



Commentary

Wherefore stoch-aptation?

Root Gorelick

Root Gorelick (Root.Gorelick@carleton.ca), Department of Biology, School of Mathematics & Statistics, and Institute of Interdisciplinary Studies, Carleton University, 1125 Raven Road, Ottawa, Ontario K1S 5B6 Canada

Abstract

There exists discordance between different levels of evolution because the whole often differs from the sum of the parts. Yet, it is not obvious that the new term ‘stoch-aptation’ clarifies these differences between evolutionary levels, especially when this term seems largely equivalent to stochastic drift, to mega-evolution, and maybe even to phenotypic plasticity with extreme environments. But this new term forces us to carefully examine what evolutionary biologists mean by randomness, drift, selection, plasticity, and mega-evolution.

Introduction

Alejandro Martínez-Abraín (2015) argues that many seemingly adaptive traits are random in nature, being the result of which species randomly managed to survived mass extinctions. He argues that some selection is deterministic, at least during normal times, while some selection is stochastic, at least during geological catastrophes that cause mass extinctions. He also parses evolution into phenomena at the species-level (‘macro-evolution’), below the species-level (‘micro-evolution’), and above the species level (‘mega-evolution’). In so doing, Martínez-Abraín (2015: 43) finds some benefit in defining the new term ‘stoch-aptation’ as a trait “later on selected just by chance during geologic periods of catastrophe.” This seems to be the evolutionary paleontological version of the sociological adage that you only find out who your true friends are in times of extreme adversity.

Selection versus drift

I fully agree with the part of Martínez-Abraín’s (2015: 44) final sentence that it is “both necessary and useful to...acknowledge the role of chance in the evolution of higher taxonomical categories, and...think of the role of geological catastrophes as generators of innovation.” However, in writing such a succinct paper, he seems to have missed a major philosophical nuance, namely the difference(s) between selection and drift. The term ‘stoch-aptation’ seems to conflate drift (stochastic) and selection (adaptation), a conflation or amalgamation that may or may not be justified.

Naively, we could conceptualize drift as random death and selection as non-random death. Philosophers of evolutionary biology have argued over this for decades (e.g. Beatty 1984, Millstein 2002, Brandon 2005). Furthermore, what is randomness? Sometimes randomness is simply something we cannot yet explain, even if the underlying cause is mechanistic. Therefore random and non-random may be indistinguishable, as when so-called random number generators are actually pseudo-random. Things that today are considered to be random genetic drift may eventually be considered non-random selection once we better understand evolutionary mechanisms. For example, randomness often comes from complex interactions between many genetic loci (epistasis; genetic background), interactions between genetic loci and the environment (norms of reaction), and developmental and regulatory cascades (e.g. heterochrony), none of which we fully know how to model. Even simple completely deterministic systems can be chaotic (Li and Yorke 1975; Feigenbaum 1978).

In some ways Gould and Lewinton's (1979) quixotic spandrels papers had it right that we egregiously ascribe too much to selection and adaptation and ascribe too little to drift and epistasis, a relative weighting of evolutionary forces that also encapsulates the long debates between Sewall Wright and Ronald Fisher (Provine 1986).

Is there a better way to distinguish selection from drift and therefore also to distinguish adaptation from stoch-aptation? By definition, selection decimates heritable variation. McShea and Brandon (2010) circumscribed drift as an evolutionary force other than mutation that increases heritable variation, which they did by logically separating out the random part of drift from the boundary conditions/absorbing states of allelic fixation in which variation is obliterated. Such a definition of drift based on resulting variation, especially if that variation is random, makes me want to simply use the term 'drift' in lieu of 'stoch-aptation'.

If drift and stoch-aptation are defined by increases in variation, then Cenozoic mammal diversity is indeed a stoch-aptation, but the 'living fossil' examples of Nautilidae and Limulidae should not be considered stoch-aptations because of their diminished diversity post mass extinction. However, it is often difficult discerning levels of diversity in 'living fossils' that only have a few extant taxa. For example, Cycadales are often considered to be 'living fossils' without much diversity (Gorelick and Olson 2011), but they also contain the only known exception to a pair of sperm cells per mature pollen tube (Norstog 1993), which is a form of cryptic diversity.

We also tend to see adaptation when it is not there, especially when reproductive isolation is driven by whole genome duplication (Gorelick and Olson 2013, Hanzl et al. 2014). For some well-studied multi-cellular eukaryotic populations, the number of traits identified by researchers as being adaptive, antithetically, can be higher than the effective population size.

Phenotypic plasticity

Phenotypic plasticity describes the combined, often non-linear, effect of genotype and environment on phenotype and, consequently, also their combined effect on fitness (Schlichting and Pigliucci 1998). The trick in quantifying norms of reaction is to measure phenotype for as wide a range of environments as possible (and also as wide a range of genotypes as possible, but we will largely ignore that here). This quantification is relatively easy to do for normal environments, but virtually impossible for ultra-extreme environments, such as super-volcanoes or huge asteroid impacts. We cannot estimate evolutionary trajectories because we cannot measure the entire norm of reaction. Maybe the effects of geological catastrophes on who survives are

perfectly predictable, but we do not yet have the tools to predict them. This is akin to the previous decade's situation with the Higgs boson, insofar as physicists could not create a sufficiently high-energy environment to measure one.

While initially Martínez-Abraín only seemed to be talking about the biological effect of extreme *abiotic* environments, he subtly morphed into also talking about the effects of extreme *biotic* environments. Instead of only talking about how species are affected by geological catastrophes, he repeatedly talked about how "species [are] successful when faced with massive extinction" (Martínez-Abraín 2015:42), e.g. when species and individuals are faced with fewer competitors, with fewer food sources, and with fewer mutualists. These extreme biotic environmental effects make measuring norms of reaction even more difficult (Wolf et al. 2004). Is it possible that stoch-aptation is nothing more than the currently unquantifiable tails of the norms of reaction?

A cursory look across Phanerozoic multicellular eukaryotes seems to indicate that plants (Archaeplastidae) have more phenotypic plasticity than animals (Metazoa). Plants have seemingly weathered mass extinctions far better than animals. Paleobotany texts barely, if ever, mention mass extinctions, especially at the Cretaceous-Paleogene boundary. Ability to withstand mass extinctions may largely be due to increased plasticity, both phenotypic and developmental plasticity, although admittedly this correlation could also reflect that most plants are terrestrial while most animals are marine.

Micro-, macro-, and mega-evolution

Parsing evolution into phenomena at the species-level ('macro-evolution'), below the species level ('micro-evolution'), and above the species level ('mega-evolution') is perfectly reasonable. Where things get confusing is in discerning which evolutionary forces are most important at each of these three levels. For micro-evolution, Martínez-Abraín only mentions selection, *not* mutation, drift, or migration, which Charles Goodnight (personal communication) refers to as the 'four horsemen of evolution'. Restricting micro-evolution to only selection seems overly adaptationist, thereby needlessly providing a sham straw comparison between normal and catastrophic environments. By stark contrast, Martínez-Abraín explicitly states that macro-evolution includes "mutations, developmental heterochronies, changes in regulatory genes or epigenetics, coupled with natural selection" (2015: 44). Finally, Martínez-Abraín (2015: 44) defines "megaevolution...as changes at taxonomical categories higher than the species, selected just by chance after environmental catastrophes, rather than by natural selection." In other

words, mega-evolution does not include selection, mutation, or migration. This seems like a strange omission. Furthermore, this definition of mega-evolution seems to be synonymous with his definition of stoch-aptation.

There also exist critiques of species-level selection, critiques that happen to reflect on phenotypic plasticity (e.g. McShea and Brandon 2010). Darwinian selection at the level of the individual describes how individuals interact with their environment. Populations also interact with their environment, such as with niche construction (Laland et al. 1999). But it is not obvious how something as diffuse as a species interacts with its environment. Not only can a species be too diffuse, both spatially and temporally, but ‘its environment’ is often too heterogeneous to describe any coherent interactions. Thus, not only am I troubled with Martínez-Abraín’s definitions of micro-evolution and mega-evolution, but also his definition of macro-evolution. While predominant evolutionary forces should be different for different levels of evolution (micro, macro, mega), it would be nice if definitions added a more consistent framework for understanding underlying evolutionary processes.

Closing remarks

In evolutionary biology and paleontology, there is a need to focus on rare, random, extreme events (e.g. Alvarez et al. 1980), albeit realizing that it is often possible to understand their statistical properties (Galambos 1978, Taleb 2010). Introduction of the term ‘stoch-aptation’ helps provide that focus and reminds us how paleontology is nowadays often forgotten in evolutionary biology.

What is the value-added in a new definition? Definitions should simplify and unify our theories, but I am not certain that the definition of stoch-aptation does. Stoch-aptation seems like a weird, albeit possibly useful, amalgam of stochastic drift and adaptation (“selected by chance”), possibly highlighting that it sometimes (often?) is impossible to consistently distinguish drift from selection or to distinguish random from non-random. In evolution, sometimes we cannot yet determine whether the proverbial dice are fair versus loaded, yet this should not cause scientific paralysis or academentia. Similarly we cannot know the full extent of phenotypic plasticity because there are too many different environments and genotypes to consider. Such unexplored portions of plasticity state-space may possibly best be folded into the umbrella of stoch-aptation. Only time will tell the utility of this new definition, for which I thank Alejandro Martínez-Abraín for opening up an important conversation.

Acknowledgments

Thanks to the Natural Science and Engineering Research Council of Canada (NSERC) for a Discovery Grant. This paper is dedicated to the memory of Edie Gorelick.

References

- Alvarez, L.W., Alvarez, W., Asaro, F., and H.V. Michel. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction: experimental results and theoretical interpretation. *Science* 208: 1095–1108. [CrossRef](#)
- Beatty, J. 1984. Chance and natural selection. *Philosophy of Science* 51: 183–211. [CrossRef](#)
- Brandon, R.N. 2005. The difference between selection and drift: a reply to Millstein. *Biology & Philosophy* 20: 153–170. [CrossRef](#)
- Feigenbaum, M.J. 1978. Quantitative universality for a class of non-linear transformations. *Journal of Statistical Physics* 19: 25–52. [CrossRef](#)
- Galambos, J. 1978. *The asymptotic theory of extreme order statistics*. John Wiley, New York.
- Gorelick, R. and K. Olson. 2011. Is lack of cycad (Cycadales) diversity a result of a lack of polyploidy? *Botanical Journal of the Linnean Society* 165: 156–167. [CrossRef](#)
- Gorelick, R. and K. Olson. 2013. Polyploidy is genetic hence may cause non-adaptive radiations, whereas pseudopolyploidy is genomic hence may cause adaptive non-radiations. *Journal of Experimental Zoology (Part B. Molecular and Developmental Evolution)* 320B: 286–294. [CrossRef](#)
- Gould, S.J. and R.C. Lewontin. 1979. Spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. *Proceedings of the Royal Society of London Series B-Biological Sciences* 205: 581–598. [CrossRef](#)
- Hanzl, M., Kolář, F., Nováková, D., and J. Suda 2014. Nonadaptive processes governing early stages of polyploid evolution: insights from a primary contact zone of relict serpentine *Knautia arvensis* (Caprifoliaceae). *American Journal of Botany* 101: 935–945. [CrossRef](#)
- Laland, K.N., Odling-Smee, F.J., and M.W. Feldman. 1999. Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences of the United States of America* 96: 10242–10247. [CrossRef](#)
- Li, T-Y. and J.A. Yorke. 1975. Period three implies chaos. *American Mathematical Monthly* 82: 985–992. [CrossRef](#)

- Martínez-Abraín, A. 2015. Stoch-aptation: a new term in the science of evolution. *Ideas in Ecology and Evolution* 8: 42–45. [CrossRef](#)
- McShea, D.W. and R.N. Brandon. 2010. *Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems*. University of Chicago Press, Chicago. [CrossRef](#)
- Millstein, R.L. 2002. Are random drift and natural selection conceptually distinct? *Biology & Philosophy* 17: 33–53. [CrossRef](#)
- Norstog, K.J. 1993. Spermatogenesis in *Microcycas*: evolutionary significance of male gametes of seed plants. Pages 270–278 in D.W. Stevenson and K.J. Norstog, editors. *The biology, structure, and systematics of the Cycadales*, Palm & Cycad Societies of Australia, Milton, Queensland.
- Provine, W.B. 1986. *Sewall Wright and evolutionary biology*. University of Chicago Press, Chicago.
- Schlichting, C.D. and Pigliucci, M. 1998. *Phenotypic evolution: a reaction norm perspective*. Sinauer Associates, Sunderland, MA.
- Taleb, N.N. 2010. *The Black Swan: the impact of the highly improbable* (2nd edition). Random House, New York.
- Wolf, J.B., Wade, M.J., and E.D. Brodie. 2004. The genotype-environment interaction and evolution when the environment contains genes. Pages 173–190 in T.J. DeWitt and S.M. Scheiner, editors. *Phenotypic plasticity: functional and conceptual approaches*, Oxford University Press, Oxford.