15 Plasticity and Evolutionary Theory: Where We Are and Where We Should Be Going

Carl D. Schlichting
University of Connecticut

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15.1 INTRODUCTION

Although the evolutionary importance of adaptive phenotypic plasticity as a mechanism of adaptation to spatial and temporal environmental variation is acknowledged as part of the mainstream of evolutionary theory, arguments for a broader importance of phenotypic plasticity are contentious, mainly hinging on its potential role as a facilitator of evolutionary change (see Futuyma 2021; Levis and Pfennig 2021; Pfennig 2021 in this volume). Some proponents of an enhanced role for plasticity have called for its inclusion as an important component of an ‘extended evolutionary synthesis’ (trait-specific changes to offspring phenotypes induced by parental environmental conditions; Pigliucci 2007; Laland et al. 2015).

In this chapter, I will show that plasticity has important ramifications for many aspects of evolutionary theory. I will highlight current research on several of these topics as a means of demonstrating the impacts of plasticity on a range of evolutionary processes. Subsequently, I will address the broader issue of how responses to ‘environmental’ variation can be more fully incorporated into our understanding of the evolution of phenotypes.

15.2 THE CONTEXT-DEPENDENCE OF GENE EXPRESSION

Although we tend to forget this, gene expression is always context-dependent (Nijhout 1990). Genes require an environmental cue to be expressed whether that cue is an external environment or the product of some other gene, and phenotypes can vary as a function of differences in those cues (see examples in Sultan 2021 in this volume). So, while one can readily assign a fitness to a DNA sequence in a computer model, in the real world, it is that sequence's expressed phenotype that has a fitness. One consequence of this 'forgetting' is that we neglect the fact that patterns of gene expression leading to 'normal' development have evolved in the context of specific ranges and frequencies of various environmental parameters (Pei et al. 2020). When organisms are placed in environmental contexts beyond the scope of their evolutionary memory, their development may no longer be predictable.

Normal developmental sequences are often considered to be 'canalized' or 'robust' to genetic or environmental changes. Within the normal range of environments, novelties in canalized developmental pathways are most likely to be produced via mutation. However, outside of those environments where canalization has evolved, reaction norms are inherently plastic and thus also inherently prone to produce phenotypic novelty (hidden reaction norms: Schlichting and Pigliucci 1998; Schlichting 2003; Ghalambor et al. 2007; Schlichting 2008). 'Hidden reaction norms' (Figure 15.1) represent plastic responses to novel or infrequently experienced conditions for which there has been no selection for either canalization of a particular phenotype or an adaptive plastic response. Collectively, the hidden reaction norms of different genotypes express 'cryptic genetic variation' (Figure 15.1). Such cryptic genetic variation has been suggested to represent a store of variability that can be revealed in novel environments or genetic backgrounds (Gibson and Dworkin 2004; Le Rouzic and Carlborg 2008; Moczek 2008; Schlichting 2008; Paaby and Rockman 2014; Schneider and Meyer 2017; Donnelly et al. 2018; Zheng et al. 2019; Pilakouta et al. 2020).

Zan and Carlborg (2020) investigated the organization of 130 yeast growth regulation genes in response to 20 different growth media. They discovered that epistatic gene interactions were significantly reorganized across environments, with a few individual loci involved in epistatic interactions on as many as 16 different growth media, but the majority were expressed in fewer than four. Thus, there were different patterns of hidden and revealed growth-regulating loci contributing to plasticity and robustness across the different growth conditions.

Adaptive phenotypic plasticity represents a type of buffering at a different scale—canalization of *responses* of different genotypes to environmental shifts (e.g., the set of parallel horizontal reaction norms for flowering in Timberline and Mather; Figure 15.1). Convergence of responses on an adaptive reaction norm will also shield unexpressed genetic variants among those genotypes from selection (Wright 1931; Schwab et al. 2019). Signor (2020) documents the canalization of reaction norms in a comparison of ethanol tolerance in *Drosophila simulans*—possessing the ancestral non-tolerant phenotype—and *D. melanogaster*—with an evolved tolerance to ethanol. She finds substantial genetic variation in the reaction norms of gene expression to ethanol of *D. simulans* but no such variation in *D. melanogaster*, a lack of variation expected if an ethanol tolerant reaction norm had been strongly selected.

FIGURE 15.1 Graph of variation in relative flowering times of *Potentilla glandulosa* clones grown at three transplant gardens. Little variation is observed at the elevations where populations are normally found (i.e., at Timberline and Mather), and the reaction norm is itself canalized between these sites. However, at the sea level garden at Stanford, clones express hidden reaction norms resulting in the expression of significant cryptic genetic variation in this population. (Data from Clausen et al. [1940]; figure modified, with permission from The New York Academy of Sciences, John Wiley & Sons, Inc., from Schlichting [2008].) A modern example of hidden reaction norms and cryptic genetic variation can be seen in Hintze et al. (2020, Figure 5A) for stem cell proliferation in *C. elegans*.

15.3 PLASTICITY MAY BE ANCESTRALLY ANCESTRAL

Futuyma (2021) raises the important question of how trait plasticity arises. Most models of the evolution of development postulate that new genotypes are initially sensitive (plastic) to environmental change, with robustness (loss of plasticity) as a subsequent evolutionary feature (Schlichting and Pigliucci 1998; Newman and Müller 2000; Nijhout 2003; Schlichting 2003; Nijhout et al. 2017; Lafuente and Beldade 2019). Evidence for sensitivity of new mutants goes back to the classic work of Dun and Fraser (1959)—who showed that the *tabby* mutation in mice increased whisker number variability—and is supported by numerous other studies showing that new mutations are relatively uncanalized (Rendel 1967; Baer 2008; Hallgrimsson et al. 2019).

Non-plasticity (i.e., canalization, robustness) is thus arguably a derived state in most biological systems (Nijhout 2003). If plasticity is the ancestral state, then the equally intriguing question for evolutionary biologists is; How does trait stability evolve? Dun and Fraser's (1959) study also showed that variation in whisker number could be decreased via selection (see Hallgrimsson 2019 for further references on

selection for canalization). There has been a resurgence of interest in how buffering of developmental processes has evolved as evidenced by the plethora of recent reviews on canalization and robustness that document the growing empirical work in this area (Bateson and Gluckman 2011; Félix and Barkoulas 2015; Geiler-Samerotte et al. 2019; Hallgrímsson et al. 2019; Klingenberg 2019; Nijhout et al. 2019). In fact, systems that have evolved genetic and environmental robustness may be more prone to produce truly novel features when these buffering mechanisms, that suppress expression of genetic variants, no longer function (Wagner 2005).

Evolutionarily fine-tuned systems of development (i.e., well buffered against environmental or genetic perturbations) likely arise via functional diversification of duplicate copies of genes. Al Asafen et al. (2020) show that the evolved robustness of dorsal-ventral patterning in the *Drosophila* embryo requires at least three mechanisms of feedback in the *Dorsal* signaling module. Ghosh et al. (2019) have shown that selection for increased canalization of development time in *Drosophila melanogaster* is effective for some environmental perturbations (density) but not for others (temperature). Green et al. (2017) examined robustness by manipulating the dosage of a critical regulator of vertebrate development, the fibroblast growth factor signaling molecule (*Fgf8*). They found that phenotypic variation in face and skull measurements of mice embryos is not related linearly to the variation in *Fgf8* expression, and that observed differences in levels of robustness among genotypes are predicted by this non-linear ‘genotype-phenotype mapping’.

Such buffered systems may subsequently be further altered for cue-specific plasticity, again by deployment of duplicate receptor and signal transduction genes modified to control new plastic responses (Smith 1990; Schlichting and Smith 2002). Ancestral patterns of plastic response may be maintained, modified, or eliminated through processes jointly referred to as ‘genetic accommodation’ (West-Eberhard 2003). Bhardwaj et al. (2020) have examined the evolution of plasticity in the classic case of seasonal ‘polyphenism’ of wing eyespots (larger in the warmer dry season) in the butterfly *Bicyclus anynana*. In *Bicyclus*, warmer temperatures induce higher production of the hormone 20E and a corresponding increase in eyespot size. Examining 12 other species of butterfly, Bhardwaj et al. (2020) found that the plasticity of hormone production to temperature is an ancestral feature. However, although receptors for 20E in the eyespot region are found in several species, only *B. anynana* shows an increase in eyespot size in response to temperature. Their results suggest that the plastic response of increasing eyespot size results from a modification of the ancestral response via derived genetic changes linking eyespot size and hormone production.

BOX 15.1 TERMS AND DEFINITIONS

Canalization or robustness. Stability of phenotypes during development following perturbation. Genetic robustness typically refers to the reduction of developmental noise, and environmental robustness refers to the reduction of plasticity.

Cryptic genetic variation. Genetic variation revealed by environmental or genetic perturbations (Gibson and Dworkin 2004).

Developmental bias. The disproportionately higher production of certain variants following environmental or genetic perturbation (Uller et al. 2018).

Developmental noise. Variation in a phenotype of a trait of a particular genotype under constant environmental conditions.

Ecological developmental biology (eco-devo). The study of how organisms' responses to their environment influence the expression of genetic and developmental programs.

Epigenetic. Originally intended to indicate organism features that arise as a consequence of developmental processes (*sensu* Waddington; see 'Genotype-phenotype mapping' below); now the term is most often used to refer to whether a particular DNA sequence or histone protein is methylated (an epigenetic mark).

Evolutionary developmental biology (evo-devo). The study of developmental processes in an evolutionary context; e.g., to infer developmental changes leading to phenotypic changes in ancestral-descendant or phylogenetic relationships.

Evolvability. The tendency of a genotype or lineage to generate genetic variability and produce or maintain phenotypic variation over evolutionary time, enabling it to pursue diverse evolutionary trajectories (Schlichting and Murren 2004).

Extended evolutionary synthesis (EES). Driven by a perception that standard evolutionary theory provides an incomplete theoretical scope, the EES proposes to include topics such as evo-devo, evolvability, niche construction, and non-genetic inheritance, and to take into account reciprocal causation (i.e., where identities of causes and effects are fluid; Svensson 2018) and context-dependence (see Müller 2007; Pigliucci 2007; Laland et al. 2015; Fábregas-Tejeda and Vergara-Silva 2018).

Genetic accommodation. A process by which phenotypic variants that are initially strictly environmentally induced are selected to become genetically determined (i.e., heritable) (West-Eberhard 2005; Schlichting and Wund 2014; Ledon-Rettig and Ragsdale 2021). Plasticity may be enhanced or refined (i.e., 'plasticity-led evolution': Levis and Pfennig 2021), or even eliminated (genetic assimilation: Scheiner and Levis 2021).

Genotype-phenotype mapping. Describes the processes that convert the genetic instructions into the visible characteristics of an organism. Explicitly considers effects of gene-gene interactions (pleiotropy and epistasis) and gene-environment interactions that lead to changes in gene expression. In the case of phenotypic plasticity, there is a one-to-many mapping of a single genotype to the alternate phenotypes possible in different environments.

Hidden reaction norms. Unpredictable extensions of reaction norms in environments outside normally encountered ranges.

Modern synthesis. Stemming from population genetics theory developed by R.A. Fisher, S. Wright, and J.B.S. Haldane, the modern synthesis melded

concepts of genetics (Mendelian and quantitative) with natural selection to illuminate evolution in natural populations of organisms. The modern synthesis was advanced during the late 1930s and 1940s by T. Dobzhansky, E. Mayr, and others.

Niche construction. The modification of environmental conditions by the actions of an organism; e.g., edifices: beaver dams, burrows, and nests; soil or water alterations: actions of lichens and earthworms, decomposers; allelochemicals of plants.

Non-genetic inheritance. Trait-specific changes to offspring phenotypes induced by parental conditions (Bonduriansky 2021). Also referred to as epigenetic or transgenerational inheritance, and maternal effects (Rossiter 1996).

Phenotypic plasticity. Any change in phenotype by a genotype in response to changes in environmental conditions. A ‘reaction norm’ is a plot of the response across a set of environments (Sultan 2021).

Polyphenism. The formation of two (or more) distinct phenotypes in response to changes in environmental factors. Classic examples include the castes of social insects, seasonal differences in eyespot size in butterflies, host plant-related larval coloration in caterpillars, and light/dark winter/summer fur or plumage in birds and mammals.

Standard evolutionary theory (SET). The set of generally accepted principles encompassed by the ‘modern synthesis’ and its post-DNA expansion. Futuyma and Kirkpatrick (2017; Chapter 1: Box 1A) provide a concise listing.

Transcriptome. Whereas a genome records the DNA sequence of an organism revealing its complement of genes, ‘transcriptomes’ record the expression levels of those genes. They are often used to contrast gene expression levels in different environments, different tissues, or at different life stages (e.g., juvenile versus adult).

15.4 PLASTICITY AS AN ORIGINATOR OF NOVELTY

Several authors have pointed out the potential role of plasticity as an originator of new phenotypes for the evolution of behavior (Wcislo 1989; West-Eberhard 1989) and development (Schlichting and Pigliucci 1998; Newman and Müller 2000; Schlichting 2003; West-Eberhard 2003; Schlichting 2008; Gavrilets 2010; Moczek et al. 2011; Wagner et al. 2019). The development of multicellular organisms is itself a continuous set of plastic responses to internally produced stimuli driving changes in gene expression (Sachs 2002). We (Schlichting and Pigliucci 1998; Schlichting 2003) have proposed that multicellularity and differentiation may have arisen through genetic assimilation of sequential plastic responses to changes in internal environments, with novel developmental phenotypes initiated plastically and subsequently canalized so that adaptive developmental sequences are repeatable under broad conditions. In this scenario, the evolution of multicellular development is a recursive process alternating between plasticity (sensitivity of the phenotype to stimuli) and the evolution of robustness (see also Nijhout 2003; Bateson 2017;

Salazar-Ciudad et al. 2019; Schwab et al. 2019). This is an area of active investigation (Ratcliff et al. 2015; Wolinsky and Libby 2016; Grochau-Wright et al. 2017; Ratcliff et al. 2017; Herron et al. 2018; Herron et al. 2019; Laundon et al. 2019; Rivera-Yoshida et al. 2019; Davison and Michod 2021).

In addition to its potential primal role in multicellular evolution, plasticity has also been implicated in the origin of several major evolutionary features. The social insects, perhaps the most successful group of organisms (Hölldobler and Wilson 2009), owe their success to features that are due to a plastic response: the production of castes and divisions of labor. Berens et al. (2014) compare ‘transcriptomes’ of fire ants (*Solenopsis*), honey bees (*Apis*), and paper wasps (*Polistes metricus*) to look for commonalities in the plasticity of gene expression across lineages. Although they found little evidence for shared responses at the specific gene level, responses were similar at the level of metabolic pathways, suggesting that these different lineages are employing a shared ‘toolkit’ for generating convergent plastic responses to nutritional signals (e.g., in the insulin/insulin-like growth signaling pathway, Corona et al. 2016). Sun et al. (2019) investigated transcriptional changes in five castes of the higher termite *Macrotermes barneyi*, documenting extensive changes between castes in both gene expression and alternative splicing.

Kapheim et al. (2020) have investigated patterns of gene expression in the facultatively eusocial sweat bee *Megalopta genalis*. This species is an ideal model because females within populations vary in their tendencies towards sociality—some are solitary and others are social. Kapheim et al. designed a comprehensive suite of analyses using an annotated genome, a set of life-stage and sex-specific transcriptomes, and a population genomic comparison of solitary and social females. They discovered very strong associations of genes that have plastic expression during development (i.e., during sexual differentiation and metamorphosis) and genes with expression differences associated with divergence among castes. This suggests that genes with plastic expression patterns were later co-opted/redeployed during the evolution of caste specification. In addition, a broader comparison among species finds that this set of genes shows signs of strong positive selection in many independently derived eusocial insects (Jones and Robinson 2018; Kapheim et al. 2020).

Several research groups have taken advantage of deviations from the canonical insect caste system to examine the origins of plasticity. The ant *Diacamma* sp. has lost morphological castes, but still has divisions of labor based on social dominance. Okada et al (2017) demonstrated rapid changes in expression levels of genes involved in nutrition (e.g., insulin signaling) that accompany changes in rank. Several studies have focused on the solitary queen species *Pogonomyrmex barbatus* to examine the plasticity of divisions of labor when social interactions are experimentally imposed and multiple queens are grouped at nest establishment. Fewell and Page (1999) found that phenotypic specialization for nest excavation arose spontaneously in nests populated with multiple queens. Subsequently, Cahan and Gardner-Morse (2013) further showed a nascent division of reproductive labor: although average productivity per queen was maintained, one queen tended to take on a larger fraction of the reproduction.

The nematode genus *Pristionchus* has delivered several examples of plasticity-based novelty. The best studied is the feeding polyphenism of *Pristionchus pacificus*—individuals with a narrow ‘mouth’ and one ‘tooth’ are bacterivores, and those with a

wider two-toothed mouth are predators on fungi and other nematodes (Bento et al. 2010). The two-toothed form is induced under low-food conditions, and two genes, the sulfatase gene *eud-1* and the sulfotransferase *seud-1*, have been identified as antagonistic controllers of this plasticity-induced novelty (Ragsdale and Ivers 2016; Namdeo et al. 2018). These genes are both duplicate members of larger gene families that apparently evolved functional specialization to control the mouth polyphenism (Biddle and Ragsdale 2020). Further analyses have identified more details of the regulatory network involved in the switch (Kieninger et al. 2016; Sommer et al. 2017; Sieriebriennikov and Sommer 2018; Bui and Ragsdale 2019): intriguingly loss-of-function *eud-1* mutants result in all one-toothed individuals, while loss-of-function *nhr-40* mutants result in all two-toothed individuals, identifying these as plasticity-specific genes. Susoy et al. (2016) identified three new species of *Pristionchus* postulated to have feeding polyphenisms; each of these species has five different mouth shape morphologies!

Griffith et al. (2017) present evidence suggesting that the decidua, a distinctive cell layer forming the maternal portion of the placenta in eutherian mammals, arose as a stress response to implantation of the embryo. They demonstrate that features of the attenuated pregnancy of marsupials, such as the inflammation response when the fetal placenta contacts the maternal endometrium, are homologous to events in eutherian pregnancy. The authors propose that this plastic inflammation response is the evolutionary precursor enabling the origin of the anti-inflammatory phase that defines eutherian pregnancy (see also Wagner et al. 2019).

15.5 GENETIC ACCOMMODATION AND PLASTICITY-LED EVOLUTION

As mentioned previously, the expansion and refinement of plastic responses represent important evolutionary changes modifying phenotypes of organisms. The general topic of genetic accommodation has been reviewed fairly extensively (Schlichting and Wund 2014; Levis and Pfennig 2017; Schneider and Meyer 2017; Jones and Robinson 2018; Velotta and Cheviron 2018; Kelly 2019), and the specific topic of plasticity-led evolution is covered by Levis and Pfennig (2021), so I will highlight just a few exemplary recent studies.

Plastic responses to low oxygen levels, both short-term (acclimation) and long-term (adaptation), are well-studied, and some short-term changes that accentuate blood flow (hypertrophy of the ventricles) may be maladaptive in the long-term (right ventricular hypertrophy can result in lung disease and heart failure). Velotta et al. (2018) compared two species of deer mice (*Peromyscus*) that occupy different elevational ranges, comparing heart muscles at normal and reduced oxygen levels (hypoxia). The species had similar right ventricle sizes in normal oxygen levels, but high elevation *P. maniculatus* had much larger left ventricles. Exposed to low oxygen levels, *P. maniculatus* did not significantly change the size of either ventricle, while the low elevation species *P. leucopus* greatly increased the size of both: under low oxygen *P. leucopus*'s left ventricle was about the same size as *P. maniculatus*, but the right ventricle was now 30% larger than that of *P. maniculatus*. Velotta et al. (2018) suggest that this represents genetic accommodation in *P. maniculatus* via an

increase in the size of the left ventricle relative to that of *P. leucopus* and a reduction of the plasticity of both ventricles in response to changes in oxygen levels.

The work of Armin Moczek and colleagues on the plasticity of horn size in dung beetles of the genus *Onthophagus* represents some of the most in-depth examination of the process and mechanisms of genetic accommodation. Males of different species of *Onthophagus* show varying degrees of nutrition-related plasticity, but in general enhanced nutrition leads to the production of significantly larger horns (Emlen 1994; Moczek 2006). Casasa et al. (2020) examined transcriptomes of adult beetles of three species: *Digitonthophagus gazella* with a small nutritional response representing the ancestral state; *Onthophagus taurus* with a derived large nutritional response; and *O. sagittarius* with a derived lack of nutritional response (Emlen et al. 2005). Comparing transcriptomes of orthologous genes across species, Casasa et al. (2020) found only 8 differentially expressed (DE) genes between small and large males of the nutritionally non-responsive *O. sagittarius*, 946 DE genes for the moderately responsive *Digitonthophagus gazella*, and 1685 DE genes for the highly responsive *O. taurus*, revealing the expected correlation between the plasticity of gene expression and morphological plasticity. Eight hundred and fifty-nine genes that were strongly up-regulated in *O. taurus* were not differentially expressed in either of the other species, indicating that many genes have evolved increased nutritional sensitivity in the polyphenic *O. taurus*. The gene expression evidence also indicates that the secondary loss of plasticity in *O. sagittarius* results from the loss of nutritional sensitivity of many genes. These results indicate widespread genetic accommodation of plastic responses, both to enhance and reduce plasticity in different species. Evidence for evolutionary changes in plasticity have also been documented among different populations of *O. taurus* (Moczek et al. 2002; Rohner and Moczek 2020).

Corl et al. (2018) examined color dimorphism among populations of side-blotched lizards (*Uta stansburiana*) occupying different substrates in southern California. Populations of typical gray and tan mottled lizards from sandy substrates and dark lizards from the Písgah lava flow (22,500 years ago; Figure 15.2a) were established in the laboratory on both lava rock and sand. Skin reflectance was measured after 1 year for each of the four groups: sand-sand (Figure 15.2b), lava-lava (Figure 15.2c), lava-sand (Figure 15.2d), and sand-lava. Lizards from both sand and lava substrates exhibited substantial phenotypic plasticity in coloration: both groups that were switched adopted coloration more similar to the new substrate (Figure 15.2e). Lizards from the lava flow were significantly darker on both substrates, and Corl et al. identified genetic differences between the sand and lava populations. Allele frequencies of two candidate genes regulating melanin production were found to differ strongly between populations: sand populations were monomorphic for the ancestral allele, but the lava population had derived alleles at each locus with frequencies >20%. Hatchling lizards carrying the derived alleles were darker. The combined results imply a scenario where plasticity present in the initial population provided an adaptive advantage to lizards living on the new lava substrate; subsequently, new alleles arose that increased the constitutive darkness of lava lizards—demographic simulations suggest that these alleles arose about 1000 generations ago and both are under positive selection (Corl et al. 2018).

FIGURE 15.2 (a) The side-blotched lizard *Uta stansburiana* on lava rock. Individuals were collected from populations on sand and lava rock substrates. In the lab, they were placed in habitats with either sand or lava gravel. After 1 year, their reflectance was measured. (b) Sand origin after 1 year on sand. (c) Lava origin after 1 year on sand. (d) The same Lava origin lizard after 4 months on sand. (e) Lizards switched both from sand to lava and lava to sand responded plastically to produce coloration more similar to the resident populations. (Panels [a], [c], and [d] are reprinted from *Current Biology* 28:18, Corl et al., The genetic basis of adaptation following plastic changes in coloration in a novel environment, pp. 2970–2977, Copyright [2018], with permission from Elsevier; [b] courtesy of Ammon Corl.)

15.6 PLASTICITY AND SPECIES DIVERGENCE

Plastic responses to environmental variation may initiate reproductive isolation between adjacent populations. This isolation can take various forms—via alterations of phenology (Rajakaruna et al. 2003; Buckley et al. 2015; Dittmar and Schemske 2017; Taylor and Friesen 2017; Osborne et al. 2019), diet or host (Smith et al. 2013; Moser et al. 2015; Silva-Brandão et al. 2017), signaling (Iglesias et al. 2018; Otte et al. 2018), or even morphology (Garduno-Paz et al. 2020). Schlichting (2004), West-Eberhard (2005), and Pfennig et al. (2010) reviewed many examples, and subsequent authors have elaborated (Levin 2009; Fitzpatrick 2012; Schneider and Meyer 2017; Otte et al. 2018).

Treehoppers (Homoptera: Membracidae) of the *Enchenopa binotata* species complex are remarkable for host-plant associated speciation across a broad diversity of host trees (from eight different plant orders). *Enchenopa* communicate via vibrational signals through the substrate (i.e., stems, leaves, and petioles), and the comparison of signals of males from 11 *Enchenopa* species (each from a different tree species) revealed extensive differentiation in all measured aspects of the signals (e.g., frequency, amplitude, and duration; Cocroft et al. 2010). The key driver of speciation appears to be the species' philopatry—females show strong preferences for laying their eggs on the tree species upon which they developed (Wood and Guttman 1982;

Stearns et al. 2013). However, signal propagation changes plastically on different plant species (Sattman and Cocroft 2003; McNett and Cocroft 2008), and Rodriguez et al. (2008) have shown not only differences in signaling of individuals on different host species, but also genetic variation in signaling on a novel host—i.e., the raw material for precipitating genetic changes.

Etges and colleagues have studied populations of the cactophilic *Drosophila mojavensis* from Baja California (ancestral) and Sonora (derived) adapted to different cactus species, *Stenocereus gummosus* (pitaya agria) and *S. thurberi* (organ pipe), respectively (Etges et al. 2010). Cuticular hydrocarbons (CHCs) are important pheromones involved in sexual discrimination among males by females, and the differences in CHC mixtures between Baja and Sonora populations are important for premating isolation between them (Etges and Ahrens 2001). Although growth on the different cactus species significantly alters CHC profiles of flies (Stennett and Etges 1997; Etges and de Oliveira 2014), a direct link between plastic changes in CHC composition and mating preferences has not been made.

Sorenson et al. (2003) documented a remarkable example of behavioral plasticity initiating components of an adaptive radiation of 19 bird species (the indigobirds, genus *Vidua*) as brood parasites on grassfinches (Estrildidae). Rapid speciation is possible because *Vidua* species acquire mating traits through imprinting on their hosts—i.e., males learn their songs from their foster parent male and females adopt preferences both for those songs and for nests of the host species. This system has recently been revisited by Jamie et al. (2020), who find that additional components of the parasitic *Vidua*'s phenotypes also mimic those of the host species, enhancing reproductive isolation among *Vidua* species. They document several putative adaptations: mimicry of nestling behavior (matching of the presence/absence of head rotation or tongue movement while begging), mimicry of the parasites' calls to those of the host species (rather than to calls of other local grassfinch species), and mimicry of hatchling mouth coloration used as signals to parents while begging (more similar to markings of host than to markings of other local grassfinch species). Such further adaptations become more likely following reproductive isolation established by the initial plastic imprinting.

Garduno-Paz et al. (2020) started with a single population of stickleback and then induced plastic benthic (shoreline) and pelagic (open-water) feeding morphologies via diet modifications. Body morphology after 10 months on each diet showed the typical differences—benthic fish with comparatively shorter heads and jaw bones and deeper bodies (each fish was given a multivariate pelagic-benthic score based on morphology relative to a benthic-pelagic continuum). 'Benthic' and 'pelagic' experimental females were then simultaneously shown size-matched mates of each morphology group. Pelagic females were significantly more likely to mate with males that were similar in their shape score, i.e., males with similar morphology. They note that coupling the sharing of feeding locations with mating preference for similar shapes could make this plastic response a 'magic' trait—i.e., a simultaneous change in the morphology and a preference for it.

Plasticity may also play an important role in character displacement with plastic responses increasing differences between sympatric populations of species (Pfennig and Pfennig 2012; Robinson and Pfennig 2013 specifically examine the case for

character displacement following competition). An example of character displacement by means of the evolution of plastic responses is seen in the competing toad species *Spea bombifrons* and *S. multiplicata* (Pfennig et al. 2007). Both species are detritivores that can plastically produce a carnivorous tadpole morph when shrimp are present—this morph is larger, with larger jaws and a shorter gut. Remarkably, in sympatry with *S. multiplicata*, *S. bombifrons* does not produce the detritivore morph. Levis et al. (2017) pinpoint some of the genetic correlates of the loss of plasticity, identifying two genes in particular that show patterns of expression that differ between diets (detritus versus shrimp) and *S. bombifrons* populations (sympatric with *S. multiplicata* versus allopatric). The protein-coding peptidase gene *Pm20d2* had higher expression in the shrimp diet, but relatively reduced expression in *S. bombifrons* populations sympatric with *S. multiplicata*. The transcription factor *Btf3* also has higher expression in the shrimp diet, but only in allopatric *S. bombifrons*; gene expression plasticity has been lost in sympatric populations. Thus, these two genes show the evolution of expression patterns; their particular functions in morph production are yet unknown.

15.7 PLASTICITY PRODUCES DISTINCTIVE EVOLUTIONARY DYNAMICS

One significant consequence of plasticity for evolutionary dynamics was pointed out by Sewall Wright—plasticity can hide genetic variation (Wright 1931). A plastic response can move organisms to a different adaptive peak, even if allelic variation is available that might otherwise facilitate adaptive evolution. If the new environment is stable, we then have adaptation via plasticity but evolutionary stasis, a fundamentally different dynamic than adaptive evolution by allelic substitution.

Another fundamental role of plasticity in altering evolutionary dynamics arises from the changes in gene expression that altered environmental conditions produce (see Goldstein and Ehrenreich 2021 in this volume). Numerous studies have demonstrated that the genetic architecture (i.e., pleiotropy, epistasis, and genetic correlations) of a population may itself be strongly modified by the environment (Draghi and Whitlock 2012; Wood and Brodie III 2015; Parsons et al. 2016; Rowinski and Rogell 2017; Gibert et al. 2019; Schou et al. 2019). Thus, if one were to raise *genetically identical populations* in alternate environments (e.g., different temperatures, water availability, pH, and predators), their divergent genetic architectures can cause them to exhibit distinctive evolutionary responses to subsequent evolutionary challenges (e.g., herbivory, predation; Schlichting 1989).

Pespeni et al. (2017) found that, in *Onthophagus* beetles, genes that are conditionally expressed, i.e., only in specific environments, showed much stronger signals of previous natural selection. This pattern is predicted because selection on such alleles is relaxed in non-eliciting environments (Snell-Rood et al. 2010). Along these lines, a meta-analysis by Noble et al. (2019) indicated that the directions of plastic responses to novel environments are aligned with those aspects of the phenotype that also have significant heritability, suggesting that integrated phenotypes respond similarly to genetic and environmental perturbations.

Thus, the dynamics of both population genetic and quantitative genetic models can be altered by plastic responses or forms of ‘non-genetic inheritance’ (changes to

offspring phenotypes induced by parental environmental conditions; Danchin et al. 2011; Bonduriansky 2021). Early models demonstrated that non-genetic modes of inheritance can significantly alter the evolutionary dynamics of populations relative to predictions of standard genetic models (Hinton and Nowlan 1987; Laland et al. 1999). These have been augmented by more general models incorporating plasticity or non-genetic inheritance (Bonduriansky and Day 2009; Day and Bonduriansky 2011; Frank 2011a,b; Klironomos et al. 2013; Bonduriansky and Day 2018), showing lags, accelerations, bumps, and plateaus in evolutionary change.

Recent models have extended findings for plasticity. Coulson et al. (2017) develop a series of integral projection models that incorporate development (i.e., genotype-phenotype mapping) and mechanisms of inheritance, and contrasted how different instantiations of phenotypic plasticity (e.g., no phenotypic plasticity, adaptive phenotypic plasticity, and non-adaptive phenotypic plasticity) can influence evolutionary responses to environmental change. Populations with adaptive plasticity, despite suffering initial declines, show the most rapid rate of adaptive evolution to new environments. Their models also suggest that some reported examples of rapid evolution are more likely to be due to initial plastic responses than to genetic evolution.

Jeremy Draghi has developed models that examine the interplay of developmental noise and plasticity. Draghi (2019) examined a model in which developmental noise is controlled by the genotype and thus can evolve. In this model, low developmental noise (i.e., canalization) is favored in constant environments but tends to impede further evolution of plasticity via the reduction in phenotypic variability. This is particularly true when the suppression of developmental noise arises through negative feedbacks (e.g., antagonistic pleiotropic effects of different genes). However, replicates that evolved canalization without pleiotropy were not as constrained, indicating that how variability is controlled will influence the evolution of the system. Draghi (2020) took a different approach, allowing developmental noise to be induced by the environment, but the results are similar in that plasticity is again more likely to evolve when environmental noise is higher because the developmental noise creates more phenotypic variability and thus more opportunities to achieve phenotypes that increase fitness.

Several recent studies have also experimentally evaluated the effects of non-genetic inheritance. Dey et al. (2016) found that *C. elegans* subjected to predictable (alternating) normal versus low oxygen environments evolved plastic anticipatory maternal effects, such that mothers increased or decreased glycogen provisioning ‘anticipating’ next-generation conditions. They modeled evolution in predictably fluctuating versus randomly fluctuating environments and found that populations that evolved anticipatory maternal effects had increased adaptability (i.e., higher fitnesses) in subsequent random environmental sequences. Samani and Bell (2016) experimentally examined the dynamics of evolutionary rescue of wild yeast populations (*Saccharomyces paradoxus*) in relation to their prior evolutionary histories. They first selected lines for 4 weeks on fructose (non-stressful) and 11 other sugars that reduced population growth rates (starvation-adapted), then subjected all lines to four novel environmental factors: high temperature, high pH, alcohol, and salt. Intriguingly, the starvation-adapted lines had *reduced* adaptive plasticity relative to the fructose lines, but a higher subsequent likelihood of adapting to the novel

challenges: the more versatile fructose lines did not adapt to any of the novel challenges. Their results suggest that initial favorable plasticity actually inhibited subsequent evolutionary rescue. The diverse results of such experimental and model studies are fueling new hypotheses about how plasticity can evolve in heterogeneous environments (Bono et al. 2020).

15.8 PLASTICITY AND EVOLUTIONARY THEORY

The core structure of the modern synthesis, population genetics, is a rigorous and successful set of models of how evolutionary forces can alter allele frequencies. Likewise, quantitative genetics is a proven model for projecting statistical changes in distributions of polygenic traits over spans of a few generations. Neither population genetics nor quantitative genetics, however, inform us about how phenotypes are produced, how development proceeds, or how environment alters gene expression (Gawne et al. 2018; Hallgrímsson et al. 2019). Because selection operates on phenotypes, and only indirectly on the alleles that produce them, it is of paramount importance to understand mechanisms by which variation in phenotypes arises and increases, whether these variants are behavioral, physiological, or developmental. Phenotypes result from ‘epigenetic’ processes (in the Waddingtonian sense) that act to produce developmental trajectories (Schmalhausen 1949; Waddington 1953). Traits of organisms and their responses to variation in local environments (both external and internal) are central to understanding how evolutionary processes of selection and drift impact trajectories of phenotypic evolution.

To answer questions about phenotypes and traits, we need disciplines including ‘evolutionary developmental biology’ (evo devo), ‘ecological developmental biology’ (eco devo; Sultan 2015), and molecular ecology and genetics to investigate phenomena such as ‘cryptic genetic variation’ (Gibson and Dworkin 2004; Ledón-Rettig et al. 2014; Zheng et al. 2019), ‘evolvability’ (Wagner and Altenberg 1996; Schlichting and Murren 2004; Payne and Wagner 2019), canalization and robustness (Flatt 2005; Nijhout et al. 2019), ‘developmental bias’ (Uller et al. 2018), ‘niche construction’ (Laland et al. 2019), non-genetic inheritance (Danchin et al. 2011), and of course phenotypic plasticity. These fields and topics represent a broad research initiative focused on understanding the processes and mechanisms underlying the production, evolution, and importance of phenotypic diversity (e.g., Rollo 1994; Schlichting and Pigliucci 1998; West-Eberhard 2003; Pfennig et al. 2010; Bolnick et al. 2011; Moczek et al. 2011; Laland et al. 2015; Sultan 2015, 2017; van Gestel and Weissing 2016; Peichel and Marques 2017; Des Roches et al. 2018; Duclos et al. 2019; Glastad et al. 2019; Müller 2019; Herrel et al. 2020).

In this essay, I have highlighted evidence that plasticity occupies a conceptual nexus with links throughout evolutionary biology, impacting all hierarchical levels of evolution—macroevolution (origin of novelties), mesoevolution (speciation), and microevolution (adaptation). As Futuyma (2021) points out, plasticity has been identified as a key concept in an array of topics that some authors have suggested raise questions for evolutionary theory, and thus merit an ‘extended evolutionary synthesis’ (EES; Müller 2007; Pigliucci 2007). The ensuing arguments and counterarguments between proponents of EES and ‘standard evolutionary theory’ (SET) have been

predictably bloody in the academic fashion, with defenders of SET asserting that it can easily encompass all these topics (Laland et al. 1999; Wray et al. 2014).

The philosophy of biology community has welcomed the controversy between the EES and SET camps as a testing ground for ideas about research programs and paradigm shifts (Fábregas-Tejeda and Vergara-Silva 2018; Lewens 2019), and as with the debates among evolutionists, there are a diversity of opinions. In both fields, many arguments revolve around ‘virtue-based’ disputes (Buskell 2020): are plasticity’s effects ‘likely’ enough, or ‘significant’ or ‘strong’ enough (Kovaka 2019; Baedke et al. 2020). Such arguments are ultimately obfuscatory, calling for decisions about whether some arbitrarily defined hurdle has been surmounted.

Rather than focusing on polarizing differences of opinion, it is probably most interesting for our purposes to be curious about these external views for their prescriptions on strategies for informing the debate. Baedke et al. (2020) call for an approach based on ‘explanatory’ power and applying explanatory standards (*precision, proportionality, sensitivity, and idealization*): “explanatory power can be assessed by comparing the range of inferences to potentially new counterfactual situations and, accordingly, of answers to *w-questions* [‘what-if-things-had-been-different’] that alternative explanations make possible. For example, an explanation of a particular population dynamic that includes developmental factors might be able to answer more questions on what would happen to this population if it was changed” (Baedke et al. 2020 pp. 7–8, see also Uller et al. 2020).

Kovaka (2019) advocates a related approach, employing evidentiary standards of ‘discrimination’ and ‘significance-relevant.’ She suggests that, at least for the debate about plasticity-led evolution, “researchers need a richer middle-range theory” (i.e., one describing the relationship between plasticity-led evolution and observable evidence). This middle-range should be focused on evidentiary support to identify the ‘traces’ that characterize plasticity-led evolution. Kovaka proposes that, although direct evidence from natural populations is important, identifying signatures of plasticity-led evolution that distinguish it from SET models may be accomplished via, for example, experimental evolution, genomic comparisons, and modeling of plasticity-led versus genotype-led evolutionary dynamics.

Uller et al. (2020) propose that it may be the representation of plasticity itself as a reaction norm that is creating a block to appreciating its ‘transformational’ role in evolution. Because reaction norms have been conceptualized as manifestations of specific genotypes, they can easily be binned as yet another example of genetic variation to be collapsed into relative fitnesses on which selection may operate. Uller et al. (2020) argue that it is this “genetic idealization of evolution by natural selection” that allows unique details of development, physiology, or behavior to be ignored because they are unnecessary to explain a pattern of evolutionary change. They suggest that adopting alternative idealizations of evolutionary dynamics may produce more satisfactory explanations of patterns of phenotypic evolution.

15.9 WHERE SHOULD WE BE GOING?

As documented in this chapter and volume, phenotypic plasticity has multifarious connections with evolutionary biology and can have striking non-canonical effects

on evolutionary processes and their outcomes. I have previously avoided joining the arguments about EES versus SET, expecting that, after the initial volleys, both sides would continue profitable work in their specialties, with eventual *rapprochement*. However, I have become frustrated as defenders of the omniscient nature of SET continually expand the list of concepts that it can accommodate—such claims appear increasingly Procrustean. There *are* areas of evolutionary biology on which the SET is silent—the origin of novelties; biases in mutation or development; evolvability; evolution of the genotype to phenotype map; and the unfolding of development. Should we be content leaving these issues to the side, settling for a theory that seems adequate, or do we want to build theories with increased explanatory power?

The SET is in no danger of being eclipsed—it is still clearly fundamental for understanding the evolution of populations subject to selection and drift, but it just as clearly is not an encompassing theory of evolutionary processes. Futuyma (2021) argues that understanding the evolutionary importance of plasticity and related concepts just requires details of “the effects of mutation, gene flow, genetic drift, and especially natural selection on the frequencies of alleles and genotypes, ... it’s still genes and selection, all the way down.” I counter that this distinctly gene-centric view of evolution, with its explicit perspective of phenotypes as byproducts, is myopic. The standard view of a genotype mapping to a single phenotype with a particular fitness is misleading at best, and likely inaccurate for most genes: via plasticity, a single genotype can produce multiple phenotypes, and each of those phenotypes will have its own environment-dependent *fitness*.

I propose that a view of evolution as a recursive process involving both the generation and sorting of variation is a more accurate and flexible perspective. Many of the topics embraced by supporters of an EES are related to the generation of variation. The SET, on the other hand, encompasses a wealth of theory about the sorting of variation. A full view sees new phenotypes produced via new mutation or exposure to new ‘environments’ (including new genetic backgrounds, new developmental milieus, and new external conditions), followed by processes that sort such variation—selection, drift, and gene flow (see e.g. Fábregas-Tejeda and Vergara-Silva 2018).

Thus, new empirical and modeling efforts to identify the roles of plasticity in evolution must explicitly recognize the complementarity of the processes involved in generating and sorting variation. Advances are already being made to construct more realistic models of evolution that incorporate separate terms for both genetic and environmental components of phenotypic variation. Such models can incorporate either of the benchmark equations of trait evolution (Breeder’s or Price’s equations) into population dynamic models for forecasting evolutionary trajectories (Coulson et al. 2020; Helanterä and Uller 2020; Rice 2020).

There are many avenues to explore on our way to a more complete understanding of how plasticity evolves. This will require building upon the recent surge of excellent work in ecological and evolutionary developmental biology and molecular ecology and genetics to get a clear picture of the genes and signal transduction pathways that control plastic responses. A better phylogenetic understanding of patterns and processes of the evolution of variation in plasticity is also needed. Results from work in these areas can then be viewed through the lens of robust models of evolution in populations that account for both genetic and environmental sources of phenotypic variation. Box 15.2 lists some suggestions for future research.

BOX 15.2 SUGGESTIONS FOR FUTURE RESEARCH

- Cryptic genetic variation and hidden reaction norms. Theory suggests that novel or rarely encountered environments should reveal cryptic genetic variation. This is an empirical question that can be addressed with experiments that expose organisms to a range of environments that span normal and unusual conditions.
- Plasticity in a phylogenetic context. Despite well-developed theory about when plasticity *should* evolve, most evidence of evolutionary change consists of comparisons of pairs of species or populations (Murren et al. 2014). There are actually very few mappings of divergence in plastic responses across phylogenies (Relyea et al. 2018). These should be produced via controlled environment studies examining responses of a group of species (e.g., congeneric taxa) to a set of environmental conditions. Such studies can answer questions about magnitude, direction, and rate of evolutionary change of plastic responses.
- Distinguishing adaptive from non- or maladaptive plasticity is experimentally difficult due to both the lack of appropriate genetic variants (highly adaptive plastic responses are likely to be fixed) and the scope of experimental designs. We need to employ the power of genomic and transcriptomic studies to uncover signatures of selection on genes and pathways related to plastic responses.
- Integration of plastic responses of phenotypes. How are plastic responses of different traits coordinated? (Schlichting 1989). There have been investigations examining pieces of this puzzle from the trait side (e.g., Buehler et al. 2012; Michimae and Emura 2012; Ellers and Liefing 2015; Rusman et al. 2018; Wright et al. 2018; Parsons et al. 2020) and many studies from the gene expression side (e.g., Mäkinen et al. 2017; Mark et al. 2019). Although examples are beginning to accumulate that link trait values and gene expression patterns (e.g., Casasa et al. 2020; Jacobs et al. 2020), there is a need for coordination of the concepts and literatures on the integration of trait plasticities and plasticity/modularity of gene expression.
- Following from Kovaka's (2019) prescriptions for detecting evolutionary signatures:
 - Contrast evolutionary dynamics of plastic versus non-plastic lineages in selection experiments. Such experiments could contrast outcomes for the evolution of plasticity from (1) experiments that select for a new trait mean versus (2) experiments that select on the plastic responses themselves. Both real and *in silico* populations could be followed (see e.g. Sikkink et al. 2019).
 - Examine the evolution of patterns of gene expression (transcriptomics) among recently diverged populations to discover characteristic patterns of change related to the evolution of plasticity (see discussion of work by Pfennig and colleagues above).

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