

Dynamics of Diversification in State Space

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America spread west in the mid-to-late nineteenth century.

In our own century, the story of the mass migration has been told and retold in countless ballads and novels. And in now-classic movie westerns, it has been epitomized in scenes of long wagon trains winding across the prairie toward the setting sun.

Census data from that period confirm the demographic aspect of the story: the mean location of Americans -- the country's

center of gravity, so to speak -- shifted westward. However, the data also show that from two broad belts occupying the middle

third of the country, the west-central states and the mountain states, about the same number of people moved east as moved west,

at least during the first part of the migration from 1850 to 1880 (data from Mitchell, 1983). Actually, slightly more moved east

during this period.

The pattern is puzzling at first. The country as a whole

spread west, while slightly more people migrated east. But it is consistent with a simple explanation, illustrated abstractly in

Figure 1A. The horizontal axis is location in space, reduced to a single dimension, east and west, and the vertical axis is time.

Suppose for simplicity that we are dealing with an asexually

reproducing species instead of people. The population begins as a

single individual. As time passes, the individual reproduces or

splits, and its progeny do likewise, causing the population to

grow. Across the country, individuals migrate east slightly more

often than they migrate west, except at one point in space where

migration to the east is blocked by a boundary, the Atlantic Ocean. The result is that, despite the slight eastward bias in the movement of individuals, the population as a whole diffuses slowly to the west. More generally, the behavior of the system at the large scale seems to be independent of its dynamics at the small scale.

The pattern after 1880 was different. The mean continued to shift west, but more people moved west than moved east from all regions (except the Pacific states; Mitchell, 1983), encouraged no doubt by the west's great natural resources and by the development of a transcontinental railroad. Figure 1B shows that the new dynamic produces a pattern broadly similar to Figure 1A. However, in this new regime, large-scale behavior -- the shift of the mean westward -- and small-scale dynamics -- the westward bias -- are more closely connected. Indeed, the large-scale behavior seems to be a direct result of the small-scale dynamics. The same disparity (Figure 1A), and congruence (Figure 1B), between large-scale behavior and small-scale dynamics can arise in a wide variety of contexts. In the above example, the diversifying group was a population and the lineages consisted of individuals. But the group could just as well be a monophyletic group of species, a clade, and the lineages could be individual species. Also, the horizontal axis was physical space. But it could equally well have been almost any "state variable" (McKinney, 1990), such as size, fitness, complexity, metabolic rate, geographic range, temperature tolerance, speciation or

extinction rate -- in principle, any feature of a species. (To emphasize the generality of the principles developed here, the one-dimensional space within which diversification occurs will be called simply a "state space," and in figures, the horizontal state-space axis will not be labeled.)

Suppose, for example, that the state space in Figures 1A and 1B were a "size space." (Size increases to the left, contrary to the convention.) The two figures could then be understood to show two possible explanations for Cope's Rule, the well-known tendency for mean size to increase in many clades. In Figure 1B, selection favors large size in all or most lineages (Newell, 1949), creating a bias toward increase, and correspondingly, an increase in the mean. In Figure 1A, a group originates near a lower bound, a lower limit on size, perhaps the result of a design constraint (Stanley, 1973). No bias is present (increases and decreases occur equally often), but mean size increases anyway as the group diversifies.

This chapter addresses two questions. First, how shall we understand the causes of large-scale behavior of clades diversifying in state space? The causes must have something to do with the small-scale dynamics of lineages, but such dynamics seem to come in many forms, producing not just biases and boundaries, but local optima and other attractors, and variations in speciation and extinction probability. To clutter the conceptual picture further, large-scale behavior for a clade includes not just trends in the mean, but stasis in the mean, and also trends

and stasis in the minimum and maximum, that is, in the locations of a clade's extremes in state space. It also includes changes and stasis in the distributions of species in state space, that is, in how many species there are in each range of size, temperature tolerance, extinction rate, and so on. At present, we have no systematic way to think about all of these factors or how they interact.

Second, how shall we understand the causes of independence between the small and the large scale when it occurs? What determines whether a change in dynamics produces a corresponding change in large-scale behavior, for example, whether an increase in speciation rate in some region of state space, produces an increase in diversity there? (It may not, if diversity is limited in that region.) What factors need to be taken into account in order to justify extrapolation across hierarchical levels, to justify inferring the behavior of a clade from the behavior of its component lineages, or vice versa? If mean temperature tolerance in a clade as a whole has been rising, does that mean that any tendency to increase exists among individual lineages? (Not necessarily; see Figure 1A.)

The overall problem can be posed in other terms. What factors control whether the distribution of species in some state space is historical or equilibrial? In other words, what controls whether a clade's distribution will be the historically probabilistic of speciation, extinction, and morphological

change) or the result of its dynamics conforming to some structuring imposed by ahistorical constraints?

For example, the present distribution of people in America could be nearly equilibrial. In other words, it might reflect the prior structuring of state space (the country), which is some function of the distribution of natural and commercial resources. (Both change somewhat as technologies and industries change, of course, so no true equilibrium is possible.) In contrast, it is clear that no equilibrium had been reached by the late nineteenth century, when the distribution of people at any given time reflected more the small-scale dynamics, the frequency of birth, death, and migration, than the actual distribution of usable resources. In retrospect, it seems clear that the early dominance of this system by its small-scale dynamics was (or is still) temporary. It could continue only until the limitations imposed by the structuring were engaged, in other words, until the country and the use of its resources reached saturation.

In the diversification of clades in state space on evolutionary timescales, the possible sources, or causes, of both the dynamics and the structuring are less easy to grasp, and the distinctions and relationships between them are less clear. This chapter is an attempt to understand and make explicit those sources, distinctions, and relationships.

I first present a conceptual scheme for organizing and thinking about the ways in which structuring can affect clade behavior and the degree of independence between small-scale

dynamics and clade behavior. The focus is on the behavior of the mean, and with some ancillary discussion of the behavior of maxima and of distribution shape. (The behavior of minima and of clade skewness were discussed in McShea, 1994.) The scheme will show that the behavior of a clade and the degree of independence between a clade's small-scale dynamics and its large-scale behavior depend partly on the nature or type of small-scale dynamics at work, but also on differences in the degree of "structuring" of those dynamics. (The word is pirated from Fisher's [1986] apt description of systems such as Figure 1A as "diffusion within a structured design space.")

I then describe three major grades of structuring, classic cases which are intended as useful reference points for discussion of structuring and independence. Finally, I try to clarify the conceptual scheme further with a discussion of two cryptic cases, two systems in which the role of structuring and its relation to the small-scale dynamics is apparently (and in one case, actually) problematic.

This analysis is not concerned with why systems are structured the way they are, but only with the effect of structuring of various kinds on large-scale behavior and on the degree of independence between the small and the large scale. Further, only some of the many possible small-scale dynamics are explored, and only some of the many possible ways of structuring, enough to enable readers who find the approach agreeable to extend the reasoning to other cases on their own. Finally, the

generate a new lineage, to speciate or branch, which it does with

Also in each time step, the lineage has the opportunity to

appropriately for the figures.)

mean zero. (The standard deviation is varied to scale the output

absolute value of a normally distributed random variable with

movement, the magnitude of the step taken in state space is the

probability p_d (probability of decrease). For both left and right

probability p_i (probability of increase) and right with

of the model, the lineage moves left in state space with

in an unspecified state space. In each time step, each iteration

begins as a single lineage, a single species, at a value of zero

computer model of clade diversification. In the model, a clade

1) A Computer Model. Figures 1A and 1B are outputs of a

II. THE STRUCTURING OF DYNAMICAL RULES

the train of thought begun in McShea (1994).

(1986), Gould (1988, 1990), and McKinney (1990), and it extends

and Gould (1974), Raup (1977), Saltz (1985, 1993), Fisher

hierarchical evolutionary dynamics of Stanley (1973, 1979), Raup

This treatment attempts to build on the foundational work on

refine, or -- as the case may be -- falsify those intuitions.

Empirical studies are an essential next step in order to verify,

to help train our intuitions and condition our expectations.

between structuring and hierarchical independence in principle,

treatment is conceptual: the point is to study the relationship

probability p_b (probability of branching), and to terminate, which it does with probability p_e (probability of extinction). When branching occurs, new lineages follow the same movement, branching, and extinction protocols as the original. Finally, the vertical line at zero in Figure 1A is a "cushioning" boundary. Lineages that try to cross it are instead assigned their original value before the attempt occurred. These protocols correspond to an "agenetic" model of evolution in that movement or anagenetic change occurs between as well as during branching events. In a cladogenetic or punctuated equilibrium version (see MCShea, 1994), lineage movement would be confined to branching events. In Figure 1B, there is a strong bias ($p_l = 0.15$; $p_d = 0.01$), and a trend in the mean results; such trends might be called "driven" (MCShea, 1994) to emphasize the fact that they occur as a result of a driving force, or bias, among lineages. In Figure 1A, there is no bias ($p_l = p_d = 0.08$); such trends are called "passive" (MCShea, 1994) to emphasize that they occur in the absence of any driving forces. In both, the branching probability was set higher than the extinction probability ($p_b = 0.15$; $p_e = 0.05$) to make diversification likely. Also in both, the model was run for 50 time steps.

The model is additive in that movement of lineages in the state space is accomplished by adding and subtracting numbers in each time step. A multiplicative model might seem more appropriate for some spaces, especially for size or other aspects of morphology, but the additive model is more versatile. It

The use of probabilistic biases and diversification parameters in the model does not deny that change or branching in each real lineage would have its own unique deterministic explanation. In a series of coin flips, the trajectory and outcome of each flip has a unique deterministic explanation, but the series as a whole can be treated statistically. Similarly, change or branching in each lineage is the deterministic result

(1994).

have to be modified. Further caveats are discussed in MCShea directionally, the model and the reasoning developed here would 1978). To accommodate such cases in which parameters change they become increasingly elaborated, or burdened (e.g., Riedl, developmental programs become increasingly resistant to change as example, the suggestion has been made that certain parts of timescales, this assumption may be decidedly unrealistic. For constant. Notice that for some morphological features, at some can assume that parameters of a system remain stochastically the model is reasonable and appropriate only in cases in which we impede the movement of lineages in another clade at all. Finally, a boundary at some value in size space for one clade may not will differ from one clade to the next, so that -- for example -- That is, p_i , p_d , p_b , and p_e as well as any structuring of these The parameters of a system are assumed to be clade specific. the state-space as a log-state-space (MCShea, 1994).

appropriately models change that is truly additive and also can be transformed to a multiplicative model simply by reconceiving

of a unique concatenation of structural and ecological factors, but an ensemble of lineages, a clade, may nevertheless have robust, statistical properties. It is those statistical properties that are captured by the model parameters. The model gives us a wide range of parameter values and value combinations to consider, and some of these are explored in McShea (1994). Here it is not a tool for exploration, however, but a heuristic, a device for visualizing clade dynamics and structuring. The model is allied with a class of Monte Carlo models developed by Raup and Gould (1974) and Raup (1977) for simulating morphological change in growing systems. Some analytical studies of such systems have also been done (e.g., Skellam, 1951; Slatkin, 1981; Toft and Mangel, 1991; and Foote, in press).

2. Definitions. The small-scale dynamics of a diversifying clade are the rules that govern the behavior of a lineage in the state space. A lineage is an ancestor-descendant sequence of species, and its behavior includes movement, branching, and extinction. Figure 2A shows the two rules that underlie the passive trend in Figure 1A. One rule -- shown as a vertical line with a reflected arrow -- is a blocking rule, which dictates that lineages attempting to traverse a place in state-space where the rule applies are blocked, and returned to their starting positions. The other -- shown as a pair of equal and opposing arrows -- dictates that movement left and right are equally probable in any place in state space where the rule applies.

3. Hierarchy. The hierarchical relationship here can be described using Salthe's (1985) basic triad of levels: focal, lower, and upper. The focal level is the clade, the lower level is the lineage (along with its dynamics), and the upper level consists of the (relatively) invariant features of the "context"

in the mean. refers to changes in those properties over time, such as trends clade that exist at a given time. And the behavior of the clade the summary statistics of, or distributions for, the members of a The clade properties of interest -- mean, maximum, etc. -- are precisely be described as a temporal cross-section of a clade. properties of what I have been calling the clade, but would more large-scale behavior refers to the behavior of certain

all lineages, at all times, throughout the space. greater probability of moving left -- and it applies equally to none of the rules is structured. There is only one rule -- uniformly everywhere to the left of the boundary. In Figure 2B, equal-probability rule is not structured at all, and it applies certain fixed value in state space, creating a boundary. The so that it applies to all lineages, arriving at any time, at a in state space. So, in Figure 2A, the blocking rule is organized arrangement of the regions of application of the dynamical rules The structuring of the small-scale dynamics is the the right.

Figure 2B shows the single rule that accounts for the driven trend in Figure 1B: movement to the left is more probable than to

If the boundary is produced by an internal developmental constraint, the constraint must apply to all or most lineages in order to constitute a boundary, and it is therefore a relatively

hierarchy.

context, and that the context is also part of an aggregative clade is physically contained within its

timescale. In this case, because the context is external, it

largely unaffected by the dynamics -- at least at the focal dynamics (Allen and Starr, 1982; Valentiné and May, 1996), and is

but because it is stable or invariant, relative to the lineage, qualifies as context not because it is external to the lineages,

clade occupying the same habitat. The selective environment

environment, perhaps competition from small species in another

combination of factors in the external abiotic and biotic

constraint. If external selection, then the context is some

could also have been the result of an internal developmental

acts only against organisms of some critical small size, but it

boundary could have been the result of external selection that

example, in the explanations offered earlier for Cope's Rule, the

include features internal to the organisms themselves. For

The role of the "context" is less clear, because it may

May, 1996) hierarchy.

structural (O'Neill et al., 1986), or aggregative (Valentiné and

the two constitute what has been called a scalar (Salté, 1993),

structures. A clade is composed of lineages, and thus together

(see below) which the clade occupies and which produces

4. Independence. Notice that in Figure 1B, the small-scale dynamics (Fig. 2B) completely account for the behavior of the clade as a whole, in particular, for the trend in the mean to the left. In other words, the behavior of the clade as a whole is a direct and obvious expression of the dynamics. In Figure 1A, however, the small-scale dynamics alone are insufficient to account for the trend. It is not enough to know what the dynamics

causes in different ways.

causes of clade behavior, but they carve the space of possible dynamics-versus-structuring distinctions have to do with the systems.) In sum, both the internal-versus-external and the example, could not be a general property of developmental no reason in principle why biases toward size increase, for not now fashionable in evolutionary discourse, although there is (Internal drives [Lamarck, 1809] -- another possibility -- are (Stanley, 1979) or developmental channeling (Alberch, 1980). well be produced by internal factors, such as directed speciation favoring large size in all or most lineages, but it could just as For Cope's Rule, it could be the result of external selection be either internal or external. For example, if a bias accounts Notice that the causes of the small-scale dynamics can also context only metaphorically.

influence it. In this case, the clade is contained within its relative to the lineage dynamics, and the lineage dynamics do not context for the lineages in that it changes slowly, at least invariant feature of the clade bodyplan. It qualifies as a

are; we must also specify their structuring, the fact that one of them is organized in space and time so as to produce a boundary. Compare the system in Figure 3A to that in 3D; both contain many blocking rules, but only in 3A are they structured in any way. This structuring supersedes the dynamics, in a sense, producing a trend that is not inherent in the dynamics alone. In other words, the trend is to some extent *independent* of the dynamics. The large-scale behavior in Figure 1A is also independent of the dynamics in another sense. Any of a number of different dynamics could have been structured to produce a boundary. The blocking rule might have dictated lineage repulsion or adsorption, rather than cushioning. Or it might have been an absorbing boundary; for example, if the state space were geographic range, then lineages with small ranges might have a higher extinction probability (Maurer and Notts, this volume). And the second dynamical rule might have specified a slight bias to the right, instead of equal probability of left and right movement. A trend to the left would occur with all of these dynamics, provided they were structured properly. Thus, to some extent, the structuring renders the small-scale dynamics invisible, or in other words, it "screens off" clade behavior from the dynamics (Brandon, 1985). Of course, a single boundary does not insulate the behavior of the clade as a whole from the small-scale dynamics under all circumstances. If the small-scale dynamics consisted of a very strong bias to the right, no trend would be produced. Initial

position can also make a difference. If the clade started much further to the left in Figure 1A, far from the boundary, no trend would be produced, at least initially. Thus, a boundary at a single value in state space is a fairly weak form of structuring which produces independence only under a restricted set of conditions. Greater degrees of structuring produce independence more reliably, under a wider range of possible small-scale dynamics (and of initial positions, as well). Some of the more structured cases are considered later.

The suggestion that systems can be independent, to some extent, of their small-scale dynamics, does not imply that they are somehow able to transcend, override, or contradict those dynamics. On the contrary, at the small scale, all behavior is a direct result of the small-scale dynamics. The expansion of a gas inside a closed box is governed by the rules of interaction of gas molecules with each other and the rules of interaction with the box. At the scale of the molecules, nothing more is going on. Viewed at a larger scale, however, different behaviors emerge. The final configuration of the gas as a whole is different in boxes of different shapes, and the behavior of the gas is different in a box with no lid. For all of these systems, the list of applicable dynamical rules is the same, but the systems differ in the structuring of their rules, in the placement of the rules in space.

Unlike gases in boxes, the list of applicable dynamical rules for lineages vary a great deal among diversifying clades.

those in which both direction and step-size are unbiased (so that those in the other (which would also produce a trend), as well as unbiased but movements or steps in one direction are larger than

would be those in which the direction of lineage movement is $p_e = 0.05$) were allowed. Examples of other unstructured systems was present, and both anagenetic change and branching ($p_b = 0.10$; present throughout the space ($p_i = 0.54$; $p_d = 0.06$), no boundary 1. The system in Figure 4A is unstructured. A bias was

increasingly constrained. structuring, in which the behavior of the system as a whole is series of instances showing successively greater degrees of (imagined.) They should instead be viewed as classic cases, a the third is not, because more highly structured systems can be first grade is an extreme, a completely unstructured system, but spaced points on a linear scale of degree of structuring. (The computer model shown in Figure 4. The grades are not equally identified. The grades are exemplified in the three runs of the Three grades, or levels of intensity of structuring, can be

III. THREE GRADES OF STRUCTURING

between the rules and clade behavior. clade as a whole, and therefore also the degree of independence influencing the behavior at the larger scale, at the scale of the structuring of the dynamical rules is also significant, strongly in large-scale behavior among clades. But like the gas, the And the variation among rules accounts for much of the variation

no trend occurs at all).

One possible example of such a system is the diversification of the horses, the family Equidae, in size space during the Cenozoic. The mean size for the clade as a whole increased, and a strong bias toward increase is evident among lineages. In a random sample of ancestor-descendant comparisons, increases outnumbered decreases nine to zero (MCShea, 1994; data from MacFadden, 1986). In addition, minimum size, or the size of the smallest horse in existence at a given time, increased as well, a pattern consistent with a bias-driven system (MCShea, 1994). In present terms, no structuring seems to be present, and the trend could well be a direct result of the small-scale dynamics, consisting entirely of the bias rule, distributed uniformly throughout size space. A likely cause of the dynamic is selection for greater size acting on all or most horse lineages.

2) The system in Figure 4B is somewhat structured, on account of the presence of two (blocking-rule) boundaries at fixed values in state space. No bias was present ($p_i = p_d = 0.50$), and again lineages move and branch ($p_b = 0.10$; $p_e = 0.05$).

Dynamics other than the blocking rule might have been used to construct the boundaries. For example, biases might have been used, perhaps biases that engage abruptly at some fixed value in state space (Fig. 3C) or perhaps graded biases that increase continuously as some fixed value is approached. Alternatively, boundaries might have been produced by abrupt increases in