Review Article

Phenotypic Plasticity and Selection: Nonexclusive Mechanisms of Adaptation

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Selection and plasticity are two mechanisms that allow the adaptation of a population to a changing environment. Interaction between these nonexclusive mechanisms must be considered if we are to understand population survival. This review discusses the ways in which plasticity and selection can interact, based on a review of the literature on selection and phenotypic plasticity in the evolution of populations. The link between selection and phenotypic plasticity is analysed at the level of the individual. Plasticity can affect an individual's response to selection and so may modify the end result of genetic diversity evolution at population level. Genetic diversity increases the ability of populations or communities to adapt to new environmental conditions. Adaptive plasticity increases individual fitness. However this effect must be viewed from the perspective of the costs of plasticity, although these are not easy to estimate. It is becoming necessary to engage in new experimental research to demonstrate the combined effects of selection and plasticity for adaptation and their consequences on the evolution of genetic diversity.

1. Introduction

How do populations adapt to their environment? This is a crucial question in evolutionary biology and greater knowledge in this field is essential if we are to understand and preserve populations in a changing environment. Adaptation is the sum of the morphological, physiological, and behavioural changes of individuals that allows maintenance of individual fitness and so leads to population and species persistence. These changes arise as a result of two mechanisms operating at the level of the individual: selection and phenotypic plasticity. Under the first mechanism, genetic selection, the frequency of favourable alleles increases over several generations while that of unfavourable ones tends to decrease. The evolution of allele frequencies results from different reproductive efficiencies (fitness between genotypes) and so tends to reduce the genetic diversity within a population. The second mechanism, phenotypic plasticity, is defined as the ability of a genotype (individual) to express different phenotypes according to its environment [1]. A number of methods exist to quantify phenotypic plasticity with the use of various indices such as the trait mean, the trait variation coefficient, the trait reaction norm, and the trait extreme values and phenotypic distances [2]. Through phenotypic plasticity, the plastic traits of individuals are modified without modifying the genetic diversity of the population. But phenotypic plasticity can influence the fitness of individuals [3, 4] and be the target of selection [5–7]. The intensity of selection for plasticity depends on the balance between a positive effect and a negative one, the cost of plasticity on fitness. This balance can lead to different levels of genetic diversity within an adapted population [8–10] (Figure 1). Genetic diversity is essential in the long term, since it increases the ability of populations or communities to adapt to new environmental conditions [11–13]. However, despite the systematic coexistence of plasticity and selection in natural populations which encounter different environments (spatial and/or temporal changes) [14–16], there is a lack of experimental information on their combined influence on the evolution of the genetic diversity of populations. The purpose of this paper is to review current knowledge on the consequences of selection and phenotypic plasticity on the genetic diversity of populations and to propose procedures to overcome the limitations of experimental data in order to identify these consequences.
2. The Consequences of Selection on Genetic Diversity

Selection occurs on a trait only if it exhibits genetic variability within a population. Selection acts on different character types, physiological processes (e.g., resistance of plants to metals [21]), behaviours (e.g., predator avoidance [22, 23]), or morphological variations (e.g., industrial melanism of the peppered moth [24]). At the phenotypic level, selection changes the mean and/or the variance of trait distributions within a population. Selection can be of three types: directional, stabilising, or disruptive. Given a normal distribution of a trait, directional selection favours individuals with a phenotype either above or below the population mean and so leads to a shift of the mean in one direction or other [25]. Stabilising selection eliminates individuals with the most divergent phenotypes leading to a decrease in trait variance [26]. Disruptive selection favours individuals with extreme phenotypes, leading to a bimodal population distribution [27].

Response to selection results in allele frequency changes of genes involved in the phenotypic variation of traits implicated in individual fitness or at loci in linkage disequilibrium with the previous genes (hitchhiking). In addition to changes in allele frequencies of specific loci, selection can change the allele frequencies globally on the genome by genetic drift, due to a decrease in the effective size of the population. A strong selection can result in a rapid allele fixation (homogenisation of all individuals) and loss of other alleles. This can have a dramatic impact on the genetic diversity of a population (Figure 1). However, selection can also maintain alleles at intermediate frequencies through heterozygote advantage (individuals having two different alleles have greater fitness), or frequency dependence (the allele advantage depends on its frequency relative to other alleles in a given population).

Directional selection tends to decrease the genetic variability of a population in a given environment. But if several populations in different environments are considered (a metapopulation), the decrease in variability within each population can be compensated for by maintenance of diversity among populations [28–31]. Each environment selects for different alleles, allowing maintenance of all alleles in the metapopulation, even if some are lost at the individual population level. The principle of diversifying selection is used in genetic conservation studies.

3. The Consequences of Phenotypic Plasticity on Genetic Diversity

Phenotypic plasticity occurs at the individual level by changing the phenotype depending on the environment [10, 32–47]. For a given trait, this change with environment can be continuous or discrete [37]. In case of continuous phenotypic changes with an environment, the relationship between environmental variables and traits is called the reaction norms. These reaction norms are often complex and nonlinear. A plant or animal with a plastic trait receives a signal from the environment that will determine the trait value [36, 48–50]. The phenotypic changes are implemented during the lifespan of an individual; that is, the effects are seen within one generation; this is not the case for selection.

Phenotypic changes of individuals within a population will lead to a modification of the distribution of the phenotypic values of this population within one generation (Figure 2). This modification is reversible without any genetic changes but in some cases this modification is conserved over several generations. Therefore, if the shift of phenotypic values is beneficial to fitness (i.e., adaptive) this adaptation
can be obtained without a decrease in genetic diversity (Figure 1). In this case the phenotypic plasticity is adaptive and moderates the effects of selection. Some genotypes, not genetically adapted to an environment, become adapted through phenotypic plasticity and thus increase their fitness. Here it is necessary to introduce the notion of an optimal phenotype for a given environment. This is the phenotype which leads to the best fitness within the population. This optimal phenotype can be obtained with or without phenotypic plasticity. In a particular environment, if a genotype shows a phenotype close to the optimal phenotype, and if this phenotype is close to the average value of this genotype within a range of environments, it will have been obtained without phenotypic plasticity. In contrast, if another genotype shows a phenotype close to the optimal phenotype, and if this phenotype is far from being the average value of this genotype within a range of environments, then this phenotype will have been obtained through phenotypic plasticity. Within a population, the ability of phenotypic plasticity to moderate selection will depend on (i) the diversity of the traits involved in the optimal phenotype, (ii) the level of plasticity of the traits involved in the optimal phenotype, and (iii) the cost of the plasticity required to reach the optimal phenotype. This cost can be defined as the difference in fitness between the genotypes showing the optimal phenotype without plasticity and that of the genotypes displaying the optimal phenotype through plasticity. If the cost of plasticity is low enough, so that plastic genotypes have fitness as good as the best non-plastic genotypes, then the plastic genotypes will be selected for in the next generation. In such cases, with different levels of plasticity among genotypes (Figure 3), selection for plasticity will occur and will lead to a decrease in genetic diversity on the loci involved in plasticity variability. These can be different from the loci involved in the variability of the trait. Scheiner and Lyman [44] have shown in Drosophila that the plasticity of a trait can respond to selection and that this response is at least partially independent of the response of the trait mean. However, this independence remains controversial [51–53]. Within a population subject to different environments, adaptation over several generations comes from a balance between phenotypic plasticity and selection for both the value of adaptive traits and their plasticity. It is extremely rare to find studies that separate and quantify the roles: (1) of selection for the traits involved in the optimal phenotype, (2) of plasticity for these traits, and (3) of selection for plasticity of these traits. Nevertheless, each of these mechanisms has a different effect on the genetic diversity of the population.

Figure 2: Scenarios for change in the mean and/or variance of a trait in a population between constitutive phenotypes expressed prior to an interaction (dark shading) and the induced phenotype following an interaction (light shading). (a) An increase in mean and variance of a trait. (b) A decrease in variance, mean unchanged. (c) An increase in variance, mean unchanged from [17].
4. Cost of plasticity

Phenotypic plasticity can act on fitness [54] which can become either closer to or further from the optimal phenotype [43]. Depending on the effect of plasticity on individual fitness, plasticity can be characterised by a number of terms. Phenotypic plasticity is termed as “maladaptive” when the effect on fitness is negative, “neutral” if it has no effect on fitness, and “adaptive” when it has a positive effect on fitness [35]. There are various examples of adaptive plastic responses. Thus, a plastic response has been shown in the case of a ciliate species following the introduction of a predator. The ciliate developed lateral wings which increased its survival by inhibiting ingestion by the predator. In turn, the predator responded plastically by increasing its gape size to accommodate the ciliate’s defence without cancelling it (mutual plasticity) [3]. Some examples of adaptive plastic responses in plants are the lengthening of internodes in the shade to better access light [55], various herbivore-resistance mechanisms [56], or adjustments to the number of simultaneously mature flowers depending on the number of pollinators present [57]. In some cases, adaptive plasticity can become maladaptive if the environment becomes too stressful [43]. For example, when competition for light is very strong, some plants can increase their internode length but if the neighbouring plant species are too tall, the plastic capacity of increasing internode length for the smaller genotypes becomes maladaptive [58–60].

Even adaptive phenotypic plasticity could come at a cost [61, 62]. Lind and Johansson [63] suggest the cost increases with the level of plasticity in the population. This cost depends on genotype, population, and environment and can have quite a large number of origins [19]. These may include (i) maintenance costs (sensory structure, metabolic regulation mechanism of plasticity) [64], (ii) production costs (a plasticity-developed structure could be more costly than a genetically determined one) [65], (iii) acquisition of information costs (the process may be risky or it requires energy or reduces feeding or breeding efficiency), (iv) cost of imprecise development (nonspecific plastic change), (v) genetic costs (genetic linkage with deleterious alleles at other loci, pleiotropy, and epistasis) [66], and ecological costs (interaction between species; e.g., the plastic response to herbivory reduces attractiveness to pollinators) [67].

The costs of plasticity are difficult to quantify [68–70], but they can be estimated by comparing the fitness of plastic genotypes to that of fixed genotypes, for the same phenotypic value in each environment using the multiple regression:

\[ W_j = \text{constant} + (B_1 \times Z_j) + (B_2 \times P_j), \]

where \( W_j \) is the fitness of family \((j)\) in one environment, \( B_1 \) is the selection coefficient on phenotypes, \( B_2 \) is the selection coefficient on plasticity, \( Z_j \) is the phenotype exhibited by family \(j\) in one environment, and \( P_j \) is the plasticity exhibited by family \(j\) in different environments [71–73]. A significantly negative regression coefficient of the plasticity term indicates a genetic cost. This cost could be different in each environment. DeWitt et al. [19] adopt this method and analyse it to quantify the relationship between the phenotype and the fitness in each environment by regression analysis or by cubic splines [74]. This adaptation has the advantage of allowing nonlinear relationships between phenotype and fitness. This mathematical relationship allows calculation of a theoretical fitness that can be compared with the observed one. To visualise the trend, the residues of the fitness equation are shown graphically, based on the genotype degree of plasticity. There is a cost when the most plastic genotypes tend to have a lower fitness than expected and also when the fixed genotypes tend to have a higher fitness than expected (Figure 4). This method is interesting but a bias occurs when the phenotypic values are correlated with phenotypic plasticity [75]. This correlation must therefore be confirmed before calculating the cost of plasticity using this method. In several studies, the most extreme phenotypes have been associated with high plasticity [56, 73], which requires a reinterpretation of the results. If costs of plasticity are very high, they may have a considerable impact on the evolution of plasticity [14, 71, 76, 77]. Although as indicated by the analysis of Van Buskirk and Steiner [78] in both animals and plants, costs of plasticity are often low and can influence phenotype evolution under stressful conditions only. The ubiquity of plasticity suggests the associated benefits outweigh the costs under a wide range of conditions [10].

5. Selection, Plasticity, and Diversity: A Balance between Gain of Fitness and Cost

If the plastic response is close to the optimal phenotype, the cost of achieving the phenotype by plasticity will determine the impact of selection on the plastic individual and therefore on allelic diversity of loci involved in trait value. If the cost of plasticity is significant, then achieving the optimal phenotype via fixed development is better than doing so via phenotypic plasticity. Individuals having a mutation that achieves the optimal phenotype directly will be selected in a stable environment. There is a kind of genetic evolution that results in reducing plasticity and in reducing the diversity of
a trait. Due to the cost of plasticity, the evolution of plasticity is slower than evolution due to maladaptive plasticity (see above) for which the selection intensity is generally stronger.

If the plastic response is still some way off from being the optimal phenotype but is still favourable, a genetic evolution by directional selection can complete it and bring it closer to the optimal phenotype. In this case, to obtain the phenotype, there is both a plastic response and a change related to selection [54].

However, depending on the conditions encountered by populations and their initial states, several hypotheses can be formulated for adaptive plasticity. Plasticity can, for example, moderate the effects of natural selection by allowing individuals to adapt phenotypically to new conditions quickly. Chevin et al. [79] have developed a model to predict population persistence in a changing environment. It can estimate how plasticity might interfere with the capacities of populations to evolve in response to environmental change.

By reducing the response to selection, phenotypic plasticity may promote the maintenance of genetic diversity within a population. If individuals have plastic traits, they can adjust their phenotypes to the environment. Different genotypes with several different phenotypes in one environment may have the same phenotype in another environment and therefore some genetic variability is maintained. Genetic variations that are few or are not expressed in an environment due to plasticity [80] become neutral if there is no cost of plasticity and thus they avoid a decrease in fitness. These predictions emerge from theoretical models [35, 81, 82] but there is little experimental data to verify them [8, 9]. In Quercus coccifera, a tree species with several ecotypes, Baquedano et al. [83] show that phenotype plasticity hides differences between genotypes which maintain a genetic variability that is inaccessible to selection.

However, we can find populations having low genetic diversity that are maintained with the help of plasticity. Plasticity can allow morphological adaptation without the need for genetic variability. The study by Geng et al. [46] compares two species in which morphological variance is small. The morphological variance in one of the species is due mainly to genotypic variations, while in the other species, which has low genetic diversity, the morphological variance is due to plasticity.

As plasticity influences genetic changes by affecting the intensity of selection, we can expect an overall change in genetic diversity through reorganisation of the evolutionary dynamics and thus of the evolution rate [84]. Intensity of selection varies with plasticity, thus upsetting the expected evolution in the absence of plasticity [17, 85, 86]. In a population of lizards (Urosaurus ornatus), a directional selection has been shown to favour the fastest-moving males. However, a seasonal plasticity increases the fitness of the slowest individuals during the breeding season. This seasonal plasticity homogenises the speed of the male population at breeding time and reduces the effect of selection for high speed [87].

To assess the impact of selection and plasticity on the evolution of genetic diversity, models allow us to assess the rate of the genetic changes caused by plasticity. Hinton and Nowlan [88] developed a model that shows how learning increases the rate of evolution. This model was modified by Behera and Nanjundiah [89] to obtain greater realism. They used a haploid population of fixed size, different levels of plasticity, and a cost associated with the plasticity. Their results indicate that plasticity slows down the pace of evolution but enhances the level of adaptation. However, other models of the same type, which explored more parameters, obtained mixed results [90–92]. To estimate the evolution rates, Ancel [93] used a quantitative model and a reaction norm
model (modelling of plasticity by reaction norm instead of by genotype, phenotype points). Ancel’s model is highly dependent on initial population conditions and on fitness. However, in most cases, the simulations obtained show that plasticity slows the evolution rate from the appearance, up to the stabilisation of the population at an optimal phenotype. When plasticity is not particularly costly, it protects suboptimal phenotypes from elimination by natural selection. In contrast, when plasticity is more costly, it fails to provide significant advantage. Furthermore, the phenotype ranges for which plasticity speeds up evolution are frequently those for which a plastic individual is less fit than its nonplastic counterpart. Paenke et al. [20] have sought conditions under which evolution is accelerated or delayed by plasticity under directional selection. According to these authors, the fitness gain gradient measures the effect of a marginal change in the degree of plasticity on the slope of the relationship between the genotypic value of the focal trait and log fitness. If the gain gradient has the same sign as the direction of selection, an increase in plasticity will magnify the response to selection. Conversely, if the two signs are opposite, greater plasticity will lead to a slower response. If plasticity acts similarly on genotypes, independently of their fitness, evolution is (i) accelerated if the log of the fitness function (defined by the relationship between phenotype and log fitness) follows a convex curve and (ii) slowed if this curve is concave (Figure 5). However, De Jong [94] considers the possibilities of evolution in the presence of plasticity and explains that there is no answer to the question of whether phenotypic plasticity promotes evolution. Everything depends on the case being studied and on the parameters associated with it.

6. Conclusion

The study of phenotypic plasticity has developed rapidly in recent decades, so we now have a clearer view of what it is and how it evolves. But for the interaction of selection and plasticity, more experimental work is required to better understand how selection acts on the reaction norm of phenotype against environments and also to better define the costs of plasticity. It should be noted that most studies focus on two environments. There is a scarcity of data on environment ranges, such as those commonly experienced by natural populations and on the changes in the selection pressures generated. In addition, measuring plasticity is difficult because the global plasticity scale of the individual is relative to the plasticity of the different traits of the individual [95]. Efforts should be made to estimate the global effect of plasticity on fitness of several traits. These studies would be improved with the development of a better understanding of the mechanisms involved, especially with regard to the genetic basis that explain plasticity. Despite numerous theoretical studies, there remains a lack of experimental data to support the results of these studies. Indeed, it is difficult to obtain experimental data in natural ecosystems where it is almost impossible to follow generations, to have replicated genotypes, and to control the environment. Ex situ experimentation could circumvent these limits by using (i) species which can be cloned or selfed and thus are easy to raise/grow and phenotype such as plant species, (ii) populations showing genetic diversity of adaptive traits and their plasticity, (iii) species with short life cycles, and (iv) semicontrolled environments. In the context of climate change, it would be interesting to conduct studies on
crops showing these characteristics to define ways which can be used to maintain production under increasingly hazardous climates events.

**Competing Interests**
The authors declare that they have no competing interests.

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**References**

[1] R. Przybylo, B. C. Sheldon, and J. Merilä, “Climatic effects on breeding and morphology: evidence for phenotypic plasticity,” *Journal of Animal Ecology*, vol. 69, no. 3, pp. 395–403, 2000.

[2] F. Valladares, D. Sanchez-Gomez, and M. A. Zavala, “Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications,” *Journal of Ecology*, vol. 94, no. 6, pp. 1103–1116, 2006.

[3] M. Kopp and R. Tollrian, "Reciprocal phenotypic plasticity in a predator-prey system: inducible offences against inducible defences?" *Ecology Letters*, vol. 6, no. 8, pp. 742–748, 2003.

[4] T. E. Reed, D. E. Schindler, and R. S. Waples, "Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate," *Conservation Biology*, vol. 25, no. 1, pp. 56–63, 2011.

[5] B. W. Robinson and D. S. Wilson, "Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gibbosus*)," *Evolutionary Ecology*, vol. 10, no. 6, pp. 631–652, 1996.

[6] D. H. Nussey, E. Postma, P. Gienapp, and M. E. Visser, "Evolution: selection on heritable phenotypic plasticity in a wild bird population," *Science*, vol. 310, no. 5746, pp. 304–306, 2005.

[7] F. Aubret, X. Bonnet, and R. Shine, "The role of adaptive plasticity in a major evolutionary transition: early aquatic experience affects locomotor performance of terrestrial snakes," *Functional Ecology*, vol. 21, no. 6, pp. 1154–1161, 2007.

[8] S. E. Sultan and F. A. Bazzaz, "Phenotypic plasticity in Polygonum persicaria. II. Norms of reaction to soil moisture and the maintenance of genetic diversity," *Evolution*, vol. 47, no. 4, pp. 1032–1049, 1993.

[9] A. H. Cheetham, J. B. Jackson, and L. A. Hayek, "Quantitative genetics of bryozan phenotypic evolution. III. Phenotypic plasticity and the maintenance of genetic variation," *Evolution*, vol. 49, no. 2, pp. 290–296, 1995.

[10] A. A. Agrawal, "Ecology—phenotypic plasticity in the interactions and evolution of species," *Science*, vol. 294, no. 5541, pp. 321–326, 2001.

[11] R. Bürger and M. Lynch, "Evolution and extinction in a changing environment: a quantitative-genetic analysis," *Evolution*, vol. 49, no. 1, pp. 151–163, 1995.

[12] S. N. Atiken, S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane, "Adaptation, migration or extirpation: climate change outcomes for tree populations," *Evolutionary Applications*, vol. 1, no. 1, pp. 95–111, 2008.

[13] A. A. Hoffmann and C. M. Sgro, "Climate change and evolutionary adaptation," *Nature*, vol. 470, no. 7355, pp. 479–485, 2011.

[14] S. E. Sultan and H. G. Spencer, "Metapopulation structure favors plasticity over local adaptation," *The American Naturalist*, vol. 160, no. 2, pp. 271–283, 2002.

[15] L. C. Latta IV, J. W. Bakelar, R. A. Knapp, and M. E. Pfrender, "Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity," *BMC Evolutionary Biology*, vol. 7, article 21, 2007.

[16] G. Röder, M. Rahier, and R. E. Naishit, "Counter-intuitive developmental plasticity induced by host quality," *Proceedings of the Royal Society of London B: Biological Sciences*, vol. 275, no. 1637, pp. 879–885, 2008.

[17] J. A. Fordyce, "The evolutionary consequences of ecological interactions mediated through phenotypic plasticity," *Journal of Experimental Biology*, vol. 209, no. 12, pp. 2377–2383, 2006.

[18] M. Pigliucci, "Evolution of phenotypic plasticity: where are we going now?" *Trends in Ecology & Evolution*, vol. 20, no. 9, pp. 481–486, 2005.

[19] T. J. DeWitt, A. Sih, and D. S. Wilson, "Costs and limits of phenotypic plasticity," *Trends in Ecology & Evolution*, vol. 13, no. 2, pp. 77–81, 1998.

[20] I. Pauenke, B. Sendhoff, and T. J. Kawecki, "Influence of plasticity and learning on evolution under directional selection," *The American Naturalist*, vol. 170, no. 2, pp. 47–58, 2007.

[21] C.-L. Meyer, A. A. Kostecka, P. Saumitou-Laprade et al., "Variability of zinc tolerance among and within populations of the pseudometallophyte species *Arabidopsis halleri* and possible role of directional selection," *New Phytologist*, vol. 185, no. 1, pp. 130–142, 2010.

[22] E. D. Brodie III, "Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*," *Evolution*, vol. 46, no. 5, pp. 1284–1298, 1992.

[23] E. D. Brodie III and N. H. Russell, "The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes," *Animal Behaviour*, vol. 57, no. 2, pp. 445–451, 1999.

[24] M. E. N. Majerus, "Industrial melanism in the peppered moth, biston betularia: an excellent teaching example of darwinian evolution in action," *Evolution: Education and Outreach*, vol. 2, no. 1, pp. 63–74, 2009.

[25] H. E. Hoekstra, J. M. Hoekstra, D. Berrigan et al., "Strength and tempo of directional selection in the wild," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, no. 16, pp. 9157–9160, 2001.

[26] X.-S. Zhang and W. G. Hill, "Competition can maintain genetic but not environmental variance in the presence of stabilizing selection," *Evolution*, vol. 61, no. 7, pp. 1532–1545, 2007.

[27] C. Rueffler, T. J. M. Van Dooren, O. Leimar, and P. A. Abrams, "Disruptive selection and then what?" *Trends in Ecology and Evolution*, vol. 21, no. 5, pp. 238–245, 2006.

[28] M. Nei, "Analysis of gene diversity in subdivided populations," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 70, no. 12, pp. 3321–3323, 1973.

[29] K. A. Jolley, D. J. Wilson, P. Kriz, G. McVean, and M. C. J. Maiden, "The influence of mutation, recombination, population history, and selection on patterns of genetic diversity in Neisseria meningitidis," *Molecular Biology and Evolution*, vol. 22, no. 3, pp. 562–569, 2005.

[30] J. Van Heerwaarden, F. A. van Eeuwijk, and J. Ross-Ibarra, "Genetic diversity in a crop metapopulation," *Heredity*, vol. 104, no. 1, pp. 28–39, 2010.
[31] A. M. Kotowska, J. F. Cahill Jr., and B. A. Keddie, “Plant genetic diversity yields increased plant productivity and herbivore performance,” _Journal of Ecology_, vol. 98, no. 1, pp. 237–245, 2010.

[32] S. Via, “Adaptive phenotypic plasticity: target or by-product of selection in a variable environment?” _The American Naturalist_, vol. 142, no. 2, pp. 352–365, 1993.

[33] A. D. Bradshaw, “Evolutionary significance of phenotypic plasticity in plants,” _Advances in Genetics_, vol. 13, pp. 115–155, 1965.

[34] C. Schlichting, “The evolution of phenotypic plasticity in plants,” _Annual Review of Ecology and Systematics_, vol. 17, no. 1, pp. 667–693, 1986.

[35] S. M. Scheiner, “Genetics and evolution of phenotypic plasticity,” _Annual Review of Ecology and Systematics_, vol. 24, pp. 35–68, 1993.

[36] S. E. Sultan, “Phenotypic plasticity for plant development, function and life history,” _Trends in Plant Science_, vol. 5, no. 12, pp. 537–542, 2000.

[37] V. Debat and P. David, “Mapping phenotypes: canalization, plasticity and developmental stability,” _Trends in Ecology and Evolution_, vol. 16, no. 10, pp. 555–561, 2001.

[38] M. Pigliucci and A. Kolodnyńska, “Phenotypic plasticity to light intensity in _Arabidopsis thaliana_: invariance of reaction norms and phenotypic integration,” _Evolutionary Ecology_, vol. 16, no. 1, pp. 27–47, 2002.

[39] B. G. Miner, S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea, “Ecological consequences of phenotypic plasticity,” _Trends in Ecology and Evolution_, vol. 20, no. 12, pp. 685–692, 2005.

[40] J. G. Swallow, J. S. Rhodes, and T. Garland Jr., “Phenotypic and evolutionary plasticity of organ masses in response to voluntary exercise in house mice,” _Integrative and Comparative Biology_, vol. 45, no. 3, pp. 426–437, 2005.

[41] G. Gorur, C. Lomonaco, and A. Mackenzie, “Phenotypic plasticity in host-plant specialisation in _Aphis fabae_,” _Ecological Entomology_, vol. 30, no. 6, pp. 657–664, 2005.

[42] M. J. West-Eberhard, “Phenotypic accommodation: adaptive innovation due to developmental plasticity,” _Journal of Experimental Zoology Part B: Molecular and Developmental Evolution_, vol. 304, no. 6, pp. 610–618, 2005.

[43] C. K. Ghambor, J. K. McKay, S. P. Carroll, and D. N. Reznick, “Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments,” _Functional Ecology_, vol. 21, no. 3, pp. 394–407, 2007.

[44] S. Scheiner and R. Lyman, “The genetics of phenotypic plasticity. II. Response to selection,” _Journal of Evolutionary Biology_, vol. 4, pp. 23–50, 1991.

[45] L. J. Chapman, F. Galis, and J. Shinn, “Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid,” _Ecology Letters_, vol. 3, no. 5, pp. 387–393, 2000.

[46] Y.-P. Geng, X.-Y. Pan, C.-Y. Xu, W.-J. Zhang, B. Li, and J.-K. Chen, “Phenotypic plasticity of invasive _Alternanthera philoxeroides_ in relation to different water availability, compared to its native congeners,” _Acta Oecologica_, vol. 30, no. 3, pp. 380–385, 2006.

[47] S. I. Peluc, T. S. Sillett, J. T. Rotenberry, and C. K. Ghambor, “Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk,” _Behavioral Ecology_, vol. 19, no. 4, pp. 830–835, 2008.

[48] R. M. Borges, “Do plants and animals differ in phenotypic plasticity?” _Journal of Biosciences_, vol. 30, no. 1, pp. 41–50, 2005.

[49] P. Beldade, A. R. A. Mateus, and R. A. Keller, “Evolution and molecular mechanisms of adaptive developmental plasticity,” _Molecular Ecology_, vol. 20, no. 7, pp. 1347–1363, 2011.

[50] A. B. Nicotra and A. Davidson, “Adaptive phenotypic plasticity and plant water use,” _Functional Plant Biology_, vol. 37, no. 2, pp. 117–127, 2010.

[51] S. Via, R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting, and P. H. van Tienderen, “Adaptive phenotypic plasticity: consensus and controversy,” _Trends in Ecology & Evolution_, vol. 10, no. 5, pp. 212–217, 1995.

[52] G. de Jong, “Phenotypic plasticity as a product of selection in a variable environment,” _The American Naturalist_, vol. 145, no. 4, pp. 493–512, 1995.

[53] G. de Jong and P. Bijma, “Selection and phenotypic plasticity in evolutionary biology and animal breeding,” _Livestock Production Science_, vol. 78, no. 3, pp. 195–214, 2002.

[54] T. D. Price, A. Qvarnström, and D. E. Irwin, “The role of phenotypic plasticity in driving genetic evolution,” _Proceedings of the Royal Society B: Biological Sciences_, vol. 270, no. 1523, pp. 1433–1440, 2003.

[55] J. Schmitt, S. A. Dudley, and M. Pigliucci, “Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants,” _American Naturalist_, vol. 154, pp. S43–S54, 1999.

[56] A. A. Agrawal, J. K. Conner, M. T. J. Johnson, and R. Wallsgrove, “Ecological genetics of an induced plant defense against herbivores: additive genetic variance and costs of phenotypic plasticity,” _Evolution_, vol. 56, no. 11, pp. 2206–2213, 2002.

[57] L. D. Harder and S. D. Johnson, “Adaptive plasticity of floral display size in animal-pollinated plants,” _Proceedings of the Royal Society of London B: Biological Sciences_, vol. 272, no. 1581, pp. 2651–2657, 2005.

[58] K. Donohue, D. Messiqua, E. H. Pyle, M. Shane Hesche, and J. Schmitt, “Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in _Impatiens capensis_,” _Evolution_, vol. 54, no. 6, pp. 1956–1968, 2000.

[59] C. Weinig, “Plasticity versus canalization: population differences in the timing of shade-avoidance responses,” _Evolution_, vol. 54, no. 2, pp. 441–451, 2000.

[60] T. Steinger, B. A. Roy, and M. L. Stanton, “Evolution in stressful environments II: adaptive value and costs of plasticity in response to low light in _Sinapis arvensis_,” _Journal of Evolutionary Biology_, vol. 16, no. 2, pp. 313–323, 2003.

[61] J. Merilä, A. Laurila, and B. Lindgren, “Variation in the degree and costs of adaptive phenotypic plasticity among Rana temporaria populations,” _Journal of Evolutionary Biology_, vol. 17, no. 5, pp. 1132–1140, 2004.

[62] M. Van Kleunen and M. Fischer, “Constraints on the evolution of adaptive phenotypic plasticity in plants,” _New Phytologist_, vol. 166, no. 1, pp. 49–60, 2005.

[63] M. I. Lind and F. Johansson, “Costs and limits of phenotypic plasticity in Island populations of the common frog _Rana temporaria_ under divergent selection pressures,” _Evolution_, vol. 63, no. 6, pp. 1508–1518, 2009.

[64] P. Edelaar, T. Piersma, and E. Postma, “Retained non-adaptive plasticity: gene flow or small inherent costs of plasticity?” _Evolutionary Ecology Research_, vol. 7, no. 3, pp. 489–495, 2005.
