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A case study in evolutionary contingency

Zachary D. Blount ^{a,b}^a BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI, USA^b Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI, USA

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ABSTRACT

Biological evolution is a fundamentally historical phenomenon in which intertwined stochastic and deterministic processes shape lineages with long, continuous histories that exist in a changing world that has a history of its own. The degree to which these characteristics render evolution historically contingent, and evolutionary outcomes thereby unpredictably sensitive to history has been the subject of considerable debate in recent decades. Microbial evolution experiments have proven among the most fruitful means of empirically investigating the issue of historical contingency in evolution. One such experiment is the *Escherichia coli* Long-Term Evolution Experiment (LTEE), in which twelve populations founded from the same clone of *E. coli* have evolved in parallel under identical conditions. Aerobic growth on citrate (Cit⁺), a novel trait for *E. coli*, evolved in one of these populations after more than 30,000 generations. Experimental replays of this population's evolution from various points in its history showed that the Cit⁺ trait was historically contingent upon earlier mutations that potentiated the trait by rendering it mutationally accessible. Here I review this case of evolutionary contingency and discuss what it implies about the importance of historical contingency arising from the core processes of evolution.

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History is subject to a tangled tension between chance and necessity. Humans have long been conscious of this fact, with one consequence being that human conceptions of history have generally fallen on a continuum between extreme poles that may be thought of as fate and fortune. In Greco-Roman mythology, fate is personified as the three stern Fates who see that history unfolds inevitably according to their inflexible plan. Fortune is personified by Fortuna, the goddess of luck and the “million to one shot.” Whereas the Fates are steady and implacable beings, the workings of whom cannot be altered even by the gods themselves, Fortuna is fickle, plays favorites as she pleases, and can whimsically change the course of events at any time. In the fatalistic view, historical outcomes are inevitable and predetermined, whereas in the view governed by fortune no historical event is inevitable until it has occurred, because chance can always intervene. Of course, both polar extremes are problematic, and most take a mixed view between the two.

Like human history, biological evolution is also subject to a tension between chance and necessity. Its core processes involve a complex interplay of the random and the deterministic (Monod, 1971). Natural selection works deterministically to adapt populations to their environments, but it must act upon heritable variation stochastically introduced by random mutation, gene flow, and recombination. Beneficial variation introduced by any of these mechanisms may be lost at random by genetic drift. Mutations can vary greatly in their effects on multiple traits (pleiotropy) and in their interactions with other genes (epistasis), so that the order in which beneficial mutations arise can change the fitness value of subsequent mutations (Lenski, Rose, Simpson, & Tadler, 1991; Mani & Clarke, 1990). Due to these effects, populations starting from the same ancestral genotype can evolve along divergent paths that vary in their evolutionary potential, thereby making evolutionary outcomes path dependent to at least some degree (Cooper & Lenski, 2000; Weinreich, Delaney, DePristo, & Hartl, 2006; Weinreich, Watson, & Chao, 2005; Wright, 1988). For instance, different evolutionary paths can lead to states with similar fitness in a prevailing environment, but very different fitness in other

E-mail address: blountza@msu.edu.<http://dx.doi.org/10.1016/j.shpsc.2015.12.007>

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environments. Seemingly subtle differences between lineages can determine which go extinct and which survive during periods of rapid and capricious environmental change (Gould, 1985; Jablonski, 1986; Lewontin, 1966).

All modern organisms are the products of unique, unbroken, and very long evolutionary histories that have played out within the broader history of a changing Earth. How important is this fact? Stephen Jay Gould suggested that it is very important. Gould focused on instances such as the body plan diversity evident in the fossils of the Burgess Shale, only a subset of which continue to exist, to suggest that there were viable alternate routes evolution could have taken (Gould, 1989, esp. 299–321, 1991, 2002, 1159–60). In Gould's view, evolution followed the path it did due in large measure to chance, including that imparted by capricious mass extinction events like the KT impact (Gould, 1989, 305–8, 2002, 1315–20). He argued that such cases show that evolutionary outcomes are sensitive to the peculiarities and quirks of history, making them fundamentally contingent, unpredictable, and path dependent (Gould, 1989, 45–52, chap. 5, 2002, chap. 12; Beatty, 2006; Beatty & Carrera, 2011). Famously, Gould suggested in *Wonderful Life* (1989, 48–51) that this contingency means that replaying the “tape of life” from points in the distant past would result in living worlds far different than the one that now exists, because evolution would be unlikely to follow the same path twice.

Gould's position has been controversial. Simon Conway Morris and others have pointed to the striking pervasiveness of convergent evolution as suggesting that natural selection and biological and physical constraints greatly restrict the range of viable evolutionary outcomes (Conway Morris, 2003, 2010; Dawkins, 1996; Van Valen, 1991; Vermeij, 2006). As Conway Morris writes in *Life's Solution* (2003, 144), “the evolutionary routes are many, but the destinations are limited.” If there are few viable end points, and the origin of life always leads to elephants, then evolution is relatively path independent (Atkins, 1981, 3). As in a Greek tragedy, the only uncertainty is that of how evolution reaches its inevitable end. In this view, replaying the tape of life would always lead to remarkably similar outcomes.

This debate has major implications for how evolution should be understood and explained as a phenomenon (Beatty, 1993; Desjardins, 2011; Sterelny & Griffiths, 1999). If evolution is highly path dependent, with many viable outcomes, then evolution must be understood in a narrative fashion (Blaser, 1999; Gould, 1985, 1989, 2002). However, if evolution's path dependence is highly constrained by few viable end states, then evolution is predictable and can be understood using robust process explanations insensitive to history, such as those in physics (Sterelny & Griffiths, 1999, 84–86). As John Beatty makes clear in his article in this issue, a narrative requires that there be possible alternatives, but if the ends of evolution are largely invariant, then narrative explanations are not appropriate.

Scientific debates must ultimately be resolved by empirical research that adjudicates which side better describes the underlying reality, and the contingency debate is no different. Gould's and Conway Morris's work does contribute to this resolution, but not directly. Each marshalled facts and findings that serve to argue for the plausibility of their respective positions (Conway Morris 2003, 2010; Gould, 1989). Their work therefore principally serves to lay out broad lines from which other researchers may develop better definitions, more focused models, and, importantly, testable hypotheses. Indeed, Gould's and Conway Morris's work has been a springboard from which numerous researchers have begun to evaluate the complex questions of evolutionary contingency (Orgogozo, 2015). Appropriately, these empirical studies have examined contingency on multiple levels, including Vermeij's examination of the timing and phylogenetic distribution of

evolutionary innovations (2006), examination of natural instances of “replaying the tape” such as radiations of *Anolis* lizards on Caribbean islands (Losos, 2010; Losos, Jackman, Larson, de Querioz, & Rodriguez-Schettino, 1998), and investigation of the effects of history on the evolution of egg-eating snakes (de Queiroz & Rodriguez-Robles, 2006) and Southeast Asian fanged frogs (Emerson, 2001). These empirical studies have made substantial contributions to a better understanding of evolutionary contingency and convergence within the context of the natural world. At the other end of the spectrum, a great deal of intriguing work has been done using experimental microbial evolution systems, in which the loss of complexity is balanced by the ability to evaluate directly the effects of history on evolution.

1. Experimental evolution with microorganisms

Experimental evolution with microorganisms involves propagating populations of microbes under controlled conditions to examine evolution as it occurs (Elena & Lenski, 2003; Kawecki et al., 2012). This approach to studying evolution was first used by William Henry Dallinger, an English Methodist minister and correspondent of Darwin's, in work he did in the 1880's that examined the evolution of thermotolerance by pond organisms (1887). Despite this early start, experimental evolution with microorganisms only began to be used as a major research approach in the 1980s, and it has since proven to be a powerful way to address a variety of fundamental questions in evolutionary biology that are difficult to examine using more traditional techniques (Elena & Lenski, 2003; Kaçar & Gaucher, 2013; Kawecki et al., 2012; Kussell, 2013).

There are many benefits to using microbes to study evolution. Microbes reproduce very quickly, making it possible to study hundreds or thousands of generations of evolution in experiments lasting only weeks or years. Large population sizes provide a steady influx of new variation from mutations. High levels of experimental replication are possible because these large populations can be kept in small containers. (A 10 mL bacterial culture may contain up to 5×10^{10} cells.) Microbes reproduce asexually, so genetically identical replicate populations can be founded. A high level of control is also possible because microbial cultures are easily maintained under a variety of conditions. Moreover, researchers can reliably manipulate important factors such as mutation supply, population size, prior evolutionary history, and the biotic and abiotic environment to study their effects (Bennett & Lenski, 1993; Bohannan & Lenski, 2000; Burch & Chao, 2000a, 2000b; Chao & Cox, 1983; Elena, Sanjuan, Borderia, & Turner, 2001; Fukami, Beaumont, Zhang, & Rainey, 2007; Lenski & Levin, 1985; Meyer & Kassen, 2007; Perfeito, Fernandes, Mota, & Gordo, 2007; Travisano, Mongold, Bennett, & Lenski, 1995; Travisano, Vasi, & Lenski, 1995; de Visser, Zeyl, Gerrish, Blanchard, & Lenski, 1999). Perhaps just as importantly, a wealth of tools, including genome sequencing and genetic engineering, allow researchers to identify evolved genetic changes and directly link them to phenotypic changes (Barrick & Lenski, 2009; Barrick et al., 2009; Bentley, 2006; Hegreness & Kishony, 2007; Herring, Glasner, & Blattner, 2003). Finally, microorganisms can be frozen indefinitely without loss of viability, so that ancestral and evolved clones¹ and populations are available for revival at will.

A number of these advantages make experimental evolution with microbes particularly useful for studying contingency.

¹ In microbiology, a clone is a population grown from a single founding cell. Because of asexual reproduction, this population will be more or less genetically identical, meaning that we can study its properties to understand the properties of the founding cell. Due to this genetic homogeneity, we also tend to use “clone” interchangeably with “genotype.”

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