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Historical Contingency and the Explanation of Evolutionary Trends

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Abstract

One "big question" of macroevolutionary theory is the degree to which evolutionary history is contingent. A second "big question" is whether particular large-scale evolutionary trends, such as size increase or complexity increase, are passive or driven. Showing that a trend is passive or driven is a way of explaining it. These two "big questions" are related in both a superficial and a deep way. Superficially, defending historical contingency and showing that major trends are passive are two complementary ways of downplaying the importance of natural selection in evolutionary history. A passive trend is one that's not explained by selection. In order to appreciate the deeper connection between the two issues, it is necessary to distinguish different senses of contingency (especially sensitivity to initial conditions vs. unbiased sorting). It's plausible that passive trends are generally due to unbiased sorting processes. Serendipitously, thinking of contingency as unbiased sorting also helps to clarify its relationship to species selection, which some think of as biased sorting. Macroevolutionary theory thus turns out to have considerable unity.

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1. Introduction

In this contribution, I explore the relationship between two major issues in macroevolutionary theory. The first issue, which Stephen Jay Gould highlighted in his 1989 book, *Wonderful Life*, is the degree to which evolutionary history is contingent. This issue has been the subject of some debate among paleontologists. Simon Conway Morris—who, ironically, was one of the heroes of Gould's book on the Burgess Shale—has argued that convergence, rather than contingency, is the hallmark of evolutionary history (Conway Morris 2003, 2008). The issue has inspired some experimental work by Richard Lenski and colleagues (Lenski and Travisano 1994; Travisano at al. 1995). Gould's argument about contingency has also had a significant, albeit indirect impact on the philosophy of biology, by way of John Beatty's classic paper arguing that the contingency of evolutionary history means that there are no distinctively biological laws (Beatty 1995). The debate about the degree to which evolutionary history is contingent is also a good example of what Beatty (1995, 1997) has called a "relative significance debate" in evolutionary biology. No one would ever deny that there are some fascinating examples of evolutionary convergence, and even the most loyal partisans of convergence would admit that some aspects of evolutionary history are contingent. They disagree over which is the dominant theme in the history of life.

The second major issue has to do with explanation in macroevolution and with the distinction between passive and driven large-scale evolutionary trends (McShea 1994; for a good introduction, see Rosenberg and McShea 2008, Ch.5). When paleontologists identify a large-scale trend in the fossil record—size and complexity increase are good examples, but see McShea (1998) for some others—one of the first questions they ask about it is whether the trend is passive or driven. Where a trend is driven, the assumption is that some force is "pushing" evolutionary change. A passive trend, by contrast, involves a random walk away from some fixed starting point. The passive/driven distinction marks two different ways of explaining trends (Grantham 1999). Here, too, one can find a Beatty-style relative significance debate. Most scientists who work on these issues try to focus on tractable questions, such as whether a morphological trend in a given clade, over a given time interval, is driven. Stephen Jay Gould (1996, 1997) has suggested that larger-scale evolutionary trends are mostly passive. Everyone acknowledges that some trends in evolutionary history are driven. And there are also some well-documented cases of passive trends (see, e.g., Jablonski 1997). But the existing body of empirical work on the subject leaves plenty of room for disagreements of emphasis.

How are these two issues—contingency *vs*. convergence, and passive *vs*. driven trends—related? One possibility is that the two issues are largely independent of one another. For example, suppose we knew that evolutionary history is highly contingent. That might make no difference at all to the question whether passive *vs*. driven trends are more prevalent. Or suppose we determine that passive trends are the rule. That might be compatible with either the convergentist or the contingentist pictures of macroevolution. In these cases, we'd have a theory of macroevolution that is compartmentalized. We'd have no story to tell about how our answers to different questions about macroevolution are related. It might turn out that this outcome is just unavoidable. But my aim here is to show that there really is an interesting and heretofore underappreciated connection between these two issues. An initial clue is that Stephen Jay Gould was consistent in his defense of both contingency and passive trends. Though he nowhere (to my knowledge) explicitly discusses the possible connections between these ideas, Gould is nothing if not a systematic thinker.

Is there a special connection between the concept of historical contingency and the concept of a passive trend? I'll begin, in section 2, by showing how this rather narrow issue is related to broader questions about the nature of explanation in historical science. Section 3 focuses on a superficial connection between the notions of contingency and passive trends. Both are, broadly speaking, non-selectionist ideas, and so defending them might be one way of downplaying the importance of natural selection. Section 4 introduces, as a working hypothesis, the suggestion that the contingency of evolutionary history explains why some evolutionary trends are passive. One immediate problem with this working proposal is that 'contingency' has different meanings. In section 5, I argue that the plausibility of the working proposal depends on which sense of 'contingency' we have in mind. If we think of contingency as sensitivity to initial conditions, then the working proposal does not fare too well. However, things look better if we think of contingency as unbiased sorting. Section 6 explores the relationship between unbiased sorting and passive trends in greater detail and argues that unbiased sorting can (partly) explain passive trends.

2. Explaining evolutionary patterns

When we think about historical science, it's natural to suppose that the explanatory targets must be particular events. For example, one might think that the explanation of the end-Cretaceous mass extinction in terms of an asteroid impact is paradigmatic. In many cases, though, paleontologists are more interested in explaining patterns and trends that show up in the fossil record, rather than particular events. One example of such a pattern is the so-called "Lilliput effect" (Harries and Knorr 2009). The animals that show up in the fossil record in the aftermath of mass extinction events tend to have smaller body sizes than the animals that preceded the mass extinction. One potential explanation of this pattern invokes species sorting. It could be that large body size increases extinction risk during calamitous times. Another possible explanation invokes within-population sorting processes: Perhaps, in the lineages that survive mass extinction events, there is strong selection pressure in favor of smaller body size (Harries and Knorr 2009, p. 7). Of course, these two hypotheses about process are not necessarily incompatible. Species sorting is compatible with natural selection working to cause dwarfism within populations. It's possible that both of these processes contribute in some way to explaining the Lilliput effect. I offer this merely as an example of the sort of explanation that is quite common in paleobiology, where the goal is to explain pattern in terms of process.

An evolutionary trend is just one kind of pattern in the fossil record. A trend is usually defined as a persisting, directional change in some variable of interest. In his classic (1994) paper, McShea treats the passive/driven distinction as a distinction between two different "mechanisms" or processes that can generate trends, so in claiming that a trend is, say, driven, one is trying to explain a pattern in terms of an underlying process. The general point is just that the investigation of passive vs. driven trends fits neatly into the larger paleontological practice of explaining patterns in terms of evolutionary processes.

One would think that if evolutionary processes were contingent, as Gould, Beatty, and others have claimed, that would matter somehow to the overall project of explaining patterns in terms of evolutionary processes. My goal here is to explore some of the ways in which contingency might matter to that explanatory project. Would the contingency of evolutionary processes make any difference at all to the way in which those processes help explain patterns and trends?

It's easier to see how the contingency of evolutionary processes might make a difference to the explanation of particular events. There are at least two ways in which contingency might constrain the explanatory options when it comes to particular events. First, suppose that contingency does imply (as Beatty 1995 argued) that there are no distinctively biological laws. That, presumably, would mean that explaining particulars by subsuming them under general biological laws is not in the cards. And some philosophers have indeed tried to show there are distinctively historical or narrative styles of explanation that do not invoke laws (Gallie 1959, Hull 1975). Second, Sterelny (1996) draws a distinction between actual sequence explanations and robust process explanations. A robust process explanation claims, counterfactually, that a given event would have happened even if initial conditions had been different. If history is highly contingent, where 'contingency' is taken to mean that later outcomes are sensitive to variations in initial conditions, then that would seem to rule out robust process explanations by definition. Although historical contingency has the potential to constrain explanation in at least these two ways, these issues both concern the explanation of particular events.

So the goal in what follows is to see if contingency matters at all to the larger project of explaining evolutionary patterns in terms of evolutionary processes. I'll pursue this by zeroing in on the somewhat narrower issue of how contingency is related to passive trends. We'll see in the next section that there is a superficial connection between the two. In order to get to the bottom of things, however, it will be necessary to examine some of the different possible meanings of 'contingency'.

3. The non-selectionist spirit

It's well known that Gould was skeptical about the prospects for using natural selection to explain many of the patterns of evolutionary history (see especially Gould and Lewontin 1979, but also Gould 2002). Much of Gould's thinking about evolution is anti-selectionist—or perhaps just non-selectionist—in spirit. Gould was also a consistent critic of the idea of evolutionary progress. One can hold that natural selection is the major cause of evolutionary change without necessarily believing in evolutionary progress. For example, one could argue that selection usually only adapts populations to local environmental conditions, without driving evolutionary change in any particular direction over longer timescales. But it is much harder to see how one could believe in evolutionary progress without emphasizing the power of natural selection. So one way to attack the notion of progress is to attack selectionism. Because progress is (partly) a normative notion, it raises further issues that might render the discussion unmanageable. So I won't say much more about progress here (but see Turner 2011, Ch. 6, for an overview). One can see contingency and passive trends as two components of a larger Gouldian critique of the power of natural selection.

To begin with, convergent evolution is usually thought to occur when distantly related lineages evolve similar adaptations under similar selection regimes, or come to occupy similar ecological niches. For example, ichthyosaurs and dolphins have remarkably similar body designs. Both have features that look like adaptations for sustained, fast swimming. Both evolved from terrestrial ancestors that returned to the water where they confronted the same biomechanical constraints. Defenders of convergence, such as Simon Conway Morris, are explicitly pro-selectionist. Clearly, one way of downplaying the importance of natural selection in evolutionary history is to downplay evolutionary convergence, and to argue that contingency is relatively more significant.

In addition, most paleontologists take it as obvious that there is a connection between natural selection and driven trends. For example, if we were to find that size increase in a given group is driven (see, e.g. Alroy's 1998 study of mammals), it would seem reasonable to conclude that natural selection is the driver. That is, the trend toward larger size is driven because natural selection is, for whatever reason, favoring larger body size. Hone and Benton (2005) discuss some of the ways in which larger body size might confer survival or reproductive advantage. Thus, for many paleontologists, investigating whether a trend is passive or driven is just an indirect way of investigating natural selection's role in evolution. There are some exceptions. McShea (2005) has argued that driven trends need not be driven by selection, and this idea also shows up in McShea and Brandon's (2010) argument that complexity increase is a driven trend, but one that's not driven by selection. Nevertheless, in spite of these recent developments, it's fair to say that most paleontologists just assume that selection is what "drives" large-scale trends. In this context, arguing that many trends are passive is another way of downplaying the importance of natural selection.

Here, then, is one interesting connection between passive trends and contingency: both ideas pose challenges to strong selectionist or adaptationist views of evolutionary history. Or coming at things from the other direction, we might say that both convergent evolution and driven trends are typical signatures of natural selection. Having made this observation, it might be tempting to stop here. But I want to press on in hopes of being able to say something deeper about the relationship between contingency and passive trends. We can say that the greater the significance of contingency and passive trends, the less important natural selection is in shaping evolutionary history. But that leaves open whether there is any tighter conceptual connection between contingency and passive trends.

4. Is there a deeper connection between contingency and passive trends?

Consider, as a first pass, the following working proposal, which is suggested by Gould's defense of both passive trends and contingency:

WP Passive evolutionary trends generally result from contingent evolutionary processes. Driven evolutionary trends generally result from non-contingent evolutionary processes.

My plan of attack will be to investigate WP in a systematic way. It will turn out to require some clarification and revision. But I'll argue that with some adjusting, tweaking, and disambiguation, WP gets things basically right. Moreover, if WP is indeed correct, then contingency does matter to the explanation of larger scale evolutionary patterns and trends. Where trends are passive, the contingency of historical processes would help explain why.

Although my main concern here is with the unity of macroevolutionary theory, WP might prove to be interesting for another reason. Scientists have developed several good empirical methods for determining whether evolutionary trends are passive vs. driven (McShea 1994). These include (i) the ancestor/descendant test, (ii) the subclade test, and (iii) the stable minimum test. Suppose, for example, that we know that mean body size increases in a certain clade over a specific time interval. Is that because there is an underlying bias toward larger size? One way to check this is by comparing ancestors with their descendants (assuming we know the phylogenetic relationships). Are the descendant species typically larger than their ancestors? Another way to check this is by looking at the size of the smallest members of the clade. Does the size of the smallest-bodied lineage of the clade increase over time? If not—if the minimum is stable—then that might suggest that the trend is passive, and that the clade is "bumping against" a fixed minimum size boundary. A third approach is to look at the size distributions in a subclade (or a sample of subclades) that is far removed from the hypothesized minimum size boundary. A pattern of size increases in those subclades suggests that the trend is driven. These methods give paleobiologists a great deal of traction when it comes to the question whether trends are passive vs. driven. There may be other questions about the causes of trends that are more difficult to answer (Turner 2009), but it is often possible to determine whether the basic dynamic is passive or driven.

Notice that WP makes specific reference to evolutionary processes. That reflects a decision to restrict the focus here to evolutionary theory. However, evolution is by no means the only context in which it makes sense to ask whether history is contingent or convergent. One can ask this about any historical processes. One especially interesting example is the history of science. Many realist philosophers of science share C.S. Peirce's faith that if scientists apply their methods consistently over the indefinitely long run, they will eventually converge on the same results no matter where their inquiries started. Anti-realists see more contingency in the history of science, and they are more open to the thought that our current scientific picture might have been very different, and yet equally well supported by the evidence (Radick 2005). Furthermore, there are many different fields of study in which researchers seek to document and explain the occurrence of historical trends, from economics to climate science. The passive/driven distinction is entirely general: any time we identify a trend, we might ask whether it is passive or driven. Thus, the relationship between historical contingency and trend dynamics is one that could be of interest to researchers in virtually any field that's concerned with historical processes. Although I will continue to focus rather narrowly on evolutionary theory, because that's where these issues have been discussed, the issues themselves could be said to belong to the philosophy of historical science more generally, an area that has received a lot of philosophical attention in recent years (Cleland 2001, 2002, 2011; Jeffares 2008; Tucker 2004; Turner 2007; among others).

If WP is correct, then these methods of determining whether a trend is passive or driven might give scientists an indirect way of addressing questions about contingency. Contingency is not easy to get a grip on empirically. Conway Morris's (2003) approach is to provide a lengthy catalogue of examples of evolutionary convergence. But Sterelny (2005) has observed that one problem with that approach is that it's not always clear whether two traits in different lineages ought to count as the same: Is the evolution of agriculture in humans and ants an instance of convergent evolution? Experimental work has yielded fascinating results, but it's not clear what conclusions we can draw about macroevolutionary history on the basis of observations of *E. coli* populations in the lab. Even more pressingly, it's not entirely clear how to assess counterfactual claims about evolutionary history (e.g., "If this or that had been different in the past, humans would never have evolved.") If, as WP says, passive trends result from contingent processes, then our methods for determining whether trends are passive could also be put to use on the question of contingency. Thus, WP could conceivably have some empirical payoff.

5. Varieties of Historical Contingency

As it stands, however, WP contains a crucial ambiguity because there are several different senses of 'contingency' (Beatty 2006, Turner 2010). The ambiguity even shows up in Gould's original presentation of the thought experiment of replaying the tape of history. At times, Gould has us imagine what it would be like to rewind the tape of life to some point in the distant past—say, the Cambrian period, some 540 mya—and then play it back again *after tweaking the initial conditions*. In his 1989 book, Gould describes in rich detail some of the bizarre creatures of the Burgess Shale, including the unimpressive *Pikaia*, a possible ancestor of the chordates. Suppose that *Pikaia* had gone extinct, but that some of the other strange organisms of the Cambrian had persisted—say, *Anomalocaris* or *Wiwaxia*? Things on Earth would look very, very different today. This idea—namely, that seemingly minor changes in upstream conditions can have major downstream consequences—is what many writers mean by contingency (see, e.g., Ben Menahem 1997). It is also very close to Beatty's (2006) notion of contingency as causal dependence. It's what we have in mind when we say that later outcomes are contingent upon earlier historical conditions. The claim that evolution is contingent, in this sense, is also what Conway Morris (2003) takes himself to be arguing against. His view is precisely that evolution by natural selection is usually *in*sensitive to variations in initial conditions. Let natural selection start out with insects, reptiles, birds, or mammals, and it will find a way to design wings every time.

There are also moments when Gould imagines replaying the tape of history multiple times from *the same starting point*, without altering the initial conditions. He suggests that if history were contingent, one would still see different downstream outcomes. This version of the thought experiment comes very close to a defense of causal indeterminism. One concern here is that if the contingency *vs*. convergence issue is supposed to be a matter of empirical scientific investigation, we might want to avoid equating contingency with causal indeterminism. The latter at least seems like a metaphysical, rather than a scientific issue, although some naturalists might think that the latest physics is our best guide to the question whether determinism is true. At any rate, it's not entirely clear why issues in evolutionary biology should hinge on the truth or falsity of causal determinism. Beatty (2006) suggests that it may be helpful here to think of contingency as *unpredictability*. On this interpretation, to say that history is contingent is merely to say that downstream outcomes are not predictable given knowledge of the upstream conditions. However, whether outcomes are predictable depends on various facts about who is doing the predicting: how much background knowledge does the predictor have, for example? How good is the predictor at processing large amounts of data? Interestingly, the degree to which the outcomes of historical processes are predictable could also depend on the degree of sensitivity to initial conditions, and perhaps also the degree of sensitivity to external disturbances. So it's possible that both versions of Gould's famous thought experiment help illustrate the view that the outcomes of evolutionary processes are unpredictable. The two versions just give different reasons for the unpredictability. For present purposes, though, I will follow Beatty's usage, and say that the unpredictability sense of contingency has to do with the second sort of case, where different outcomes result from the same initial conditions.

Gould was likely influenced by the MBL model, an early attempt by a group of paleontologists meeting at the Marine Biological Laboratory at Woods Hole, Massachusetts, to simulate macroevolution using computers (Sepkoski 2012, Ch. 7). The MBL model treats species sorting as a stochastic process, so that it's a matter of chance whether a species goes extinct, speciates, or persists with no change during each time step of the model. This is a bit speculative, but it seems plausible that when Gould talks about "rewinding the tape of history" he may well have in mind the early magnetic tape that was used in computers. This suggests another way of thinking about contingency as unbiased species sorting (Turner 2010, 2011, Ch. 8). On this reading, when Gould says that evolutionary history is contingent, he's making a very specific claim about macoevolutionary mechanisms—namely, that macroevolution works in somewhat the same way as the MBL model. This interpretation has the advantage of drawing a connection between Gould's views about contingency and his defense of what is sometimes known as the hierarchical expansion of evolutionary theory, or his view that in order to understand macroevolutionary patterns, we need to consider distinctively macro-level processes such as species selection. Although different theorists think of species selection in different ways (see Turner 2011, Chs. 4 and 5), one view is that species selection is merely biased species sorting. Biased *vs*. random species sorting would then be analogous to the processes of natural selection and drift at the population level. The precise nature of the relationship between natural selection and random drift has been the subject of much controversy in recent philosophy of biology, and so one must tread very carefully here. However, some do think of the difference between selection and drift as a matter of biased *vs*. unbiased sorting (or sampling). Putting all of this together, Gouldian contingency might be a kind of macro-evolutionary, species-level drift. I'll call this *contingency as unbiased sorting*.

We have, then, three different senses of historical contingency: sensitivity to initial conditions, unpredictability, and unbiased sorting. What happens when we plug these different senses of contingency into WP?

Contingency as unpredictability

WP says that passive trends usually result from contingent processes. If we plug in the unpredictability sense of contingency, WP does not fare very well. The problem is that passive trends are eminently predictable. If you take a computer simulation designed to generate a passive trend—that is, one where increases and decreases in the value of the variable being tracked are equally probable, and where the state space is structured by a fixed boundary—and let it run over and over, you will see much the same pattern on each run, even though it's impossible to predict whether the value being tracked will increase or decrease over one "turn" or time interval. The simulation will do a random walk away from the fixed boundary. Passive trends are predictable in precisely the same sense in which the distribution of heads and tails in a series of coin tosses is predictable: We may not be able to predict the outcome of a single toss, but we can predict that as the number of trials increases, the ratio of heads to tails will approximate 50:50. If we think of contingency as unpredictability, then WP comes out false.

Contingency as sensitivity to initial conditions

WP fares much better when we think about contingency as sensitivity to initial conditions. The issues here are a little more complicated, however, because the notion of sensitivity to initial conditions has more moving parts. There are, as it were, a variety of different initial conditions that one could hypothetically manipulate:

(i) the starting value of the trait.
(ii) the strength of the directional bias in the state space. (The directional bias is akin to the probability that an unfair coin will come up heads. The probability of heads might be .6, or it might be .8, or it could have any number of other values.)
(iii) the location of the fixed boundary in the state space.

With respect to (i), sensitivity to variation in the starting value of the trait, there is an interesting difference between passive and driven trends. A passive trend with respect to some variable, such as mean body size, is indeed sensitive to the starting value of the variable. A passive trend requires that the initial setting for the variable be at or near the fixed boundary in the state space, so that there is nowhere to go but up. A driven trend, on the other hand, is less sensitive to variations in the starting value of the variable in question. If natural selection always drives increases in body size, then it doesn't really matter what the starting body size of the clade might be; whatever the starting size, the mean body size will subsequently increase. Thus, there does seem to be a connection between passive trends and contingency, in the sense that passive trends are sensitive to variations in the starting value of the trait.

What about (ii) sensitivity to variations in the strength of the directional bias in the state space? Note that in principle, the strength of the bias could remain constant, but that it could also change over time, creating what I have elsewhere called a "shifting bias" trend (Turner 2009). It might help to think of a passive trend as the limiting case in which the bias is set to zero. If you introduce a bias at all, the trend is technically no longer passive. Changing the strength of the bias can certainly also change the shape of the resulting driven trend. Differences in the strength of the directional bias could reflect differences in the strength of natural selection. For example, it's possible that while organisms are small, there is strong selection in favor of larger body size, but that as size increases, the strength of selection flags. The shape of the resulting trends will be sensitive to changes in the strength of the bias. By analogy, the expected distribution of heads and tails in a series of coin tosses will differ depending on whether one is using a mildly weighted coin (Prob heads = .6) *vs*. a strongly weighted one (Prob heads = .8). Pulling all of this together, driven trends are sensitive to changes in the directional bias in a way that passive trends are not.

A third parameter that can be set in different ways is (iii) the fixed boundary in the state space. There is, plausibly, a minimum size for mammals, below which the mammalian *Bauplan* just isn't biomechanically or physiologically feasible. The smallest mammals living today—the pygmy shrew or the bumblebee bat—are probably at or near that size minimum. What if the size minimum were different? For example, what if it were a great deal smaller? Imagine a hypothetical scenario in which mammals start out the size of house cats, but where much smaller, insect sized mammals are biologically possible. In that case, the starting body size would be far away from the fixed boundary, and so the conditions would not be right for a passive trend. For passive trends, what matters is the distance (in the state space) between the fixed boundary and the starting value of the trait, so passive trends are sensitive to changes in both of those variables. Driven trends could, however, also be sensitive to the presence or absence of a fixed boundary in the state space. Instead of a size minimum, imagine that there is a maximum size for a given clade that's similarly imposed by biomechanical or physiological constraints. We can imagine that natural selection would drive the mean body size of the clade upward until it hits the ceiling of biological impossibility, so to speak. Change the location of the ceiling, or the floor, and you can change the resulting trend. Elsewhere I call such trends shifting boundary trends (Turner 2009).

The relationship between passive trends and sensitivity to initial conditions is thus rather messy and complicated. There are three different sorts of initial conditions to which trends might be sensitive. It's only in case (i) that we get a result that looks good for WP—namely the result that passive trends result from contingent evolutionary processes while driven trends do not. But (ii) and (iii) also represent potentially interesting kinds of sensitivity to initial conditions.

There is another obstacle that confronts any attempt to understand WP in terms of sensitivity to initial conditions. Sensitivity to initial conditions comes in degrees (Ben-Menahem 1997). In the limiting case, virtually any initial condition would result in the same outcome. This limiting case is well illustrated by a simple equilibrium model provided by Sober (1988), who imagines a ball released from some point along the rim of a bowl. It makes no difference what the release point is; the ball will always come to rest at the same place at the bottom of the bowl. Think of this as a simplified landscape (Inkpen and Turner 2012 develop the landscape metaphor as a way of thinking about historical contingency). In a more complex landscape—say, a basin with an uneven floor—the point of release would make more of a difference to the outcome. The sensitivity of the outcome is a matter of degree, and it depends on the nature of the topography. The trouble is that the distinction between passive and driven trends does not seem to be a matter of degree. Because the strength of the "driver" can vary, we can distinguish between stronger and weaker driven trends (Rosenberg and McShea 2008, p. 148). And of course, trends themselves can be more or less pronounced. But the passive/driven distinction seems like an either/or distinction.

One scientist has argued that passive and driven trends "represent extremes of a continuum" (Wang 2001, p. 851). However, Wang's point has to do with scaling effects (see Turner 2011, pp. 134-5 for discussion). For example, if mean body size increase in a clade is driven, it might be driven in 75% of the subclades and passive in the other 25% of subclades. So we might want to say that the trend is "mostly" driven. Contingency is also scale-dependent in much the same way (Inkpen and Turner 2012). If we resolve to focus on a given clade at a particular temporal scale, the question whether the trend is passive *at that scale* will often have a yes/no answer. For example, the stable minimum test might show that the trend in a particular clade at a particular level of resolution is passive. By contrast, contingency, understood as sensitivity to initial conditions, always comes in degrees.

Because contingency as sensitivity to initial conditions is a matter of degree while the passive/driven distinction is not, the contingency/inevitability distinction does not map onto the passive/driven distinction in the way that WP suggests. In many contexts, it is illuminating to think of contingency as sensitivity to initial conditions, but if we want to understand how contingency is related to passive trends, we should keep looking.

Contingency as unbiased sorting

Some proponents of species selection take the view that all that's required for species selection is biased sorting of lineages. That just means that different lineages have different probabilities of branching, persisting, or going extinct. If it helps to do so, we can think of those probabilities as species-level fitnesses. Some theorists think that more than this is required for species selection (see Turner 2011, Ch. 5, for an overview). For present purposes, we don't need to worry about what does and does not count as species selection. It's enough to work from some simple and hopefully uncontroversial observations: First, lineage sorting does in fact occur in nature. Lineage sorting is the process that generates the Darwinian tree of life. Second, lineage sorting can (indeed, must) be either biased or unbiased. The MBL model of the early 1970s shows what unbiased lineage sorting would look like. One thing we might mean when we say that history is contingent is that it involves unbiased sorting processes. Indeed, I suspect that this is one thing that Gould (1989) did mean by contingency. One major theme of *Wonderful Life* is that the sorting of *Baupläne* in the early history of the metazoans was unbiased. Beatty (2006, p. 345) has also observed that Gould seems to be talking about something like "sampling error at the level of lineages." Gould (1993, p. 307) also writes sympathetically about the "random model" of lineage sorting during mass extinction events, though he doesn't use the term 'contingency' in that context.

Some of the puzzles that arose when we tried to understand the second version of Gould's thought experiment disappear if we think of contingency as unbiased sorting. If one were to "rewind" the MBL model and play it back again in a series of trials—and that, in fact, is just what the MBL group did—then the unbiased sorting process would lead to different outcomes on every run, even when the model runs from the same starting conditions. And although it might look like Gould was flirting with causal indeterminism in the second version of his thought experiment (and maybe he was), Millstein (2000) points out that unbiased sorting processes can occur in a metaphysically deterministic universe. A series of fair coin tosses is an unbiased sorting process. But no one thinks it possible to refute determinism by tossing a coin.

At the very least, there is a strong analogy between (a) the distinction between biased and unbiased sorting processes, and (b) the distinction between driven and passive trends. The claim that some historical trend is passive amounts to the claim that history is chancy or unbiased, or more precisely, that changes in one direction are no more or less probable than changes in another. The claim that history is contingent, on the current proposal, also amounts to the claim that history is chancy or unbiased. This suggests that there is a more general issue about whether historical processes are biased or unbiased. Unbiased sorting and unbiased directional change are just two ways in which history can be chancy.

My view is that *both* unbiased sorting and sensitivity to initial conditions are extremely interesting and important concepts in evolutionary biology. And both of these concepts are in play in Gould's classic (1989) discussion. Both are interesting and important because of the way in which they generate empirical questions. Once we appreciate that historical processes can vary with respect to their degree of sensitivity to initial conditions, then it's an empirical question how much sensitivity to initial conditions is exhibited by any particular historical process. Likewise, once we appreciate that sorting processes can be biased or unbiased, then it's a live empirical question whether any particular sorting process is unbiased.

The main claims of this section can be stated without using the term 'contingency' at all: The relationship between the notion of a passive trend and the notion of a process that exhibits sensitivity to initial conditions is not at all straightforward. We cannot explain why a trend is passive by pointing out that the historical processes that generated it are sensitive to initial conditions. By contrast, I'll argue in the next section that the relationship between passive trends and unbiased sorting processes is much more straightforward. I tend to think of both of these notions – unbiased sorting and sensitivity to initial conditions – as different senses of 'contingency', and part of the reason for that is historical. Gould used the term 'contingency' in both ways. Since Gould, however, philosophers and scientists alike have tended more to use 'contingency' to refer to sensitivity to initial conditions. If someone wanted to insist on that usage and to deny that unbiased sorting is really one kind of historical contingency, that terminological disagreement would just require me to reformulate the take-home message of this paper. For those who insist that contingency is sensitivity to initial conditions, the claim would be that it's not quite right to say (without a lot of qualifying and clarifying) that passive trends result from contingent processes. The claim that passive trends result from unbiased sorting processes has much more going for it.

6. Passive trends and unbiased sorting

Substituting “unbiased sorting processes” for “contingent evolutionary processes” in WP yields the following:

WP* Passive evolutionary trends generally result from unbiased evolutionary sorting processes with proper fixed boundary conditions. Driven evolutionary trends generally result from biased evolutionary sorting processes.

WP* seems plausible. I won’t try to offer a full defense of it here; I just want to suggest that it has some advantages, and that it represents an improvement over WP. To begin with, the second half of WP* coheres extremely well with the standard understanding of driven trends. As noted earlier, most scientists assume that the “driver” of driven trends is cumulative natural selection. And natural selection is readily understood as a biased sorting process. Body size increase will be a driven trend if body size makes a difference to (or biases) the sorting processes going on at the population level.

WP* also preserves the analogy between micro- and macroevolutionary theory that animated some of the efforts of the scientists who participated in the “paleobiological revolution” of the 1970s and 1980s (see especially Stanley 1975 for an especially clear example). Trends in gene frequencies in a population can be passive or driven. Passive trends in gene frequencies are usually associated with random genetic drift, whereas driven trends are associated with selection. Some philosophers of biology have at times seemed to want to identify selection with driven trends in gene (or trait) frequencies, arguing that is not a cause of evolutionary change but rather a certain sort of statistical trend (Matthen and Ariew 2002; Walsh, Ariew, and Lewens 2002). One could similarly say that drift just is a passive trend. Or one could say that driven trends in gene frequencies are caused by selection, whereas passive trends are caused by drift. The precise nature of the relationship between selection and drift is much contested. For present purposes, all that matters is that at the micro-level, it’s plausible to say that biased sorting generates driven trends in trait frequencies, whereas unbiased sorting generates passive trends.

I argued above that the distinction between passive and driven trends does not map neatly onto the distinction between historical contingency (understood as relative sensitivity to initial conditions) and historical inevitability or convergence. That's because sensitivity to initial conditions comes in degrees. We avoid this problem completely when we think of contingency as unbiased sorting. The distinction between biased and unbiased trends perfectly parallels the distinction between passive and driven trends. Biased sorting does come in degrees, since the strength of the bias can vary, but this, as we saw earlier, is also true of driven trends.

In section 2, I observed that no one had really shown how the contingency of evolutionary processes might be relevant to the explanation of evolutionary patterns and trends. WP* makes this much clearer. Suppose we find that a trend (in a given clade, over a given time interval) is passive. This tells us something about the processes that generated the trend, but we might wish to know more? Why is the trend passive? One part of the answer to that question will be a story about the fixed boundary in the state space. For example, why might there be a minimum size for mammals? Is that lower bound policed by natural selection? Is it due rather to biomechanical or physiological constraints? But even if we knew the cause of the fixed boundary, we would not have the whole story about why the trend is passive. We might also want to know why there is no directional bias in the state space. For example, why are size decreases and increases equally probable? One answer to that question is that the relevant sorting processes are unbiased with respect to size. That might be true of the sorting processes occurring within the relevant populations (at the "micro" level), and it might also be true of the sorting among lineages. If we think of contingency as unbiased sorting, then it turns out that the contingency of history really is relevant to the larger project of explaining patterns in terms of processes.

As noted at the end of section 5, some philosophers might prefer to reserve the term "contingency" for sensitivity to initial conditions. That's just a terminological issue. What I hope to have shown here is that from the perspective of explanation in paleobiology, the concept of unbiased sorting is more helpful than the concept of sensitivity to initial conditions.

8. Conclusion

There are four or maybe five big ideas in macroevolutionary theory, depending on how you count: punctuated equilibria, species selection, historical contingency (a term that may cover two rather different concepts), the distinction between passive and driven trends, and perhaps also idea that evolutionary history is characterized by major transitions (Maynard Smith and Szathmary 1995). To the extent that scientists wish to develop a unified account of how evolution works at large scales, it is important to explore the relationships among these ideas. This is a highly theoretical undertaking to which philosophers of biology may have something to contribute. Here I have tried to shed some light on the connections between two of these big ideas: historical contingency and the distinction between passive and driven trends. The issues are complicated owing to the different senses of contingency. Although it's common—and in many contexts, very useful—to think of contingency as sensitivity to initial conditions, I've argued that we can make more headway by thinking of contingency as unbiased macro-level sorting. Not only does that help illuminate the connection between contingency and passive trends, but it serendipitously highlights a tight conceptual connection with yet another of the big ideas of macroevolutionary theory: species selection. Recall that on some of the looser conceptions of species selection, it is nothing other than biased species sorting. Roughly: Contingency is to species selection as drift is to selection. Eldredge and Gould's theory of punctuated equilibria is also related to these ideas, though as I've argued elsewhere (Turner 2010), that connection is a weaker one that's best understood in terms of theoretical "suggestiveness." The connections between these ideas and the major transitions have yet to be explored (though Calcott and Sterelny 2011 provide a good starting point). The theory of macroevolution that paleontologists have forged and refined over the last couple of decades has its share of unity and elegance.

Beginning in the 1970s and 1980s, in an episode in the history of science that David Sepkoski (2012) has documented, a number of paleontologists self-consciously undertook to show that their discipline had something significant to contribute to evolutionary theory. In order to accomplish that goal, these paleontologists—including Gould, Niles Eldredge, David Raup, Jack Sepkoski, Thomas Schopf, Elisabeth Vrba, Steven Stanley, and others—had to do two things. First, they had to make some theoretical innovations. Because the fossil record is the special purview of paleontology, and the fossil record also happens to be our main source of evidence concerning macroevolution, most of the new theory had to do with macroevolution. Second, they had to show that these new ideas could do some explanatory work that could not be done in any other way, and that you really need punctuated equilibria, species selection, etc., in order to make sense of patterns in the fossil record. One of the things at issue here is the overall explanatory power of macroevolutionary theory. If I am right, and (some of) the theoretical innovations that paleobiology has seen over the last few decades turn out to hang together very well, then it might make sense to talk of a single body of macroevolutionary theory that can be deployed to explain a wide variety of patterns in the historical record.

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References

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals, Science 280: 731-734.

Beatty, J. 1995. The evolutionary contingency thesis. In G. Wolters and J. Lennox, eds., Concepts, theories, and rationality in the biological sciences. Pittsburgh, PA: University of Pittsburgh Press, pp. 45 – 81.

Beatty, J. 1997. Why do biologists argue like they do? Philosophy of Science 64(4 supp): S432-443.

Beatty, J. 2006. Replaying life's tape. Journal of Philosophy 103(7): 336-362.

Ben-Menahem, Y. 1997. Historical Contingency, Ratio 10: 99-107.

Calcott, B., and K. Sterelny, eds. 2011. The major transitions in evolution revisited. MIT Press.

Cleland, C. 2001. Historical science, experimental science, and the scientific method, Geology 29: 987-990.

Cleland, C. 2002. Methodological and epistemic differences between historical and experimental science, Philosophy of Science 69: 474-96.

Cleland, C. 2011. Prediction and explanation in historical natural science, British Journal for the Philosophy of Science 62(3): 551-582.

Conway Morris, S. 2003. Life's solution: Inevitable humans in a lonely universe. Cambridge University Press.

DesJardins, E. 2011. Historicity and experimental evolution. Biology and Philosophy 26: 339-364.

Gallie, W.B. 1959. Explanations in history and the genetic sciences, in Patrick Gardiner, ed., Theories of History. Glencoe, IL: The Free Press, pp. 386-402.

Gould, S.J. 1993. Eight little piggies. W.W. Norton.

Gould, S.J. 1996. Full house: The spread of excellence from Plato to Darwin. W.W. Norton.

Gould, S.J. 1997. Cope's rule as psychological artefact, Nature 385(6613): 199-200.

Gould, S.J. 2002. The structure of evolutionary theory. Harvard University Press.

Gould, S. J. and R. Lewontin 1979. The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme," Proceedings of the Royal Society B 205: 581-598.

Grantham, T. 1999. Explanatory pluralism in paleobiology. Philosophy of Science 66 supp: S223 – S 236.

Harries, P.J. and P. O. Knorr 2009. What does the "Lilliput effect" mean? Paleogeography, Paleoclimatology, Paleoecology 284: 4 – 10.

Hone, D.W.E., and M.J. Benton 2005. The evolution of large size: How does Cope's rule work? Trends in ecology and evolution 20(1): 4-6.

Inkpen, R., and D. Turner 2012. The Topography of Historical Contingency, Journal of the Philosophy of History 6: 1-20.

Jablonski, D. 1997. Body size evolution in Cretaceous mollusks and the status of Cope's rule, Nature 385: 250-252.

Jeffares, B. 2008. Testing times: regularities in the historical sciences, Studies in History and Philosophy of Biological and Biomedical Sciences 39: 469-475.

Lenski, R.E. and Travisano, M. 1994. Dynamics of adaptation and diversification: A 10,000 generation experiment with bacterial populations. Proceedings of the National Academy of Sciences 91: 6808-6814.

Matthen, M. and A. Ariew. 2002. Two ways of thinking about fitness and natural selection. The Journal of Philosophy 99(2): 55-83.

Maynard Smith, J. and E. Szathmary 1995. The major transitions in evolution. W.H. Freeman.

McShea, D.W. 1994. Mechanisms of large-scale evolutionary trends, Evolution 48: 1747-1763.

McShea, D.W. 1998. Possible largest-scale trends in organismal evolution: eight 'live hypotheses', Annual review of ecology and systematics 29: 293-318.

McShea, D.W. 2005. The evolution of complexity without natural selection: a possible large-scale trend of the fourth kind, Paleobiology 31(supp): 146-156.

McShea, D.W., and R.N. Brandon 2010. Biology's first law. University of Chicago Press.

Millstein, R. 2000. Chance and macroevolution. Philosophy of Science 67(4): 603-24.

Radick, G. 2005. Other histories, other biologies. Royal Institute of Philosophy Supplements 80(56): 21-47.

Raup, D.M., and Gould, S.J. 1974. Stochastic simulation and the evolution of morphology - towards a nomothetic paleontology, Systematic Zoology 23: 305-322.

Raup, D.M. Gould, S.J., Schopf, T.J.M., and Simberloff, D. 1973. Stochastic models of phylogeny and the evolution of diversity, Journal of Geology 81: 525-542.

Rosenberg, A., and D.W. McShea 2007. Philosophy of biology: A contemporary introduction. Routledge.

Sepkoski, D. 2012. Rereading the fossil record: The growth of paleontology as an evolutionary discipline. University of Chicago Press.

Sober, E. 1988. Reconstructing the past: parsimony, evolution, and inference. MIT Press.

Stanley, S. 1975. A theory of evolution above the species level. Proceedings of the National Academy of Sciences 72(2): 646-650.

Sterelny, K. 1996. Explanatory pluralism in evolutionary biology. Biology and Philosophy 11: 193 – 214.

Sterelny, K. 2005. Another view of life, Studies in History and Philosophy of Biology and Biomedical Sciences 36: 585-593.

Travisano, M., Mangold, J.A., Bennett, A.F., and Lenski, R.E. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution, Science 27(5194): 87-90.

Tucker, A. 2004. Our knowledge of the past: a philosophy of historiography. Cambridge: Cambridge University Press.

Turner, D. 2007. Making prehistory: Historical science and the scientific realism debate. Cambridge: Cambridge University Press.

Turner, D. 2009. How much can we know about the causes of evolutionary trends? Biology and Philosophy 24: 341-357.

Turner, D. 2010. Gould's replay revisited, *Biology and Philosophy* 26: 65-79.

Turner, D. 2011. Paleontology: A philosophical introduction. Cambridge University Press.

Walsh, D.M., A. Ariew, and T. Lewens. 2002. The trials of life: Natural selection and random drift. Philosophy of Science 69(3): 452-473.

Wang, S.C. 2001. Quantifying passive and driven large-scale evolutionary trends, Evolution 55(5): 849-858.