

The Evolution of Evolution: Reconciling the Problem of Stability

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Abstract Evolutionary Science has, at least since the publication of *Origin*, been less concerned with the continuation of species in stable forms, than with the reconfiguration of forms into a host of varieties. So influential has this emphasis been that, over the years, “variation” has become a cardinal desideratum, even taking precedence over the macroevolutionary landscape. This orientation has made it much more difficult to objectively assess the meaning of non-change patterns such as periods of stasis, which appear to be widespread in most species. Yet, if stasis is an expectable outcome of evolutionary activity, this raises the possibility that there may be mechanisms and processes at many causal levels, acting on its behalf, without reference to the impetus toward persistent variation. Researchers have been reluctant to attribute stasis to a macroevolutionary tendency toward ‘stability’ despite the commonality of stasis in many species, and notwithstanding the many biological/behavioral processes that seem inclined to produce and maintain conformance, regulation and consistency. Speciation, paradoxically, is the best evidence for an overriding influence toward stability in that stability would seem to be a necessary condition prior to the development of isolating mechanisms. An alternative macroevolutionary model of biological activity is offered consisting of two tendencies, “variety” counterpoised with “stability” both acting in the service of the persistence of life.

Keywords Stability · Punctuated equilibrium · Stasis · Macroevolution · Regulation · Conformance · Speciation

Introduction

While some theorists would quibble with Eldredge and Gould’s assessment that “pronounced stasis” is the “usual fate of most species” (Mayr 1992, p. 32; also see Gould 1982:86), there is now substantial evidence that slow, gradual change is not the only observable mode of evolution over time. There is increasing evidence that evolution may move at different rates, sometimes quite rapidly (see Hendry et al. 2007; Coyne and Orr 2004). At the other extreme, species’ stasis (Eldredge and Gould 1972; Stanley 1979), where phenotypes may not significantly diverge in morphology for millions of years, is now well documented in a variety of lines (Goldman 1995; Jackson and Cheetham 1999; Lieberman et al. 1994; for a review see Eldredge et al. 2005). Hunt (2007) statistically analyzed the fossil sequences of more than 250 documented cases of phenotypic traits in 53 fossil lineages and applied a statistical “best-fit” analysis using three models of evolutionary activity over time, directional change, unbiased random walk, and stasis. He found that “directional change” was “rarely observed within lineages (5% or less) traced through the fossil record” (p. 104) and “unbiased random walk” only agreed with the data about 47% of the time. In the other 47% of sequences, “stasis” was the best-fit to explain the data. Added to the accumulating evidence from a variety of single species, both extant and extinct (Gould and Eldredge 1993, for a compendium of support; and Levinton 2001, and Hoffman 1989, for opposition), this result suggests that the pattern of stasis is a fairly common “fate” of species. This pattern can be viewed for what it does not indicate, i.e., directional change, or for what it does show, a significant trend toward stability. Gould and Eldredge, who brought stasis to modern attention, highlighted the importance of the latter. On the twenty-first

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anniversary of their original article on “punctuated equilibria” (1972), they concluded that “maintenance of stability within species must be considered a major evolutionary problem” (1993:224). But, how *major* is major? What does the commonness of species’ stability imply about living things generally? Moreover, is ‘stability’ a macroevolutionary outcome that implies more than simply the absence of change? If this is so, then are there independent mechanisms and processes that act so as to establish and maintain species in a relatively *unchanged* form for long periods, just as there are mechanisms and processes of persistent change?

The Hunt analysis mentioned above doesn’t simply justify ‘stasis’ as an evolutionary pattern, nor indicate only that stability is possible. While about 47% of the lines show evident stasis by Hunt’s criteria, as many as 95% meet a broader standard (e.g., Gould 1982). This is because another 47% show evidence of unbiased random walk, i.e., uncoordinated, unsystematic change that nevertheless accumulates. Interestingly, of the species involved in these cases of random walk, more than half remained morphologically identical, changing only in size; while of those that remained, changes were consistent with drift. Thus, depending upon the standard employed, between 47 and 95% of the total lineages, demonstrated evidence of long periods of stability of form with at most, relatively minor change within adaptive optima. If these proportions are typical, then species stability over paleontological time-scales is not just possible, it’s highly likely, especially in phenotypes that have lived long enough to leave fossil remains. What is more, assuming that some species are only recently evolved, this proportion may be an underestimate of the commonness of ‘stability of form,’ since evolving species may take many generations before becoming stable. This pattern, if borne out by additional evidence, strongly suggests that ‘stability of form’ is more than a gradual, somewhat unpredictable outcome of microevolutionary processes. It is deeply woven into the fabric of living things. This begs the question of whether ‘stability’ has an important part to play in both the evolutionary and macroevolutionary domains, as a tendency, as an objective, and/or as the outcome of specifically stabilizing processes and mechanisms. Unfortunately, the founding posture of evolutionary science has rendered it particularly unwelcoming to this sort of amendment.

Macroevolution and the Imperative of Change

It has been customary in evolutionary science, to portray all living processes and mechanisms that have an effect over time, as acting to either produce variation, or to oppose it. Anything that cannot be construed in this way,

like collaborative behavior or self-regulation, is commonly considered to be mistakenly conceived (really a process of variation in disguise) or literally extraneous to evolution. As a result, mechanisms that produce stability and homogeneity, have come to be alternately conceived of as constraints on change (for a review, see Futuyma 2010) or, in lieu of that, considered to be evolutionarily irrelevant. At the same time, ‘variation’ has been given special importance; so much so, in fact, that it is treated as an a priori assumption of primary significance, even when attempting to derive general, transspecific rules. Needless to say, these issues make assessment of stability difficult and inhibit multidisciplinary synthesis.

While there is growing interest, over the past half century, in the broader inquiry into all aspects of evolutionary ‘construction’ and ‘design,’ a focus that is potentially free of historical imperatives and is compatible with processes that act on behalf of persistence generally without reference to change, the old habits of evolutionary thought continue to have a constricting effect on the theoretical landscape. With ‘continuous variation’ well entrenched in its superordinate niche, no other influence has been able to be entertained as similarly pertinent, let alone as equally important in evolutionary scenarios. Thus, when evidence of regulatory systems within a host of organisms became well known, it was not seen as reflecting a common, transspecific impulse toward stability, but as the natural selection of a series of specific, similarly constraining, characters of change. In the same way, when Simpson (1944) brought from Paleontology, evidence of lineage patterns that were inconsistent with the phyletic gradualism that persistent variation predicted, he, himself, shrank from writing an alternative narrative (Gould 1995). Gould and Eldredge, in their turn, reminded evolutionary science of Simpson’s work when they published their paper on “punctuated equilibria” in 1972, but they interpreted the pattern in the framework of the existing orthodoxy; that is, they saw it as a series of alternations between ‘change’ and ‘not change.’ Moreover, as paleontologists, their emphasis was at and above the *species* level, which restricted speculation to those mechanisms that could have an ultimately resolving effect on the species as a whole. Since then, research into stasis, driven by the conviction that macroevolutionary patterns, no matter how convincing, could not deviate from known change-driven mechanisms and causes, has focused on microevolutionary processes that may explain the shape called “stability,” in a landscape where continuous variation is the only desideratum. In other words, virtually all research has looked for microevolutionary processes that explain why changes, during periods of stasis, have *not* occurred, or why they have occurred less often, or why changes were not conserved generally, or why the effects of these changes, inevitable though they

may be, have *not* been evident over time (for a review of the various approaches, see Estes and Arnold 2007).

This is not to say that ‘stability,’ generally has had no attention in macroevolutionary discussions. Niles Eldredge has written about the subject for his entire career and Gould, Lieberman, Jablonski, and others have made important contributions (Gould 1982; Gould and Eldredge 1993; Lieberman et al. 1994; Lieberman and Dudgeon 1996; Jablonski 2000, 2007; Estes and Arnold 2007; Eldredge et al. 2005; Hunt 2007). Gould and Lewontin (1979) aroused interest in history, architectural trends and pathways of development that have channeled and limited phenotypic design over time. They argued that, as evolution acted over many generations, there was an accumulating effect of form, function and process, which shaped living things and provided them with an underlying structure within which future evolution was bound. Their argument, however, couched in the familiar framework of change-driven processes, saw evolution as open-ended and boundless. As such, it did not conceive of the resulting stability and consistency as the outcome of countervailing causal mechanisms. Rather, the model viewed Bauplan and development, as random obstacles or biophysical impediments to the natural flow of change, the way trees, mountains and rock formations channel and constrain a river shaping it into opportunistic pathways and determining its shape and course. Gould (2002) provided a role for species’ stability in a transspecific context in his last book, an elaborate model of macroevolution based on the mechanisms and processes of microevolution. In his “Grand Analogy,” ‘species’ takes the familiar role served by the organism in Darwinian evolution and ‘species sorting’ takes the role of selection. However, stability, once again, is forced into its customary, subsidiary role. In his system, species compete for resources with one another and succeed or fail through the passive selection of their differences. The energy for the whole mechanism comes from “drives” to vary, expressed through anagenesis and biased production of offspring (directional speciation), both directional and both associated with the spread of novelty. Thus, the role of stability is familiar; in this case, in two parts, first, in opposing anagenesis by stasis during regimes of punctuated equilibrium, and second as an outcome of the general structures within species which constrain novelty, to the extent that they are cladistic, originate in the Bauplan, or are associated with the rate of speciation.

The notion of *species’ sorting* is not limited to Gould (for a review, see Grantham 1995). In systems of sorting, stability plays a role, but not as an overriding tendency, instead as an outcome of evolution that becomes a quality of species. The involvement of stasis is, as one of the measures or criteria of species’ viability, a contributor to something that might be compared to species’ fitness. The

more fit the species, the more likely it is to persist. Gould and Eldredge (1993) described it this way:

“Most macroevolution must be rendered by asking what kinds of species within a clade did better than others (speciated more frequently, survived longer), or what biases in direction of speciation prevailed among species within a clade” (p. 224)

As can be seen, in this scenario, stability itself is not macroevolutionary. It is a scalable, taxonomic quality of species like mating selectivity, rather than an imperative or a process evident across genealogies. Only the selection (or sorting) itself can be viewed as a macroevolutionary event. Nevertheless, the implications of species’ level stability in macroevolution are fascinating and potentially important. Vrba’s “turnover-pulse hypothesis” (1985) particularly, offers a fresh approach to temporally correlated speciations across taxa. This has been explored with good result in association with species stasis and with isolation by Lieberman et al. (2007).

In Ecology, the general progress of the discipline impacts on aspects of stability through its interest in species’ relationships, biotic-abiotic equilibriums, and how originally competing species come to specialize in their use of resources in order to establish a supportive, presumably safe and stable niche. Nevertheless, ecology is less concerned with intraspecific or transspecific stability than with ecological stability. It is not clear whether the discipline views biotic stability as an objective of natural behavior and a direction for organisms, or simply as a subcategory of ecological stability, viewed as a constellation of interactions between climate, food webs, organisms and terrain. In support of an overall imperative toward stability, is the Gaia hypothesis (Lovelock 1995) which proposes that all organisms alter their physical environment to maintain conditions that are conducive to their persistence. Thus, the biosphere, taken as a whole, is stable and self-regulating and all interactions, both interspecific and biotic-abiotic must be consistent with an overriding tendency toward stability. Free and Barton (2007), however, have pointed out, that because Darwinian Theory and Gaia are fundamentally incompatible (Lenton 1998), that conventional evolutionary biologists have tended to ignore Gaia, while Gaia theorists have tended to “ignore much biological theory and, especially experiment” (p. 611). Gaia theory, too, tends to be interested in processes of stability such as homeostasis, only in the ways that they can be assembled or magnified to reflect the global unifying assumption.

The question remains: Is the *macroevolutionary* pattern of stasis, seen in the fossil record, an indication of a *macroevolutionary* tendency toward stability, or is it simply an after-effect of the *microevolution* of living things as they adjust and change to accommodate their

circumstances? Clearly, there can be no hope of absolute proof on either side. However, I will argue that there is strong support for the independence and importance of stability and stabilizing mechanisms in their own rights, within the evolutionary realm.

Discussion

If the slowly growing interest in stasis is an indication of a generally broadening, more catholic approach to evolutionary activity, then it is worth revisiting whether variation alone can explain all the fundamental questions which may be raised in the science consistent with this larger context. Whatever the pretensions and assumptions of the traditional model, *something* seems to produce superorganisms, characteristic affiliations, prey-predator equilibria, engineered niches, balanced ecosystems, long periods of species' stasis, floral-faunal codependencies, host-parasite and symbiotic relationships. Ultimately, the tendency to vary may prove insufficient to explain the persistence of life in all these shapes. Moreover, something must be offered to explain why species acquire characters that make them more stable within their environments. Further, I suggest, that without a correlate tendency to *hold steady* or to repeat in kind, variations of any kind are fundamentally powerless to proliferate, and such stable relationships as mentioned above never come into existence. I submit that there exists a single imperative or tendency to stability, in the same manner as there is a single imperative or tendency to persistently vary. I base this assertion on logical argument, on the perpetual repetition of “nearly” exact phenotype for virtually every form of life, and on the evidence of many kinds of stabilizing mechanisms, some of which cannot be explained with reference to variation, or solely by appeal to the tendency to vary.

Evolutionary theory, to a great extent, began as an answer to the more popular idea that life's many forms emerged through *generative* processes, especially where there was the participation of a single *creator*. By contrast, Darwin proposed the idea that change was slow, gradual and un-agented. As such, one of the essentials came to be that life proceeds through *reproduction*. Yet reproduction depends upon “nearly” exact replication. Moreover, sexual reproduction, which Mayr viewed as fundamental to the biological concept of species (1996, p. 264), takes as necessary that most organisms live in relatively stable, at least minimally collaborative communities of highly similar conspecifics. Still, despite what would appear to be a heavy reliance on processes of replication, persistent affiliation, and mechanisms that maintain conspecificity, macroevolution has nevertheless been viewed as a distillation, or more appropriately, an amplification of the

processes of change, ‘writ large.’ Notwithstanding this emphasis, ‘replicability in kind,’ reliability, stability, regulation, and consistency in phenotype both between individuals and between generations, can be writ large, also. Perhaps, in this light, it may be reasonable to infer a parallel tendency, occurring even as populations diverge, to hold most similarities *unchanged*, even as the visible phenotype may slowly alter driven by the imperatives of change.

Possibly the best argument for stability's place among the pantheon of macroevolutionary influences is, paradoxically, the presumed process of *speciation*, or at least speciation in certain typical forms. Speciation is best viewed, not as an objective, but as a mechanism—a solution to a particular problem of existence. In this light, speciation, either in a gradual form, like anagenesis, or more abruptly, in an outright branching of a clade, can most fundamentally be viewed, at least in its final outcome, as the making permanent of a new, divergent phenotype, by its isolation. In keeping with this principal function, the cardinal and certainly the defining act of speciation, is the construction of reproductive barriers to all other living things (Dobzhansky 1937, for a review, see Mayr 1996). This seminal act preserves and protects the integrity of the new founding population from the invasive and unsettling influence of variations from the outside. However, the erection of reproductive barriers against all other organisms, even including close cousins, is a drastic step. Once in place, most isolating mechanisms cannot be violated; they constitute a one-way door. Moreover, once completed, the transition prevents any and all variations arising in any other organisms from affecting the newly created gene pool. Therefore, it is of the most vital concern for the future of the incipient species that essential variations be incorporated and fully proliferated throughout the population, *before* the selection of any potentially isolating mechanisms commences. If this were not the case, then the fledgling species might well be prematurely and injudiciously separated from the larger wellspring of useful and practical novelties which could arise within the originating deme, in the service of supporting the diverging form's search for an acceptable balance between its shape and the set of adaptive optima prevailing. This is especially true in that isolating mechanisms, like all variations, are liable to arise in only a subset of the founding deme, and spread through selection (Levinton 2001). Until the generalization of these variations was complete, over many generations, the presence of isolating mechanisms in some, but not all members of a population would render the splinter group's future, highly precarious. Additionally, all stress and perturbation, which might signal the need for further adaptive alteration, must similarly be at a minimum prior to the erection of a reproductive barrier, on the same grounds.

As a consequence, it is highly likely that speciation *will not* occur (or not take its most crucial step) until a founding population is stable in relation to all biotic and abiotic influences. But, this would mean that stability can be viewed as a crucial milestone prior to the final (or primal) act of speciation, and that the memorialization of speciation in the form of reproductive isolation, is the preservative act occurring only *after* a founding population has reached a stable condition.

Additionally, genetic structure seems to bear out the co-importance of variety and stability in evolution. DNA does not, by its configuration, indicate that ‘change’ is the only overriding function or objective of the genome. While the double helix design, transcription, translation, recombination, mutation, and even drift, suggest that variation is a fundamental instrument of change, much of the body of the DNA molecule is taken up with a virtually flawless recapitulation of phylogeny, one that permits organisms to produce a functionally endless stream of “almost” identical offspring. Moreover, in any narrative of genetic evolution, no variations arising independently could be conserved unless the species’ structure retained the ability to produce not only the original form, but the identical genetic nuance in addition, over and over again throughout the population. At most, then, on the issue of ‘variability’ versus ‘stability,’ DNA equivocates. Both variability and stability seem well represented as simultaneous, somewhat rival influences on life’s overall design.

Yet, none of these arguments would be of any consequence, if it could be shown that the most compelling examples of stability were, in fact, explicable with reference to mechanisms of variation. Important in this regard is the effort to demonstrate that species’ ‘stasis’ can be subsumed under ordinary microevolutionary processes. Species’ stasis is a significant test case since, what better advertisement for stability is there than the apparent steadiness of form over millions of years within lineages? While supporters of Darwinian orthodoxy will quarrel with ‘punctuated equilibrium’ as a model, even its most severe critics allow that periods of stasis are common (e.g., Levinton 2001). But, if stable states can be successfully attributed to microevolutionary mechanisms, then there is no reason to amend the macroevolutionary landscape. True, stasis comes into specific relief as a result of an observed pattern across many species on a paleontological timescale. However, if such patterns prove tractable to explanations rooted in processes of change, then the argument that stability is a byproduct of “normal” evolution will be convincing. Still, some have argued that “character” explanations do not apply to species stasis. Stanley (1979) argued that microevolutionary processes cannot logically be extrapolated to explain macroevolutionary patterns (also, see Eldredge and Cracraft 1980).

Rensch (1959; also see Vrba 1983) has argued that pattern producing processes (like species selection) would necessarily operate above the level of the population.

Nevertheless, the literature on stasis does claim to have identified the causes of long periods of little change in the fossil record of species; causes that emerge from traditional sources. Estes and Arnold (2007) developed statistical models for six of the seven underlying factors that they had identified as having been historically associated with stasis. Using these models, they tested, by means of “best-fit” analysis, each of the factors against a large dataset by Gingerich (2001). They concluded that the best fit was to a pattern modeled after “stabilizing selection” (Charlesworth et al. 1982) operating in the presence of an adaptive peak, constrained within an optimal range. While this seems like evidence of a general tendency toward stability, the authors did not intend it as such, and stabilizing selection has not been conceived of in this context. For example, stabilizing selection is abundant in rapidly evolving lines (Mayr 1992). Additionally, Kaplan (2009) has correctly pointed out, that curve fitting does not create a causal chain between the inferences associated with an artificial curve and phenomena in the natural world. Also, the failure of some models to match an overall pattern does not indicate that the processes inferred to be associated with those models have had no effect on the outcome. For example, human athletic performance is affected by ambient temperature; yet, one could not accurately predict performance based on temperature alone. Moreover, stabilizing selection has not been shown to operate systematically outside populations (Eldredge et al. 2005), so its effectiveness within a species is difficult to justify, even if it follows a recognizable pattern across populations.

Lieberman et al. (2007), expanding on an earlier argument (Eldredge et al. 2005; Lieberman and Dudgeon 1996), indicated that in broadly distributed species the fact that they tend to be broken up into distinct geographic populations or demes with quasi independent evolutionary histories is the primary contributor to stasis. They further suggested that this would be a reason why stabilizing selection would be unlikely to promote stasis: because it would not act consistently across such species. However, this motif involving many, widely separated demes with disparate selection regimes, is only one of many extant patterns of dispersal. Not a few narrowly dispersed or habitat tracking species never meet the minimum conditions of range and distribution the authors argue are essential for the development of evolutionary stasis. Additionally, some species are not likely to produce population adaptations, despite varying habitats and conditions. For example, extinction is more likely than adaptation for many habitat-selecting species in the face of alterations to their environment. Many species actively

alter their environment (Day et al. 2003), which consequently constrains the selection regime they experience. It is also not impossible that all demes of a given species, already in stasis, might meet relatively similar conditions and/or be so constrained by Bauplan, architecture, niche habituation, and established conformance to a wide range of abiotic conditions, that stasis will persist over any dispersal conditions and set of selection regimes, regardless.

Processes and Mechanisms of Stabilization

There is considerable evidence for transspecific mechanisms and processes of stability, involving living entities at many levels including the cell, organ, organism, group and society. These processes result in conformance, accommodation, adjustment, mutuality, cohesion, regulation, or consistency, or reduce competition, or diminish divergences and novelties in behavior. While mechanisms that increase conformance passively, or reduce divergence and novelty, are equivocal with regard to their representation as either ‘stabilizing’ or ‘anti-variational,’ it is hard to make a case that processes that regulate state within optima, forestall competition, encourage repetition and consistency, foster cohesion, or that help an organism respond flexibly to stress or perturbation, or engineer the environment to be compatible with existing character, can be well explained by appeal to the single imperative of ‘persistent variation.’

Other than “stabilizing selection” (Charlesworth et al. 1982), there has been little attention in the literature to mechanisms or processes of stability, *per se*. Yet there is an extensive literature on constraints of variation that may alternately be viewed as acting on behalf of stability. Futuyma (2010) has argued that there may be some value in distinguishing constraints into two categories: *character* constraints that operate “on particular characters or character complexes,” and *systemic or organismic* constraints, that “apply widely across the genome and phenotype.” (pp. 1865–1866). By far, the largest body of literature concerns character constraints, since they can be viewed purely as microevolutionary processes and mechanisms. Epistasis, antagonistic pleiotropy and linkage disequilibrium can limit the appearance of variations individually and by so doing, collectively prevent the generation of novel genotypes (Barton and Partridge 2000), as can alternative selection (Falconer and Mackay 1996). Cooper and Lenski (2000) have shown that despite an increase in genetic variations over time, phenotypic evolution declined in succeeding generations of *Escherichia coli* supporting the existence of adaptive peaks (Wright 1931), the foundation of stabilizing selection (Charlesworth et al. 1982). Interbreeding tends to spread common genes and suppress

invasive ones (Wilson et al. 2009). Futuyma (2010) identified six kinds of evidence for constraints on evolution at the genetic level. These include evidence of: (1) reduced or absent variation; (2) characters that, in combination are antagonistic to the direction of selection (with particular reference the **G** matrix); (3) “regressive evolution” such as in the loss of genes in endosymbionts, parasites and troglolobites; (4) limited mutation rates that limit the variance available for selection; (5) selective sweeping of linked variations by novelties with fitness advantages; and (6) character overload, in which too many characters compete for adaptation simultaneously in too many dimensions. A detailed exposition of genetical constraints is beyond the scope of this paper but is available elsewhere (see Hansen and Houle 2004; Eldredge et al. 2005; Blows and Hoffmann 2005; Walsh and Blows 2009; Futuyma 2010).

Cells, have stabilizing mechanisms that create and maintain: (a) membrane potential (Wright 2004); (b) the electrochemical energy of ion and solute gradients (Aronson et al. 2003); (c) cell size (Strange 2003); and (d) *ph* levels (Boron and De Weer 1976). Organisms often include specific cells, organs, symbionts, etc., arrayed in elaborate internal regulatory subsystems coordinating many participating entities. There are as many as eleven regulatory subsystems (muscular, skeletal, integumentary, respiratory, digestive, circulatory, immune, excretory, nervous, endocrine, and reproductive systems) which complex animals include in their physiology. These systems use negative feedback control mechanisms, such as TSH (blood levels of TSH serve as feedback for production of TSH), and positive feedback mechanisms, such as oxytocin (which is produced by uterine contractions in mammals, and subsequently accelerates the contractions during childbirth) to regulate their operation.

Organisms appear to have a great variety of stabilizing mechanisms. The survival of all metazoan organisms is dependent on the regulation of O₂ delivery and utilization to maintain a balance between the generation of energy and production of potentially toxic oxidants (Semenza 2007). Populations of many species have been shown to evolve to match adaptive peaks (e.g., see Benkman 2003). The size of populations, for many species, is carefully controlled within upper and lower limits, often regulated by available resources (e.g., Sinervo and Licht 1991), or by the presence and concentration of other species such as in prey-predator or host-parasite ecologies (e.g., see Harrison 1979; Holling 1965). Many species from social insects to primates have mechanisms for monitoring a shared range or territory (e.g., in lions, see Mosser and Packer 2009). So-called *superorganisms* (Hölldobler and Wilson 2009) have highly regulated habitats. For example, many species of the taxon *Isoptera* build similar, highly sophisticated, temperature regulated mounds that include function-specific chambers

seemingly with allometric pre-calculation (Turner 1994). Sexual selection, to the extent that it encourages, on average, qualities like fertility, strength, size, dominance, etc., can arguably be said to regulate novelty and encourage an average phenotype. For example, within populations, many species regulate novelty through: (a) reproductive suppression associated with dominance (Hass and Jenni 1991), or social stress (Heistermann and Schulke 2008), (b) mate selection of intermediate phenotypes (Mead and Arnold 2004; Brooks et al. 2005), (c) aggressive culling of non-conforming or *dismorphogenic* offspring (Wright 1968), and (d) band expulsion of subordinate rivals (Clutton-Brock et al. 1998). Evolutionary ecology has identified numerous examples of animal-environment interactions that regulate elements of both. Niche-constructing processes (Odling-Smee et al. 2007) generate feedbacks which alter natural selection on the niche constructors themselves and on organisms sharing the same environment (Lenton 1998). Microbial ecologists use the term ‘syntrophy’ to refer to situations where an unselected feedback process evolves into an adaptive feedback mechanism, such as when two microorganisms increase the output of their waste products, which are consumed by the other (Sachs et al. 2004, or, for a general discussion of stability in complex ecologies see Free and Barton 2007). Some species actively preselect environments (*habitat selection*) that are more predictable and more suitable for their own characteristics (e.g., in birds, see Norris and Marra 2007), a suitability which uses a priori conformance to diminish large post-choice discrepancies between existing traits and adaptive peaks. By reducing these large discrepancies preemptively, forms may remain relatively stable. In the same way, *habitat tracking* (e.g., see Dalen et al. 2007), provides the same service to a relatively established population by ensuring the persistence of a similar level of conformance into a new ecology.

There is also some evidence within nature of processes that seem to serve both stability and variation simultaneously. This contradictory or paradoxical action can be seen in polymorphism of dispersal. Rather than uniform dispersal within a species, Mayr (1963) predicted a proportional polymorphism of geographic habitation preferences, with some offspring highly committed to the local environment (“philopatric”), most (“vagrants”) tending to scatter but not very far and returning to reproduce, while a small minority (“nomads”) venturing great distances and establishing new colonies hundreds of miles away from the founding population. This pattern has been seen in birds (Brown 1974; Stacey and Ligon 1987), reptiles and mammals (e.g., Goossens 2006). While most of the contemporaneous explanations for these phenomena have been microevolutionary, involving “relative fitness components of dispersing and philopatric individuals” (Belichon et al.

1996:504, also see Johnson and Gaines 1990, for a review), this is an unlikely cause since the behavior itself ought to produce homogeneous populations which reproduce selectively for nomadic or philopatric tendencies. Ambivalent macroevolutionary forces may be a better fit, with “philopatry” due to the stabilizing tendency, “vagrancy” related to pure ambivalence, and “nomadism” associated with the impulse to vary.

Implications

While some of the reason that stability has not been proposed as playing a more central role in the macroevolutionary landscape is, no doubt, paradigmatic, it is also true that, were stability recognized as important, it would complicate the picture of evolutionary process in ways that would require rethinking of some basic principles. Seen as a pivotal player in macroevolution, ‘stability of form’ is a direct rival to the tendency for forms to persistently change. As such, it would have bearing on evolutionary process at several causal levels. For example, just as there are molecular processes of change, there ought to be molecular processes of stability. As has already been pointed out, there are such mechanisms, although they are not currently conceived of as such (see “character” constraints, above). At the organismic or population level, a tendency to hold form steady would amend the standard microevolutionary narrative of trait adaptation. This tendency might manifest itself in different ways. First, stabilizing characters at this causal level might directly oppose the establishment of specific variations. More likely, novel change variations may be rendered unnecessary as a result of an acquired characteristic that permits persistence without the need for phenotypic change. For example, behavioral plasticity, by ensuring flexibility in a variety of disparate circumstances, produces stability by eliminating the need for additional adaptations; yet, it is not a constraint on any particular character. Affiliation within a species, too, acts to forestall the need for individuals (even fragile, relatively defenseless varieties), to independently construct habitats, defend themselves, hunt alone, and locate mates, etc., without acting to constrain particular variations. There may also be characters that, rather than fostering changes in the phenotype, act to stabilize the current form, for example by reconciling two rival variations. More generally, stability may act so as to maintain consistency in character throughout the population. In other words, there may also be a transspecific mechanism to hold the phenotype *unchanged*, which acts against any variant. There are implications, too, for the concept of fitness which, as a measure of the distance from

optimality, may be more associated with stability than variation. We, too often, view a fitness difference as purely an indication of the effects of a trait on behalf of some variation, yet it may indicate a test of whether a given variant aided the phenotype in moving toward greater consistency of the population, toward greater stability of the individual, toward some combination of characteristics that might result in greater personal or population stability, or toward greater stability of two diverging subgroups within the population, instead. Also, it is clear that variants are differences, suggesting that traits may be tested based on whether they bestow a sufficient advantage to the individual to override the *potential loss* in fitness that accrues from deviation from the population's current, average intermediate phenotype. In other words, every change, for an individual and a population, may signal both a potential increase and a potential loss in fitness.

The most compelling implication of including a general tendency toward stability in the macroevolutionary landscape is that the conception of organisms and, to some extent, higher levels of organization like groups and societies, may take on the characteristics of active living systems in balance, rather than passive instruments of change. This would argue for the inclusion of elements of adaptive engineering and strategic behavior, beyond sexual selection, more directly in evolutionary discussions, and suggest that destabilizing conditions, like stress and perturbation, had an impact on both the slope of radiations, and the rate of speciations (for a novel mechanism that might explain these rate changes at a molecular level, see Zeh et al. 2009). What is more, to the extent that higher levels of organization are self-regulating, the characteristics of regulatory systems would have to be inferred to exist in such entities. Thus, for example, a self-regulating society like a superorganism would have to include: sensory *mechanisms of recognition* of disturbance, *central control* to select among and implement available options for correction, and *effecting mechanisms* to restore the regulated condition. If such mechanisms were found, then it would lend considerable power to the argument that centrally controlled organizations of living things above the level of the organism, like the group, population and society, are, themselves, living entities subject to and capable of the same processes and mechanisms of evolution as cells and organisms. Miller (1978), after a careful and thorough systems analysis of living entities, concluded that cohesive organizations of living things do indeed include such mechanisms (although species do not), and that they are, as a result, living systems. An exploration of these possibilities is beyond the scope of this paper, but the implications are dramatic and far-reaching, and would seem to offer many opportunities for future research.

Summary

Evolutionary science has known for some time that there were processes of regulation at all levels of organization, that organisms gradually establish themselves in comfortable niches where their persistence is more likely, that shape is gradually constrained over time, that demic adaptations generally reduce the discrepancy between adaptive optima and the population, that organisms come to affiliate in stable groups that insulate them from individual threats and dangers, that resources are balanced between species in complex ecosystems, that populations control their own size, that societies interact with precision and coordination, that variation could not alone have caused life to be maintained without consistency and repetition, in short, that life seems to move toward stability at many levels. However, these observations place no obligation on the discipline to encompass stability within its theoretical framework. Nevertheless, the science does have an obligation to verify that its existing model is the best available, one that explains most of the phenomena that is widely considered evolutionary. But, what is the proper domain of evolutionary phenomena? In the past, too often, the discipline has limited itself to the elements and mechanisms of change. Yet, the now burgeoning bodies of literature demonstrating stasis and its consequences, not to mention behavioral plasticity, developmental regulation, and the conservation of morphology, along with the literature on the role of species' stability in the maintenance of ecologies, argue for a broader context of evolutionary design and construction. In short, Evolutionary Science may wish to itself, evolve, and define a larger realm encompassing all the elements of biological persistence. This broadening of phenomena may, by itself, indicate the need to consider alternative models of the macroevolutionary landscape. The one that is suggested here includes both processes of stability and processes of change.

As for stasis, stability in the fossil record may be a direct reflection of the coming to exist of a balance between these tendencies to change and to stay the same. To the extent that that is true, then Gould and Eldredge were prophetic when they used the word "equilibrium" in their model. The pattern called "punctuated equilibrium" further may be a reflection of a stage, within the history of a lineage, where stability and variation are in a rather settled period of an ongoing contest that frequently results in the mastery of stability for long intervals. Stasis, would reflect the processes of stability offsetting the processes of change, while periods of rapid divergence would reflect sudden change fostered by a disturbance in this balance, for example, when demes become reproductively isolated in unusual ecosystems for long periods, when anomalies in novel environments are discovered through dispersal, or more

generally in the case of dramatic climatic change, habitat invasion, perturbation, stress, or abrupt changes in the pattern of biotic interactions.

Gould and Lewontin (1979), more than thirty years ago, touched on the importance of macroevolutionary architecture and on stability particularly when they wrote, that:

“organisms must be analyzed as integrated wholes, with *Baupläne* so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs” (p. 581).

Thus, stasis may be reminding us that we are missing a key element of the big picture of micro- and macroevolution: that the tendency of living systems to stabilize is transspecifically correlated with the tendency to persistently vary, and cannot be ignored in any evolutionary scenarios. Further, that these two tendencies may collaborate toward optimality, or they may result in processes that come to rival one another and among which, organisms are driven to find an acceptable compromise between varying and staying the same. In either case, both would seem to be necessary for life in the natural world.

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