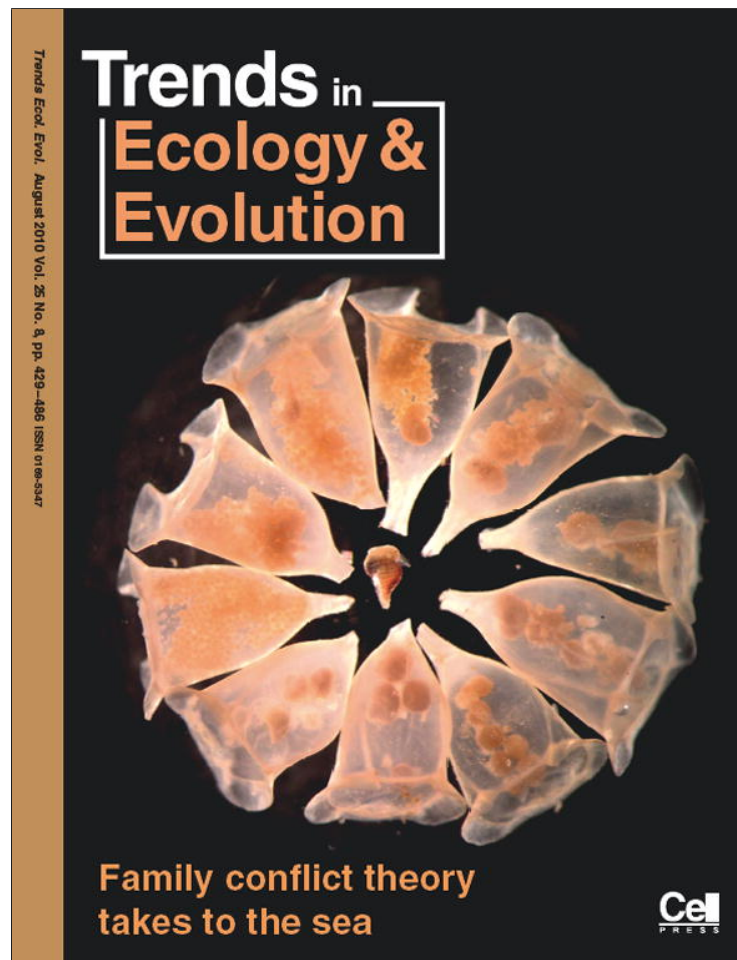


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Phenotypic plasticity's impacts on diversification and speciation

David W. Pfennig¹, Matthew A. Wund², Emilie C. Snell-Rood³, Tami Cruickshank³, Carl D. Schlichting⁴ and Armin P. Moczek³

¹ Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA

² Department of Biology, The College of New Jersey, Ewing, NJ 08628, USA

³ Department of Biology, Indiana University, Bloomington, IN 47405, USA

⁴ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA

Phenotypic plasticity (the ability of a single genotype to produce multiple phenotypes in response to variation in the environment) is commonplace. Yet its evolutionary significance remains controversial, especially in regard to whether and how it impacts diversification and speciation. Here, we review recent theory on how plasticity promotes: (i) the origin of novel phenotypes, (ii) divergence among populations and species, (iii) the formation of new species and (iv) adaptive radiation. We also discuss the latest empirical support for each of these evolutionary pathways to diversification and identify potentially profitable areas for future research. Generally, phenotypic plasticity can play a largely underappreciated role in driving diversification and speciation.

Plasticity and diversification

A major goal of evolutionary biology is to understand how and why living things diversify. Historically, research has concentrated on genetic and ecological causes of diversification [1–5]. By contrast, development's contribution has received much less attention. Nevertheless, it is increasingly clear that the responsiveness to changes in the environment commonly seen in development (Figure 1), and the evolution of this sensitivity (Figure 2), might play a key role in diversification and speciation [6–10].

Phenotypic plasticity is the capacity of a single genotype to produce different phenotypes in response to varying environmental conditions [11]. Although phenotypic plasticity has had a long history in evolutionary biology, its evolutionary significance remains controversial [6]. On the one hand, a central tenet of the modern synthesis of evolutionary biology is that phenotypic change wrought by the environment does not influence the genes that an individual transmits to its offspring [12]. Accordingly, many evolutionary biologists have long held that plasticity has no relevance for the evolutionary process other than to perhaps impede it by dampening the effects of selection (Box 1). On the other hand, early evolutionists, most notably Weismann, Goldschmidt, Schmalhausen, and Waddington, maintained that plasticity is central in the origin of phenotypic differences between species [13].

Recently, there has been renewed interest in clarifying phenotypic plasticity's role in evolution [6–9,13,14]. This renaissance has spawned innovative theory and data,

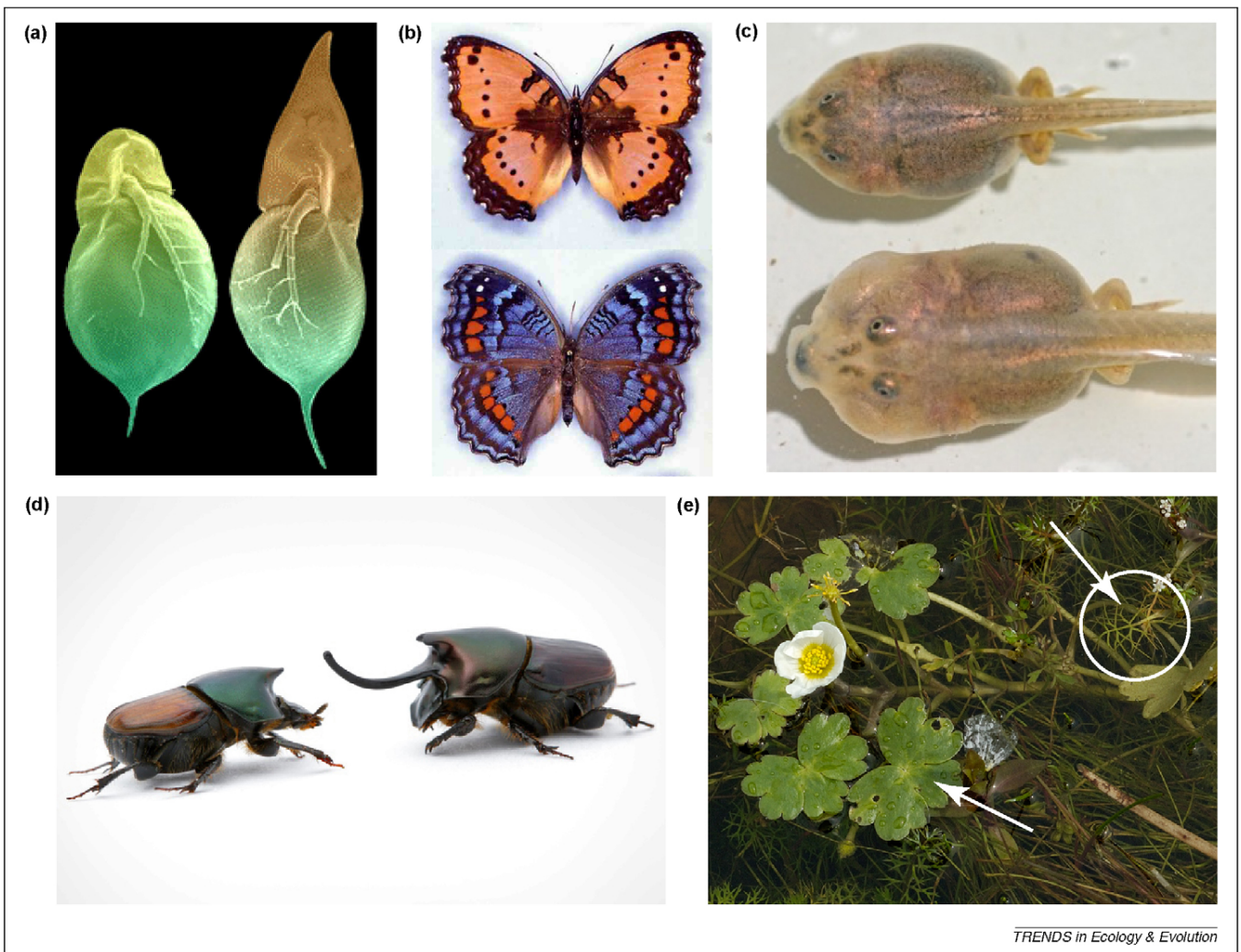
which implicate plasticity in two of evolution's most fundamental events: the origin of novel, complex traits [9,15,16] and the origin of new species [10,14,17,18]. Although plasticity's importance in promoting diversification and speciation has garnered widespread acceptance among researchers in the emerging field of ecological developmental biology [6,19], these ideas remain controversial for many evolutionary biologists. For example, recent reviews of speciation [1,2,4,5] generally fail to discuss phenotypic plasticity, indicating that workers in this field do not recognize a significant role for plasticity in speciation. The reasons for this controversy are varied and complex [7,9,20], but they range from the difficulties of incorporating environmental complexity into existing theory and empirical studies to a mistaken invocation of Lamarckianism.

Our goal is to move beyond this debate and instead explore how these ideas can enrich our understanding of how and why living things diversify. We specifically focus on adaptive plasticity and describe recent theory on how such plasticity promotes diversification at four different levels of biological organization: (i) the origin of novel phenotypes and divergence within populations, (ii) the evolution of divergence among populations and species, (iii) the formation of new species and (iv) adaptive radiation. We also discuss the latest empirical support for each pathway to diversification and outline profitable avenues for future research.

Plasticity's role in promoting novel phenotypes and divergence within populations

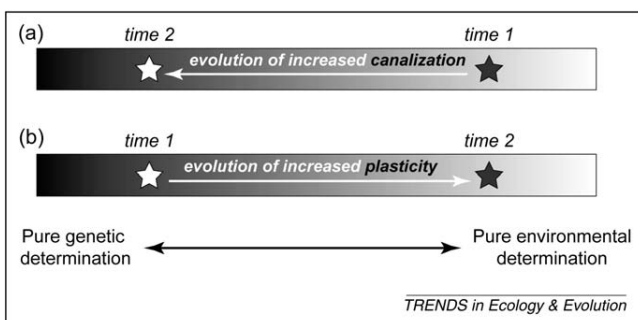
Because of its unique ability to generate an immediate phenotypic response to the environment [9], phenotypic plasticity plays a key role in fostering divergent phenotypes within populations and subsequently driving diversification. In particular, when either directional or disruptive selection favors novel or divergent phenotypes, the developmental genetic pathways underlying plasticity provide both an immediate, population-wide response to the environment [21] and the genetic variation on which selection can act, promoting the evolution of diverse phenotypes. Once induced, environmentally initiated phenotypes can be refined by selection through the processes outlined below. In contrast to the rapid response produced by plasticity, if the production of newly favored phenotypes

Corresponding author: Pfennig, D.W. (dpfennig@unc.edu).



TRENDS in Ecology & Evolution

Figure 1. Representative examples of environmentally induced alternative phenotypes (polyphenism). **(a)** Normal (left) and predator-induced (right) morphs of water fleas, *Daphnia cucullata* (photo courtesy of Ralph Tollrian); **(b)** wet-season (top) and dry-season (bottom) gaudy commodore butterflies, *Precis octavia* (photo courtesy of Fred Nijhout); **(c)** omnivore (top) and carnivore-morph (bottom) spadefoot toad tadpoles, *Spea multiplicata* (photo by David Pfennig); **(d)** small-horned (left) and large-horned (right) dung beetles, *Onthophagus nigriventris* (photo by Alex Wild); **(e)** broad, aerial leaves and narrow, submerged leaves (circled) on the same water crowfoot plant, *Ranunculus aquatilis* (photo by John Crellin/Florallimages).



TRENDS in Ecology & Evolution

Figure 2. A schematic depicting the evolution of development, which emphasizes the continuum between genetic and environmental influences on phenotypes. Individuals might vary phenotypically because they possess different genes or because they experienced contrasting environments and trait differences arose through phenotypic plasticity. These two proximate mechanisms are best thought of as occupying different positions along a continuum in which strict genetic determination of trait production resides at one end and pure environmental induction resides at the opposite end. Most (perhaps all) traits, however, lie between these two extremes. Moreover, a trait's position along this continuum can change over evolutionary time. For example, in **(a)** a trait evolves reduced environmental sensitivity (i.e. it undergoes genetic assimilation), whereas in **(b)** a trait evolves increased environmental sensitivity. Such shifts can have profound impacts on diversification and speciation.

requires new mutations, the waiting time for such mutations can be prohibitively long and the probability of subsequent loss through drift can be high [22].

Phenotypic plasticity can promote diversification because the developmental pathways that underlie environmentally induced phenotypes consist of many genetic components that can potentially respond to selection. For instance, these genetic components might regulate the likelihood or degree to which a phenotypic response to an environmental signal is triggered or the critical period during which external cues must be detected to produce an environmentally induced phenotype [23]. More generally, gene expression throughout development is sensitive to both internal and external environmental cues [24–26]. Variation in gene expression is also often underlain by genetic and gene by environment interaction components [27].

Additionally, because selection operates on suites of traits, plasticity in one trait can influence selection on linked or correlated traits. An environmentally induced change in morphology, for instance, is often accompanied by changes in behavior and physiology [28,29]. Hence,

Box 1. Why does plasticity sometimes impede and sometimes facilitate diversification?

Evolutionary biologists have long argued that phenotypic plasticity should dampen selection for diversification [8], for two reasons. First, plasticity allows a single genotype to produce multiple phenotypes in response to different environmental (and hence, selective) regimes, and thus genetic alternatives are not required for attaining fitness optima. Second, different genotypes can produce the same phenotype via plastic responses, thus hiding genetic differences between them from the discerning eye of selection. Here, we consider three factors that can influence whether plasticity impedes or facilitates evolutionary change and diversification.

The first factor is the genetic architecture of the focal trait and its plasticity [8]. If there is a strong genetic correlation between the trait and its degree of plasticity, trait evolution will be inhibited. However, if there is a weak correlation, trait evolution might be slowed but will not be halted. Natural selection does not care how phenotypes near the optimum for that environment are produced, and thus both adaptive plastic responses and alleles that move the trait mean will be favored.

A second factor that can influence whether plasticity impedes or facilitates diversification is the degree of plasticity expressed in a population [9,14]. Generally, diversification is most likely to occur in populations that express moderate levels of phenotypic plasticity [9,14]. Such levels are optimal in both permitting population survival in a novel environment and bringing populations into the realm of attraction of an adaptive peak [14]. By contrast, low levels of plasticity are less likely to do either, and, whereas high levels of plasticity increase the probability of population persistence, they also reduce the likelihood of genetic change. This is because high levels of plasticity tend to place the population close to an adaptive peak, thereby dampening the effects of selection for novel genetic variants [14].

Finally, whether plasticity impedes or facilitates diversification also depends on plasticity's effects on gene flow. Plasticity can promote gene flow between selective environments by allowing dispersers to adapt to alternate conditions [81], which could in turn either inhibit or spur adaptive divergence between populations [91].

In sum, to assess whether plasticity impedes or facilitates diversification, it is important to consider the combined effects of genetic architecture, selection, and gene flow, as these factors can influence plasticity's impacts on adaptive divergence in natural systems.

induction of one phenotype can indirectly influence the expression of numerous other traits and expose them to novel selective pressures. Environmentally induced change in behavior can also alter the nature of selection on morphological traits. For example, learning to exploit a new niche (a manifestation of plasticity) facilitates survival in novel environments [30], exposing resource-use traits to new selection pressures [14].

Furthermore, phenotypic plasticity promotes the accumulation and release of cryptic genetic variation (i.e. variation that is only expressed under certain environmental or genetic conditions) [31,32]. As we describe in greater detail below, such variation can provide the raw material for diversification and speciation. Plasticity facilitates the building up of genetic variation, both because the effects of novel genetic variants are buffered by compensatory plastic responses [15,33,34] and because environment-specific genes are subject to relaxed selection in the non-inducing environment [35–37]. The buildup of cryptic genetic variation can lead to further phenotypic novelty in subsequent generations when such genetic variation is revealed through a change in the environment or genome (via mutation, recombination and/or epistasis). Such unmasking

of standing genetic variation facilitates evolutionary change [38]. This variation can also supply the raw material for genetic accommodation [9]. Genetic accommodation is a mechanism of evolution wherein a novel phenotype, generated either through a mutation or environmental change, is refined into an adaptive phenotype through quantitative genetic changes [39]. Genetic accommodation can result in either increased or decreased environmental sensitivity of a plastic phenotype (Figure 2a,b). When induced phenotypes lose their environmental sensitivity, they undergo genetic assimilation (Figure 2a) whereby an induced phenotype becomes, through evolutionary time, a constitutively expressed trait [40].

Both genetic assimilation and genetic accommodation are potentially important in diversification. When an induced phenotype becomes expressed constitutively, environmentally induced variation within populations or species can be translated into diverse phenotypes between populations and species. Thus, genetic assimilation generates diversity because it produces fixed (genetic) differences among populations due specifically to the shift from a plastic to a nonplastic phenotype. Theory has demonstrated genetic assimilation's capability for promoting diversification [41,42], and empirical studies find that phenotypic plasticity produces intraspecific variation that parallels interspecific variation within the same clade [43–47]. Further support for genetic assimilation's role in evolution comes from studies showing that phenotypic plasticity in an ancestor mirrors, in magnitude and direction, fixed phenotypic differences observed between populations [16,48–51] or species [52–54]. These studies are complemented by selection experiments demonstrating the feasibility of genetic assimilation [39,40].

Genetic accommodation is also potentially important in diversification [9]. Experiments have shown that genetic accommodation can lead to an evolutionary gain of plasticity (e.g. through the evolution of novel response thresholds) [39]. Genetic accommodation might even promote the evolution of an extreme form of plasticity known as polyphenism [23]. Polyphenic development arises when individuals with identical genomes respond to different environmental cues by expressing alternative developmental pathways [24,25], which results in distinctively different, adaptive phenotypes. Polyphenism provides some of the most dramatic examples of diversity within populations (Figure 1). Furthermore, as we explain in greater detail below, the evolution of such divergent phenotypes might often instigate the process of speciation.

Future research should seek to: evaluate the relative importance of polyphenism versus other mechanisms of plasticity for diversification; identify the relative frequency of genetic assimilation versus accommodation; determine whether the developmental genetic mechanisms of plasticity are concordant with the genetic basis of phenotypic differences between higher taxa, as proposed by recent work [55,56].

Plasticity's role in promoting divergence among populations and species

At the most obvious level, phenotypic plasticity promotes divergence among populations by directly producing

phenotypic differences when populations experience different environmental circumstances. If these differences are strictly environmental in origin, they might ultimately be trivial. However, if genetic variation in plasticity exists (or arises), then a response to selection can ensue. With environmental induction, even weak selection can cause dramatic shifts in trait distributions between populations [57,58].

Phenotypic plasticity also promotes population divergence by facilitating peak shifts or valley crossing on the adaptive landscape [8,14,59,60]. Imagine two hypothetical populations, each of which initially occupies one of two possible peaks on an adaptive landscape. Suppose environmental conditions in one population change abruptly, such that the population no longer resides at a fitness optimum. To reach an alternative peak through a traditional process of incremental evolution, a population must, through the accumulation of small genetic changes, first cross a fitness valley of maladaptive intermediate forms. Such valley crossing is normally prevented by selection. However, with plasticity (and especially polyphenism), valley crossing unfolds in developmental, rather than in evolutionary, time. Thus, a population can traverse a valley rapidly, potentially in one generation, by facultatively expressing an alternative phenotype closer to the fitness optimum. Consequently, populations experiencing different environmental conditions can diverge rapidly.

Once populations begin to diverge, plasticity further enhances divergence by promoting the differential fixation of alternative phenotypes in populations that no longer experience both environments. The loss of plasticity and the subsequent fixation of the induced, favored phenotype occurs through genetic assimilation and can proceed via two routes. First, when maintenance or expression of plasticity is costly [36], selection can actively eliminate it, causing one phenotype to be fixed in the population. Second, plasticity can be lost through mutational degradation or genetic drift [61], thereby leading to genetic assimilation. Experiments have demonstrated the loss of plasticity [39], and data from natural populations indicates that the resulting differential fixation of alternative phenotypes in different populations can drive phenotypic (and possibly, genotypic) divergence between populations [62,63] and species [64]. Moreover, when different populations evolve different response thresholds, genetic accommodation can accentuate divergence between populations.

Plasticity promotes divergence not only between populations, but between species as well. Individuals of many species use phenotypic plasticity to facultatively alter their phenotype in response to the presence of other species, be they mutualists, enemies or commensals [65]. For example, many species respond adaptively to competitors by facultatively producing a resource-use phenotype unlike that of their competitor [64]. Similarly, numerous species respond adaptively to predators by facultatively producing a predation-resistant phenotype in the presence of predators [65].

Phenotypic change induced in one species might induce additional changes in the other species. This reciprocal selection can generate a 'runaway' process in which each

population evolves ever greater plasticity [11], thereby exaggerating divergence between species. Alternatively, such reciprocal selection might cause either species to lose plasticity if specific different phenotypes are favored in each species, thereby causing fixation of species differences. For example, data from natural populations have shown that species that respond to competitors through plasticity can become fixed for dissimilar phenotypes [64], possibly via genetic assimilation. As we describe in the next section, such fixation could promote speciation between populations that have, and have not, undergone such divergence [66].

Plasticity's role in promoting speciation

Speciation begins when populations become genetically isolated from each other (e.g. owing to spatial segregation). This process culminates when these populations diverge because of either selection or genetic drift until they can no longer successfully interbreed [2]. Historically, phenotypic plasticity was not thought to contribute to this process. However, phenotypic plasticity's tendency to facilitate population divergence (see above) might be crucially important in speciation, because any process that promotes population divergence should also facilitate speciation [1,4].

Recent data suggest that plasticity might play an important role in promoting speciation. For example, as noted above, phenotypic plasticity generates phenotypic variation within species that often parallels variation between species of the same clade, implying that environmentally induced, intraspecific variation might form the basis for interspecific diversification [10]. The challenge has been to discover how plasticity might actually facilitate speciation [9,11]. Here, we review a plausible, and potentially common, mechanism.

We specifically focus on the role of polyphenism in speciation [18]. The evolution of a resource polyphenism, i.e. divergent, environmentally triggered, resource-use phenotypes within a population (Figure 1c), is a critical early stage of speciation in some models [17,18,67,68]. Indeed, recent research has revealed that populations differing in expression of resource polyphenism often exhibit ecological and genetic differences and even partial reproductive isolation (Table 1), indicating the presence of incipient species [17,67,69–71].

The evolution of alternative resource-use morphs might be particularly effective at facilitating speciation because the same conditions that promote resource polyphenism simultaneously foster speciation's three components: genetic isolation, divergence and reproductive isolation [18]. Genetic isolation can arise between morphs because alternative resource-use morphs typically differ in the locations and times that they seek their separate resources [67] and thereby, potentially, where and when they seek mates. Such isolation between ecotypes can enable natural selection to enhance existing differences between alternative morphs (and also between populations that differ in the expression of such morphs). In particular, natural selection will generally favor morph-specific traits that improve a morph's ability to exploit its particular niche [72]. Moreover, even

Table 1. Representative examples in which populations that differ in the expression of alternative, environmentally influenced, resource-use morphs appear to be evolving reproductive isolation.

Species	Type of divergence	Citation for evidence of reproductive isolation	Citation for evidence of environmental influence on morph determination
Numerous species of phytophagous insects	Different host plants	[78]	[85] ^a
Sticklebacks (<i>Gasterosteus aculeatus</i>)	Benthic and limnetic niches	[86]	[16]
Midas cichlids (<i>Amphilophus</i> sp.)	Benthic and limnetic niches	[87]	[68]
Spadefoot toads (<i>Spea multiplicata</i>)	Omnivore and carnivore niches	[66]	[64]
Crossbills (<i>Loxia curvirostra</i>)	Different food types	[88]	[89] ^a
Darwin's finches (<i>Geospiza fortis</i>)	Different food types	[90]	[89] ^a

^aAn individual's resource-use phenotype might be influenced by learning, a type of plasticity.

small-scale ecological separation can influence patterns of sexual selection, which could further enhance divergence between morphs [73].

Once alternative morphs begin to accumulate these ecological and genetic differences, matings between them should produce offspring with low fitness [74], thereby favoring the evolution of reproductive isolation between such divergent individuals [4,75]. Furthermore, matings between populations that differ in expression of phenotypic alternatives should also produce offspring of low fitness [76], again favoring the evolution of reproductive isolation between such populations [66]. For example, imagine that selection has favored a high inherent propensity to respond to an environmental cue and produce a particular morph in one population, but a low propensity to produce this same morph in another population. Assuming additive inheritance, the offspring of matings between such populations would have a maladaptive propensity to produce this morph and would therefore be disfavored [76]. In such situations, selection should favor assortative mating by ecotype or population, leading to complete reproductive isolation and, possibly, speciation.

Although the above process can occur even when alternative morphs are not environmentally induced and are instead specified by alternative alleles [67], speciation can proceed especially rapidly when morphs are environmentally induced, because a sudden change in the environment can simultaneously induce and select for a single alternative phenotype [64]. If there is underlying genetic variation in the degree to which individuals respond to the environmental change, this process can have important genetic consequences. In particular, once only a single morph is expressed in a population, selection should favor alleles that regulate expression of the newly favored trait through the process of genetic accommodation. By contrast, alleles that regulate expression of the alternative, 'hidden' phenotype(s) would not be exposed to selection and would be at greater risk of chance loss through genetic drift, thereby possibly leading to fixation of the favored morph through genetic assimilation. Thus, population differences that initially arose through plasticity might eventually become genetically fixed. This process might thereby contribute to the rapid accumulation of genetic differences between populations that, in turn, enhance reproductive isolation.

Recent comparative data indicate a possible causal link between polyphenism and species formation. Fish and amphibian clades in which resource polyphenism has

evolved are more species rich than sister clades lacking resource polyphenism [18] (Figure 3). However, more direct tests of whether and how polyphenism specifically, and plasticity more generally, promotes speciation are needed. Organisms with short generation times that facultatively shift hosts and mate on their hosts, such as certain microbes [77] and phytophagous insects [78], might prove especially useful for these tests. For example, such organisms could be used to determine whether lineages with higher levels of plasticity are more likely to evolve reproductive isolation (or evolve it faster) than lineages with lower levels of plasticity when different populations of each lineage are experimentally exposed to contrasting selective environments. Future research should also evaluate the possible contributions to speciation of forms of polyphenism other than resource polyphenism. For instance, recent research has shown that the selective loss of polymorphic mating types is associated with speciation [79], indicating a possible role in speciation for mating polyphenism (Figure 1d).

Plasticity's role in promoting adaptive radiation

Phenotypic plasticity might also promote adaptive radiation, influencing both the likelihood of occurrence and the patterns of diversity that emerge. In adaptive radiation, a single ancestral lineage diversifies rapidly in response to divergent selection pressures across numerous environments [1]. 'Replicate radiations' arise when many descendant species evolve parallel ecotypic variation in response to similar selection pressures [1]. Theoretically, plasticity could facilitate each step in this process: persistence in novel environments, rapid evolutionary response to altered selection pressures via genetic accommodation, and repeated evolution of phenotypes matched to specific environments. Here, we describe how plasticity can represent a key innovation that catalyzes adaptive radiation in general and replicate radiation in particular.

In a new environment, plasticity rapidly produces new phenotypic variants, increasing the likelihood of survival of at least some individuals. Empirical evidence indicates that plasticity can promote successful colonization of novel environments [18,80,81] and adaptive responses to new selection pressures [82]. Thus, by increasing phenotypic variance, plasticity might increase persistence under novel circumstances [81], providing an opportunity for subsequent adaptive radiation. Moreover, by generating new targets for selection within a single generation,

plasticity promotes a hallmark of adaptive radiation: rapid evolution. Whereas a new mutation occurs in a single individual and must spread through the population over many generations, a change in environment often leads to the simultaneous expression of novel, induced phenotypes in many individuals [9].

This model of evolution can help explain the repeated evolution of specific ecotypes and the replicate nature of many adaptive radiations. Parallel ecotypic variation is often ascribed to similar selective pressures acting on separate populations [83]. However, considering the contribution of ancestral plasticity could explain why isolated derivatives repeatedly evolve the same solutions to the same problems. According to the 'flexible stem' hypothesis [9], an adaptive radiation arises when ecological circumstances favor diversification in an ancestral taxon that expresses phenotypic plasticity in the types of traits that characterize the adaptive radiation. Under such circumstances, when individuals are exposed to the same selective environments, plasticity in the ancestral lineage repeatedly reveals the same sets of phenotypes. Although this model is not radically new [1], it does emphasize the critical role of the environment in not only exerting parallel selection pressures but also in generating a parallel distributions of traits in the first place, leading to a highly deterministic outcome.

If the outcome of adaptive radiation is contingent upon initially plastic phenotypes, then phenotypic variation revealed by ancestral plasticity should resemble derived, adaptive variation. A challenge to testing this prediction is that ancestral populations are usually no longer available for study, rendering it difficult to characterize ancestral reaction norms (but see Box 2). One way to circumvent this problem is to identify systems with extant ancestral populations. This approach has been used in the threespine stickleback radiation (*Gasterosteus aculeatus*), in which the modern marine population has changed little since giving rise to the diverse freshwater radiation [84]. Diet-induced plasticity in marine stickleback (representing the ancestral colonists) produced phenotypes similar to those expressed in derived

Box 2. Plasticity and rapid diversification in a natural setting

How does one demonstrate that plasticity plays a role in diversification in natural populations? Here, we highlight a recent study [63] that illustrates a thorough approach for answering this question. The study involves *Daphnia melanica* in alpine lakes in California. Normally, the degree to which an individual is pigmented varies facultatively with its UV exposure. However, predatory salmonid fish have been introduced to certain lakes in the last century. Associated with these introductions are recurrent reductions in *Daphnia* pigmentation, which renders *Daphnia* less vulnerable to predation [63]. This evolutionary change in pigmentation results from a reduction in plasticity of melanin production, owing to genetic accommodation of particular genetic pathways; specifically, changes in the expression of *dopa decarboxylase* and *ebony* in response to UV exposure [63]. The strengths of this approach include: knowledge of the polarity of character evolution, identification of both the phenotypic and genetic targets of selection, and evidence of genetic change in reaction norms that have led to rapid evolutionary responses.

Box 3. Evidence highlighting plasticity's role in diversification and speciation

Direct evidence

- plasticity can mediate rapid and adaptive divergence between populations (e.g. house finches [62]) and species (e.g. spadefoot toads [64])
- plasticity in traits that influence mate choice [92], resource or habitat use [71](Table 1), or phenology [93] can promote rapid reproductive isolation
- clades in which resource polyphenism has evolved are more species rich than sister clades (Figure 3)
- the occurrence of homoplasy in conditionally expressed traits (e.g. paedomorphosis in ambystomatid salamanders [94])
- the prevalence of replicated adaptive radiation involving environmentally induced traits (e.g. postglacial fish [95], cichlids [68], anole lizards [46])

Phenomena that can be illuminated by considering plasticity

- maintenance of cryptic genetic variation [96]
- peak shifts on adaptive landscapes [8]
- origins of novel traits [15] and body plans [97]

freshwater benthic and limnetic ecotypes [16]. An alternative approach is to infer ancestral reaction norms in a phylogenetic context. This approach has been used in spadefoot toads to indicate that ancestral plasticity predated adaptive radiation in this group [43,54]. Other replicate radiations also hint at possible roles for ancestral plasticity [46,67].

In sum, plasticity could represent a key innovation that catalyzes adaptive radiation. Indeed, species-rich clades more often exhibit greater levels of ecologically relevant plasticity than closely related, species-poor clades [18] (Figure 3). Thus, plasticity can potentially explain not only why adaptive radiations occur, but also why some lineages are more prone to diversify broadly and rapidly than others.

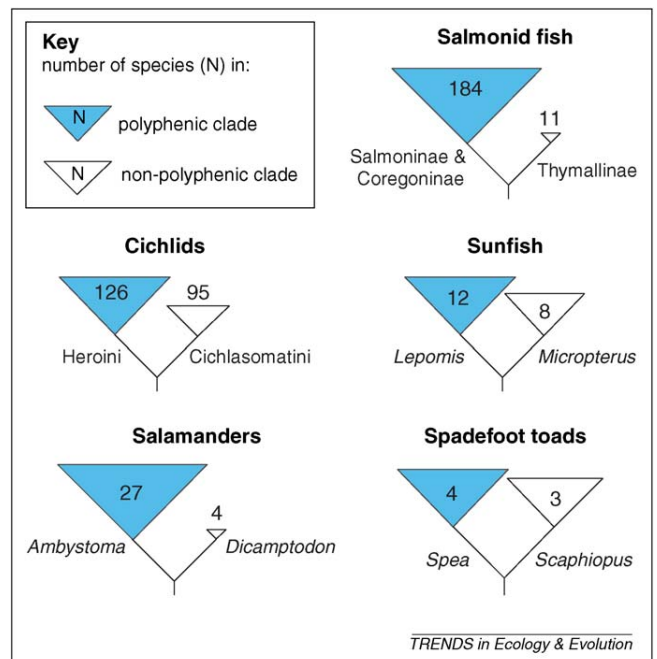


Figure 3. Evidence that resource polyphenism is associated with greater species richness in various clades of fish and amphibians. From [18].

Box 4. Some key challenges for the future**Theoretical**

- incorporate knowledge of developmental regulatory mechanisms more effectively into both theoretical population genetics and genetic accommodation theory
- determine whether the evolutionary implications differ for continuous reaction norms versus polyphenism
- explore parameter space over which plasticity promotes rather than impedes diversification

Empirical

- use experimental evolution studies to determine whether more plastic genotypes evolve more rapidly than less plastic genotypes when confronted with novel selective regimes
- investigate if the developmental mechanisms underlying plasticity parallel those responsible for generating interspecific diversity
- assess whether polyphenism promotes speciation and identify the mechanisms by which it does so
- ascertain whether plasticity promotes lineage persistence and identify the mechanisms by which it does so
- evaluate whether ancestral plasticity generally influences the nature of phenotypic diversity in adaptive radiations

Concluding remarks

Recent theory and data implicate phenotypic plasticity as playing a key role in promoting diversification at numerous levels of biological organization, often through the action of similar processes, such as genetic accommodation and genetic assimilation (Box 3). Although these ideas are fundamentally consistent with the modern synthesis (in that they ultimately rely upon genetic changes to mediate evolution), they enhance our understanding of evolution by emphasizing the importance of environmentally initiated change [6,7,9,11]. Traditionally, the environment was thought to play a single role in evolution by selecting among genetically fixed phenotypic variation. However, by incorporating plasticity into the evolutionary framework, the environment assumes an additional role: it both selects among phenotypic variation, and it generates that variation in the first place [6]. Consequently, these ideas illuminate a broader array of evolutionary phenomena (Box 3). Further tests (Box 4) promise to provide additional important insights into how and why living things diversify.

Acknowledgements

This paper grew out of a working group sponsored by the National Evolutionary Synthesis Center (NESCent) and organized by Pfennig and Moczek. We thank the other members of our working group; Susan Foster, Ehab Abouheif, Ian Dworkin, Cris Ledón-Rettig, Fred Nijhout, Sonia Sultan, and Mary Jane West-Eberhard, as well as Karin Pfennig, Josh Auld, Aaron Leichty, Ryan Martin, and three anonymous referees for discussions and comments on the manuscript.

References

- Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- Coyne, J.A. and Orr, H.A. (2004) *Speciation*, Sinauer Associates
- Carroll, S.P. (2005) *Endless Forms Most Beautiful*, W. W. Norton
- Rundle, H.D. and Nosil, P. (2005) Ecological speciation. *Ecol. Lett.* 8, 336–352
- Grant, P.R. and Grant, B.R. (2008) *How and Why Species Multiply: The Radiation of Darwin's Finches*, Princeton University Press
- Gilbert, S.F. and Epel, D. (2009) *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution*, Sinauer Associates
- Pigliucci, M. (2007) Do we need an extended evolutionary synthesis? *Evolution* 61, 2743–2749
- Schlichting, C.D. (2004) The role of phenotypic plasticity in diversification. In *Phenotypic Plasticity: Functional and Conceptual Approaches* (DeWitt, T.J. and Scheiner, S.M., eds), pp. 191–200, Oxford University Press
- West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*, Oxford University Press
- West-Eberhard, M.J. (2005) Developmental plasticity and the origin of species differences. *Proc. Natl. Acad. Sci. U. S. A.* 102, 6543–6549
- Whitman, D.W. and Agrawal, A.A. (2009) What is phenotypic plasticity and why is it important? In *Phenotypic Plasticity of Insects* (Whitman, D.W. and Ananthakrishnan, T.N., eds), pp. 1–63, Science Publishers
- Futuyma, D.J. (2009) *Evolution*, Sinauer Associates
- Jablonka, E. and Lamb, M.J. (1995) *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*, Oxford University Press
- Price, T.D. (2003) The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. London B Biol. Sci.* 270, 1433–1440
- Moczek, A.P. (2008) On the origins of novelty in development and evolution. *Bioessays* 30, 432–447
- Wund, M.A. *et al.* (2008) A test of the 'flexible stem' model of evolution: ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *Am. Nat.* 172, 449–462
- Skúlason, S. *et al.* (1999) Sympatric morphs, populations and speciation in freshwater fish with emphasis on arctic charr. In *Evolution of Biological Diversity* (Magurran, A.E. and May, R.M., eds), pp. 70–92, Oxford University Press
- Pfennig, D.W. and McGee, M. (2010) Resource polyphenism increases species richness: a test of the hypothesis. *Philos. Trans. R. Soc. London B Biol. Sci.* 365, 577–591
- Sultan, S.E. (2007) Development in context: the timely emergence of eco-devo. *Trends Ecol. Evol.* 22, 575–582
- Sultan, S.E. (2003) The promise of ecological developmental biology. *J. Exp. Zool.* 296B, 1–7
- Martin, R.A. and Pfennig, D.W. (2010) Field and experimental evidence that competition and ecological opportunity promote resource polymorphism. *Biol. J. Linn. Soc.* 100, 73–88
- Phillips, P.C. (1996) Waiting for a compensatory mutation: phase zero of the shifting-balance process. *Genet. Res.* 67, 271–283
- Nijhout, H.F. (2003) Development and evolution of adaptive polyphenisms. *Evol. Dev.* 5, 9–18
- Aubin-Horth, N. and Renn, S.C.P. (2009) Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Mol. Ecol.* 18, 3763–3780
- Snell-Rood, E.C. *et al.* (2010) Developmental decoupling of alternative phenotypes: insights from the transcriptomes of horn-polyphenic beetles. *Evolution*
- Hodgins-Davis, A. and Townsend, J.P. (2009) Evolving gene expression: from G to E to GxE. *Trends Ecol. Evol.* 24, 649–658
- Windig, J.J. *et al.* (2004) Genetics and mechanics of plasticity. In *Phenotypic Plasticity* (DeWitt, T.J. and Scheiner, S.M., eds), pp. 31–49, Oxford University Press
- Cornwallis, C.K. and Birkhead, T.R. (2008) Plasticity in reproductive phenotypes reveals status-specific correlations between behavioral, morphological, and physiological sexual traits. *Evolution* 62, 1149–1161
- Bourdeau, P.E. (2009) Prioritized phenotypic responses to combined predators in a marine snail. *Ecology* 90, 1659–1669
- Sol, D. *et al.* (2005) Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl. Acad. Sci. U. S. A.* 102, 5460–5465
- Gibson, G. and Dworkin, I. (2004) Uncovering cryptic genetic variation. *Nat. Rev. Genet.* 5, 1199–1212
- Le Rouzic, A. and Carlborg, O. (2008) Evolutionary potential of hidden genetic variation. *Trends Ecol. Evol.* 23, 33–37
- Sutter, M. and Kawecki, T.J. (2009) Influence of learning on range expansion and adaptation to novel habitats. *J. Evol. Biol.* 22, 2201–2214
- Sangster, T.A. *et al.* (2004) Under cover: causes, effects and implications of Hsp90-mediated genetic capacitance. *Bioessays* 26, 348–362

- 35 Lahti, D.C. *et al.* (2009) Relaxed selection in the wild. *Trends Ecol. Evol.* 24, 487–496
- 36 Snell-Rood, E.C. *et al.* (2010) Toward a population genetic framework of developmental evolution: costs, limits, and consequences of phenotypic plasticity. *Bioessays* 32, 71–81
- 37 Van Dyken, J. and Wade, M.J. (2010) The genetic signature of conditional expression. *Genetics* 84, 557–570
- 38 Barrett, R.D.H. and Schluter, D. (2008) Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44
- 39 Suzuki, Y. and Nijhout, H.F. (2006) Evolution of a polyphenism by genetic accommodation. *Science* 311, 650–652
- 40 Waddington, C.H. (1953) Genetic assimilation of an acquired character. *Evolution* 7, 118–126
- 41 Masel, J. (2004) Genetic assimilation can occur in the absence of selection for the assimilating phenotype, suggesting a role for the canalization heuristic. *J. Evol. Biol.* 17, 1106–1110
- 42 Lande, R. (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J. Evol. Biol.* 22, 1435–1446
- 43 Gomez-Mestre, I. and Buchholz, D.R. (2006) Developmental plasticity mirrors differences among taxa in spadefoot toads linking plasticity and diversity. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19021–19026
- 44 Badyaev, A.V. and Foresman, K.R. (2000) Extreme environmental change and evolution: stress-induced morphological variation is strongly concordant with patterns of evolutionary divergence in shrew mandibles. *Proc. R. Soc. London B Biol. Sci.* 267, 371–377
- 45 Bull-Herenu, K. and Arroyo, M.T.K. (2009) Phenological and morphological differentiation in annual *Chaetanthera moenchioides* (Asteraceae) over an aridity gradient. *Plant Syst. Evol.* 278, 159–167
- 46 Losos, J.B. *et al.* (2000) Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* 54, 301–305
- 47 Huizinga, M. *et al.* (2009) The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, *Poecilia reticulata*. *J. Evol. Biol.* 22, 1860–1866
- 48 Shaw, K.A. *et al.* (2007) Ancestral plasticity and the evolutionary diversification of courtship behaviour in threespine sticklebacks. *Anim. Behav.* 73, 415–472
- 49 Latta, L.C. *et al.* (2007) Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity. *BMC Evol. Biol.* 7, 21
- 50 Aubret, F. *et al.* (2004) Evolutionary biology: adaptive developmental plasticity in snakes. *Nature* 431, 261–262
- 51 Keogh, J.S. *et al.* (2005) Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes. *Evolution* 59, 226–233
- 52 Palmer, A.R. (2004) Symmetry breaking and the evolution of development. *Science* 306, 828–833
- 53 Otaki, J.M. (2007) Stress-induced color-pattern modifications and evolution of the painted lady butterflies *Vanessa cardui* and *Vanessa kershawi*. *Zool. Sci.* 24, 811–819
- 54 Ledon-Rettig, C.C. *et al.* (2008) Ancestral variation and the potential for genetic accommodation in larval amphibians: implications for the evolution of novel feeding strategies. *Evol. Devel.* 10, 316–325
- 55 Alaux, C. *et al.* (2009) Honey bee aggression supports a link between gene regulation and behavioral evolution. *Proc. Natl. Acad. Sci. U. S. A.* 106, 15400–15405
- 56 Young, R.L. and Badyaev, A.V. (2007) Evolution of ontogeny: linking epigenetic remodeling and genetic adaptation in skeletal structures. *Integr. Comp. Biol.* 47, 234–244
- 57 Schlichting, C.D. and Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*, Sinauer Associates
- 58 Svanbäck, R. *et al.* (2009) Fluctuating population dynamics promotes the evolution of phenotypic plasticity. *Am. Nat.* 174, 176–189
- 59 Pál, C. and Miklos, I. (1999) Epigenetic inheritance, genetic assimilation and speciation. *J. Theor. Biol.* 200, 19–37
- 60 Pfennig, D.W. *et al.* (2006) Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. *Ecology* 87, 769–779
- 61 Masel, J. *et al.* (2007) The loss of adaptive plasticity during long periods of environmental stasis. *Am. Nat.* 169, 38–46
- 62 Badyaev, A.V. *et al.* (2002) Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science* 295, 316–318
- 63 Scoville, A.G. and Pfrender, M.E. (2010) Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. *Proc. Natl. Acad. Sci. U. S. A.* 107, 4260–4263
- 64 Pfennig, D.W. and Murphy, P.J. (2002) How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* 56, 1217–1228
- 65 Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294, 321–326
- 66 Rice, A.M. and Pfennig, D.W. (2010) Does character displacement initiate speciation? Evidence of reduced gene flow between populations experiencing divergent selection. *J. Evol. Biol.* 23, 854–865
- 67 Smith, T.B. and Skúlason, S. (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* 27, 111–133
- 68 Meyer, A. (1993) Trophic polymorphisms in cichlid fish: do they represent intermediate steps during sympatric speciation and explain their rapid adaptive radiation? In *New Trends in Ichthyology* (Schröder, J.-H. *et al.*, eds), pp. 257–266, Blackwell
- 69 Hendry, A.P. (2009) Ecological speciation! Or lack thereof?. *Can. J. Fish. Aquat. Sci.* 66, 1383–1398
- 70 Mallet, J. (2008) Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philos. Trans. R. Soc. London B Biol. Sci.* 363, 2971–2986
- 71 Adams, C.E. and Huntingford, F.A. (2004) Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biol. J. Linn. Soc.* 81, 611–618
- 72 Schluter, D. (1993) Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. *Ecology* 74, 699–709
- 73 Boughman, J.W. (2001) Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 411, 944–948
- 74 Hatfield, T. and Schluter, D. (1999) Ecological speciation in sticklebacks: environment-dependent hybrid fitness. *Evolution* 53, 866–873
- 75 Nosil, P. *et al.* (2002) Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* 417, 440–443
- 76 Pfennig, D.W. and Rice, A.M. (2007) An experimental test of character displacement's role in promoting postmating isolation between conspecific populations in contrasting competitive environments. *Evolution* 61, 2433–2443
- 77 Duffy, S. *et al.* (2007) Evolution of host specificity drives reproductive isolation among RNA viruses. *Evolution* 61, 2614–2622
- 78 Bush, G.L. and Ritchie, M.G. (2004) Sympatric speciation in insects. In *Adaptive Speciation* (Dieckmann, U. *et al.*, eds), pp. 229–248, Cambridge University Press
- 79 Cori, A. *et al.* (2010) Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *Proc. Natl. Acad. Sci. U. S. A.* 107, 4254–4259
- 80 Yeh, P.J. and Price, T.D. (2004) Adaptive phenotypic plasticity and the successful colonization of a novel environment. *Am. Nat.* 164, 531–542
- 81 Ghalambor, C.K. *et al.* (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* 21, 394–407
- 82 Reale, D. *et al.* (2003) Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. London B Biol. Sci.* 270, 591–596
- 83 Schluter, D. and Nagel, L.M. (1995) Parallel speciation by natural selection. *Am. Nat.* 146, 292–301
- 84 Cresko, W.A. *et al.* (2007) Studies of threespine stickleback developmental evolution: progress and promise. *Genetica* 129, 105–126
- 85 Papaj, D.R. and Prokopy, R.J. (1989) Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Entomol.* 34, 315–350
- 86 Rundle, H.D. *et al.* (2000) Natural selection and parallel speciation in sympatric sticklebacks. *Science* 287, 306–308
- 87 Barluenga, M. *et al.* (2006) Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature* 439, 719–723
- 88 Smith, J.W. and Benkman, C.W. (2007) A coevolutionary arms race causes ecological speciation in crossbills. *Am. Nat.* 169, 455–465
- 89 Slagsvold, T. and Wiebe, K.L. (2007) Learning the ecological niche. *Proc. R. Soc. London B Biol. Sci.* 274, 19–23

- 90 Huber, S.K. *et al.* (2007) Reproductive isolation of sympatric morphs in a population of Darwin's finches. *Proc. R. Soc. London B Biol. Sci.* 274, 1709–1714
- 91 Crispo, E. (2008) Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *J. Evol. Biol.* 21, 1460–1469
- 92 Irwin, D.E. and Price, T. (1999) Sexual imprinting, learning and speciation. *Heredity* 82, 347–354
- 93 Levin, D.A. (2009) Flowering-time plasticity facilitates niche shifts in adjacent populations. *New Phytol.* 183, 661–666
- 94 Shaffer, H.B. (1984) Evolution in a paedomorphic lineage. I. An electrophoretic analysis of the Mexican ambystomatid salamanders. *Evolution* 38, 1194–1206
- 95 Robinson, B.W. and Wilson, D.S. (1994) Character release and displacement in fish: a neglected literature. *Am. Nat.* 144, 596–627
- 96 Schlichting, C.D. (2008) Hidden reaction norms, cryptic genetic variation, and evolvability. *Ann. New York Acad. Sci.* 1133, 187–203
- 97 Newman, S.A. and Müller, G.B. (2000) Epigenetic mechanisms of character origination. *J. Exp. Zool.* 288, 304–317