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*New Idea*

# Stoch-aptation: a new term in evolutionary biology and paleontology

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## Abstract

Following two seminal papers published in the journal *Paleobiology* by Stephen Jay Gould and Elisabeth Vrba several decades ago, I suggest a new term (stoch-aptation) to refer to those individual traits or sets of traits that provide, just by chance, fitness advantages to species when faced with catastrophes (i.e. geological events triggering massive mortality), and that may lead to the origin of taxonomical entities above the species level. I provide as an example of stoch-aptations the set of features that helped mammals pass the Cretaceous-Paleogene transition, as well as traits behind the success of living fossils. However, the identification of specific stoch-aptations can be difficult. This missing term is necessary and useful to (a) consolidate the idea of selection at different hierarchical levels, (b) acknowledge the role of chance in the evolution of higher taxonomical categories and (c) think of the role of geological catastrophes as generators of innovation.

Key Words: missing term, megaevolution, geological catastrophes, hierarchical selection, stoch-aptation, chance.

Stephen J. Gould and Elisabeth S. Vrba published decades ago a famous paper in *Paelobiology* (Gould and Vrba 1982) where they pointed out the inadequacy of the use of the term “preadaptation” to refer to features now enhancing fitness but originally evolved by natural selection for a different role. Instead they proposed the term “exaptation” to prevent the idea of anticipation that the word preadaptation entails in common language. This term has been of a great utility to the scientific community. It has been applied not only to evolutionary biology but also to the social sciences and even the evolution of language. Gould and Vrba made evolutionary scientists think more deeply about the role of re-utilization (of genes and their functions) as a generator of innovation in evolution. The history of success of the term is depicted in Figure 1, where we can see that its use is more alive now (thirty years after its proposal) than ever.

Among his great scientific achievements, Gould not only proposed a new term, giving support to a relevant concept already suggested by Darwin in his *opus magna* (“metamorphism of function”), but also defended the idea that natural selection acts at different structural or hierarchical levels (i.e. genes, organisms, species). Indeed, another notorious *Paleobiology* paper by Gould (Vrba and Gould 1986) developed the argument that not only physical individuals but several other biological entities, notably the species, can behave as “individuals”, as units, in relation to selection by natural means (see also Gould 2004).

Due to the occurrence of catastrophic events in the history of life some species are benefited (“selected”) and others perish. Importantly both Raup (1991) and Jablonski (1989) developed the view that features that make species predictably successful during the long periods of background extinction are not the same that make species successful when faced with massive extinction. That is, features that provide fitness gains to species experiencing catastrophes (i.e. extreme perturbations along the environmental stochasticity

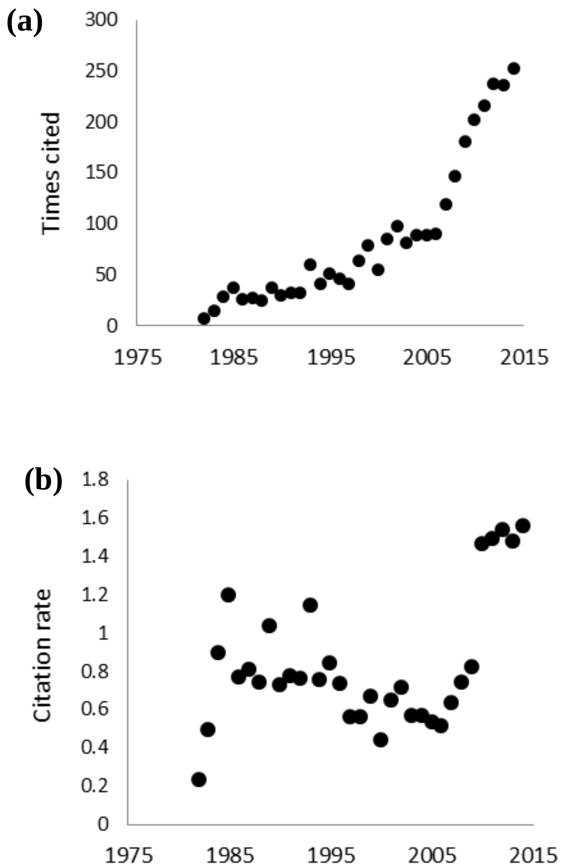


**Figure 1.** Citation rate of the term exaptation in the scientific literature from 1982 to 2014. (a) Raw rate calculated as the number of times papers with the term "exaptation" in the title were cited annually by others during the study period (source: ISI Web of Science). (b) Standardized rate, calculated as the number of times papers with the term "exaptation" in the title were cited annually by others divided by the number of papers published annually with the word "evolution" in the title.

continuum) are unpredictable. However these authors do not offer a new term for that situation.

I am writing here to suggest that these unpredictable features that make species successful after periods of massive extinction lack a name in evolutionary biology and paleontology, and, as indicated by Gould and Vrba (1982), unnamed ideas run the risk of being unconsidered or at least underconsidered. Following the logics behind the term exaptation, I propose to name those features that provide fitness gains to species surviving geological catastrophes as stoch-aptations. The reason for choosing the prefix "stoch" is obvious (i.e. selected by chance) and "aptation" is borrowed from Gould and Vrba (1986) to refer to any character currently subject to positive selection regardless of how it evolved. Stoch-aptations could first evolve by genetic drift or as local adaptations by means of classical neo-Darwinian processes, but they are later on selected just by chance during geologic periods of catastrophe. Features that provide evolutionary success after periods of mass extinction should necessarily be considered stochastic. Nobody could predict beforehand that any of those features was going to be advantageous at the long run simply because natural selection is short-sighted and it only works in relation to local conditions. There is no way for natural selection to advance the arrival of a geological catastrophe, nor to foresee the new environmental conditions (in the form of both abiotic and biotic pressures) that will turn out after a catastrophe; conditions that can be dramatically different compared to those before the crisis.

Along the same line of thought presented by Gould and Vrba (1982) when introducing the term exaptation, I want to stress that the term preadaptation is not an adequate substitution of stoch-aptation because it gives a wrong idea of prediction at the long run, and after massive environmental change, which does not correspond to reality. In addition, stoch-aptation does not compete with the term exaptation because the latter entails a change in trait function that is not required in stoch-aptations (although it could also happen).

Recall that the term I am suggesting here relies on the concept of species selection (considering the species as the unity of selection) (Vrba and Gould 1986), and hence stoch-aptations are necessarily species-level features. Identifying what represented a specific stoch-aptation can be difficult, especially because stoch-aptations could well often be trait complexes rather than single traits. This was probably the case with the set of mammalian features, such as small size, nocturnal life, homoeothermic metabolism or non-vegetarian diet, that provided an unpredictable advantage to mammals during the Cretaceous-Paleogene crisis, leading to its later radiation. Brachiopoda groups surviving until present from Cambrian times (e.g. Lingulata) must have had some local adaptations that can be viewed as stoch-aptations, providing unpredictable fitness advantages during catastrophic periods, over the geological time scale, compared to many other extinct Brachiopoda groups. This is necessarily true for other living fossils such as Nautilidae (a diversified group in the Mesozoic with only two surviving genera at present) or horse-shoe crabs (Limulidae), a diverse group from the Ordovician that has only three extant genera.

Finally, stoch-aptations would not be responsible for microevolution (defined here as additive genetic variation coupled with natural selection leading to local adaptation and with the individual as the unit of selection) or even of macroevolution (defined as changes at the species level driven by a number of mechanisms including *sensu lato* mutations, developmental heterochronies, changes in regulatory genes or epigenetics, coupled with natural selection, working at the individual level. Stoch-aptations would rather be responsible for megaevolution, defined here specifically as changes at taxonomical categories higher than the species, selected just by chance after environmental catastrophes, rather than by natural selection.

Thus, this missing term (stoch-aptation) is both necessary and useful to (a) consolidate the idea of selection at different hierarchical levels, (b) acknowledge the role of chance in the evolution of higher taxonomical categories, and (c) think of the role of geological catastrophes as generators of innovation.

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**Response to referee**

I appreciate Dr. Gorelick’s (2015) comments on my brief paper introducing the new term “stoch-aptation”. Although he agrees that we must acknowledge the role of chance in the evolution of higher taxonomical categories as well as the role of geological catastrophes as generators of innovation, he argues that my new term may be unfortunate because it mixes the ideas of stochastic drift (stoch) and deterministic selection (aptation). Actually I do not see that as a problem because genetic drift is a source of non-adaptive genetic variation (neutral traits), whereas stoch-aptations do provide adaptation (they are positive for survival and reproduction), although it is not natural selection what makes the *triage* but just chance, because adaptation is provided over the geological time scale (after massive geological catastrophes). So you can have a trait or set of traits evolved locally by genetic drift or by classical natural selection that is now subject to the trial of a geological catastrophe and ends up being positive for survival in a completely different natural system, just by chance. By random I mean simply unpredictable. Forces selecting the original trait were not part of the evolutionary pressures shaping the trait in its former local environment. There is selection (at the species level). It is only that this selection is not deterministic but random, because unpredictable selection forces did the job this time.

Stoch-aptations are not necessarily sources of radiation and innovation. In some cases they just help some individual species to survive in geological time (i.e. the case of living fossils), and in some other fortunate cases it can lead to massive radiation (i.e. the case of mammals surviving the Cretaceous-Paleogene transition).

I would not try to link phenotypic plasticity and stoch-aptations because that implies introducing a deterministic (somehow predictable) component in the process of selection by geological catastrophes. Again, traits with the potential of being selected by ultra-extreme events such as super-volcanoes and asteroid impacts are unpredictable. One could make a list of traits having helped species to survive a massive extinction period, but you could only do this *a posteriori*, as in Raup (1991). A new catastrophic event could end up selecting for different traits that would turn out to be new stoch-aptations. Plants, despite their high phenotypic plasticity, have indeed suffered major loses over the geological time scale. For example European forests are more decimated in species than Asian or North American forests simply because of the East to West orientation of the major mountain ranges that acted as barriers preventing the movement of species southwards during the Quaternary glaciations. Mediterranean shrubs, evolved in the Oligocene, that now are the main representatives of Mediterranean shrublands (genus *Pistacia, Chamaerops, Arbutus, Olea, Phillyrea, Smilax*) are good examples of plant species necessarily bearing stoch-aptations, despite the difficulty in identifying what traits (evolved under Tertiary climatic conditions) have been responsible for the success of those genera under the climatic conditions of the Quaternary. One might argue that everything is predictable and that stochasticity is just a matter of huge complexity. I would agree to calling those models that include a huge number of additive variables and their interactions with non-linear effects as random.

Regarding micro, macro and megaevolution I just simply mean evolution of adaptations by the traditional routes of neodarwinism, evolution of species (including mostly evo-devo mechanisms, epigenetics, gene regulation, plant hybridization) and evolution of higher taxonomical categories, respectively. Stoch-aptations are not synonymous with megaevolution because the former are traits and the latter are processes. But yes, I suggest that stoch-aptations may be key for the evolution of new genera and families. These probably have an indirect rather than a direct relationship. Stoch-aptations allow some species to survive massive catastrophes whereas species not holding those traits perish. Hence surviving species have more chances to radiate and occupy ecological niches. These niches (defined by the new abiotic and biotic conditions) may be radically different and hence chances are that large innovations appear giving rise to new higher taxonomical categories. Alternatively, as in the case of living fossils, megaevolution may not occur—just survival of ancient lineages. Megaevolution does include selection; but it is a non-deterministic type of selection. Species environments are indeed heterogeneous and this is central to the geographical mosaic theory of coevolution by Thompson (2005). The reason why, despite all this heterogeneity, some traits are finally fixed and others are not (which has puzzled the followers of this theory), could be connected with Ramón Margalef's (1978) old ideas linking evolution and ecological succession (eco-evo). There is a directional factor acting in ecosystems: succession. The traits that are finally fixed could be those corresponding to the final stages of succession (climax).

Finally I thank Dr. Gorelick (2015) for an inspiring discussion of my proposal. I hope this new term will give evolutionary biologists pause to think more often on selection at different hierarchical levels, reflect more about the role of pure chance in evolution and help highlight the importance of paleontology for evolution, along the lines that Stephen Jay Gould opened up decades ago.

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