Proc. Natl. Acad. Sci. USA
Vol. 90, pp. 595–599, January 1993
Evolution

Species selection on variability

(hierarchical selection theory/emergent characters/aggregate characters/adaptation)

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Contributed by Stephen Jay Gould, October 14, 1992

ABSTRACT Most analyses of species selection require emergent, as opposed to aggregate, characters at the species level. This "emergent character" approach tends to focus on the search for adaptations at the species level. Such an approach seems to banish the most potent evolutionary property of populations—variability itself—from arguments about species selection (for variation is an aggregate character). We wish, instead, to extend the legitimate domain of species selection to aggregate characters. This extension of selection theory to the species level will concentrate, instead, on the relation between fitness and the species character, whether aggregate or emergent. Examination of the role of genetic variability in the long-term evolution of clades illustrates the cogency of broadening the definition of species selection to include aggregate characters. We reinterpret, in this light, a classic case presented in support of species selection. As originally presented, the species selection explanation of volutid neogastropod evolution was vulnerable to a counterinterpretation at the organism level. Once this case is recast within a definition of species selection that reflects the essential structure and broad applicability of hierarchical selection models, the organism-level reinterpretation of variability loses its force. We conclude that species selection on variability is a major force of macroevolution.

Selection

We begin with some basic distinctions. Most important is the difference between a process and an outcome of that process; in this case, selection is the process, and evolutionary change is the outcome. The process of selection involves an interaction between an entity and its environment or, more specifically, between a particular trait of an entity and particular aspects of its environment. Part of the fitness calculated for an entity represents the particular value conferred by having a specific trait in a specific environment. In other words, the component of fitness associated with a trait is the representation, in an evolutionary model, of the process of selection.

The selection process itself must be contrasted with the result or outcome of that process. Sorting is simply the differential birth and death of individual entities in a population, while selection is a potential cause of that sorting (ref. 1, p. 217). Sorting at a particular level has a variety of potential causes; it can arise from selection acting at that level or occur as a consequence of chance or of selection processes at either a higher or a lower level.

Species Selection

A number of attempts have been made to apply the basic notion of selection to the species level. Vrba, Eldredge, Gould, and others (1–7) in several articles have defended the idea that selection at a particular level requires characters to be heritable and emergent at that level and to interact with the environment to cause sorting. Species-level properties are divided into aggregate and emergent characters. Aggregate characters are based on the inherent properties of subparts and are simple statistics of these properties, while emergent characters arise from the organization among subparts (ref. 4, p. 146). Possible emergent characters among species include population size, distribution, and composition (4).

According to this argument, which we shall call the "emergent character" approach, one need only show that a trait in question is aggregate, not emergent, in order to demonstrate that species are not functioning as units of selection in a particular case (1, 2, 4).

We shall contrast the emergent character approach with an "emergent fitness" or "interactor approach," which emphasizes the nature of fitness values, rather than type of character. Under this approach (presented in more detail in *Emergent Fitness or Interactor Approach*), the relationship between character and environment becomes the key issue. This relationship is represented in the fitness parameters. Selection processes are delineated by distinctive attributes of the fitness parameters. Interactors, and hence selection processes themselves, are individuated by the contributions of their traits to fitness values in evolutionary models; the trait itself can be an emergent group property or a simple summation of organismic properties. This definition of an entity undergoing selection is much more inclusive than in the emergent character approach, since an entity might have either aggregate or emergent characters (or both); this distinction between emergent and aggregate characters does not usually appear in quantitative models of species selection (e.g., see ref. 8). The emergent fitness approach requires only that a trait have a specified relation to fitness in order to support the claim that a selection process is occurring at that level (cf. refs. 7, 9, and 10; see *Emergent Fitness or Interactor Approach* and *Appendix*).

Adaptations

An important component of the emergent character approach is its focus on adaptations. The existence of an emergent character at the species level is taken as equivalent to the existence of a potential species-level adaptation (ref. 11, p. 388; ref. 12, p. 132).

The focus on characters rather than fitnesses is related to this requirement for adaptations. Emergent characters are always potential adaptations. Not all selection processes produce adaptations, however. The key issue, in delineating a selection process, is the relationship between a character and fitness. The emergent character approach is more restrictive than alternative schemas that delineate selection processes, for only some selection processes at the species level (perhaps very few) result in the evolution of emergent characters or adaptations. The emergent character approach picks out a subset of cases given by the interactor approach;

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it is, to be sure, an especially interesting subset—namely, species-level adaptations. Nevertheless, if one is interested in discussing evolution by species-level selection processes *per se*, then this approach is too restrictive.[‡] Let us return to the emergent fitness approach to see how aggregate traits, which are not adaptations, could function in a species selection process.

Emergent Fitness or Interactor Approach

As the guiding idea behind our hierarchical view of selection models, we hold that selection processes are best described in terms of interactors (see refs. 15–17). An interactor is an entity that has a trait; the interactor must interact with its environment through the trait, and the interactor's expected survival and reproductive success are determined, at least partly, by this interaction. In other words, the interactor's fitness covaries with the trait in question.

If we have an interactor, we should expect to find a correlation between the interactor's trait and the interactor's fitness.[§] For evolution by selection to occur, both the trait and the correlation between trait and fitness must be at least partly heritable (in the sense of narrow heritability). Heritability depends, in turn, on the additive genetic variance of the trait by definition. It should be recalled that fitness itself can be analyzed into components, each correlated with a trait that affects fitness. In selection models, the interactions *per se* of trait and environment are not represented; rather, the evolutionary effect of this interaction is represented by the selection coefficient (fitness parameter). We can model the selective effects of interactions by partitioning the overall fitness into levels where the proper correlation between a trait and a component of fitness can be represented. In selection models, then, those interactions between trait and environment that yield evolutionary changes are represented by an additive component of variance in fitness correlated with variance in the trait in question.[¶] In considering a hierarchy of selection models, we are simply generalizing this principle that relates the efficacy of natural selection to additivity. Note that this view can accommodate more than one level of selection operating simultaneously.

Clearly, a potential problem exists here. Suppose the correlation between trait and fitness at a higher level is a simple effect of the traits and fitnesses at a lower level. Since we do not want to count these lower-level interactions twice, we must avoid representing selection at the higher level in this case. This is done by describing interactors at the lower level first. If a higher-level interactor exists, the higher-level correlation of fitness and trait will appear as a residual fitness contribution at the lower level; we must then go to the higher level in order to represent the correlation between higher-level trait and higher-level fitness. Hence, species-level fitness is not defined as an average or sum of the organismic fitnesses within a species (see refs. 7, 10, and 19).

More simply put—the operative notion in all examples of higher-level selection is some sort of interaction effect or context dependence (e.g., ref. 20; see ref. 21, chapt. 7; here, "context" refers to the other entities in the same population and not to the environment). Intuitively, the properties of the other members of your group must make a difference, and there must be a correlation between group type and fitness.

One might object that the above approach to delineating interactors is overly reductionist. After all, it seems that this view simply embodies G. C. Williams's famous and misleading maxim: don't even consider any higher level of selection unless the lower-level model proves empirically inadequate (ref. 22, p. 55). The problem with Williams's maxim is that different selection processes may sometimes yield identical gene frequency predictions. In these cases, additional information about population structure, group membership, and group-level fitnesses is needed in order to tell which model best fits the system at hand (see ref. 19, pp. 86–96).

The approach that we support is intended not as a research strategy, as Williams's maxim has often been used, but as a method of evaluation or calculation. Our recommended method for assessing selective levels is used only after all the information has been obtained, including data about population structure, group composition, and group-level fitnesses. In the method we advocate, and as a crucial difference from Williams's approach, this information is not collected under a reductionist research program; for in such a program, the lowest-level selection model is accepted without even testing whether a higher-level model might be more adequate (see refs. 17, 19, 20, and 23–25).

Variability

Dobzhansky, in his *Genetics and the Origin of Species* (26), considered variability as a species-level character related to species survival (cf. refs. 27–30). Dobzhansky notes that a reservoir of genetic variation within species acts as a hedge against extinction (ref. 26, p. 127). He sees a trade-off involved in variability; species that concentrate adaptations very narrowly are favored by natural selection at a given moment, but they sacrifice plasticity, "the flexibility that retention of a goodly amount of genetic variation affords against the (inevitable) change in position of the adaptive peak" (ref. 12, p. 199; ref. 8; cf. ref. 9, p. 15; ref. 31).

Eldredge acknowledges that the reservoir of genetic variability discussed by Dobzhansky could play a role in species survival (ref. 12, p. 182; see ref. 32). But while Lewontin (33) talks of selection contributing to or maintaining variation, Eldredge claims that variation is not being selected because it conveys an advantage; rather, the maintenance of variation is just an effect of ordinary selection on organisms. While Eldredge agrees that variability is correlated with long-term species survival, he rejects the possibility that this might count as species selection because variability is not an adaptation. We claim, in contrast, that variability is a perfectly good species-level trait that can be associated with genuine species-level fitness (see ref. 19, pp. 110–112).

Many evolutionists shared Dobzhansky's interest in variability and its involvement in long-term species survival. During the early 1950s, evolutionists produced genetic models of the relation between variability and what were then called (improperly, by our definitions) species adaptations

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[‡] Dawkin's arguments against species selection are refreshingly clear about this distinction. Following his admission that species selection is, in principle, possible, he expresses skepticism that species selection may be important in explaining evolution. He then continues "This may just reflect my biased view of what is important. . . what I mainly want a theory of evolution to do is explain complex, well-designed mechanisms like hearts, hands, eyes, and echolocation" (ref. 13, p. 265). We would reply that a theory of evolution has many more, and equally important, things to do. Dawkins may be revising his view, since he has now offered a species-level selection interpretation for an aggregate species-level trait (14).

[§] Several methods are available for expressing such a correlation. For instance, under the covariance approach, the change in the mean value of a trait under selection can be expressed as a covariance between relative fitness and the character value (i.e., quantitative description of the trait). Actually, it is somewhat imprecise to refer to "an interactor's fitness"; this quantity should be understood as the probability associated with the interaction of the interactor and its environment.

[¶] Damuth and Heisler (7) claim "selection can be occurring at a level only if there is a relationship between some character of the units at that level and the fitnesses of those units." They assess the existence and intensity of this relationship through the regression of the fitness on the character value [see the selection gradient analysis, a phenotypic approach (18)].

(29, 33). Why was this subject dropped? We suggest that the virtually universal failure to distinguish between adaptations and selection processes led to this abandonment. The attack on group adaptations, led by Williams (22), was interpreted as an assault on the possibility of group-level selection processes in general, although such a conclusion does not follow. Hence, we suggest, species-level variability, like other group-level properties, was discredited through its association with unsupportable arguments for group-level adaptationism (ref. 32, p. 491). We would like to revive interest in the relation between genetic variability across groups and lineages, and long-term success of lineages, by placing this subject in the context of hierarchical selection theory.

Williams did a service to the community of evolutionary biologists by refining the definition of adaptation and by insisting on strict standards of proof for adaptedness. His analysis drove a wedge between fitness (expected reproductive success) and adaptedness, where only adaptedness signifies adaptation (34, 35). Unfortunately, biologists seem to have lost track of those selection processes that do not yield cumulative adaptations. (A stronger link may exist between adaptation and selection at the organism level than at higher levels. This might constitute a genuine and interesting difference between these levels.) If evolutionary theory is to yield accurate models of all selection processes, however, then the set of available models must be expanded.

Once the definition of species selection has been brought into alignment with other hierarchical selection models, species selection gains potential for a greatly expanded role in evolution.[‖] For example, let us turn to the key item barred by the emergent character approach but included under the emergent fitness approach—variability. We next offer a reinterpretation of a classic case presented in support of species selection. The original interpretation, advanced by Gould, is vulnerable to a counterinterpretation at the organism level. When the case is recast in terms of variability, however, the organism-level reinterpretation loses its force.

Neogastropods

Cases that suggest no clear adaptive explanation for trends in organismal phenotypes are promising for species selectionists. Trends may occur because some species speciate more often than others. For example, many clades of marine invertebrates exhibit a trend toward increased frequency of stenotopic species (stenotopes are narrowly adapted to definite environmental factors; eurytopes can tolerate a broad range of environments; see refs. 41–46). Sometimes this trend leads to elimination of eurytopes completely, as in the volutid neogastropods (43). Analysis of this clade shows a much greater rate of speciation among stenotopic species, which helps to produce the trend even though stenotopes also suffer a higher rate of extinction.

The higher rate of speciation in stenotopes has been interpreted as resulting from isolation of small populations; speciation may be enhanced because stenotopes generally brood their young, while eurytopes tend to have planktonic larvae—and species with planktonic larvae exhibit high levels of gene flow (ref. 42, p. 96). Jablonski (45) argued that different modes of larval development confer different population structures, which could be counted as species-level traits. (We part with Jablonski's analysis in that he supported the claim for species selection by characterizing larval ecology as an "emergent property," while we concentrate on tying the population structure to lineage-wide genetic variability.) The trend is interpreted as a case of species selection because stenotopic species take over the clade by differential speciation, which is not sensibly explained by organismic-level natural selection (ref. 42, p. 97; see discussion in ref. 10; ref. 45).

But why call this species selection? The trend toward stenotopy in the lineage can be seen as an effect of an organismic-level property—namely, the tendency for larvae to be nonplanktotrophic. The key factor in the higher rate of speciation is isolation, and a primary cause of isolation is the feeding habits of individual offspring. Hence, a species-level pattern is produced but does not arise from a true species-level property. In fact, those who require a species-level adaptation would certainly reject nonplanktotrophy, as it is a property of organisms. Therefore, the organismic selectionist might argue, there is no species selection operating here; this is just a case of organismic-level selection producing a higher-order effect (e.g., see ref. 13, p. 266).

In response to this challenge, we would like to recast this case in terms of variability and its role in the evolution of lineages. Consider the case in which eurytopes have been eliminated from the lineage: A species with nonplanktotrophic young has a tendency to develop isolated populations—hence, a tendency to speciate. Speciation leads (in this case) to more genetic variability across the lineage (counting from some ancestral gene pool; see ref. 29). These species also have a relatively high probability of becoming extinct. [Jablonski (46) provides additional support for the argument that variability provides a target for species selection. He documents the role of geographic range in species persistence and heritability.] But, for the overall lineage, enhanced speciation leads to success.[**] Note that the immediate cause of success is the tendency to speciate, but the long range explanation of success could be related to variability.

The species with planktotrophic young do not speciate much, as a result (partly at least) of extensive gene flow; hence, they present fewer alternative strategies for facing environmental challenges. These species are longer-lived relative to the stenotopes—but note that, in the case of the volutes, the eurytopes are all extinct (36).

Let us reconsider the trait, "tendency to speciate." Gould (42) originally considered this feature both (*i*) an emergent property, and (*ii*) a property resulting from a larval strategy—i.e., an individual-level trait. But in this case, stenotopes not only tend to speciate more; the extinction rate, even though higher than in eurytopes, is also lower than the speciation rate. Hence, stenotopes are the only long-term survivors in the lineage. That is, there is advantage (to the original gene pool) in speciating more. We propose that the advantage comes from success in some of the experiments that occur during speciation. If one counts the total genetic variability across the whole lineage, then stenotopes as a collective lineage maintain more variability than eurytopes. This variability is expressed in the speciation experiments, and the

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[‖] Discussions of the evolution of sexual reproduction have sometimes involved species- and lineage-level selection processes. Stanley, for example, argued that a sexually reproducing ancestral species produces a much greater ecological diversity of descendant species than an otherwise identical asexual species; this greater diversity makes the sexual lineage less vulnerable to extinction than the asexual one (cf. refs. 36–40). Vrba, who formerly emphasized the limited role of species selection in evolution, based on the requirement that it must involve species level adaptations (2, 3, 11), now thinks that species selection will be "quite common" (ref. 3, p. 162).

[**] As a rough notion of success, we can borrow Thoday's definition of the fitness of a "unit of evolution," which is equal to the probability that it "will survive for a given long period of time, such as 10^8 years,"—i.e., it "will leave descendants after that lapse of time" (ref. 29, p. 98). Similarly, Arnold and Fristrup define success as a measure of the relative increase or decrease in descendants of a lineage (and fitness as the expectation of that success; ref. 10, p. 120; cf. ref. 47).

presence and maintenance of variability contribute to the long-term success of the stenotopic lineages.

This is not the only possible evolutionary scenario that could be given for this case, of course, but it is a possible and testable candidate. A lineage-level component of fitness based on variability can, in principle, be quantified and entered into the models previously discussed. By taking this alternative seriously, we avoid thinking that simply because a higher-level trait in a species is, in fact, caused by the behavior of individual organisms, species selection cannot be operating (ref. 19, chapt. 7; refs. 48 and 49). Hence, in our view, a trait can ordinarily be considered as a genic- or organismic-level trait, but it can nevertheless participate causally in species selection. The existence of such cases will expand the amount of evolutionary change explicable by species selection.

Macroevolutionary Significance of Species Selection on Variability

We have shown, by an argument based on a logical analysis of evolutionary theory, that variability and other aggregate traits can figure in species selection defined by emergent fitnesses under the interactor approach. But while cogent logic may define the philosopher's task, it can only represent the starting point for a practicing biologist. The authors of this paper, as a collaboration of both professions, must therefore pose a further question: is species selection on variability important in evolution; does it display a high relative frequency among the causes of trends? Almost all major questions, and great debates, in natural history revolve around the issue of relative frequency: for example, selection and neutrality, adaptation and constraint.

The centrality of this point was recognized by Fisher (50). He acknowledged that the logic of species selection was unassailable but denied this process any important role in evolution by arguing that it would always be overwhelmed by his (and Darwin's) favored mode of selection on organisms. The number of organism births overwhelms species births by so many orders of magnitude, Fisher argued, that nothing much can accumulate by selection among species relative to organisms.

This argument might work in Fisher's world of uniformity, isotropy, and universally effective (and therefore nonrestrictive) intraspecific variability. But the geological stage of macroevolution presents a situation most uncongenial to Fisher's assumptions—a world that suggests an important relative frequency for selection on species level variability. Consider just two aspects of the fossil record.

(*i*) Punctuated equilibrium. Despite continuing arguments about interpretation (51–54), nearly 2 decades of study and debate have established a high relative frequency for the geometry and topology underlying this theory (55, 56)—geologically abrupt appearance and later stasis of most morphospecies in the fossil record. Fisher's argument fails because most species may be constrained to remain stable, thus rendering irrelevant the orders of magnitude advantage of individual births, and making rare events of speciation "the only game in town." Trends must therefore arise as differential success of species, and clades with greater interspecific variability due to more copious speciation, may gain a macroevolutionary edge. (Our explanation for volute evolution in the last section presents an argument in this mode.)

(*ii*) Mass extinction. If differential removal of species during rapid and worldwide episodes of mass extinction sets the basic pattern of life's diversity through time, then failure to maintain variation becomes an especially potent cause of species death, since survival through unanticipated environmental challenges of such magnitude must often depend on fortunate success of a few variants, while narrow adaptation and limited variability must often lead to elimination.

Thus, in the actual and uncertain world that geology has set for the history of life, differential success of species must regulate many trends—and variability across species within clades must be a major component of success or failure. Species selection on variability is probably a major force of macroevolution.

Appendix

Here we review briefly one possible approach to modeling species selection. This approach, developed by Damuth and Heisler (7), uses covariance models to express selection differentials (they also present a set of regression models in their appendix; see refs. 10, 18, 57–59). The basic idea is that a selection process can be occurring at a level only if there is a special relationship between some character of the units at that level and the fitnesses of those units. The existence and intensity of this relationship can be analyzed or expressed through the covariance between fitness and the value of the character (alternatively, the regression of the fitness on the character).

For example, Damuth and Heisler describe a multilevel selection analysis in which the group-level character is the mean, $Z_{i.}$, of the individual characters in each group. Note that group fitness is most often not the same as mean individual fitness. A new term, Ω_i, is introduced to represent group relative fitness, regardless of its relationship to organismic level fitness (ω_i). Also, the covariances are expectations defined over the distribution of groups. The total selection differential on the group character (ref. 7, p. 415) is written as

$$S_{\mathrm{T(G)}} = \mathrm{Cov}_{(u)}(\omega_{ij}, Z_{ij}) + \mathrm{Cov}(\Omega_i, \Delta Z_{i.}) + \mathrm{Cov}(\Omega_i, Z_{i.}). \quad [1]$$

From the point of view of an individual organism, the group or species is represented as a context affecting individual relative fitness. The total selection differential on an individual character, $S_{\mathrm{T(I)}}$, can be written as a partition of the total covariance between character and fitness, as follows:

$$S_{\mathrm{T(I)}} = \mathrm{Cov}_{(u)}(\omega_{ij}, Z_{ij}) + \mathrm{Cov}(\omega_i, \Delta Z_{i.}) + \mathrm{Cov}(\omega_i, Z_{i.}). \quad [2]$$

Z_{ij} denotes the measured phenotypic value and W_{ij} is the absolute fitness of the jth member of the ith group. Let $Z_{i.}$ denote the mean phenotypic value and $W_{i.}$ the mean absolute fitness of the members of group i (where the dot subscript indicates averaging over the relevant subscript). Damuth and Heisler define the relative fitness of individual j within group i as $\omega_{ij} = W_{ij}/W_{i.}$, where $W_{i.}$ is the mean of the individual fitnesses for group i. Similarly, the relative mean fitness of group i is defined as $\omega_i = W_{i.}/W_{..}$, where $W_{..}$ is the mean of the individual fitnesses for the entire population. The first term in Eq. 2 is the unweighted mean of the within-group covariances, and the middle term is the covariance between the average relative fitness of individuals within a group and the change in the group mean of the character due to lower-level selection ($\Delta Z_{i.}$).

Damuth and Heisler demonstrate the conditions (which are quite broad) under which Ω_i will have an emergent relationship with ω_{ij} (that is, the conditions under which species selection can be said to be occurring, according to our approach; ref. 7, pp. 422–423). For more on the relations between the two models given above, see Damuth and Heisler (7) and Heisler and Damuth (60).

We would like to thank Joel Cracraft, John Damuth, Michael Dietrich, Niles Eldredge, James Griesemer, David Hull, Richard

Lewontin, Judith Masters, Montgomery Slatkin, Steven Stanley, Hamish Spencer, and David S. Wilson for their helpful comments.

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