

Developmental capacitance, genetic accommodation, and adaptive evolution

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SUMMARY The concept of genetic accommodation remains controversial, in part because it remains unclear whether evolution by genetic accommodation forces a revolution, or merely a shift in emphasis, in our understanding of how evolution produces adaptive new traits. Here I outline a perspective that largely favors the latter view. I argue that evolution by genetic accommodation can easily be integrated into traditional evolutionary concepts. At the same time, evolution by genetic accommodation invites novel empirical and theoretical approaches that may allow biologists to push the boundaries of our current understanding of the process of evolution and to solve some long-standing controversies. Specifically, I discuss the role of

developmental mechanisms as natural, and likely ubiquitous, capacitors of cryptic genetic variation, and the role of environmental perturbations as mechanisms by which such variation can become visible to selection on an individual to population-wide scale. I argue that in combination, developmental capacitance and large-scale environmental perturbations have the potential to facilitate rapid evolution including the origin of novel adaptive features while circumventing otherwise powerful genetic and population-biological constraints on adaptive evolution. I end by highlighting several promising avenues for future empirical research to explore the mechanisms and significance of evolution by genetic accommodation.

GENETIC ACCOMMODATION

Genetic accommodation has been proposed as a mechanism whereby environmentally induced phenotypic changes that provide a selective advantage are genetically stabilized, or accommodated, through the subsequent selection of genetic modifiers available in a population (West-Eberhard 2003, 2005a, b). As a consequence, genetic accommodation may result in altered sensitivity to the originally inducing environment, including genetic assimilation via complete loss of sensitivity in extreme cases (Waddington 1953; Gibson and Hogness 1996; Pigliucci and Murren 2003). Genetic accommodation is thus thought to provide a mechanism by which interactions between environment and development become able to generate adaptive phenotypes, accompanied by selection for genetic modifiers, which ultimately permit these new phenotypes to become heritable across generations. Ever since its introduction, the concept of evolution by genetic accommodation has generated debate, to say the least, in part because it has remained unclear whether evolution by genetic accommodation forces a revolution of how we view and understand the process of evolution, or merely a shift in emphasis (de Jong and Crozier 2003; Levinton 2003; Pigliucci and Murren 2003; Braendle and Flatt 2006; Pigliucci et al. 2006). In this perspective article I dissect the concept of evo-

lution by genetic accommodation and discuss the minimum four ingredients necessary, as I see them, for evolution by genetic accommodation to occur. I then argue that none of these ingredients represents a novel component in biologists' thinking about the process of evolution. Nevertheless, I suggest that evolution by genetic accommodation forces a shift in emphasis away from genes and mutations on one side and environmental sensitivity on the other, toward a deeper appreciation of how developmental mechanisms link genetic and environmental variation, ultimately providing organisms with the capacity to evolve, at least some of the time, via genetic accommodation.

ENVIRONMENTAL SENSITIVITY, CANALIZATION, AND DEVELOPMENTAL CAPACITANCE

The nature of developmental processes provides three of the four basic ingredients required for the process of evolution by genetic accommodation: environmental sensitivity, canalization, and capacitance (Box 1). Below I argue that each of them is well recognized and understood, at least in part, by biologists, but that their significance for evolution, especially in combination, is generally underappreciated (but see Wilkins 2003). The first ingredient is environmental sensitivity, or

Box 1 Definitions of terms used in this article*Plasticity/environmental sensitivity*

Plasticity or environmental sensitivity have been defined in a variety of ways over the years. On a most fundamental level (and as used in this article) both terms simply refer to an organisms' ability to respond to changes in the environment via changes in the expression of a phenotype. These responses may be adaptive, neutral, or nonadaptive, continuous or discrete, and may occur at any level of biological organization including behavior, physiology, gene expression, morphology, etc.

G × E

Different genotypes may respond differently to the same environmental change. *G × E* stands for *genotype × environment interaction* and is a quantitative genetic term referring to the fraction of the total phenotypic diversity in a population that can be attributed to differences between genotypes in their ability to respond to the same environmental change. From a quantitative genetic perspective, existence of significant *G × E* in a population is one of the prerequisites for the evolution of adaptive phenotypic plasticity.

Canalization

Canalization can be defined as a measure of the ability of a genotype, organism, or developmental process to produce the same phenotype in the face of genetic and environmental perturbations. The more canalized a developmental process, the more robust it is to perturbations through variation in genetic and environmental inputs.

Epistatic variation

The effect of genes on a phenotype often depend on which genes are present at other loci, preventing genes from having strictly additive effects on a given phenotype. Epistatic variation refers to the fraction of the total phenotypic variation in a population that arises from all possible interactions between gene products that deviate from strict additivity.

Developmental capacitance

Developmental capacitance refers to the ability of developmental processes to act as capacitors of genetic variation and shielding such variation from being visible to selection. For example, highly canalized developmental pathways are likely to allow a large number of allelic combinations to yield the same phenotype without fitness differences.

Cryptic genetic variation

Individuals within a population can be genetically different from each other without leaving a signature of this difference in their phenotypes and reproductive success. Such cryptic, or hidden, genetic variation is invisible to selection, but may be exposed under certain circumstances. The accumulation of cryptic genetic variation may be facilitated by strong epistatic interactions among loci or a high degree of canalization of developmental processes.

plasticity, of development. The ability to respond to environmental conditions by altering some component of development is not something organisms had to evolve, instead it came for free as a function of the biochemical and biophysical context within which the development of organisms takes place. Environmental sensitivity is therefore the ancestral character state of any developmental process (Nijhout 2003). Environmental influences on development, including phenotypic outputs of development, are nothing new to evolutionary biologists. In quantitative genetics terms such influences are subsumed as the environmental variance component, or V_E , or in laypersons' terms as environmental noise. What organisms did have to evolve was the ability to respond reliably in certain aspects of development to certain changes in environmental conditions. This was made possible through what we now recognize as ubiquitous heritable variation in how different genotypes respond to the same environmental change, or in quantitative genetic terms the existence of widespread and significant *G × E* interactions in natural populations. Such heritable variation in environmental sensitivity facilitated the evolution of what we generally refer to as adaptive phenotypic plasticity (Schlichting and Pigliucci 1998). Heritable variation in environmental sensitivity also

facilitated the evolution of another phenomenon that, I would argue, most biologists do not consider when discussing plasticity and environmental sensitivity, namely canalization. Canalization refers to a given developmental mechanism's ability to translate a range of environmental and genetic inputs into a single, nonvariable, "canalized" phenotypic output (Scharloo 1991). In contrast to environmental sensitivity, canalized development is a derived condition of developmental mechanisms, and I argue that it represents the second major ingredient required for the process of evolution by genetic accommodation, as outlined next.

Canalized development permits organisms to produce the same phenotypic output in the face of environmental and genetic variation. It is a phenomenon well known to developmental biologists as well as evolutionary biologists and geneticists (Wilkins 1997; de Visser et al. 2003; Flatt 2005). For example, canalization is manifest in the absence of significant *G × E* interaction terms, but also low penetrance in mutant phenotype screens or experimental knock-down of transcript levels via interfering RNAs. Importantly, canalization is often more than "insensitivity" or lack of ability to respond to external changes, in that it commonly reflects a developmental machinery capable of buffering and compensating for envi-

ronmental and genetic perturbations. However, no developmental system, no matter how robust, is perfectly canalized. This was particularly well illustrated in a simulation study by von Dassow et al. (2000) who studied the dynamics and robustness of the arthropod segmentation network, one of the best understood developmental regulatory networks. The main observations were that the network was remarkably robust against perturbations and capable of absorbing orders of magnitude of changes in parameter values without altering the final phenotypic output. Despite this tremendous canalization, new phenotypes eventually emerged as parameter values exceeded certain thresholds. Canalization therefore allows organisms to buffer aspects of their development to environmental and genetic variation until confronted with above-threshold perturbations. Canalization's ability to absorb environmental changes directly counteracts the ancestral environmental sensitivity of all developmental mechanisms discussed above. However, canalization's ability to absorb variation in genetic inputs adds a new dimension, and one that is crucial to the process of evolution by genetic accommodation, because it permits genetic variation to arise and accumulate in natural populations while hiding it from selection.

Hidden, or cryptic, genetic variation is once again nothing new to evolutionary biologists and population geneticists, who for decades have been accustomed to dealing with a particular kind of cryptic genetic variation: epistatic variation. Epistatic variation is traditionally defined as the phenotypic variance component arising from nonadditive genetic interactions at two or more loci, that is, the observation that the phenotypic effect of a given allele for a certain locus depends on which allele(s) are present at other loci. A less formal way to look at epistatic variation is that it captures the fraction of the phenotypic variation in a population that arises from all possible interactions between gene products that deviate from strict additivity (Rice 2000). Epistatic variation is shielded from selection, but can be converted into additive genetic variation, for example, when a fraction of the epistatically interacting loci become fixed for certain alleles, as envisioned during founder flush speciation events (Meffert 2000; Regan et al. 2003). Alternatively, epistatic genetic variation may be converted into additive genetic variation, following changes in environmental conditions. Simply put, loci may interact with each other epistatically in one environment but not in others, thus altering their ability to contribute to a given population's response to selection (Gibson and Dworkin 2004). However, cryptic genetic variation as envisioned in the hypothesis of evolution by genetic accommodation (West-Eberhard 2003) is not limited to epistatic genetic variation as defined in quantitative genetic terms, though it may be a major component. Instead, cryptic genetic variation includes the sum total of all genetic variation made available to selection, following environment-mediated perturbations of developmental pathways.

For example, this definition of cryptic genetic variation would include the range of allelic combinations at various loci that due to the buffering or canalizing architecture of a given developmental pathway all yield the same phenotype until the buffering capacity of said developmental pathway becomes compromised by above-threshold environmental perturbations. An additional, yet somewhat different type of cryptic genetic variation may arise from loci which under regular environmental conditions simply do not contribute to a given phenotype, but suddenly do so once environmental perturbations alter the range of genetic inputs into the underlying developmental pathways. Variation at such loci, no matter how large, would be invisible to selection under regular environmental conditions but could fuel rapid selection responses following above-threshold environmental perturbations. Recent experimental and simulation studies leave no doubt that at least some, but more likely most, developmental processes are natural capacitors for cryptic genetic variation of one kind or another (Rutherford and Lindquist 1998; Queitsch et al. 2002; Cowen and Lindquist 2005; Dworkin 2005a, b; Nijhout et al. 2006; Suzuki and Nijhout 2006). Developmental capacitance for the origin, accumulation, and ultimately release of cryptic genetic variation then represents the third, and arguably, most crucial ingredient required for the process of evolution by genetic accommodation. It is presently unclear, though likely, that the degree to which developmental processes may be capable of accumulating hidden genetic variation may depend on a given developmental process' level of canalization. Similarly possible is that the degree to which environmental perturbations permit cryptic genetic variation to become visible to selection may depend on whether or not such perturbations exceed the buffering capacity of canalized development. Apart from these details, which await empirical examination, one thing that appears to be certain, is that exactly what kind of new phenotypic and previously hidden genetic variation may be made available by this process should be *random* with respect to the initiating environmental perturbation. There is no mechanism available that would allow development to preferentially generate phenotypes that will subsequently prove adaptive and selectable, a point that deserves emphasis because it divorces evolution by genetic accommodation from any Lamarckian overtones. Just like the vast majority of mutations are prone to be either neutral or detrimental, the vast majority of environment-induced new phenotypes will probably be nonadaptive or nonselectable. However, if *by chance* a certain environmental perturbation alters development in a way that it happens to produce an adaptive phenotype, and if *by chance* the same environmental perturbation results in the release of previously cryptic genetic variation, selection on which could stabilize the newly adaptive phenotype, then we have the principal ingredients in place for evolution by genetic accommodation to occur and to allow environmentally induced phenotypic vari-

ation to become heritable. It is one of the challenges to the current generation of evolutionary biologists to determine how frequently these two situations indeed co-occur. Below I argue that even though this scenario may appear improbable at first, it may become far more feasible if we consider the spatial and temporal scales of natural environmental changes, which combined provide the forth major ingredient for the process of evolution by genetic accommodation.

GEOGRAPHIC AND TEMPORAL SCALE OF ENVIRONMENTAL PERTURBATIONS

Whereas mutations by necessity originate in individuals and must overcome the burden of rarity in order to become a property of a population or species, environmental perturbations can operate immediately on the level of populations or even communities. By operating on a large number of individuals at once, environmental perturbations have the capacity to generate phenotypic changes in a large number of individuals at once, as well as to make a large amount of previously cryptic genetic variation available to selection (West-Eberhard 2004). As emphasized above, whether induced phenotypes ultimately prove adaptive and selectable is a chance event, but by virtue of operating on the level of populations rather than individuals, the probability of such an event to occur within a certain window of time is much increased. Furthermore, as environmental perturbations persist over generations, environmental induction of adaptive new phenotypes and the appearance of genetic modifiers suitable for their subsequent accommodation no longer have to co-occur in the same individual or even generation but can be temporally dissociated. Lastly, if environment-induced phenotypes happen to be selectively favorable *and* suitable genetic modifiers happen to exist in a population, such modifiers may well surface in many more than just a single individual. As the proportion of individuals in a population increases in which the same environmental perturbation induces adaptive new phenotypes as well as the appearance of genetic modifiers suitable for their subsequent accommodation, the chances of new phenotypic variants to persist and even spread within a population are much increased.

NEITHER GENES NOR ENVIRONMENT LEAD (BUT DEVELOPMENT MEDIATES)

To many evolutionary biologists, and certainly to many lay people, a traditional view of evolution is one that starts with random mutations generating variation in fitness, which natural selection can then act on. Environmental conditions are important here because they contribute to the nature and direction of selection but are denied a creative force in the

evolutionary process. In response to this “mutations first” view of the evolutionary process, West-Eberhard (2003) characterized genetic accommodation as a process by which the environment leads, whereas genes follow. I argue that genetic accommodation assigns a critical role to environmental perturbations, but the assignment of a leadership role obscures the mechanisms that mediate evolution by genetic accommodation. For genetic accommodation to work, cryptic genetic variation must be present in a population, so clearly some kind of *a priori* genetic contribution is fundamental to the process of genetic accommodation. Yet at the same time genetic accommodation will not occur unless environmental perturbations decrypt genetic variants. One could argue of course that clearly only those phenotypes will be genetically accommodated for which there happen to be decryptable genetic variants that permit accommodation through subsequent generations, giving genetic variation a kind of lead in the process. But because not all environmental changes are likely to lead to the same release of cryptic genetic variation, one could also argue that only those phenotypes will be genetically accommodated where the “right” environmental perturbations generate a new adaptive phenotype alongside a corresponding release of genetic variation. Genetic accommodation thus clearly requires both cryptic variation and a variable environment, neither of which can be designated a leading role in the process. The second major reason why a “genes first” versus “environment leads, genes follow” discussion is ultimately unproductive is because it obscures the larger issue that evolution by genetic accommodation is first and foremost an emergent property of the way developmental processes build organisms. The intrinsic ability of developmental processes to (i) produce different phenotypes in response to changes in some environmental conditions while producing the same, canalized phenotype in response to changes in others, combined with (ii) development’s ability to hide genetic variation until freed by above-threshold environmental perturbations, put developmental mechanisms and their properties at the center stage of evolution by genetic accommodation. Not that development leads the process either, but it more than anything determines when, where, and to what degree it may be possible. Thus, to learn more about the process of evolution by genetic accommodation, developmental processes and how they link genetic and environmental variation in space and time deserve to become the conceptual foci of future research.

GENETIC ACCOMMODATION IN ACTION—WHAT TO LOOK FOR AND WHERE?

Evolution by genetic accommodation has already been demonstrated convincingly in several elegant laboratory studies in a variety of organisms (Rutherford and Lindquist 1998;

Queitsch et al. 2002; Cowen and Lindquist 2005; Suzuki and Nijhout 2006). However, studying genetic accommodation in the field and in natural populations is a far more challenging proposition, for the following reasons. Evolution by genetic accommodation differs from a traditional view of the evolutionary process merely in that it begins with environmental perturbations, which through their effects on developmental processes alter the amount and nature of genetic variation visible to selection. There are no new mutations required, only new phenotypes, some of which, however, must be paralleled by the environment-induced surfacing of genetic modifiers suitable for the subsequent accommodation of these new phenotypes should they be favored by selection. Evolution by genetic accommodation thus differs from traditional perspectives on adaptive evolution in that it ascribes specific roles to environmental perturbations, developmental processes, and the interactions between them, in making previously cryptic genetic variation available to selection. Traditional perspectives on adaptive evolution make no such statements but are of course perfectly compatible with them. Consequently, demonstrating that evolution by genetic accommodation has occurred requires a comparison of how development generates phenotypes before and after environmental perturbation, as well as a comparison of quantitative genetic properties such as the heritability of particular phenotypes before and after environmental perturbations allowed previously hidden genetic variation to surface. Once evolution by genetic accommodation has occurred, it is indistinguishable from a process driven by selection on standing genetic variation that required no special function of environment, development, hidden genetic variation, and the respective interactions between them. Distinguishing the latter from the former can be accomplished in laboratory settings, especially in the context of artificial selection experiments, where starting genetic composition of experimental populations and their developmental properties in the presence and absence of environmental perturbation can be controlled and measured, both before and after artificial selection in the presence and absence of perturbing environments has taken place. This is far more daunting in the field, but I would argue that several opportunities exist, today more than ever before, that promise the possibility to catch evolution by genetic accommodation in the act as well as in the wild. The first of two that I would like to highlight is global climate change and its dramatic effects on environmental conditions experienced by a wide range of organisms. Global climate change is, by definition, a global event, affecting individuals, populations, species, and communities (Hansen et al. 2006; Lensing and Wise 2006). Global climate change alters not only average temperatures, but with it a dramatic list of biotic and abiotic factors (e.g., rainfall, salinity, exposure, nutrient turnover, species ranges, spatial, and temporal availability of resources, etc.), and as a consequence is likely to have a profound effect on the physiology,

development, and life history of a wide range of organisms. Most importantly, for many organisms global climate change is likely to alter environmental conditions significantly within one to a few generations and is unfortunately likely to exert its effects for many generations to come. Global climate change thus supplies a major and lasting environmental perturbation of widespread ontogenetic significance and invites a comparison of developmental, quantitative genetic, and ecological properties of populations across generations as well as taxa that are experiencing these perturbations.

Similar arguments can be made for invasive species and the communities they invade. Biological invasions happen on an unprecedented scale and threaten to homogenize global biodiversity (Simberloff 1997; Low 1999; Carlton 2000; Hobbs 2000). At the same time biological invasions offer the opportunity to study rapid evolution in action in the context of at least seminatural experiments (e.g., Tsutsui et al. 2000; Moczek 2003; Siemann et al. 2006; Carroll 2007). Invasive species typically encounter biotic and/or abiotic environmental conditions very different from their native habitat. Source, age, and direction of invasions are often known, and invasions from the same source population often occur repeatedly into the same or different exotic environments. Repeat invasions in particular offer the unprecedented opportunity to contrast developmental plasticity and evolvability of native populations on one side and conspecific exotic populations of varying age on the other. As the frequency of, and opportunities for, biological invasions are only increasing, there should be no shortage of taxa that would qualify for such an approach.

Regardless of choice of taxa, documenting evolution by genetic accommodation in nature would still not be easy, but arguably possible. As discussed above, evolution by genetic accommodation makes explicit statements regarding the roles of environmental perturbations, developmental processes, and the release of previously hidden genetic variation. A proof of evolution by genetic accommodation in nature then becomes an exercise in documenting that each of these interactions have indeed occurred, that is, (i) a population was unable to evolve a certain phenotype until (ii) environmental perturbations induced such a phenotype (or at least precursor of it), which (iii) was in turn accompanied by the release of cryptic genetic variation, (iv) selection on which ultimately allowed this phenotype to become heritable over generations. In other words, it would require documenting the ontogenetic responses of populations to environmental perturbations by quantifying changes in the distribution of phenotypes of interest, accompanied by quantifying those same populations' ability to respond to selection on a particular phenotype of interest before, during, and after environmental perturbations have occurred. Which phenotypes to focus on would, as so often, be crucial for such a study, but I would argue that we know enough about the evolutionary ecology of many

organisms to make at least good guesses. In the context of global climate change, for example, rising temperatures are likely to affect growth dynamics of many poikilothermic organisms (Edmunds 2005; Yan et al. 2006). Many insects, for example, respond to increases in rearing temperature with accelerated development leading to a smaller final adult body size (Berrigan and Charnov 1994; Atkinson et al. 2006). At the same time, rising temperatures are likely to reduce dissolved oxygen levels across biota. Insects with gill-breathing aquatic larval stages may be particularly affected as their ability to grow and sustain themselves is often limited by dissolved oxygen levels (Nebeker et al. 1996; Buchwalter et al. 2003), hypothetically leading to selection for smaller body sizes and a larger gill surface-to-insect volume ratio. If correct, this may generate a situation in which rising temperatures will generate smaller sizes simply by altering developmental properties, in a direction that at the same time may happen to be favored by selection in at least some organisms. All that is needed to fuel an evolutionary change in body size via genetic accommodation is that rising temperatures, by altering development, facilitate the conversion of hidden genetic variation into variation that is visible to selection. An analysis of the developmental and quantitative genetic properties determining body size before, during, and after temperature has had an opportunity to alter population-wide developmental properties would provide most if not all of the data necessary to determine whether body size evolution, if occurring, was possibly mediated by genetic accommodation. Similar examples can of course be constructed for many other contexts, such as biological invasions. Here, a particular advantage lies in the fact that source populations are often known, and descendant native populations may provide acceptable proxies for the ancestral developmental and genetic properties of focal populations before invasion and possible evolution by genetic accommodation.

CONCLUSION

Evolution by genetic accommodation represents a valuable shift in emphasis to traditional evolutionary thinking by emphasizing environmental and developmental contributions to the origin of heritable variation. As discussed above, genetic accommodation can be integrated into existing concepts and frameworks familiar to evolutionary biologists. However, evolution by genetic accommodation forces a revision of how we think about how environmental and developmental properties mediate evolutionary change in general, how certain environmental changes may facilitate particularly rapid evolution, and how developmental properties such as degree of canalization guide or bias kind and magnitude of evolutionary change possible within a lineage. It will be up to the current generation of evolutionary biologists to devise the

kind of creative yet rigorous theoretical and experimental explorations necessary to document scope and significance of evolution by genetic accommodation in nature, but there is every reason to be confident that this stimulating concept will spawn a wave of exciting and insightful work in the future.

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