Explanatory Pluralism in Paleobiology

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Abstract: This paper is a defense of "explanatory pluralism" (i.e., the view that some events can be correctly explained in two distinct ways). To defend pluralism, I argue that a certain class of macroevolutionary trends (what I call "asymmetrical passive trends") can be explained in two distinct but compatible ways. The first approach ("actual sequence explanation") is to trace out the particular forces that affect each species. The second approach treats the trend as "passive" or "random" diffusion from a boundary in morphological space. I argue that while these strategies are distinct, both kinds of explanation can be true of a single trend. Further, since neither strategy can be reduced or eliminated from paleobiology, we should accept that both strategies can provide correct explanations for a single trend.

Explanatory Pluralism in Paleobiology

Philosophers of science generally accept the view that there is a single complete and correct explanation for every event. Call this view "explanatory realism."[1] Salmon (1971), for example, seems to embrace explanatory realism when he argues that there is a single complete and correct set of statistical relevance relations for every event. And according to Kim's (1993) explanatory exclusion principle, two complete and independent explanations of a single event cannot coexist. In this paper, I will argue that philosophers of science who are concerned to be faithful to scientific practice ought to reject explanatory realism in favor of explanatory pluralism (i.e., the view that some events can be correctly explained in two distinct ways).

My argument comes in three phases. Section 1 presents a set of necessary and sufficient conditions for demonstrating explanatory pluralism. Section 2 provides a brief introduction to macroevolutionary trends and the mechanisms that cause them. Based on this background, I argue that paleontologists employ two distinct (but compatible) explanatory strategies to explain "bounded passive trends." Finally, I argue that both explanations should be viewed as "correct" in the sense that neither strategy can be reduced or eliminated (section 3). Since we have two distinct (but compatible) explanations and neither explanatory strategy can be eliminated, I maintain that we have a genuine case of explanatory pluralism.

1. The Argumentative Strategy.

Let me begin by discussing two standard (but ultimately unsatisfying) arguments for pluralism. Identifying the weaknesses of these arguments will allow us to develop a more forceful argumentative strategy.

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[1]A note about terms. "Explanatory realism" (in my sense) is essentially identical with the thesis that Waters (1991) labels "causal realism." I have opted for the term "explanatory realism" to keep the focus on explanation. Kim's (1993) usage differs significantly from mine. For him, explanatory realism is simply the supposition that explanations can be true or false.

Several biologists have advanced "instrumentalist" arguments for pluralism. For example, Maynard Smith (1987) argues that argues that sex ratio evolution can be appropriately modeled in three different ways: game theory, population genetics, and Wilson & Colwell's intrademic group selection model. The three models possess different strengths and weaknesses, but all make the same predictions. According to Maynard Smith, "in such cases, we are not obliged to choose between [the models]" (p. 130). We can take advantage of the benefits of all three kinds of models. Dugatkin and Reeve have recently summarized this line of argument: "although the gene/individual and trait-group selection approaches are mathematically equivalent, each has its own heuristic value relative to (1) economy of explanation, (2) modeling simplicity, and (3) hypothesis-generating potential. Certain ecological scenarios are best approached from the individual selection road, whereas others are best traversed from a trait-group-selection path. Behavioral ecologists can only profit by having the "nuts and bolts" of each approach in their conceptual toolbox" (1994:130). While I believe that this argument reveals important shortcomings in methodological reductionism, philosophers who are interested in reductionism as an issue about the epistemology of the sciences are not (in general) moved by instrumentalist arguments. If the various models make <u>identical</u> predictions, then they are only verbally distinct and the appearance of pluralism disappears. But if they are truly distinct explanations, then only one of them can be true. *If* one adopts instrumentalism, then it is clearly possible to have multiple "correct" explanations because there can be more than one *useful* explanation. Instrumentalist arguments fail to address the crucial question, however: can there be more than one *correct* (true and complete) explanation. Similarly, arguments that presuppose a pragmatic (answer to a why question) view of explanation can establish a form of pluralism. If explanations are just answers to why questions, then (in different contexts) the same event might be correctly explained in two different ways. But again, philosophers with a penchant for realism will question the implicit theory of explanation. These brief reflections suggest that neither strategy is promising. Both strategies require extensive defense of controversial positions, and even then are unlikely to persuade realists. Thus, I intend to pursue a different strategy.

What would it take to provide a more convincing defense of explanatory pluralism? It seems that four conditions are necessary and sufficient:

1. *Two distinct explanatory strategies must offer explanations for a single event.* Unless these strategies are truly distinct, any case of pluralism will be merely apparent.

2. *Both strategies provide <u>correct</u> explanations for the same event.* I do not intend to provide a full analysis of what it means to provide a "correct" explanation. Roughly, I mean that the explanation is "true" and complete. Showing that an explanation has heuristic advantages is not sufficient.

3. *The explanatory strategies are compatible.* To satisfy the realist, both explanations must be true. Thus, it must be possible for particular instances of both strategies to provide true explanations of a single event. Presumably, if the strategies are truly distinct, they will diverge in some cases as well.

4. *Neither strategy is "eliminable."* That is, neither explanatory strategy can be reduced or completely eliminated from our most complete theory of the domain.

The strategy of this paper is to present a single case which meets these four conditions.

2. Distinct, Yet Compatible Explanations.

In this section I argue that biologists are currently pursuing two distinct (but compatible) ways of explaining asymmetrical passive trends. Before discussing the two explanatory strategies, I briefly summarize a bit of paleobiology as background for my argument.

2.1: A Bit of Paleobiology.

A macroevolutionary trend is a "directional evolutionary change that persisted long enough to be detectable in the fossil record" (Ridley 1993, p. 559). It is important to distinguish two different kinds of evolutionary change that are commonly called "trends." The first class of trends -- "anagenetic" or "phyletic" trends -- occur when there is sustained directional change in a single (non-branching) lineage. For example, if the members of a clam species steadily grew larger with no new species "branching" off of the lineage, then the trend is anagenetic. But if the trend arises in a whole family of species (a "clade"), then the trend is considered "cladogenetic." This paper will focus on cladogenetic trends.

Paleobiologists have identified several different "patterns" of clade-level evolution. Figure 1 provides a classification of different kinds of patterns that are evident in the fossil record. Clades can increase in variance (first row), decrease in variance (second row), or maintain constant variance (third row). Further, clades can

display symmetrical or asymmetrical patterns (columns). Paleobiologists have asked several different questions about these possible patterns of evolution: Which patterns actually occur in the history of life? How common are the different patterns? Why are some patterns more common than others? What mechanisms produce these patterns? For the moment, I want to highlight the last question. This classification does not make any assumptions about the mechanisms that cause these patterns, so biologists have suggested different possible explanations for each pattern. For the purposes of this paper, I'll focus on the asymmetrical ("bounded") increase in variance pattern (e.g., Figure 1b and 1c). What could cause this pattern of evolution?

McShea (1994) distinguishes between two kinds of mechanism that can cause an asymmetrical increase in variance. First, the trend could be "driven" by some force that consistently favors an increase in the trait under consideration. The "driving" force is typically natural selection, though other forces could (in principle) drive a trend. Consider, for example, a trend toward large body size: species with small body size will either be driven toward larger body size, or will be driven into extinction. According to this model, (nearly) all species within the clade experience selection pressure for large size and this consistent "driving" force explains the trend. In the long run, one expects that a driving mechanism will produce a pattern more like Figure 1i, but over the short run (or if the driving force is weak), a driven trend can display the bounded increase in variance pattern.

The second approach views cladogenetic trends as "passive diffusion" of species away from a boundary. Consider, again, the example of body size. Stanley (1973) argued that body size evolution will often be subject to important constraints. In particular, many body plans are not effective below a specific minimum body size. If the founding species of a new clade happens to be at or near this minimum body size, then even if large size is not always selectively advantageous (that is, even if the trend is not driven), "passive diffusion" away from this size boundary can lead to an increase in both the maximum body size and the mean body size. Just as molecules of gas that are placed near one wall of a box will expand away from that wall, a clade that begins near a boundary will passively diffuse into open morphological space. Passive diffusion models treat the direction of evolution (i.e., direction of both phyletic and speciational changes) as "random" in the sense that evolution is equally likely

to produce larger or smaller species.[2] It is important to recognize that this "randomness" is compatible with

determinism. Even if the evolution of each lineage is completely deterministic, we can treat the direction of

evolution as "random" if the species are equally likely to increase or decrease in size. Consider again the analogy

of the molecules in a box. Even if the motion of each molecule is completely determined by physical forces,

physical theory can treat molecular motions as "random" because in the long run, each molecule is equally likely

to go left or right. Just as randomly moving molecules will passively diffuse away from the wall of a box,

random speciation will lead a clade to evolve away from a minimum size boundary. (McKinney (1990a, 1990b)

and McShea (1994) offer more detailed analysis of passive diffusion models.)

One reason passive diffusion models (PDMs) are *philosophically* interesting is that they hold out the

possibility of a new interpretation of "progress" in the history of life. Trends toward increased complexity have

sometimes been cited as evidence of progress. But McShea (1991, 1993) has argued that complexity increases

are not always driven. Diffusion models recognize that morphological complexity has increased over time, but

they strip away the idea of a pervasive force that drives species toward greater complexity. If passive diffusion

models provide the correct explanation for increases in complexity, then there is no global drive toward

complexity. Rather, increases and decreases occur and both can be locally advantageous. (For more on the issue

of progress, see the essays in Nitecki 1988).

To address the issue of progress, we need techniques for distinguishing passive and driven trends.

Fortunately, such techniques are available (McShea 1994). Consider, for example, the well-known trend toward

large size among horse species (Figure 2). Is this trend toward large size passive or driven? Two pieces of

evidence suggest that this trend is driven. First minimum body size in the clade increases over time.

Mathematical models suggest that the minimum body size will remain roughly constant in a passive system, but

we expect the minimum body size to increase if the trend is driven. Thus, the increase in the minimum body size

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[2]For ease of discussion, I will often say that the "direction of speciation" is random. That is, I'll speak as though nearly all evolutionary change occurs at the time of speciation. But passive diffusion models do not presuppose the truth of punctuated equilibrium. The crucial point for passive diffusion models is that once species are away from the boundary, the direction of evolution (both within a lineage and during speciation) is random.

suggests that the trend is driven. Second, MacFadden's (1986) study of ancestor-descendant pairs confirms that

this trend is driven. Recall that in a passive system, the direction of speciation is random. Thus, daughter

species should decrease in size 50% of the time.[3] But in a driven system, the force of selection should "bias" the

direction of speciation so that "daughter" species will (in general) be larger the parent species. By studying pairs

of ancestral and descendant species, MacFadden has shown that the direction of speciation is biased in the

direction of large size. Of the nine well-documented ancestor-descendant pairs which are not in the vicinity of the

boundary, all nine get larger. In the clade as a whole (including species near the boundary), the ratio of size

increases to size decreases is 19:5.

Although the well-known case of horse evolution turns out to be a driven trend, other significant trends

appear to be passive. McShea (1994) argues that the evolution of spinal column complexity is a passive system.

And Gould (1988, 1990) argues for the pervasiveness of passive trends. In one of the first systematic studies of

body size evolution, Jablonski (1996, 1997) shows that 25% of mollusk genera display a symmetrical increase

in variance pattern (i.e., Figure 1a). Furthermore, because this is "the pattern expected for a large population of

clades branching stochastically to larger and smaller sizes", these increase-in-variance trends are probably passive

(Jablonski 1997, p. 251). While passive trends may be relatively common, the specific pattern I am focusing on

(i.e., passive diffusion away from a boundary) does not appear to be a dominant pattern in the history of life. In

Jablonski's (1997) examination of body size trends, only 5% of the mollusk clades increase in variance away

from a lower boundary. Although we need more data before drawing general conclusions, the best available

evidence suggests that passive diffusion away from a boundary is a relatively rare (but not insignificant) pattern

in the history of life.

2.2: Two Strategies for Explaining Passive Diffusion Away From a Boundary.

To illustrate how two distinct explanations for a single trend are possible, consider the following

example (loosely based on McShea 1993 and 1994). Imagine that a clade of vertebrates grows from a single

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[3]Speaking strictly, this is only true of species that are not in the immediate vicinity of the boundary.

ancestral species with a very simple spinal column into a family of species with variation in spinal complexity. While some species retain simple spinal columns, others evolve highly differentiated (i.e., complex) spines. Our fictional clade will display a trend toward complexity in two senses: both the maximum and average degrees of vertebral complexity will increase over time. Suppose further that we have good evidence to believe that the trend is passive (e.g., the minimum degree of complexity remains (roughly) constant and a study of ancestor-descendant pairs confirms that complexity is equally likely to increase or decrease). My thesis is that this kind of trend can be correctly explained in two distinct ways. (See Table 1).

The first strategy is simply to explain the trend by appealing to a passive diffusion model (PDM). That is, we explain the trend by saying that whenever the founding species of a new clade is close to a boundary and the direction of speciation is random, a passive trend is likely. In this case, the "lower bound" is a completely undifferentiated spine. If the various evolutionary forces in this bounded morphological space are, on average, equally likely to favor an increase or a decrease in complexity, then a trend toward increasing complexity is very likely. Thus, PDMs identify certain (rather abstract) conditions under which a passive increase in variance trend is likely. We explain particular passive trends by noting that these conditions are met.

Although it is more cumbersome, neodarwinians could also provide an explanation of this trend. Neodarwinians explain the trend by providing a detailed account of the evolutionary forces affecting each species in the clade. (Call this style of explanation "actual sequence" explanation). The key point is that PDMs do not involve any distinctive higher-level mechanisms. Thus, by explaining each evolutionary transition, a neodarwinian could (at least in principle) provide a detailed history of the causes which produced the trend toward complexity. According to one influential defense of neodarwinism, "In the neo-Darwinian theory, phylogenetic patterns are supposed to be predominantly due to natural selection *acting in each lineage*" (Charlesworth et al. 1982, p. 490, emphasis added). It is a daunting task to explain the fate of each major evolutionary transition in each lineage over millions of years, but it is (at least in principle) possible to do so.

Passive diffusion and actual sequence explanations invoke fundamentally different explanatory strategies. Whereas actual sequence explanations provide a detailed account of the causal forces acting on each

lineage, PDMs abstract away from the specific causes driving each lineage in order to identify more abstract

"structuring" causes.[4] In this case, the morphological space is structured by the boundary. If diversity increases

in the clade and the direction of speciation is random, then a passive trend toward increasing complexity will

arise. (It is worth noting that passive diffusion explanations are also quite different from any of the other

standard explanations of trends [e.g., directional selection, species selection]).

> While passive diffusion and actual sequence explanations are distinct, I maintain that they are compatible

in the sense particular explanations of both types might be true of a single event. The models are compatible

because PDMs do not postulate any non-darwinian causal forces acting within lineages. The boundaries and the

"random direction of evolution" are (presumably) realized by the ordinary neodarwinian forces of mutation,

natural selection, genetic drift, etc. Given this claim about compatibility, you will certainly wonder whether

passive diffusion explanations are reducible. It is to this question that I now turn.

3. Is either explanation eliminable?

I have argued that actual sequence explanations and passive diffusion explanations are distinct (but compatible)

explanatory strategies. In this section I mount an argument to show that neither strategy is likely to be eliminated

from paleobiology. The structure of my argument is relatively simple. (1) The neodarwinian "actual sequence"

strategy for explaining trends is an important part of contemporary biological thought and is unlikely to be

eliminated. (2) If we aspire to explain the relative frequency of bounded passive trends, then we are committed

to retaining a passive diffusion explanations. In particular, I will argue that while actual sequence explanations

can explain particular trends, they cannot explain the <u>frequency</u> of asymmetrical bounded passive trends. Since

(3) no other explanatory strategies are available to explain the frequency of bounded passive trends, I conclude

that if we aspire to explain the relative frequencies of different patterns of macroevolution then passive diffusion

models cannot be eliminated.

> (1) Neodarwinian "actual sequence" explanations are so central to contemporary neodarwinism that one

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[4]My account of these two explanatory strategies is influenced by Sterelny's (1996) discussion of "actual sequence" and "robust process" explanations.

cannot imagine their elimination. This is a primary strategy for explaining macroevolutionary trends --

particularly adaptive radiations (see e.g., Bock, 1979). Thus, I cannot foresee the elimination of this pattern of

explanation.

(2) I do not believe that passive diffusion models can be eliminated from our account of macroevolution.

In order to make this point, I want to shift our attention to the problem of explaining the frequency of

asymmetrical passive trends (rather than explaining particular trends). Paleobiologists are concerned to

understand why certain patterns of evolution are more common than others. In particular, we'd like to know

why bounded passive trends are relatively rare. (Recall Jablonski's data). Here's one story:

> (E): asymmetrical passive trends arise if and only if (1) the founding species of an emerging clade occurs
> close to a boundary, (2) the direction of speciation is "random", and (3) the speciation rate exceeds the
> rate of extinction.[5] Since conditions (1) and (2) are only rarely met, asymmetrical passive trends are
> relatively rare.

On the face of it, this seems to be a reasonable explanation. We cite a generalization about the conditions under

which asymmetrical passive trends are likely to arise and note that these conditions are only rarely met. The

discussion of the previous section has, I trust, made it clear that these conditions are individually necessary and

jointly sufficient for the occurrence of an asymmetrical passive trend. Paleobiology has not (yet) determined how

often these conditions are met, but as the data come in, we should be able to strengthen our understanding of

how often conditions (E1)-(E3) are met, and this will strengthen our understanding of why asymmetrical passive

trends are not a dominant pattern in the history of life. Thus, we seem to have a legitimate explanation of the

frequency of this kind of pattern.[6]

Noting that (E) is a possible explanation for the frequency of passive trends does not, of course, show

that this explanation is ineliminable. To demonstrate ineliminability, I will argue that actual sequence

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[5]The third condition is a way of stipulating that the number of species increases. If the clade does not grow, no trend may emerge.

[6]Note that if (E) is correct, then passive diffusion explanations of particular trends must be correct. (E) offers necessary and sufficient conditions for the occurrence of a passive trend. If one accepts that this generalization has the explanatory power to explain the frequency of passive trends, then this generalization must certainly have the explanatory power to explain the occurrence of a particular trend.

explanations do not "reduce" (E). First, note that even if a neodarwinian could provide an actual sequence explanation for every particular asymmetrical passive trend, this collection of explanations would not explain why this kind of trend is relatively rare. Actual sequence explanations simply don't address the issue of relative frequency. Second, (E) depends crucially on the concepts of "boundary" and "random direction of speciation" and these concepts are not reducible. While each particular boundary and each instance of "random speciation in a clade" will be realized by some particular set of neodarwinian forces, there are an indefinite number of actual sequence realizations. The problem here is not merely that these terms are multiply realizable (though they certainly are). The deeper difficulty is that even if we identify all the realizations of "boundary" and "random direction of speciation" that have actually occurred so far, we have not identified the salient (counterfactual supporting) predicates. To see this, consider the claim all passive trends display random direction of speciation. To reduce the "random direction of speciation", we might list (in a massive disjunction) all of the known lower-level realizations of random speciation. But we cannot infer that all passive trends will have one of these realizations (because other lower-level realizations are possible). Thus, I claim that the generalizations that are crucial in explaining the frequency of passive trends cannot be reduced. (See Kincaid 1997 for a more general defense of the claim that supervenience does not entail reducibility). If the passive diffusion explanation for the frequency of passive trends cannot be reduced, then we must accept this strategy of explanation as ineliminable.

Thus, my argument for pluralism goes roughly as follows: asymmetrical passive trends can be explained by both actual sequence and passive diffusion accounts. The two accounts involve distinct (but compatible) explanatory strategies. Further, we cannot eliminate the passive diffusion accounts (by reducing them to neodarwinian accounts) because we need the passive diffusion account to explain the frequency of asymmetrical passive trends. If we accept the burden of explaining the frequency of different kinds of trends (something paleobiologists are committed to), then passive diffusion explanations are here to stay.

(3) One might object that I've overlooked some of the explanatory resources of the neodarwinian theory. So far, I have focused solely on two approaches: actual sequence explanation and passive diffusion models. But (the critic continues) neodarwinians have additional explanatory resources. In particular, one might explain the occurrence of an asymmetrical passive trend by appeal to the principle of "competitive exclusion." The principle

of competitive exclusion asserts that "competing species cannot indefinitely coexist if they are limited by precisely the same resources" (Futuyma 1986, p. 30). That is, if two species occupy the same niche, one species will eventually drive the other species into a new niche or into extinction. Thus, if a clade is founded near a boundary, then (assuming that speciation exceeds extinction) the clade will expand away from the boundary.

While I do not want to deny the reality of competitive exclusion, I do not believe that a competitive exclusion account can replace or reduce (E). First, to explain passive increase in variance trends, the competitive exclusion account must make reference to "boundaries" in morphological space -- a concept that is not reducible (see above). Second, competitive exclusion concerns species that occupy largely or precisely the same niche. The fact that two species share the same space along one morphological axis (e.g., complexity of vertebrate spine) does not guarantee that these species occupy the same ecological niche. The third point really just generalizes from the second: the ecological language of "competitive exclusion" does not map onto the cladogenetic framework of paleobiology. Clades are fundamentally genealogical (not ecological) units. The fact that two species of the same clade occupy overlapping regions in morphological space does not guarantee that they are _ecological_ competitors. (Remember: virtually identical "sibling species" do exist within clades). Two species that overlap in one dimension of morphospace may (a) differ in other (ecologically significant) traits, or (b) occur in physically distinct locations. Thus, while competition between species is certainly an important factor leading to asymmetrical passive trends, competitive exclusion will not provide an adequate _general_ account of the frequency of this class of trends.

To summarize: neither actual sequence nor competitive exclusion explanations are able to provide reduce (E), and I can see no other viable neodarwinian alternatives. Thus, it appears that if we retain the goal of explaining the relative frequency of different kinds of cladogenetic trends, we remain committed to using PDMs. In using PDMs to explain the frequency of passive increase in variance trends, paleontologists presuppose that we can also explain particular passive trends using PDMs. Furthermore, since it is clearly possible to give actual sequence explanations for particular passive trends, we are committed to the claim that some trends can be explained in two distinct (though compatible) ways.

Let me conclude this section with a brief caveat. Ideally, to establish a case of pluralism, one should

show that both explanatory strategies are ineliminable. The argument of this section falls short of this goal.

Despite the occasional pronouncements of the "end of science" (e.g., Horgan 1997), we are not in a position to

make decisive pronouncements about future developments in science. The best we can do is to assess what

explanatory strategies (based on current evidence) seem so central that we cannot foresee their abandonment.

Though many of you will likely be unfamiliar with passive diffusion models, my claim is that a careful

assessment of paleobiology supports the claim that passive diffusion models will be very hard to eliminate. As

long as we remain committed to the task of explaining the relative frequency of different patterns of cladogenetic

evolution, we will need passive diffusion models. While this falls short of demonstrating that these models are

ineliminable, it is the best naturalistic philosophers of science can hope for. That is to say, my defense of

explanatory pluralism has enough empirical content to be defeasible.

4. Concluding Reflections.

The pluralism I defend is intended to be a constrained form of pluralism that is rooted in a naturalistic

approach to the philosophy of science. The pluralism is constrained because the conditions I offer are

stringent. Because these criteria are stringent, I do not expect pluralism to be a widespread phenomenon. But

nor do I feel comfortable ruling out pluralism on the basis of philosophical arguments that do not attend to the

practices of particular sciences. Despite the intuitive pull of Kim's (1993) metaphysical arguments for

explanatory exclusion, I remain unpersuaded. A close examination of current science shows that

paleobiologists use two distinct strategies to explain passive trends, and that both explanations seem to be

correct and complete. Although one might save Kim's principle by noting that the two explanations are not

completely independent (e.g., the higher-level properties depend on lower-level realizations), we still seem to

be forced to accept both explanations because neither can be eliminated. Since the thesis of explanatory

realism does not fit with the best account of contemporary science, I argue that we should accept pluralism.

cladogenetic trends: sustained directional change within a clade (i.e., the "family" of species that have evolved from a common ancestor).

Two kinds of cladogenetic trends:

A. Driven: Trend "driven" by some consistent force (e.g., natural selection) that affects nearly all species; direction of evolutionary change is biased by the driving force.

B. Passive: Trend arises through "diffusion" away from a boundary in morphological space; direction of evolutionary change is "random."

Two ways of explaining bounded passive trends:

1. Actual sequence explanation. Traces the specific forces affecting each species.

2. Passive diffusion model. Identifies the "structuring cause" of passive trends: random diffusion away from a boundary.

Table 1: Paleobiological Terminology. There are two different kinds of cladogenetic trends: driven and passive. Passive trends can be explained in two distinct (but not incompatible) ways.

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