

Commentary: The Promise of Ecological Developmental Biology

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In a persuasive essay on the promise of developmental evolution, Wagner (2000) argued that this synthetic discipline can make a unique explanatory contribution to evolutionary biology. Identifying developmental and molecular mechanisms and how they have changed at crucial junctures is key to understanding the range of phenotypic possibilities available through evolutionary time, and hence major steps in morphological evolution. Here I discuss a second recently emerged discipline that can profoundly enrich our understanding of the evolutionary process and of biological diversity, as well as of development itself. Ecological development investigates the development of organisms in their natural contexts. This investigation shifts our focus to the immediate interactions between individual organisms and their environments (and to the underlying mechanisms of those interactions). "Eco-devo" thus illuminates the ecological and hence microevolutionary implications of development, providing the critical complement to the macroevolutionary focus of the evolutionary development problematic (Gilbert, 2001).

The goal of ecological developmental biology is to include the environment in studying both the developmental causes and the ecological consequences of phenotypic variation. This inclusion of the environment is not a contemporary innovation but rather a restoration of an earlier, more holistic approach to understanding individual development. Early twentieth-century German biologists viewed the genotype as a repertoire of environmentally contingent phenotypic potentialities or "norm of reaction" to the environment, rather than as a rigid developmental blueprint (Sapp, '87; Sultan, '87; Stearns, '89; Sarkar, '99). Accordingly, every phenotype was understood to represent a genotype-by-environment interaction: the expression of a given genotype under its particular environmental influences. With the growing professional dominance of transmission genetics in studies of heredity (Amundsen, 2001), the adoption by New Synthesis evolutionists of a determi-

nate, strictly Mendelian notion of gene expression (Sultan, '92), and an increasing focus on "model" organisms chosen specifically to express minimal environmental responses (Bolker, '95; Gilbert, 2001), the phenotype came to be seen instead as the direct, fixed outcome of the genotype. Accordingly the earlier genotype/environment paradigm was displaced by purely gene-based models in both developmental and evolutionary biology. Evolutionary biologists such as Schmalhausen and Waddington who took an integrative approach remained outside the mainstream. Neo-Darwinian theory became, in R. A. Fisher's phrase "a genetical theory of natural selection" that defined evolution as change in allele frequencies rather than in organisms.

One clear consequence of this approach, which has dominated evolutionary biology since its origin during the mid-twentieth century, was the exclusion of developmental biology from studies of evolutionary change in populations (Hamburger, '80; Amundsen, 2001). However, starting in the late 1970's ecological geneticists and life history theorists sought increasingly to integrate the complexity of environmental response into their understanding of evolutionary processes [e.g., the seminal work of Stearns ('77, '82); Jain ('79); Gupta and Lewontin ('82); and Scheiner and Goodnight ('84)¹]. Since that time a considerable body of work in ecological development has emerged, together with insights and approaches that hold the promise of redressing this disjunc-

¹Growing interest in this new direction was reflected in the 1989 publication of an important symposium on phenotypic plasticity in the journal *Bioscience*, presenting a range of ecological development studies and pointing to the critical importance of phenotypic response to environment for evolutionary theory (Stearns, '89 and references therein).

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tion. Investigating the phenotypes produced in natural environments and their realized levels of fitness in those environments both broadens our understanding of developmental processes, and furthers the integration of developmental biology into microevolutionary theory.

Development as a genotype-environment interaction: phenotypic plasticity and the norm of reaction revived

Although in casual parlance genes are often said to “control” development, or to code directly for specific traits, the dynamic physical and biochemical processes that give rise to individual form reflect a subtle nexus of influences which include major and epistatic gene effects, physical and biotic conditions of the organism’s external environment, and the resulting internal environment (see Lewontin, 2001; Nijhout, 2001). Since development is a Markovian process, these influences are not distinct and additive, but rather they interact in complex feedbacks throughout ontogeny. For this reason, the phenotype is most accurately described as the joint outcome of these internal and external genetic and environmental forces (Gray, ’92). It is important to recognize that developmental studies under controlled laboratory conditions do not identify purely genetic sources of form in the absence of environmental influences, but simply reveal the form produced in that particular environment. In other words, an organism can never develop in the absence of an environment, so under laboratory conditions one is simply studying a single point on its norm of reaction. For molecular biologists studying signaling pathways in gene transcription to understand broadly shared developmental mechanisms, this is one of several necessary and reasonable experimental simplifications (working on laboratory-bred strains rather than naturally-occurring genotypes is another). However, since neither the genotypes nor the biotic and abiotic conditions in such studies occur in nature, information on phenotypic expression from these studies cannot be extrapolated to organisms in the real world (Gilbert, 2001). If we seek to understand how organisms function and evolve in their environments, and if we furthermore seek to mitigate the human-mediated disruption of these living systems over the coming decades, this gap in our biological knowledge is a serious one.

Ecological development research seeks to fill this gap by characterizing the phenotypic expres-

sion of naturally-occurring organisms in environments relevant to their field distributions. In so doing, it examines the ecologically significant ways that individuals may differ as a result of the environmental heterogeneity that most lab studies are designed to eliminate. The past fifteen years has seen an explosion of interest in the phenotypic modifications that may be expressed by a given organism under contrasting conditions, or *phenotypic plasticity*. To date, developmental plasticity has been reported in land plants, algae, lichens, marine and freshwater invertebrates, insects, fish, amphibians, reptiles, and mammals, in response to such diverse environmental factors as light quantity and spectral quality, temperature, substrate chemistry or texture, relative humidity, day length, food type or availability, the presence of herbivores, predators, and pathogens, population density, social interactions, and the concentration of atmospheric carbon dioxide and other biologically active molecules (references in Sultan, 2000, 2003; Gilbert, 2001). In some cases, environmental effects are mediated by the organism’s own physical activities and experience, through phenotypic effects of biomechanical stress and neurological stimuli (references in Losos et al., 2000; Gilbert, 2001). Environmental influences may also carry over to the offspring generation, through effects on maternal tissue status and life-history (Mousseau and Fox, ’98). Yet we have only begun to examine the developmental potentialities of naturally evolved organisms in response to the kinds of environmental variation that occur in nature. Further eco-devo studies will certainly lead to a richer understanding of these phenotypic repertoires and of the complex genotype by environment transduction mechanisms that generate them.

The norm of reaction concept provides a powerful and flexible experimental approach for studies of developmental response to environment. In practice, the norm of reaction is defined as the set of phenotypes produced by a given cloned or inbred genotype in a range of environmental conditions (Gupta and Lewontin, ’82; Sultan and Bazzaz, ’93a,b,c; Schlichting and Pigliucci, ’98; and references therein). The phenotypic impact of specific environmental factors or factor combinations are tested by conducting norm of reaction experiments in series of controlled conditions. These individual norms, or patterns of genotype-environment response, are expressed graphically by plotting for each genotype the phenotypic state it expresses in each of the test environments;

phenotypic differences among the various environments can be assessed statistically using standard quantitative genetics techniques (e.g., above references, this paragraph).² Environmental response patterns can also be characterized for populations or species by calculating mean norms of reaction for robust samples of constituent genotypes. In organisms that are not amenable to inbreeding or cloning, well replicated plasticity experiments that measure distinct genotypes in each treatment can also provide good information as to environmental effects on development at the population and species levels (though without the same statistical precision, since genotype-environment interactions are subsumed within the overall treatment effects).

Norm of reaction and plasticity studies thus take into account the context dependency of development through precise tests of genotypic and environmental effects on phenotypic variation. Because of this context dependency, the results of these studies will depend critically on both the set of genotypes and the particular environmental conditions considered (De Jong and Stearns, '91). If the information is to be interpreted in an ecological or evolutionary context, it is essential to study genotypes sampled from natural populations, and to examine their morphogenetic responses to major resources or stresses that vary in the field (Sultan, '95). Depending on the organism, key environmental factors may include abiotic factors such as temperature, mineral resources, pH, and so on, as well as biotic factors such as the identity and density of competitors, prey, or predators. When factors interact, they may be tested in multifactorial designs or in combinations based on field measurements. Ideally, specific treatment levels are chosen to reflect the actual range of variability in populations or geographic regions under study. This is particularly important because norms of reaction are not necessarily linear (Scheiner, '93), so patterns of phenotypic variation may be strongly influenced by the precise treatment levels chosen. Thus appropriate design of ecological development studies demands a careful determination of salient

aspects of the environment and their ranges of variability.

Evolutionary insights from ecological development

Though clearly important for understanding the causes of developmental variation in natural contexts, an eco-devo approach affords even more profound insights into the micro-evolutionary consequences of this variation (Lewontin, 2001). Since natural selection acts based on actual phenotypic differences among individuals in their environments, these are the differences we must study to understand the evolutionary process (Schmalhausen, '49). This requires taking into account the complex ways that genetic inheritance and environmental influences—including some that are themselves inherited, such as cytoplasmic factors, maternal effects, and endosymbionts—jointly give rise to phenotypic outcomes across generations. However, until recently, environmental influences on phenotype were rigidly excluded from consideration by New Synthesis evolutionists, who posited that such effects were evolutionarily trivial because they were not (usually) inherited (e.g., Maynard Smith, 2000; critiqued by Griffiths, 2001). This view led to the paradoxical notion (discussed in Sultan, '92) that although environmental influences can lead to substantial phenotypic differences among individuals in natural populations, such environmentally-induced variation is somehow irrelevant to natural selection. On the contrary, to understand and correctly predict the process of adaptive evolution, we must know the sources of phenotypic diversity and their distribution, and study the effects of that diversity on fitness in nature (Sultan, '87; Stearns, '89; Nager et al., 2000, Lewontin, 2001).

Ecological development studies illuminate two distinct and equally fundamental ways that environmentally-induced phenotypic variation can influence the process of natural selection. First, environmental effects can directly enhance or reduce an individual's fitness relative to others in the population, through inevitable effects of resource levels or stress on development and function. Second, phenotypic responses to environment may entail ecologically beneficial developmental plasticity that constitutes adaptation at the individual level. Below I briefly explain these two critical insights and their implications for adaptive evolution.

²Note that the norm of reaction inherently weights environmental and genetic influences equally as developmental causes, effectively expressing the biological truism that trait expression depends on both types of factor. In this way this approach departs from the common practice of ascribing a unique or primary status to the "information" carried in DNA. See Griffiths, 2001 and Oyama et al., 2001 on the issue of information and information metaphors in molecular biology, and for discussion of a more inclusive "developmental systems" approach.

Environmental effects on individual fitness

Over evolutionary time, natural selection is understood to fit populations genetically to their particular environments by favoring the most well-adapted genetic variants, due to their correspondingly high reproductive success or fitness relative to others in the population. In order to predict trajectories of adaptive genetic change in populations, micro-evolutionary models assign specific, constant fitness levels to alternative genotypes. This simplification underlies the elegant mathematical apparatus of population genetics. However, like other aspects of the phenotype, fitness is not an intrinsic property of genotypes but rather depends on both the physical and biotic environment. It is now recognized that variable environmental effects on fitness, which were previously treated as evolutionarily irrelevant “noise,” may in fact slow or even prevent predicted selective outcomes (Barton and Turelli, '89).

Variation in environmental quality can confound genotypic differences for all aspects of fitness, a phenomenon termed the “silver spoon effect” (Grafen, '88; Primack and Kang, '89; Travis, '94; Jordan and Snell, 2002). This term, arising from a wry description of privileged upbringing as a cause of general success in life, denotes the fact that favorable environmental circumstances during development (or their absence) may result in a suite of positively correlated fitness-related traits. For instance, individual biomass and offspring number are generally highly correlated with environmental resources such as water, food supply, or (for plants) light intensity. In natural populations, these key resources are often patchily distributed, creating a mosaic of differential fitnesses that typically outweigh more subtle genotypic differences (Dobzhansky, '41; e.g., Sultan and Bazzaz, '93a,c). These environmental effects on fitness may vary at surprisingly fine spatial scales (Stratton, '94), and in addition often vary temporally within and among seasons. Their fitness impact may depend on the factors involved as well as on the timing, duration, and variance of specific factor levels (Shine and Harlow, '96; Weinig, 2000; Chakir et al., 2002).

As a result of these environmental fitness correlations, even traits that appear to be under direct selection such as size and reproductive output can be kept in evolutionary stasis (Sultan, '87; Nager et al., 2000, and references). The

precise evolutionary impact of environmental effects on fitness depends on the distribution of environmental states and on differences among genotypes in their response patterns to those states. Variation among genotypes in norms of reaction for fitness components is quite well known. In natural populations, which inevitably encounter environmental heterogeneity, this aspect of genotype-by-environment interaction leads to the maintenance of genetic variation for traits that would otherwise be predicted to show selective change (Mitchell-Olds and Rutledge, '86; Bazzaz and Sultan, '87; Moussou and Roff, '87; Gillespie and Turelli, '89) Thus, the most evolutionarily informative ecological development studies will examine the genotype-specific fitness effects of variation in key environmental factors, based on measured patterns of spatial and temporal variability in natural populations.

Developmental plasticity as a mode of adaptation

Perhaps the most fascinating aspect of phenotypic response to environment is the adaptive nature of that response for a wide array of organisms, traits, and environmental challenges (reviewed by Travis, '94; Gotthard and Nylin, '95; Sultan, 2000; Gilbert, 2001; see Kingsolver and Huey, '98; Schmitt et al., '99 on adaptive interpretation of plasticity). For instance, depending on its developmental habitat the common sunfish *Lepomis gibbosus* will develop into either a littoral, mollusk-feeding form with a deep body and short pectoral fins, or an open-water planktivorous form with a more fusiform body and longer fins (Robinson et al., '96); such habitat and food-based polyphenisms are known in other fish species, in insects, and in marine invertebrates. Insects may also express plasticity for wing pigmentation in response to seasonal variation in temperature (Nijhout, '91; Kingsolver and Huey, '98 and references). The presence of predators induces adaptive morphological defenses in a number of invertebrate species (Harvell, '90 and references) as well as in larval anurans (Relyea, 2002 and references) and in at least one species of flowering plant (Young, '87). Plants also may respond adaptively to abiotic stresses, through developmental adjustments in proportional tissue allocation and organ size and structure that maximize the availability of limiting resources (Sultan, 2003, and references therein). Since plant morphogenesis is generally indeterminate, plants

also exhibit dynamic plasticity in response to fluctuating environmental conditions, adjusting spatial root deployment so as to track soil resources, and elongating specific stem internodes depending on the changing above-ground competitive environment (Weinig, 2000; Sultan, 2003).

The environmental cues for adaptive plastic responses may be direct and immediate, or indirect and predictive: for example, in several amphibian species increased population or prey density, sensed by swimming contact or ingestion, serves as a proximate indication of pond drying and cues rapid metamorphosis (Pfennig, '92; Denver et al., '98). Depending on the trait, environmental cues may be effective only at specific developmental periods (Chakir et al., 2002), and they may be surprisingly subtle, as in the case of a whitefly species that develops into ecologically distinct phenotypes depending on the leaf hairiness of its host plant during the crawling stage of its larval development (Guershun, 2001). The accuracy and timing of the organism's perception and developmental response to these environmental cues are ecologically critical, and may influence the types of environmental factor and the specific phenotypic traits predicted to evolve in plastic systems (Kingsolver and Huey, '98; Sultan and Spencer, 2002 and references therein). Cue perception and response systems themselves may evolve adaptively to reflect local differences in environmental predictability (Moran, '92).

One particularly intriguing aspect of individual adaptive response is cross-generational plasticity: changes in offspring phenotype that are adaptive to environmental stresses experienced by the parent organism. In cases where these stresses are likely to be constant across generations, for instance in organisms with limited dispersal, this constitutes a remarkable form of non-genetically inherited adaptation (Mousseau and Fox, '98). Agrawal et al. ('99) showed cross-generational developmental plasticity in both animals and plants: adult *Daphnia* exposed to a predatory dipteran's chemical signal produced offspring with a defensive "helmet" morphology, even when they themselves developed in a predator-free environment. Adult *Raphanus* plants predated by *Pieris* larvae produced offspring with increased defensive trichome density as well as higher concentrations of defensive secondary chemicals.

With the publication of these and many other intriguing case studies over the past decade and a half, individual plasticity for ecologically impor-

tant traits has increasingly been recognized as a major source of adaptive phenotypic diversity. This recognition dramatically alters our understanding of organismic diversity by adding an individual, developmental mode of adaptation to the neo-Darwinian process of selective diversification. Indeed, adaptive differences among populations assumed to reflect evolutionary change under local selection pressures may be shown by appropriate ecological-development studies to result from developmental plasticity (e.g., Losos et al., 2000).

Clearly, the potential for this within-genotype adaptive diversity has important implications for our understanding of the evolutionary process and its possible outcomes within and among populations. These outcomes can be more complex and indeed more interesting than a simple selective sorting of narrowly adapted genotypes into particular environments. The selective enhancement of plasticity itself—the ability to accommodate various environmental circumstances—poses a distinct, alternative evolutionary endpoint to the classic view of continual selective diversification. Depending on environmental heterogeneity, patterns of genotype by environment interaction, migration rates, and aspects of plastic response systems such as environmental predictability and perception, developmental lag time, and possible underlying costs, selection may favor either specialized, canalized genotypes or plastic "generalists" within as well as across populations (relevant models reviewed by Scheiner, '93 and Schlichting and Pigliucci, '98; see also Tufto, 2000; Sultan and Spencer, 2002). Consequently, these organismic and external aspects of environmental response systems can powerfully influence selective outcomes and patterns of adaptive population (and ultimately species) diversification. Individual plasticity may also contribute to evolutionary diversification by allowing colonization of a novel or extreme habitat so as to permit subsequent selective adaptation to that habitat (Schmalhausen, '49; West-Eberhard, '89; Losos et al., 2000). Thus, knowing the adaptive repertoires of genetic individuals in various species will profoundly inform our interpretation of existing biological diversity as well as our predictive understanding of adaptive evolution.

Conclusions and future directions

Evolutionary development addresses major phenotypic innovations and constraints; ecological

development completes this synthesis by illuminating the causes and consequences of phenotypic variation at the individual level. Together, these newly emerging disciplines promise to fully integrate development and evolution, and to restore to these processes the rich and complex “real world” contexts in which they occur.

Several areas in ecological development may prove particularly valuable for pursuing these goals. One such area is the genetic basis of plastic response, which remains largely unknown (Scheiner, '93; Nager et al., 2000). In general, mechanisms of environmental perception and developmental response in diverse organisms remain to be elucidated (but see Denver et al., '98 for a well-studied exception). Mechanisms for cross-generational environmental effects offer a particularly fascinating and largely unexplored research area. At the comparative level, differences in patterns of individual plasticity among species comprise a central issue. At present little is known about such differences, which may influence relative ecological breadth and invasiveness, as well as comparative prospects for persisting in the face of rapid habitat and atmospheric change (Travis, '94; Sultan, 2000). Finally, an ecological development approach may provide new insights into the nature and evolutionary consequences of species interactions, which often involve various aspects of developmental as well as biochemical and behavioral plasticity (Agrawal, 2001).

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