

EVOLUTIONARY CONSTRAINT AND ECOLOGICAL CONSEQUENCES

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One of the most important shifts in evolutionary biology in the past 50 years is an increased recognition of sluggish evolution and failures to adapt, which seem paradoxical in view of abundant genetic variation and many instances of rapid local adaptation. I review hypotheses of evolutionary constraint (or restraint), and suggest that although constraints on individual characters or character complexes may often reside in the structure or paucity of genetic variation, organism-wide stasis, as described by paleontologists, might better be explained by a hypothesis of ephemeral divergence, according to which the spatial or temporal divergence of populations is often short-lived because of interbreeding with nondivergent populations. Among the many consequences of acknowledging evolutionary constraints, community ecology is being transformed as it takes into account phylogenetic niche conservatism and the strong imprint of deep history.

KEY WORDS: Community ecology, ephemeral divergence, evolutionary constraint, genetic variation, genostasis, limits to adaptation, phylogenetic conservatism, stasis.

Since the centennial celebrations of *The Origin of Species* 50 years ago, evolutionary biology has experienced phenomenal growth and change. I do not think any of the changes, with the possible exception of a modified version of Kimura's neutral theory of molecular evolution, fit the much abused phrase "paradigm shift," if by that we mean Kuhn's (1962) revolutionary shift to an incommensurably different theory, occasioned by a crisis in confidence in the reigning theory. The neo-Darwinian (Charlesworth et al. 1982) or more properly the Synthetic (Mayr and Provine 1980) Theory has largely stood firm despite many proclamations of failure (e.g., Gould 1980; Ho and Saunders 1984). Natural selection, for example, remains the virtually undisputed explanation for adaptation. Nevertheless, contemporary evolutionary theory has clearly been enormously expanded. It also has been modestly revised, if only by shifts in emphasis and appreciation of the significance of previously acknowledged phenomena and processes whose importance had not been widely recognized.

Among the most salient such phenomena are those that imply limits on rates and directions of adaptive evolution. The postulated limiting factors are often referred to as constraints, although

this term has a variety of interpretations. "Constraints" often restrain evolution ("quantitative constraints" of Mezey and Houle 2005) rather than being absolute, and it is in this sense that I will usually intend "constraint" to be understood. Although I can make few, if any, new contributions to the subject, I aim in this review to develop several points. (1) Recognition of constraints (*sensu lato*) is one of the most profound and important shifts in the views of evolutionary biologists, comparable to acceptance of "non-Darwinian" neutral evolution. Continuing resistance attests to the significance of this shift, although its magnitude and implications are perhaps not fully appreciated. (2) A focus on limiting factors is both motivated by and draws our attention to paradoxical, seemingly contradictory observations, and so propels research in new directions. Indeed, we are led to confront an overwhelmingly important question that highlights the immaturity of our science: how can we predict whether a population (or species) will adapt or become extinct in the face of environmental change? (3) Different kinds of limiting factors may explain different phenomena. In particular, it may be useful to distinguish "character constraints" (on particular characters or character complexes) from

“systemic or organismal constraints” that may apply widely across the genome and phenotype. (4) This theme is a major meeting ground for the subdisciplines of evolutionary biology. Students of evolutionary history—paleontologists and systematists—have been the most insistent advocates of the importance of constraint, and consequently of history and contingency. The theme now engages the attention of theoretical and experimental evolutionary geneticists and it highlights the importance of understanding developmental and physiological mechanisms. It may find some of its resolution in ecology, and certainly has enormous ecological implications.

The Traditional View and Challenges to It

The central issue is the nature and sufficiency of genetic variation, and the consequent ability of a population to respond to selection on one or more characters. By the 1970s, the revelation of genetic variation in fitness and later in proteins, and especially the response of almost any trait or pairs of traits to artificial selection, had led to a widely held consensus that, as Lewontin (1974, p. 92) put it, “genetic variation relevant to all aspects of the organism’s development and physiology exists in natural populations,” for “[t]here appears to be no character—morphogenetic, behavioral, physiological or cytological—that cannot be selected in *Drosophila*.” Stebbins (1971) wrote in an elementary textbook that “mutations are rarely if ever the direct source of variation upon which evolutionary change is based. Instead, they replenish the supply of variation in the gene pool.” The textbook by Dobzhansky et al. (1977) asserted that “[t]he balance model of the genetic structure of populations has now become definitely established” (p. 35), and that “the pervasiveness of genetic variation in natural populations is evident from the success of artificial selection . . .” (p. 38). In the first edition of my own textbook (Futuyma 1979), I noted that “some characteristics, to be sure, do not respond greatly to artificial selection,” but I immediately brushed hesitation aside: “the ubiquity of genetic variation leads one to wonder whether its amount ever limits a population’s rate of evolution or its ability to adapt to environmental changes” (p. 209). Genetic variation has been viewed as sufficient not only for immediate adaptation to altered selection, but also for long-term evolution. The eminent quantitative geneticist Kenneth Mather (1955) wrote that “[i]n a long term sense the possibilities of response to selection are limited only by the possibilities of mutation,” but “given time, genes and gene combinations can arise to do anything. The nature of the selection itself then becomes decisive in determining the response.”

Many evolutionary geneticists have echoed the theme that adaptation is not limited by genetic variation. For example, “[T]he simplest possible evolutionary constraint, viz. lack of genetic vari-

ation, would appear not to be important” (Barker and Thomas 1987). Several authors have noted that rates of long-term evolution of morphological traits are far slower than is compatible with mutation and genetic drift, much less directional selection (e.g., Lynch 1990). Barton and Partridge (2000) infer that neither mutation rate nor genetic variation limits evolutionary rates: “Genetic variation and, more specifically, lack of mutations should not and, it seems, does not limit at least straightforward selection response.” The ubiquity of genetic variation is an important basis for rejecting challenges to adaptationism (e.g., Reeve and Sherman 1993).

The view that rates of adaptive evolution are limited more by natural selection than the availability of genetic variation is unquestionably based on abundant evidence. Exceptions to Lewontin’s generalizations about the ubiquity of genetic variation and responsiveness to artificial selection are rarely reported (although some of those exceptions are particularly interesting, as I will detail). Examples of rapid adaptive divergence among populations, especially in response to human alterations of environmental factors, are legion (Thompson 1998; Palumbi 2001; Carroll et al. 2007; Hendry et al. 2008), and even speciation can occur with an astonishing speed in some clades (Hendry et al. 2008). These rates are much greater than those seen in episodes of morphological change in fossil lineages that are rapid by geological standards (Gingerich 1983), rates that can be easily accommodated by models based on realistic mutation rates and (mostly stabilizing) selection (Charlesworth et al. 1982; Barton and Partridge 2000; Estes and Arnold 2007).

In this light, myriad observations, of many kinds, appear utterly paradoxical, for they suggest that there are substantial limits on the adaptability—the evolvability (Wagner and Altenberg 1996; Kirschner and Gerhart 1998)—of populations and species. A nonexhaustive list of paradoxical kinds of data might include the following.

First, the most extreme evidence of failure of adaptation is, obviously, extinction, the fate of the vast majority of species. It is also of extreme concern today because of anthropogenic environmental changes, and even the most optimistic evolutionary biologist surely expects untold numbers of species soon to become extinct, as some already have. Of course, it may be protested, this is to be expected, given the extreme rate of human-induced change; but if the many cases of rapid adaptation to anthropogenic alterations are evidence of the adequacy of genetic variation and natural selection, why should we not expect the great majority of populations and species to do likewise?

Second, limits on the geographical and habitat ranges of species remain an unresolved problem (Futuyma and Moreno 1988; Bridle and Vines 2006). In an important paper on “genostasis and the limits to evolution,” Anthony Bradshaw (1991), who pioneered the study of plants’ rapid adaptation to

metal-contaminated soils, asked how it could be that a species of tree may be abundant near the edge of a marginal habitat such as a salt marsh, raining millions of seeds into it over the course of centuries, yet fail to adapt. Limits to geographic and ecological ranges are generally explained by trade-offs, often in concert with gene flow—a subject to which I will return. It is also supposed that expansion is prevented by superior competing species. But some species have broad ranges or niches, so genetic change seems to have mitigated trade-offs in some but not all species. (Breadth of host range in herbivorous insects, for example, seems to have evolved almost equiprobably in both directions between specialist and generalist states [Nosil 2002; Winkler and Mitter 2008].) And almost every plant species that has expanded its geographic range, or has diverged in habitat use from its ancestors, has done so in a fully vegetated landscape, so interspecific competition is not necessarily an insurmountable obstacle.

Third, most notably in his book *Wonderful Life* (1989), Gould emphasized historical accident or contingency. Pace skeptics (e.g., Conway Morris 2003), Gould's argument had been advanced earlier and repeatedly by leaders of the evolutionary synthesis, such as Simpson (1964) and Mayr (1988), who, in the context of arguing the extreme improbability of detecting intelligent life elsewhere in the universe, emphasized that “even slight changes in earlier parts of the history [of evolution] would have profound cumulative effects of all descendant organisms” (Simpson) and that “if evolutionists have learned anything . . . it is that the origin of new taxa is largely a chance event” (Mayr). The emergence of a lineage with human faculties was the one-off event at issue, but we know of thousands of one-off, or at most rarely paralleled, adaptations: the feather, the prehensile nose (of elephants), the neural crest (of vertebrates), the tracheid (of tracheophytes). The prevalence of convergent versus unique evolutionary changes may depend on the level of detail or of functional similarity specified, but the synapomorphies of higher taxa provide many instances of rare or unique events.

Fourth, as a consequence, there exist many seeming lacunae in the economy of nature, what I would controversially consider “empty niches,” implied by geographic and temporal imbalances in the distribution of adaptive forms. The “unbalanced” biota of islands—even of large, ancient islands such as New Zealand (Gibbs 2006)—is only an extreme case of a more general condition. Is there really no ecological space in the Atlantic for sea snakes, which are limited to the Indo-Pacific region? The canopy in wet forests of the Old World is thick with epiphytic ferns and orchids, but only in the New World is it festooned with water-holding plants (bromeliads) that provide distinct ecological opportunities for animals. Ecological communities with different evolutionary histories have far less convergent structure than ecologists once optimistically expected (Schluter and Ricklefs 1993). Paleontology concurs. A bivalve-drilling gastropod lineage evolved in the

Triassic, but became extinct at the period's end, not to be replaced for the next 120 million years, when modern oyster drills evolved (Fürsich and Jablonski 1984). Predators certainly ate bivalves in the meantime, but we can hardly suppose that they vacated “ecological space” only when the modern lineage evolved its drilling habit. Much of the history of increased biotic diversity has been explained by increasing occupancy of “ecological space,” associated with morphological or physiological innovations (Bambach 1985; Signor 1990), and there is no reason to think that this history has come to an end. Although alleviation of incumbent competition certainly has enabled ecological shifts in many lineages, there is no guarantee that lineages will evolve to take advantage of apparent ecological opportunity.

Fifth, an increasingly appreciated phenomenon that requires explanation is “phylogenetic niche conservatism” (Wiens and Graham 2005), an ecological parallel to the equally puzzling conservative morphological characters that are often the synapomorphies of higher taxa. Niche conservatism is prevalent among both plants (Ricklefs and Latham 1992; Ackerly 2003) and animals (Peterson et al. 1999; Wiens and Donoghue 2004), among which herbivorous insects provide many salient examples, with lineages having retained associations with particular plant families since the early Cenozoic or even the mid-Mesozoic (Mitter et al. 1991; Winkler and Mitter 2008). In morphology, I find it astonishing that the large fly family Sepsidae is distinguished from all other acalypterate families by the possession of bristles on the posterior margin of the metathoracic spiracle, and that the closely related families Calliphoridae (blowflies) and Sarcophagidae (flesh flies) can be distinguished by whether the hindmost posthumeral bristle is located laterad or mesad of the presutural bristle (Triplehorn and Johnson 2005). Dobzhansky (1956) likewise marveled that all the 600 species of *Drosophila* of which he knew possess three orbital bristles, of which the anterior curves forward and the others backward. That the Drosophilidae, and indeed the 65 families of acalypterate flies, vary so little in details of wing shape and venation impresses some evolutionary geneticists even today (Hansen and Houle 2004).

Finally, of course, is the “stasis” in the fossil record that Eldredge and Gould (1972) and Stanley (1979) made famous, and which has been corroborated by many studies (e.g., Stanley and Yang 1987; Goldman 1995; Jackson and Cheetham 1999; Hunt 2007a). Morphologically delimited species persist without appreciable change for millions of years. What is noteworthy, and perhaps insufficiently emphasized, is that the stasis is not limited to specific characters, but marks all the detectable morphological features, that is, is organism-wide. Taxonomists often distinguish species of both living and fossilized organisms by very slight morphological differences, as long as they are consistent (e.g., Jackson and Cheetham 1999); so to say that a named form persists without changing into another named taxon is tantamount to saying that

no morphological feature has changed over the interval. In the vast literature on stasis, explanations range from developmental constraint (Eldredge and Gould 1972) to (most commonly) stabilizing selection (e.g., Charlesworth et al. 1982) to the effects of population structure (Eldredge et al. 2005).

The possible limiting factors and constraints on evolution are many, and it is quite possible that the most common explanations will prove to vary not only among characters and taxa, but also among the several phenomena I have described. I suggest that explanations of single-character stasis within populations or species may need to be amplified to explain phylogenetic conservatism among species in a clade, and that the most likely explanations of organism-wide stasis may be altogether different.

I will begin by reviewing theoretical considerations of possible limits on selectable genetic variation, and then proceed to evidence. I will assume that environmental sources of directional selection exist, and that the problem is to explain what might limit a response to selection. My treatment overlaps the insightful reviews by Hansen and Houle (2004), Blows and Hoffmann (2005), and Walsh and Blows (2009).

What Might Limit Response to Selection?

To describe adequately the theoretical literature on genetic constraints is beyond both available space and my abilities, so I will enumerate them with relatively little comment or explanation.

First, the “character” does not exist except in our imagination. Gould and Lewontin (1979) cautioned against “reifying” characters that might not correspond to the underlying biology, citing the human chin as a (disputed) case in point. Most phenotypic traits are, very largely, “black boxes” in terms of their underlying components or their developmental or biochemical pathways. Hence, the trait we think we are measuring might be most meaningfully described as a set of distinct traits, or it might not even exist in a meaningful way. *Drosophila melanogaster* has four precisely situated bristles on the scutellum, which some authors have treated as a single canalized character controlled by an underlying, continuously variable “morphogen.” Yet several lines of evidence showed that the anterior and posterior pairs, and perhaps the four individual bristles, act as separately controlled characters (Scharloo 1991). I might find no variation in a feeding response of a host-specialized insect to an alien plant (Futuyma et al. 1995), but this would hardly be surprising if I were to learn that the insect’s behavior is so dependent on a receptor tuned to a specific stimulatory compound that the plant is not detected as a potential food item. “Feeding response” might be no more meaningful a character in this case than “tooth number” is in a bird. Haldane (1932, p. 110) wrote that “a selector of sufficient knowledge and power,” working on the human species, “could

not produce a race of angels. For the moral character or for the wings he would have to await or produce suitable mutations.” Alas, humans, like all tetrapods, lack a developmental pathway for scapular wings.

It is possible that many “failures” to adapt are ascribable to “lack of character.” We know that unused characters are lost in evolution, and (despite increasing reports of the demise of Dollo’s law) that the developmental or molecular foundations may become irretrievably lost as some underlying genes become pseudogenes. If a pathway such as photosynthesis in a parasitic plant, or a protein such as hemoglobin in some notothenioid icefish can be lost, it can also not have arisen in the first place.

Second, suitable mutations are rare, and the rate of evolution is limited by the rate at which they arise. This might be the case for several reasons. (A) Some characters may be based on so few genes that they are a small “target” for mutation (Houle 1998); likewise, advantageous mutations in a gene might be limited to those that alter only a few of the protein’s amino acids (Wichman et al. 2000). For many traits, it appears that variation within and among populations is based on loci with an exponential distribution of allelic effects, hence fewer effective loci than in the traditional “infinitesimal” polygenic model (Orr 2005). (B) The character may be a threshold trait, so that only mutations of large effect on the hypothetical underlying character are phenotypically expressed. (C) It is generally supposed that more potentially adaptive genetic variation may be stored in a population if it is maintained by balancing selection than by mutation–selection balance. Under the latter model, the amount of variation that is potentially “usable” by selection will be less if most mutations that affect a trait are deleterious under many or all environmental conditions than if their disadvantage is highly context-specific (Houle et al. 1996; Hansen and Houle 2004). Positive genetic correlations in the fitness of variant phenotypes across environments may signal that much of the underlying genetic variation is not likely to be the stuff of new adaptations. (e.g., fitness components of herbivorous insects and parasitic plants are often positively genetically correlated across different plant species, whether these are normal hosts of the insect or not [e.g., Ueno et al. 1999; Ahonen et al. 2006; Futuyma 2008; Vorburger and Ramsauer 2008].) (D) Similarly, under some forms of epistasis, a mutation may be potentially advantageous only if placed on certain genetic backgrounds, and be “useless” except in the company of specific alleles at one or more other loci (e.g., Blount et al. 2008). Such epistasis underlies Wright’s (1931 et seq.) models of multi-peaked adaptive landscapes, Dobzhansky’s (1955) “coadapted gene pools,” Mayr’s (1963) “unity of the genotype,” and Lewontin’s (1974, p. 318) assertion that “context and interaction are of the essence.” (E) Traditional models of quantitative (i.e., most phenotypic) traits assume that variation is based on loci that are not only numerous but substitutable, so that a given phenotypic deviation can

be achieved by many combinations of alleles at various loci. If, instead, the loci are not substitutable—if each has a distinct identity and plays a different developmental role—then advantageous new phenotypes may be based on a smaller number of possible allele combinations, and are correspondingly less likely. This is clearly related to the issue of complexity, treated below.

Third, a “genetic correlation” between a directionally selected focal character and a character subject to antagonistic selection is universally acknowledged to slow down or possibly prevent response to selection. Extensions of this principle are a major topic of current theoretical research, and are becoming perhaps the most popular explanation for constrained evolution.

Hansen and Houle (2004, 2008) define the conditional evolvability of a trait y as its evolvability when constraining correlated characters are not allowed to change. (Here, “evolvability” is the additive genetic variance, V_A , scaled by the squared character mean. Wagner and Altenberg [1996] use “evolvability” to mean the genome’s ability to produce adaptive variants, whether they are actually present in a population or not.) As Dickerson (1955) first pointed out, character y may be unable to respond to selection if it is correlated with multiple other characters, even if each pairwise genetic correlation is less than 1.0. As Bürger (1986), Blows and Hoffmann (2005), Kirkpatrick (2009), and others have emphasized, pleiotropic correlations among multiple characters may constrain additive genetic variance to few axes in the multivariate character space, effectively reducing the dimensionality of genetic variation; individual characters, although variable, may not have free V_A , and may not respond to selection. For example, much or most of the V_A may be along a single principal component, often referred to as $g_{\max}$, calculated from the matrix of genetic variances and covariances of the characters ($\mathbf{G}$). Evolution in certain multivariate directions will be absolutely constrained if $\mathbf{G}$ has any zero eigenvalues (Gomulkiewicz and Houle 2009). Abundant pleiotropy not only may limit the response to selection; it also may constrain the evolution of the $\mathbf{G}$ matrix itself, lending it long-term stability that is manifested as similarity among species in a clade (Jones et al. 2003). On an “intermediate” time scale of perhaps hundreds or thousands of generations, $\mathbf{G}$ is shaped by both selection and by $\mathbf{M}$, the matrix of variances and covariances generated by mutation, which itself might be molded by selection over very long time scales (Draghi and Wagner 2007; Jones et al. 2007; Arnold et al. 2008). Thus, knowledge of mutational matrices $\mathbf{M}$ and of the consistency of $\mathbf{G}$ among species will cast a bright light on the evolvability of traits.

It is important to recognize, as did Schmalhausen (1986, first published in 1949), Wright (1931), Mayr (1963), and many other forbears, that selection stems not only from ecological factors extrinsic to the organism, but also from intrinsic factors, for the first test of an allele’s fitness is its impact on viability or reproduc-

tion via its developmental or physiological effects. Some authors, such as Schwenk and Wagner (2004), think that “internal selection” may be the most common basis of pleiotropic effects on fitness, and of genetic and phenotypic stability, and suggest that the term “constraint” be restricted to intrinsic fitness effects of deleterious genotypes.

Fourth, insufficient genetic correlation among traits might sometimes be as constraining as too much genetic correlation. In some circumstances, genetic variation in many dimensions (many independent characters) may reduce the response to directional selection along one axis in phenotype space, because stabilizing selection on the other characters accounts for most of the genetic load—it “uses up” the genetic deaths (or the reduced reproductive output) that are inherent in selection (Bürger 1986; Wagner 1988). Along the same line, adaptation may be slow if it requires coupled change in multiple, genetically independent but perhaps functionally interdependent characters. In that case, the frequency of superior genotypes is reduced, the greater the number of traits—and the response to multivariate selection is increasingly opposed by recombination, which breaks apart advantageous trait combinations. (This is the traditional objection to “phase 3” of Wright’s [1931] shifting balance theory, in which superior gene combinations are supposed to spread to other demes and pull them to the same high adaptive peak [Crow et al. 1990].) This problem of complexity may be reduced by genetic correlations among characters (e.g., modularity, Wagner and Altenberg 1996; Barton and Partridge 2000). Whether genetic correlation would facilitate adaptation or not depends on the degree of alignment between vectors of character variation and ridges of the adaptive landscape. (Such alignment could be fortuitous, or it could be a consequence of past selection if there has been a long history of correlational selection along the same vector, as in functional allometric relationships among some characters [Arnold et al. 2008].)

Closely related to this cost of complexity is the dimensionality of selection, the number of environmental variables that may differ when a population experiences a change of environment. It is simplistic to suppose, for example, that an increase in average environmental temperature would select only for higher thermal tolerance. Depending on the biology of the organism, it may also select for change in water balance, in the phenology of multiple life-history traits, and in perhaps many interactions with other species. The consequence could be selection on many genetically independent traits.

Evidence that Genetic Variation Can Limit Evolution

As I noted at the outset, there is no question that standing genetic variation in many traits enables a rapid response to selection. The

question is whether any of the genetic constraints described by contemporary theory have nevertheless been important, and could explain the failures of adaptation that cry out for explanation. The evidence for the several kinds of genetic constraints is limited and in some cases merely suggestive at this point, but the literature is growing rapidly.

GENETIC VARIATION SLIGHT OR UNDETECTABLE

In the prescient and inspiring essay to which I have already referred, A. D. Bradshaw (1991) argued that “evolutionary failure is commonplace,” and that “there are limits to evolution, for which the controlling agent is the supply of variation.” He noted that wherever rapid adaptation has been observed in some species, such as the evolution of herbicide or insecticide resistance, many other equally exposed species have failed to adapt. Likewise, although a few plant species have adapted to metal-contaminated soil, the floras in such sites remain extremely depauperate, and much ground typically remains bare. Moreover, genetic variation for copper tolerance could be found in “normal” populations of all of the eight sampled species that have formed copper-tolerant populations, but in none of seven species that have not. (Macnair 1997 reports similar results.) Plant breeders, Bradshaw noted, have sometimes succeeded in obtaining desired traits, such as disease resistance, by selection within the population of interest, but very often have found the required genetic variation only in other populations of the crop, or in related (crossable) species. He remarked, “that the necessary gene or genes may not be present within a species is, of course, the fundamental justification for the modern genetic engineering industry.”

In an effort to determine if genetic constraints or biases might cast light on the pattern of phylogenetic divergence and conservatism in the host plant associations of specialized herbivorous insects, my laboratory screened four species of *Ophraella* beetles (Chrysomelidae) for quantitative genetic variation in larval and adult feeding responses to, and capacity to survive on, the host plants of their congeners. A phylogeny based on mitochondrial DNA sequences indicated that shifts among plant genera within tribes of Asteraceae have been more frequent than between tribes (Funk et al. 1995). Evidence of genetic variation, liberally taken to include variance among dams and not just sires in a half-sibling design, was detected in only 21 of 39 tests of feeding responses and in only two of 16 tests of larval survival; and the presence versus apparent lack of variation was modestly but significantly correlated with the propinquity of relationship between the beetle species’ normal host and the plant with which it was challenged (Futuyma et al. 1995). (In some cases, no individuals fed on a plant, so both variance and mean were zero.) We suggested that the history of host shifts may have been guided by the nature of genetic variation, a satisfying and perhaps remarkable instance of the relevance of contemporary estimates of genetic variation

to long-term evolution—what Schluter (1996) termed “evolution along genetic lines of least resistance.”

A few other authors have reported lack of detectable genetic variation in, for example, certain locomotor and life-history traits of a treefrog (Watkins 2001) and in desiccation resistance in two rainforest species of *Drosophila* (Hoffmann et al. 2003; Kellermann et al. 2006; van Heerwaarden et al. 2008). The same research group (Kellermann et al. 2009) also found that additive genetic variance for desiccation and cold resistance was significantly lower within populations of 15 species of *Drosophila* with restricted tropical distributions than in 15 broadly distributed species, and suggested that the “specialist” species may lack genetic variation necessary to expand their range. Insufficiency of selectable genetic variation in a population is also implied when adaptation is facilitated by an infusion of genetic variation into a population by gene flow or hybridization with other species; Arnold (2006) provides many examples. It appears that not all traits are genetically variable, perhaps especially some ecologically most interesting traits.

CHARACTER COMBINATIONS AND GENETIC CORRELATIONS

Genetic correlations do not in themselves necessarily imply constraint, nor are genetic constraints necessarily expressed as genetic correlations. Nevertheless, genetic correlations among characters sometimes conform to the trade-offs that are postulated to account for patterns in life histories, ecological amplitude, and other traits, and sometimes are demonstrably antagonistic to the direction of selection. Recent studies emphasize especially the **G** matrix for multiple traits. Neither male attractiveness nor female mate preference responded to experimental selection in guppies (*Poecilia reticulata*), in which male attractiveness may be correlated with low fecundity (Hall et al. 2004). In a similar experiment in *Drosophila bunnanda*, male mating success failed to respond to selection, because of the “virtual absence of genetic variance in the combination of CHCs under sexual selection”—even though individual CHCs vary genetically (McGuigan et al. 2008). The absence of genetic variance was attributed to persistent directional selection by female choice. A very similar result was described for a set of male call properties in a cricket (Hunt et al. 2007). Such cases support Bradshaw’s (1991) conjecture that usable genetic variation will often have been depleted by directional selection. Without venturing to attribute lack of variation to selection, Smith and Rausher (2008) determined in *Ipomoea hederacea*, as Caruso (2004) had in *Lobelia siphilitica*, that the predicted response to selection on floral traits was constrained by the genetic correlations among them. Male and female fitness components are negatively correlated in a number of animal and plant species and may have important constraining effects (Kirkpatrick 2009). For instance, the strong positive genetic correlation in size, but divergent

selection, between the sexes in the collared flycatcher causes the predicted selection response in female tarsus length to be opposite from the direction of selection (Merilä et al. 1998). In one of the most ecologically relevant such studies, Etterson and Shaw (2001) reciprocally planted families of a prairie legume (*Chamaecrista fasciculata*) from three latitudes in all three locations and estimated the selection gradient on several adaptively relevant characters, to judge how northern populations would evolve in a response to a warming climate, as is presently typical further south. Although additive genetic variance was found in each individual trait, the predicted rate of adaptation was slow, because numerous genetic correlations among traits were antagonistic to the direction of selection on multiple traits (or pairs of traits) taken together.

That the correlation structure of the **G** matrix can have long-term effects on evolution was famously shown by Schluter (1996), who provided evidence that the direction of divergence among species of finches, mice, and fish is largely along the axis of maximal multivariate genetic variation (g_{max}). Deviation from this axis increased over time, but the effect nonetheless appeared to last for up to 4 million years (my)—suggesting also a long-term conservation of the basic structure of **G**. (Similar inferences were drawn by Futuyma et al. [1995] from their study of *Ophraella*.) Evidence for evolution along lines of least resistance (g_{max} or its phenotypic equivalent p_{max}) has also been described for species of crickets (Bégin and Roff 2004), stalk-eyed flies (Baker and Wilkinson 2003), and platyrrhine primates (Marriog and Cheverud 2005), among others (Hunt 2007b). Using multiple shape measurements in 51 fossil populations of *Poseidonamicus* ostracodes, distributed over 40 my, Hunt (2007b) found that the direction and the rates of change, both in ancestor-descendant transitions and in divergence among lineages, was close to the axis of maximal variation, and that this effect lasted for several million years. In this and several other instances, there was a reason to think that at least some of the evolution was caused by natural selection rather than drift.

Similarly, the matrix of character variation and covariation among species in a clade corresponds, in some instances, to the intraspecific pattern of variation (e.g., Ackerman and Cheverud 2002; Blows and Higgie 2003; Hansen et al. 2003). Hansen and Houle (2008), comparing divergence in wing shape among drosophilid species with the estimated **G** of *D. melanogaster*, concluded that “broad characteristics of the **G** matrix are preserved over the more than 50 million years of evolution captured in this clade of flies.” Differences in the genetic variance in eight male traits (CHCs) among populations of *Drosophila serrata* are mostly along the major axes of variance within populations (Hine et al. 2009). The correspondence between divergence and **G**, like the similarity of **G** among populations and species, is not very strong in all such studies (Steppan et al. 2002), but that should not be surprising, because **G** is measured with often considerable

error. Moreover, selection is likely to cause short-term variation among populations and over time, whereas long-term divergence among species may average over such variation, and be guided by an “average” **G** that is determined largely by mutation (**M**, which is likely to evolve much more slowly).

PSEUDOGENES AND THE LOSS OF EVOLUTIONARY POTENTIAL

That lineages may simply lack the genetic and developmental basis for some imaginable adaptations is vividly illustrated by the loss of such bases, despite some fascinating evolutionary reversals that call Dollo’s law into question (Collin and Miglietta 2008). “Regressive evolution” has long been recognized, and is now being associated with the silencing and loss of genes in endosymbionts and parasites (e.g., Moran et al. 2009) and in troglobites (e.g., Leys et al. 2005). In angiosperms, the oft-repeated transition to selfing from self-incompatibility, which appears never to have been reversed, is associated with multiple loss-of-function mutations at the *S* locus (Igic et al. 2008). An evolutionary change in flower color is associated with degeneration of the anthocyanin pathway in a species of *Ipomoea* (Zufall and Rausher 2004). Enamel-specific loci have become pseudogenes in the toothless mysticete (baleen) whales (Demere et al. 2008), and although rudimentary odontogenesis can be induced in birds, functional bird teeth with enamel covering are an “impossibility” because two key genes have degenerated (Sire et al. 2008). Most Antarctic icefish species have lost the adult β -globin and have a truncated α -globin pseudogene (Near et al. 2006). Neurotoxicity has been reduced in a specialized egg-eating sea snake, in which the toxin gene is frame-shifted and truncated (Li et al. 2005). Many chemoreceptor genes have lost function in both chimpanzee and human, which have quite different olfactory receptor repertoires (Wang et al. 2004; Go and Niimura 2008), and the independent evolution of host specialization in two species of *Drosophila* is associated with a fivefold acceleration of loss of chemoreceptor genes (McBride and Arguello 2007). Because many steps in developmental pathways are controlled by key genes (not by interchangeable polygenes), the loss of one or two genes may spell the irreversible loss of a character.

THE ROLE OF MUTATION RATE

Ceteris paribus, the mutational variance V_m of a trait, the increment of variance per generation due to new mutations, is proportional to the number of loci that contribute to the trait’s development. Houle (1998) provided evidence that the standing variance of traits is correlated with V_m , and argued that both are related to the number of loci, or “target size” for mutation. The smaller the mutational target, the more likely the rate of mutation is to limit the variance available for selection. For example, genes with unique, key roles in developmental pathways provide

small targets. That many traits provide relatively small targets for mutation is suggested by evidence that the distribution of allelic effects underlying variation in quantitative traits is often exponential, with a few loci accounting for much of the variance, and these often mapping to known candidate genes (e.g., Long et al. 1995; Bradshaw et al. 1998; Albert et al. 2007; cf. Orr 2005).

This conclusion is strengthened by cases in which adaptation is based on rare mutations or on independent evolution at the same locus (parallel genotypic evolution: Wood et al. 2005; Arendt and Reznick 2008). For example, organophosphate insecticide resistance in the mosquito *Culex pipiens* can be based on three loci, but many populations around the world owe their resistance to long-distance migration of only a few independent mutations at one esterase locus (Raymond et al. 2001). Target site resistance to pyrethroids and DDT is based on mutations of the same sodium channel gene in at least three orders of insects (Pittendrigh et al. 1997). Resistance to the herbicide triazine is based on the same amino acid substitution in the D1 protein of photosystem II throughout diverse families of dicots and monocots (Warwick 1991; Trebst 1996). Transgenic experiments indicate that changes in or near the *Leafy* locus underlie the independent evolution of rosette morphology in three lineages of Brassicaceae (Yoon and Baum 2004). Pelvic reduction appears to be based on parallel evolution of expression of the *Pitx1* gene in two genera of sticklebacks (Shapiro et al. 2006). Wood et al. (2005) list many other examples of parallel genotypic adaptation. As they note, the number of pathways between phenotypes is more limited in an oligogenic model of inheritance than in the infinitesimal model, under which there should be numerous paths from one phenotype to another. Mounting evidence suggests that homoplasy may sometimes owe as much to design limitation as to selection (Wake 1991).

ADAPTATION FROM NEW MUTATIONS

Although the traditional theory of population and quantitative genetics mostly concerned evolution based on standing variation and largely ignored evolution based on de novo mutation (Stolzfus 2006), recent theory has increasingly explored the role of mutation (e.g., Phillips 1996; Hartl and Taubes 1998; Orr and Unckless 2008). A rapidly growing literature concerns signatures of selective sweeps (reduction of sequence variation) that may provide evidence of positive selection, which “occurs when a new (or previously rare) mutation confers a fitness advantage” (Nielsen et al. 2007). In contrast, selection of an allele that has persisted for many generations at low frequency might be expected not to sweep away linked variation, because the selected site will have more nearly approached linkage equilibrium with linked variants (Barrett and Schluter 2008). Abundant selective sweeps have been described in *Drosophila* and human populations (Glinka et al. 2003; Nielsen et al. 2007) and in candidate genes for cer-

tain adaptations in other species (e.g., Kane and Rieseberg 2007; Linnen et al. 2009), and have been interpreted as evolution based on de novo mutations. However, such observations must be interpreted cautiously because selection on standing variation can sometimes yield a similar pattern (Hermisson and Pennings 2005; Przeworski et al. 2005).

THE DIMENSIONALITY OF VARIATION

As discussed above, the constraining effects of genetic correlations among characters increase as the number of character correlations grows. Genetic correlations reduce the effective number of dimensions of variation. In empirical datasets, most genetic variance is accounted for by a few principal components, so that the number of genetic “degrees of freedom” is considerably lower than the number of traits measured (Schluter 2000, p. 221). If the number of principal components (the rank of **G**) is less than the number of characters, there exists an absolute constraint on evolution of some character combinations. How frequently this is the case is uncertain; for instance, the **G** matrix for 10 aspects of wing shape in *D. bunnanda* had only five detectable dimensions in females and two in males (McGuigan and Blows 2007), but in a similar study of 20 aspects of wing shape in *D. melanogaster*, Mezey and Houle (2005) detected 20 dimensions, and concluded there is little evidence of bidirectional absolute constraints. Kirkpatrick (2009) has defined the “effective number of dimensions” n_D as the sum of the eigenvalues divided by the largest eigenvalue of **G**, and finds that n_D is less than 2 in datasets that include as many as 21 measured traits. For many traits, the response to selection would be substantially reduced, especially if the selection gradient is not oriented along the axis (g_{max}) of greatest variation.

On the other hand, the rate of adaptation may be greatly slowed if it requires simultaneous change in too many dimensions, that is, too many independent characters. Complex characters, in which function depends on the fit or interaction among multiple components, are a case in point. The “character” we measure, say leg length, may actually have several components, such as its several segments or, for that matter, its skeletal, muscular, circulatory, and nervous components. The latter are presumably developmentally integrated (i.e., have high positive genetic correlations if we were to measure them separately), but if they were not, evolution of leg length might be difficult. On the other hand, genetic correlations among the leg’s segments might facilitate or retard adaptive evolution of leg length, depending on various aspects of function.

In many cases, we know little about the components that compose a complex trait. For instance, who would have expected, without careful study, that facial grooming in laboratory strains of house mice (*Mus musculus*) consists of at least three independently inherited components (Vadász et al. 1983)? “Host preference” is commonly scored in phytophagous insects as the

frequency of choice between two or more plant species, and is said to have evolved when related species “prefer” different plants. But “preference” may be a highly complex “character” (cf. Bernays and Chapman 1994; Schoonhoven et al. 1998; Futuyma 2008). Oviposition or feeding on a plant often includes several steps (e.g., long-distance orientation to plant, settling on plant, “contact evaluation,” and acceptance), each of which may be governed by different chemical (or other) plant characteristics. Acceptance is often based on reactions to both positive stimuli (e.g., certain plant compounds) and to negative stimuli that deter oviposition or feeding on nonhost plants. Although we have only rudimentary knowledge of the genetic bases of these reactions, we know that they stem from a number of peripheral chemosensory characters (e.g., distribution and identity of a variety of receptor proteins on both “positive” and “negative” cells) and on central nervous integration of stimuli. Adult and larval host acceptance appears genetically independent in at least some species (Forister et al. 2007), and the behaviors that compose “host preference” are generally genetically independent of postingestive physiological traits that determine growth and survival on a plant that the insect consumes (Thompson 1988; Fox 1993; Forister 2005). Thus, some imaginable host shifts—perhaps to chemically very different plants—may require unlikely combinations of alleles that affect many traits. If so, it is not surprising that large samples from an insect population may display no genetic variation in feeding response to certain plants, and in some instances uniformly refuse to feed (Futuyma et al. 1995), nor that many large clades of insects are restricted to a limited range of related, chemically similar plants (Ehrlich and Raven 1964; Becerra and Venable 1999; Winkler and Mitter 2008).

The degree of pleiotropic correlation among functionally related traits is a major consideration in the evolution of morphological integration (Olson and Miller 1958) and modularity (Cheverud 1996; Wagner and Altenberg 1996; Klingenberg 2008). There is some genetic evidence of developmental modules (e.g., high correlations among measurements within, but not between the tooth-bearing part of the mouse mandible and the ascending ramus), but there are no unequivocal examples of adaptive modularity, that is, the evolution of adaptive developmental integration among functionally interacting morphological structures (Klingenberg 2008).

Stasis of Characters and of Organisms

Considering the relative recency of substantial study of possible genetic constraints, there is enough evidence to suggest that all the several classes of genetic limitation I have discussed may limit evolution in some instances. Lack of genetic variance (perhaps due to lack of genetic and developmental foundations) and low mutation rate (based on small target size) may restrain adapta-

tion in some cases. However, it is likely that multivariate genetic correlations will prove the major constraints on certain characters within species, and complexity (functional integration of multiple characters) a major constraint on adaptation to multidimensional environmental changes. Phylogenetic conservatism may in some cases stem from genetic limits on particular characters, but probably more often from the need for complex changes.

I think it unlikely, however, that these genetic factors explain the phenomenon of long-term stasis, as described by paleontologists, because (as I noted earlier) stasis appears to characterize essentially all the visible characters in a fossil lineage. It stretches credulity to suppose that these “internal” genetic limitations can constrain all of an organism’s visible features. Eldredge and Gould (1972), drawing on the view of genetic integration promulgated by Wright, Dobzhansky, and Mayr, initially attributed stasis to pervasive genetic (or developmental) constraint stemming from gene interactions, but in the face of the many counterarguments by population biologists (e.g., Charlesworth et al. 1982), retreated from this position (e.g., Eldredge 1995; Gould 2002). It seems inescapable that true stasis requires explanation by “external” factors. Several such explanations have been proposed. (See Jablonski’s [2000] comprehensive overview.)

STABILIZING SELECTION

Stabilizing selection was proposed early as a simple explanation of stasis (e.g., Charlesworth et al. 1982). Recently, Estes and Arnold (2007) concluded, based on computer simulations, that stabilizing selection best explains data on a wide range of time scales. Aside from indications that stabilizing selection is not as common as once supposed (e.g., Kingsolver et al. 2001), we must ask what sources of selection might account for stasis in so many characters. A good possibility is that by active habitat selection, a species remains associated with much the same effective environment, and may shift its geographic range if its habitat moves, as it may during periods of climatic change (Maynard Smith 1983; Eldredge 1989); however, this hypothesis requires us to explain why habitat selection behavior does not evolve when environments change (Hansen and Houle 2004), and it does not apply to plants and many other organisms. Some paleontologists have suggested that stabilizing selection may be exerted by a species’ biotic interactions in long-lasting assemblages of species, or communities (e.g., Morris et al. 1995; Lieberman et al. 2007). This suggestion warrants further study, but I find it not entirely convincing for two reasons. First, it assumes that such interactions exert selection on all or most characters, which calls for empirical evidence. Second, it appears to conflict with some observations, including those by some of the same authors. For example, Lieberman and Dudgeon (1996) found that two Devonian brachiopod species varied less across faunistically different paleoenvironments than they did through time in a single such environment (echoing similar

observations on bivalves by Stanley and Yang [1987]), and these authors drew attention to the relative instability of the composition of many “communities.” Great changes in the composition of species assemblages during Quaternary climate oscillations (Webb and Bartlein 1992) had little effect on the morphology of beetles, plants, and other organisms (e.g., Coope 1979; Cronin 1985; Bennett 1990; Willis and Niklas 2004).

In advocating stabilizing selection, Estes and Arnold (2007) note that it may have not only external (environmental), but also internal sources. For example, strong genetic correlations or functional interactions can have this effect, as noted earlier. Genetic constraints and internal selection are closely related (Schwenk and Wagner 2004), so internal stabilizing selection returns us closely to the Wright/Dobzhansky/Mayr viewpoint that Eldredge and Gould espoused.

LIMITS ON NICHE EVOLUTION

I think it is not controversial to suppose that most adaptive character changes are advantageous under a relatively restricted set of ecological conditions, and transpire when a population adapts to a different fundamental ecological niche (Futuyma 1987; Levin 2005). The factors most frequently cited as limitations on niche width or niche shift are fitness trade-offs and gene flow, usually acting in concert (Futuyma and Moreno 1988). Gene flow is widely thought to constrain adaptation unless opposed by sufficiently strong selection (Rasanen and Hendry [2008] review examples), and to be a major factor in limiting expansion of a species' geographic range (e.g., Kirkpatrick and Barton 1997; Angert and Schemske 2005).

Recent theory, initiated by Holt and Gaines (1992) and elaborated by Holt (1996 et seq.) and others (Kawecki 1995; Whitlock 1996; Cohen 2006), has emphasized that even without trade-offs between fitness in different habitats, the demography of selection can restrain niche evolution (reviewed by Kawecki [2008]). If a “major” (more “productive”) habitat (or resource) contributes more to population numbers than a “minor” (less “productive”) habitat (which may be a population “sink”), advantageous mutations that enhance fitness in the major habitat will increase faster than comparable mutations that affect fitness in the minor habitat, even if their per capita fitness effects are equal. A similar asymmetry applies to the efficacy of purifying selection against habitat-specific deleterious mutations. A common consequence is that mean fitness (adaptation) increases faster with respect to the major than the minor habitat, in which fitness may actually decline (due to random fixation of more deleterious mutations). Gene flow between habitats often, but not always, enhances this effect. In general, this demographic effect should lead to evolution of a narrower niche (Whitlock 1996; Cohen 2006), specialization on abundant habitats or resources, and niche conservatism. Although this theory of niche conservatism has been little tested,

Losos et al. (1994) suggested that it explains the unexpected retention of ecological specialization in certain *Anolis* populations.

STASIS AS A CONSEQUENCE OF EPHEMERAL DIVERGENCE

In 1987, in an effort to reconcile the punctuated pattern of evolution claimed by Eldredge and Gould (1972) with broadly held views in population genetics, I suggested that stasis may be explained not as a genetically constrained inability of populations to respond to selection, but as a failure of locally evolved adaptations to persist long enough to be registered in the fossil record (Futuyma 1987). I shall call this the hypothesis of “ephemeral divergence.” Similar suggestions have since been advanced by other authors (e.g., Eldredge et al. 2005).

Before proceeding, I should note that “punctuated equilibrium” has been used to refer both to a paleontological pattern of rapid shift between long-persisting “static” phenotypes, and to the hypothesis that Eldredge and Gould (1972) advanced to explain this pattern, namely that evolutionary change occurs almost exclusively during speciation, that is, the cladogenetic formation of a phenotypically divergent, reproductively isolated “daughter” biological species from a “parent” species that continues relatively unchanged. Support for this hypothesis requires evidence of cladogenesis, that is, temporal overlap of two descendants of the ancestral form (Gould and Eldredge 1993). The hypothesis gains no support from examples of distinct successive forms that may be named as different species (i.e., chronospecies). Many paleontologists affirm that “most morphological transitions take place during speciation” (Lieberman et al. 2007), and cite examples of temporal overlap between ancestral and derived phenotypes.

In proposing an explanation for stasis and for a possible association between morphological transitions and speciation, I assumed that most new adaptations are fairly narrowly context (niche) specific and that they are based on polygenic traits. Often they are based on several such traits; for example, an animal's use of a food type or habitat often entails both behavior and morphological or physiological features. Because recombination breaks down associations among traits, and among loci that contribute to even a single polygenic trait, “the constellation of characters associated with adaptation to an ecological niche will generally not be maintained intact in a sexual population if it is locally sympatric with and interbreeds with another such population that is likewise adapted to another niche” (Futuyma 1987, p. 466). In contrast, of course, reproductive isolation between two such populations enables persistence of distinct gene combinations.

Without reproductive isolation, a polygenic niche-adaptation that arises by selection in a local or regional population (1) may often be unable to spread through intervening conspecific populations to other areas in which the niche (e.g., habitat) also occurs; and (2) is likely to be lost eventually to interbreeding with the

ancestral type, as shifts in the mosaic distribution of their niches cause episodic but massive gene flow: a collapse of population structure. Either of these processes can prevent new adaptive traits from being registered in the fossil record of a species, because they are too temporally or spatially localized.

In 1987, I emphasized that without reproductive isolation (speciation), interbreeding will cause the adaptations of a local population to be ephemeral, and to leave little or no trace in the fossil record, because of gene flow—not “trickle” gene flow between neighboring populations as we typically observe at any one point in time, but the more substantial gene flow that can be caused by extinction and colonization of populations (Slatkin 1977; McCauley 1993). For example, the geographic distribution of species changed markedly and repeatedly during the Pleistocene due to extinction of some populations and colonization of new sites—a process that can mix the descendants of diverse source populations. Moreover, microhabitats and resources (e.g., the host plants of phytophagous insects) that were formerly geographically segregated may become mixed together, as we know from the individualistic Pleistocene shifts in plant species and the formation of different species associations (Davis 1976). Both the collapse of population structure of a geographically variable species and shifts in the distribution of the populations’ distinct resources can increase gene flow and erase niche differentiation. This process will result in the appearance of stasis if gene flow results in the loss of the newly divergent characters, and persistence of the ancestral phenotype. This is likely if the ancestral type is adapted to a more abundant and widespread niche: the demography of selection modeled by Holt and Gaines (1992), Kawecki (1995), and Whitlock (1996) then favors conservation of the ancestral niche.

The same appearance of stasis will result if there is a high rate of extinction of local populations that diverge from a stable, large parent population. Bell (2001) showed that since the Miocene, marine three-spined sticklebacks (*Gasterosteus*), with a static phenotype, have frequently colonized lakes, where they evolve distinct phenotypes but quickly become extinct because lakes are geologically short-lived.

The proposition that climatic instability inhibits speciation, and therefore anagenesis, by increasing extinction/colonization dynamics has been advanced also by Dynesius and Jansson (2000; also Jansson and Dynesius 2002), who emphasize especially Milankovitch oscillations on a timescale of 10–100 thousand years, caused by changes in the Earth’s orbit. Although occurring throughout the Earth’s history, they have been pronounced and best studied during the Pleistocene.

I remarked in 1987 that reproductive isolation enables a new, niche-differentiated form to spread and retain its association with its resource. I expanded on this idea in a later paper (Futuyma 1988), noting that if the habitat to which a plant ecotype is adapted

shifts geographically, the spread of the ecotype from old sites to new is likely to be prevented by gene exchange and recombination with intervening populations that occupy different (e.g., ancestral) habitats. Much the same ecotype might be reconstituted anew by selection in the new sites (perhaps with a different genetic basis), but if genetic variation were insufficient for the repeated origin of the ecotype, its appearance on the evolutionary stage would be local and brief. In contrast, a reproductively isolated ecotype could persist as long as it could disperse from one temporary site to another. Only if the ecotype is widespread and long-lasting does it have much chance of appearing in the fossil record.

I am now inclined to think that the difficulty a new polygenic adaptation has in spreading may be at least as important as the gene flow that stems from extinction and colonization of populations. Eldredge et al. (2005) have also emphasized the problem of spread, although they focus more on metapopulation dynamics than recombination. In a related vein, Lieberman and Dudgeon (1996) suggested that selection on most characters is too geographically variable to enable a widespread species *qua* species to evolve much, and Thompson (1999, 2005) has made a similar point about the “geographic mosaic” of selection stemming from biotic interactions, with the result that “few coevolved traits spread across all populations to become fixed traits within species” (Thompson 2005, p. 103). This is undoubtedly true as long as all the populations remain one species, but reproductive isolation enables an association with a prey species or symbiont to spread to the various sites in which the associated species occurs.

Therefore, adaptive phenotypic evolution may be associated with speciation, not because speciation in itself accelerates evolution by releasing gene pools from epistatic constraints (as Eldredge and Gould suggested), but because it enables long-term retention of divergent characters. (In his final work, Gould [2002, pp. 798–802] welcomed this argument, and viewed it as a reconciliation of punctuated equilibrium with population genetics, as it was intended to be.) Might speciation also enhance the rate of neutral evolution? Perhaps. Many presumably neutral molecular variants vary in frequency among conspecific populations, because of genetic drift. An allele that has a relatively high frequency in a population that evolves reproductive isolation has a greater probability of fixation than it would in the species as a whole, in which it is more likely to be lost because of its lower frequency. Any such population has relatively high-frequency variants at some sites, and these will have a “head start” toward fixation. Pagel et al. (2006) note that if species are formed by small founder populations, drift will increase the rate of neutral evolution, and reproductive isolation will preserve such founder effects (and, they note, adaptive divergence as well). However, the evidence for founder-effect speciation is meager (Coyne and Orr 2004).

DOES EVOLUTIONARY CHANGE DEPEND ON SPECIATION?

The two sides of the Ephemeral Divergence hypothesis are that (1) reproductive isolation of a population enables evolutionary shifts from ancestral states to be retained indefinitely, and that (2) phenotypes appear static unless such shifts are captured by reproductive isolation, for otherwise they are likely to be localized and transitory, leaving neither a paleontological imprint nor long-term effects. I have not thought of unique predictions or tests of this hypothesis, but it is consistent with many observations, especially (1) evidence that elevated evolutionary rates are associated with speciation (the original theoretical claim of punctuated equilibrium), and (2) evidence that divergence is enhanced by stability rather than change of climate.

The variance of species means of a phenotypic trait in a clade may be a consequence of both anagenetic (gradual) and cladogenetic (punctuated) changes. Ricklefs (2004) proposed to distinguish these effects on the basis that the variance increases linearly with time in a neutral gradual model, but with the logarithm of the number of species in a purely cladogenetic model. He reported that morphological evolution in passerine birds is strongly associated with cladogenesis, but later (Ricklefs 2006) acknowledged that this approach does not distinguish between the models. One difficulty with using phylogenies of extant species in such tests is that not all speciation events are visible in a phylogeny because of extinction. Bokma (2008) has extended Ricklefs's approach by proposing a Bayesian algorithm to simultaneously estimate speciation and extinction probabilities. Applying this to a molecular phylogeny of nearly all the extant species of mammals, Mattila and Bokma (2008) estimated that only 20–35% of the variance in body mass is accounted for by gradual divergence, with speciation accounting for most of the variance. Taking a different approach to divergence at the molecular level, Pagel et al. (2006) propose that the path length (number of nucleotide substitutions) from the root of a tree to an extant species can be written as $x = nB + g$, where n is the number of nodes along the path, B is the contribution of speciation to evolution at each node, and g is the gradual contribution to the path, measured as the sum of the internode lengths. In a set of 100 clades of plants, animals, and fungi, Pagel et al. reported that speciation contributed significantly to path lengths in 35, and in these it accounted for 30% of molecular diversity, on average. The few analyses, then, suggest that evolution of both morphological and molecular traits is associated with speciation.

Whether climatic instability inhibits speciation (and therefore anagenesis) is the focus of considerable controversy, centering on the effects of Pleistocene Milankovich oscillations. Until recently, the Pleistocene was thought of as a time of active speciation, due to isolation of populations in separated refugia; for example, Haffer's (1969) suggestion that Pleistocene speciation in Amazonian refuges contributes greatly to tropical species rich-

ness was widely accepted. Clearly, some speciation occurred during the Pleistocene (e.g., Knowles 2001; Lister 2004), but both fossil and genetic studies now suggest that in trees (Willis and Niklas 2004), lampropeltine snakes (Pyron and Burbrink 2009), many marine taxa (Jackson and Johnson 2000), and arid-zone Australian animals and plants (Byrne et al. 2008), most species arose before the Pleistocene (see Bennett 2004). Klicka and Zink (1997) called the supposed prevalence of Pleistocene speciation a "failed paradigm" for birds, setting off a debate that seems to have settled on the conclusion that speciation rates were not elevated during the Pleistocene, though leaving it uncertain if they were actually depressed (Zink et al. 2004; Zink and Klicka 2006). In an analysis of phylogenies of Neotropical birds, Weir (2006) found evidence of a Pleistocene decline in speciation rates for lowland taxa, but an increase for highland (Andean) taxa, as reflected in their high degree of endemism (Fjelds  et al. 1999). Whereas differentiation of lowland populations can be broken down by gene flow when climate changes, montane populations may simply shift vertically over short distances, while remaining separated from each other (Jansson and Dynesius 2002).

In contrast to these studies, Weir and Schluter (2004) concluded from analysis of coalescence of superspecies that speciation in boreal birds (in contrast to subboreal and tropical birds) was commonly initiated during the Pleistocene, probably as a result of a direct fragmentation of ranges by ice sheets. Furthermore, Weir and Schluter (2007) found that sister species of birds are younger at high than at lower latitudes, and concluded from applying birth–death models that speciation and extinction rates, and hence turnover rates, are greatest at high latitudes. These results seem not to accord with the expectation that speciation would be inhibited by the pronounced climatic changes at high northern latitudes. On the other hand, phenotypic diversification among populations of birds, indexed by numbers of subspecies, is higher at lower latitudes (Martin and Tewksbury 2008). Jansson (2003) found that the number and proportion of endemic species of vertebrates and vascular plants in various regions of the world are negatively correlated with recent climatic instability, and proposed that climatic stability allows speciation to be completed.

Although study of extant sister species pairs does not reveal how much of the phenotypic difference between them has accumulated gradually since speciation, the fossil record shows that in many cases, their morphology dates to the Pliocene or earlier (Jackson and Johnson 2000; Bennett 2004). Coope (1979, 2004) has emphasized that late Cenozoic fossil Coleoptera, almost without exception, are identical in fine morphological detail to living species, and attributes this stasis to local extinction and gene flow. Cronin (1985) reported that Cenozoic ostracodes showed their greatest stasis during major climatic oscillations. Sheldon (1996) summarized many other examples in support of his contention

that evolution occurs mostly in stable environments and that stasis is the norm in widely fluctuating environments. Although he attributed the pattern to clade selection (persistence of more tolerant, generalized lineages), it is consistent with the hypothesis of ephemeral divergence.

Implications of Developing Views on Constraints

To acknowledge intrinsic and extrinsic constraints or biases in evolution is not to deny that genetic variation does enable many traits to respond rapidly to selection. Still less does it deny a major (or the major) role for natural selection in phenotypic evolution when it does happen. Many or most phenotypic characters probably originated as adaptive traits—with the reservation that some may be pleiotropic correlates of adaptations (Dobzhansky 1956). But evolutionary biology has been enriched by considering not only how adaptation happens, but also why it often does not happen, or at least does not happen as we might naively expect. Eldredge and Gould's (1972) proposed cause of punctuated evolution was wrong, and I think Gould and Lewontin (1979) were far too skeptical in their criticism of the “adaptationist program,” but these challenges to the Modern Synthesis drew attention to puzzling phenomena and alternative explanations, and contributed to an efflorescence of new theoretical and empirical analyses of phenotypic evolution and its limits. Just as Eldredge and Gould found lack of change interesting (stasis is data), we now recognize that lack or paucity of genetic variation in a trait or trait combination, resistance to selection, the differences in evolutionary rates assessed at different time scales, and phylogenetically conserved characters are important and interesting phenomena that call for explanation.

Among the fields most affected by an appreciation of restraints on adaptation is community ecology, which is being radically altered by the recognition that phylogenetic history is an indispensable element in explaining the species composition and diversity of communities (Ricklefs 1987, 2004; Webb et al. 2002; Emerson and Gillespie 2008; Cavender-Bares et al. 2009). The main reason for this is phylogenetic niche conservatism, carrying the implication of restraint of the evolution of ecologically important characters. For example, it is increasingly clear that many of the species in a community did not evolve their features in situ, but retain much the same ecological character as their ancestors that dispersed to that region from elsewhere (Brooks and McLennan 1991). As Donoghue (2008) remarks, “it's easier for organisms to move than to evolve,” as the history of range shifts during the Pleistocene illustrates (see above). For example, Ackerly (2004) found that the sclerophyllous leaves and other traits characteristic of shrubs in California chaparral did not evolve in situ; the Californian species are members of widely distributed clades that

evolved these traits elsewhere, long before California developed the Mediterranean climate in which chaparral is characteristic. Futuyma and Mitter (1996) determined that the great majority of host-specialized species of leaf beetles in New York State feed on the same plant family as their congeners in Europe or tropical America, and were presumably able to spread into (or possibly from) northeastern North America only because those plant families were present. Consequently, historical biogeography, by tracing the origin and spread (and vicariance) of lineages and thus of their membership in regional biotas, regains its position as a key contributor to community ecology (Donoghue and Smith 2004; Donoghue 2008).

This historical perspective does not replace, but instead supplements, the ecological theory of species interactions that became the main framework of community ecology in the 1960s (Cavender-Bares et al. 2009). Examination of local co-occurrence of species of plants (e.g., Webb 2000; Cavender-Bares et al. 2004), birds (Lovette and Hochachka 2006), and other organisms shows that closely related species may co-occur more frequently than expected at random, presumably because of shared physiological tolerances, or less frequently than expected, presumably because greater similarity of close relatives engenders more intense competition. Phylogenetic conservatism can have either effect, depending on the characters.

Of all ecological subjects, explanation of geographic patterns in species diversity (richness) is probably being most extensively revised by historical and phylogenetic considerations (Ricklefs 1987, 2004; Wiens and Donoghue 2004; Mittelbach et al. 2007). The latitudinal gradient in diversity, conspicuous in many terrestrial and marine taxa, has been the most common focus. History-based explanations of greater tropical diversity (e.g., Fischer 1960) were prevalent before the development, in the 1960s, of ecological theories of competition and niche packing that were intended to explain local diversity by species interactions under the influence of contemporary climate. This approach has strong adherents today (see Willig et al. 2003 for review), but it has not yielded a satisfactory explanation of latitudinal differences in diversity (Currie et al. 2004). Today, there is growing acceptance of history-based explanations, of two kinds.

First, rates of speciation may be higher, and/or of extinction lower, at lower than at higher latitudes. Although evidence of lower extinction rates is equivocal, rates of diversification, and of speciation in some groups, appear higher in tropical regions (Cardillo 1999; Cardillo et al. 2005; Davies et al. 2004; Hawkins et al. 2007).

Second, the “tropical conservatism hypothesis” (Wiens and Donoghue 2004), a recent elaboration of an earlier suggestion (Farrell et al. 1992; Latham and Ricklefs 1993), proposes that many or most clades originated in tropical environments, simply because these characterized much of the Earth until about

45 million years ago. Most species in these clades retain adaptation to those environments; few clades have made the transition, and these are mostly recently, to the climate (perhaps especially freezing) that now prevails at higher latitudes. Hylid frogs, among others, conform to this hypothesis: basal clades are tropical, only a few clades show transition to the temperate zone, and the species richness of a clade in a region is correlated with the time since the clade arrived there (Wiens et al. 2006). Fine and Ree (2006) also found evidence that both time and area explain diversity: the current species diversity of trees in a biome on each continent is correlated with the biome's area not at the present time, but integrated over the area of that biome's climate since the early Tertiary. Jablonski et al. (2006) showed that there has been a long history of clades originating in tropical regions and expanding into higher latitudes, while persisting at low latitudes—a process that, *ceteris paribus*, would produce the latitudinal gradient. A simulation of range fragmentation by climate change, speciation, and niche evolution predicted spatial diversity patterns resembling that of South American birds (Rangel et al. 2007). Among all the factors that were varied in many runs, the one that maximized the fit to the data was a high level of climatic niche conservatism.

The themes of evolutionary history and constraint are starting to influence other areas of ecology; for example, the functional features of species that affect ecosystem properties vary among clades. The amount of phylogenetic diversity within a community has a greater effect on productivity than simple species diversity (Cadotte et al. 2008; see also Maherali and Klironomos 2007). In population ecology, restraints on evolution are paramountly important for understanding range limits and, most urgently, for judging the likelihood of species' survival versus extinction in the face of massive and accelerating anthropogenic changes in the environment—especially global climate. The maximal rate of sustained evolution of a character that influences survival in a directionally changing environment depends on the mutation rate, and may fail to maintain the population if the rate of change in the optimal character state is too great, especially if the environmental change reduces the population size (Bürger and Lynch 1995; Orr and Unckless 2008). Indeed, sufficiently strong selection toward a new optimum in an altered environment can cause a negative rate of population growth, hence extinction; such demographic limitations on the rate of adaptation “can convert quantitative evolutionary constraints into insuperable barriers to adaptation” (Gomulkiewicz and Houle 2009).

There is a great need for experiments that identify characters which limit environmental tolerance or geographic ranges, such as the report by Griffith and Watson (2006), who by transplanting cocklebur (*Xanthium strumarium*) seedlings beyond the northern range limit and manipulating their photoperiod, concluded that a population could persist there if it evolved earlier reproduc-

tion. Such information, coupled with analysis of genetic variation and its correlated effects, could provide a basis for judging the likelihood of adaptation, should the species' range shift with the temperature regime (assuming the species could establish new populations fast enough, which for many species is dubious, especially because of habitat fragmentation). Experiments like that by Etterson and Shaw (2001), described earlier, can provide insight into the likelihood that populations might adapt in situ to climate change. If genetic restraints prove to be more important than traditionally thought, the outlook for the future of biodiversity will be so much the grimmer.

Challenges and Opportunities

Many of the operational difficulties in understanding constraints, such as accurately estimating *G* (and even knowing what characters to include), are well known. Here are a few challenges and opportunities for research that I think are especially intriguing.

First, is there any justification for distinguishing, as I have, between stasis of characters and “species stasis” as it was described by advocates of punctuated equilibrium? Or is “species stasis” merely stasis of many individual characters? Do they call for different explanations, as I have suggested, or do intrinsic genetic constraints provide a comprehensive explanation?

Second, what is the relationship between “genetic constraints,” for example, lack of variation along some multidimensional axes, and “developmental constraints”? So far, the expectation that evolutionary developmental biology (evo-devo) would describe and explain constraints has been largely unmet; in fact, some authorities in evolutionary developmental biology have expressed skepticism on constraints, citing the uncoupling of genetically correlated characters by artificial selection (Beldade et al. 2002). Perhaps these experiments merely indicate that “constraints” are really “restraints.” In any case, the pattern of variation in characters expressed by *G* must describe outcomes of the development of the characters.

Third, what are the mechanistic bases of constraints (or restraints) such as pleiotropy, lack of genetic variance, or apparent irreversibility? By understanding developmental or biochemical pathways, or the cellular or molecular basis of traits (e.g., chemoreceptors involved in an insect's host plant preference), we can better understand what our reified “characters” are and the extent to which genetic correlations are “necessary,” and can pursue deeper genetic analysis. Knowing that the genetic basis of a trait has degenerated into pseudogenes, for example, provides greater understanding than a simple phylogenetic determination that it has not been regained.

Fourth, how do we determine which among the many possible kinds of intrinsic and extrinsic constraints (including selection and gene flow) best explains a trait's slow evolution?

Fifth, is it possible to develop generalizations about what kinds of characters are most likely to be constrained? For instance, might nonredundant biochemical pathways be more constrained than fecundity or other fitness components because they differ in mutational “target size”? Might characters that have long been subject to fluctuating selection be more “evolvable” than those, such as desiccation tolerance in rainforest flies, that have not?

Sixth, finally, and most sweepingly, what do we need to know to predict the evolvability of a trait, or the capacity of a population to survive a specified environmental change by adaptation? We have long known that our ability to predict the trajectory of a selected trait for more than a few generations is quite limited. But surely the most lofty goal of our discipline, conceived in our most idealistic and optimistic moments, must be to understand how and when evolution enables lineages to persist and to defer extinction. And surely, as we contemplate human assaults on the biosphere, no goal can be more important.

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