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New Idea

Black Swans in ecology and evolution: The importance of improbable but highly influential events

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Abstract

The role of improbable but highly influential events in ecology and evolution is poorly understood. Recent works in economics and finance emphasize the importance that these events, so-called Black Swans, can have for the behavior, predictability, and ultimately understanding of complex economic systems. Ecology and evolution are also complex systems that involve the interaction of organisms with their environment in different time scales; therefore, they should also experience Black Swans. Here, we briefly discuss the nature of Black Swans, and their potential role in ecology and evolution. Traditionally, ecological and evolutionary research has been mostly focused on normal or regular events, while rare events have been usually ignored. However, several highly consequential events in ecology and evolution could qualify as Black Swans. For example, the sudden emergence of a new deadly pathogen, or, the rapid extinction or diversification of a lineage could be considered Black Swans. Thus, including the Black Swan phenomenon in ecological and evolutionary thinking may be necessary for a better understanding of these subjects.

Keywords: Black-Swans, ecology, evolution, improbable, highly-influential

What are Black Swans?

The role of improbable but highly influential events has historically attracted limited attention in ecology and evolution. Despite the fact that there is active research on improbable but highly influential events (e.g. mass extinctions, appearance of novel key traits in lineages, global change and uncertainty) (Alroy 2010, Polasky et al. 2011), these phenomena are still not an integral part of the generalized ecological and evolutionary thinking. Today, more research is devoted to investigate predictable and frequent events, and our statistical tools are better suited to deal with this type of data. It is not surprising that the research community has traditionally focused on investigating the rule and not the exception, as events that rarely occur can be perceived as less important, more anecdotal, or more difficult to approach than more frequent events. However, what if these rare events are also pivotal for our understanding of ecological and evolutionary systems? Taleb (2007) asks a similar question in relation to economic and financial systems, and named such rare but highly consequential events "Black Swans" after the shocking discovery, for the European travelers, of black swans in Australia, disproving the previous view in Europe that all swans were white. Taleb (2007) describes and discusses how Black Swans can be of key importance for understanding the

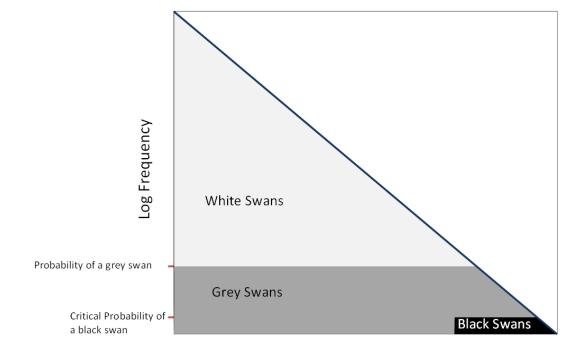
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Log Event Magnitude

Figure 1. Hypothetical definition of Black, Grey and White Swans in relation to the frequency of occurrence and the magnitude of their effect.

functioning of complex economic systems. Specifically, he indicates that focusing on normal or regular events may not be informative for a comprehensive understanding of such systems. Other works in finance also stress the importance of investigating and understanding the role of outliers (Sornette 2009). Nevertheless, the idea of exploring rare events is not new: Francis Bacon wrote approximately 400 years ago in Novum Organum, "Errors of Nature, Sports and Monsters correct the understanding in regard to ordinary things, and reveal general forms. For whoever knows the ways of Nature will more easily notice her deviations; and, on the other hand, whoever knows her deviations will more accurately describe her ways".

White, Grey and Black Swans

Producing a statistical and/or mathematical framework that defines and serves to identify Black Swans goes beyond this work. However, here we provide a preliminary idea on how to define a Black Swan event based on its magnitude and probability of occurrence (Figure 1). In this conceptual schema (Figure 1) we indicate White, Grey and Black Swans. Frequent or predictable events with a limited magnitude—White Swans—are normally used as a basis for expecting or predicting future events. Organisms also tend to adapt to regular conditions, as those conditions are the most likely to be

encountered in the near future. Grey Swans may be associated with events that are rarer than White Swans, with consequences ranging from large to irrelevant (Figure 1). Recurrent volcano eruptions and earthquakes in some parts of the world that have limited predictability (e.g. some earthquakes in Chile or Japan) would be good examples of Grey Swans. In contrast to the previous examples, Black Swans are very rare, virtually unpredictable, and highly consequential events (Figure 1). For example, the HIV emergence, or the 9/11 attacks on the World Trade Center could qualify as Black Swans.

Examples of Black Swans in ecology and evolution

It has been proposed that "[o]ne of the most remarkable emergent properties of natural and social sciences is that they are punctuated by rare large events, which often dominate their organization" (Sornette 2009: 1). This tenet agrees with the Punctuated Equilibrium theory of evolution (Gould and Eldredge 1977), which indicates that periods of evolution occur as very rapid events and, most of the time, species do not show any appreciable evolutionary change. It may be possible that these bursts of evolution were Black Swans, or consequences of Black Swans. In a retrospective analysis, it is possible to detect several potential Black Swans in evolution (see Table 1 for a non-exhaustive list; Figure 2). For

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Events	Examples
Unexpected invasion and impact	The invasion, dominance and high impact of the Argentine ant due to
	low levels of genetic variation (see text)
Geological events	The emergence of the Panama Isthmus and the consequential invasion of
•	South America by placental mammals, which contributed to the
	extinction of numerous marsupial species (see text)
Unexpected long distance dispersal	Cactaceae in Africa (Nyffeler 2002)
Key innovation	Evolution of the wing in birds initially not related to flight (Dial 2003)
Extinctions	The passenger pigeon was the most abundant bird in North America, and
	in a period of few decades it became extinct (see text)
Climate change	Extinction of large mammals in part due to climate change in the last
	glacial period (Barnosky et al. 2004)
Astronomical events	Possible extinction of dinosaurs due to a meteorite impact (see text)
Some cases of co-evolution or	Fungi and plant (mycorrhiza) interactions in early colonization of land
association	by plants (Wilkinson 2001)
	Fungi and Algae (lichens)
	Plastids and Mitochondria in the eukaryotic cell (Margulis 1970)
The emergence of new species with	Humans
highly influential effects on the	Cyanobacteria (generation of an oxygenic atmosphere that promoted the
biosphere	evolution of other organisms)

example, the emergence of life (but see Kauffman 1995), the appearance of the eukaryotic cell, the origination of mitochondria (Margulis 1970), multi-cellularity, and possibly the mind (Wilson 1992), may all be considered evolutionary Black Swans. Other events that could also be Black Swans in evolution include the meteorite impact that appears to have generated a mass extinction in the Cretaceous-Tertiary (Alvarez et al. 1980), or the connection of landmasses owing to continental drift, bringing together previously isolated fauna and flora (Cox and Moore 2005) and promoting colonization and extinction events. In a contemporary context, Black Swans in evolution could be represented by key innovations (i.e. a large increase in the fitness of a species as a product of an unlikely process). For example, mutations in viruses that allow them to infect a completely new host could qualify within this category. This could be the case of the 1918 flu virus that killed about 50 million people and which likely derived from an avian host shortly before the pandemic (Taubenberger et al. 2005).

Diverse potential Black Swans can be also found retrospectively in ecology. For example, the successful invasion and dominance of the Argentine ant (*Linepithema humile*), which, by reducing intraspecific competition and promoting the formation of supercolonies (Tsutsui et al. 2000, LeBrun et al. 2007), triggered an invasion of large geographic proportions with a tremendous impact on native biodiversity (Sanders et al. 2003). Other potential Black Swans could be the extinction of the passenger pigeon in North America, which was at one time the most abundant bird on the continent (Ellsworth and McComb 2003), or the

extinction of the golden toad in Costa Rica (Pounds et al. 2008). Similarly, the tremendous invasion of Monterev pine (*Pinus radiata*)—a narrowly restricted pine in its native environment (Lavery and Mead 1998) throughout the southern hemisphere may qualify as a Black Swan. Other examples may include the loss of competitive ability by a dominant plant species with the unexpected arrival of a new pathogen (Gandhi and Herms 2010), or the extreme and rare ecosystem perturbations that may reveal unexpected behaviors of ecosystems (Murawski et al. 2010). Single and extreme climatic events such as floods or storms could also qualify as Black Swans and drastically affect community structure and abundance of species (Valone et al. 1995, Westbrooke et al. 2005, Thibault and Brown 2008). Finally, the exponential growth of the human population during the last 200 years and its large impact on the entire biosphere could also qualify as a Black Swan.

How to study Black Swans?

Black Swans may be deeply rooted in the myriad of interactions present in complex ecological and evolutionary systems, and, therefore, may be a characteristic feature of them. Hence, future studies should explore more thoroughly the impact of Black Swans in ecology and evolution. Still, studying Black Swans is a challenging task, as one aims to investigate events that are, by definition, rare and beyond our expectations. Once an event happens, we can identify it as a Black Swan, but we cannot do so before it occurs (Taleb 2007); so, how do we proceed? There is no straight-forward

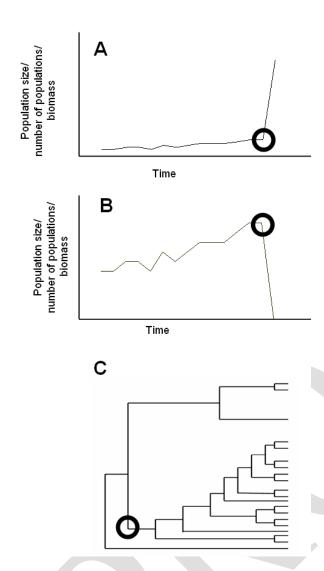


Figure 2. Examples of hypothetical Black Swans (unexpected, surprising and highly influential events) in different systems (black circles). A) Increase in the size/number/biomass of a given species, due to its unpredicted, successful invasion of new areas, or a change in given areas, allowing the species to became dominant. B) Unexpected extinction of a species or population due to, for example, climatic change, a volcanic eruption, or the appearance of a new disease. C) Phylogeny of a group that has diversified extensively due to a key innovation, colonization of a new area, or the extinction of competitors.

answer; but still, simple actions may help us integrate Black Swans into the subjects of ecology and evolution. For example, increasing our awareness of the potential importance of rare and highly influential events may prompt researchers to investigate outliers when they occur instead of ignoring them. Studies in finance encourage investigating these rare events (Taleb 2007, Sornette 2009). In ecology, Hilborn (1987) and Wintle et al. (2010) suggested that in certain circumstances, planning for unknown unknowns (that is, possible Black Swans) may be an appropriate strategy for the management of ecological systems.

Studying Black Swans in ecology and evolution using a theoretical and experimental framework will require substantial effort. This will likely need a close interaction between biologists, mathematicians, statisticians, and computer scientists. Fortunately, some inspiration in this respect can be borrowed from the financial world, where Black Swans are being studied (Taleb 2007, Sornette 2009). For example, a recent and mostly theoretical work investigated meaningful outliers, which have been named Dragon-kings (Sornette 2009). Dragon-kings are large outliers that do not fall within the realms of power laws (that is, a probability distribution where very few events have a large impact, while most of them have a low impact). Another work entitled "Financial black swans driven by ultrafast machine ecology" exemplifies how we can gain insight on Black Swans by analyzing those emerging from fast computer interactions that are not controlled by humans (Johnson et al. 2012). These works suggest that we could gain insight on the effects of Black Swans in ecology and evolution by performing computer simulations (e.g. simulating ecosystems using artificial and interacting organisms). Then, it may be possible, for example, to estimate the distribution of Black Swans according to their magnitude and frequency (at least for these artificial systems). In addition, experiments could also serve to investigate the effects of Black Swans in biological systems (e.g. exposing experimental communities to unique and extreme disturbances). Such experiments could be carried out, for example, with microbial communities, which have fast generation times and large populations sizes. Furthermore, observatories could be established to investigate Black Swans when they happen in natural biological systems (e.g. in natural communities). When studying Black Swans, it is also important to consider that timescale may be playing a role in how we define these events. For example, an extreme event that drastically changed the evolution of a linage over a decadal time scale (e.g. a deadly microbial pathogen) may only be perceived as a Black Swan after substantial time following the event has occurred. The same event may be perceived as a Grey Swan if studied while it is happening.

Conclusion

Rare and highly-consequential events, so-called Black Swans, may be an inherent feature of ecology and evolution. Much evidence suggests that several Black

Swans have occurred during the history of the evolution of life. In addition, Black Swans can also occur and affect contemporary ecological and evolutionary systems. Investigating the impact of Black Swans in ecology and evolution is challenging, but research in other fields (such as finance) can serve as inspiration for ecologists and evolutionists. Despite the obvious difficulties, research in this direction will serve to provide better understanding of the role of uncertainty in ecology and evolution. This may be especially important for the management of natural resources, where black swans could have irreversible effects (e.g. species extinctions or changes in the functioning of ecosystems). Therefore, it may be critical to plan for Black Swans (Hilborn 1987, Wintle et al. 2010). In summary, we propose that ecology and evolution may be better understood if we consider the effects of both improbable but highly influential events (Black Swans), as well as more predictable or regular events (White Swans).

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