and spread in new environments. These population dynamics effects likely then cascade to indirect influences on communities and ecosystems. Plasticity likely also has direct influences on communities and ecosystems. As one example, trophic traits are often strongly influenced by plasticity, which will then have many community and ecosystem consequences. Similarly, plant traits are often very plastic and so many of the ecological effects of those traits (most obviously individual plant biomass) will also be fundamentally altered by plasticity. For all of these reasons, plasticity needs to be an integral part of any conceptual framework and empirical investigation of eco-evolutionary dynamics.

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