BIOGEOGRAPHY

Unlikely Yet Pivotal Long Dispersals

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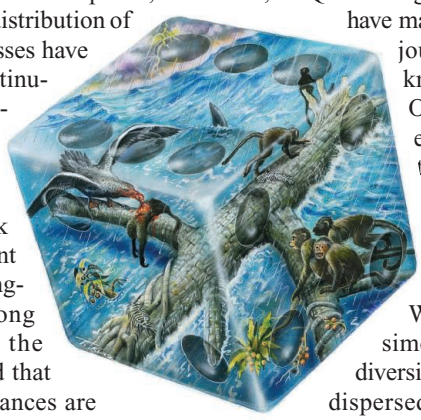
Long-distance dispersal can enable a species to colonize new areas far from its range, with potentially drastic consequences for ecology, evolution, and biogeography. In *The Monkey's Voyage*, Alan de Queiroz argues that long-distance dispersals are necessary to explaining the evolutionary histories of many animals and plants across the world. Although Charles Darwin (*1*) and Alfred Russel Wallace (*2*) came to the same conclusion over a century ago, the dispersalist view has long been strongly resisted. In particular, the acceptance of plate tectonics in the 1960s expedited an alternative view, known as vicariance biogeography, which soon gained forceful support.

This alternative uses vicariance (splitting) events, such as those driven by the rupture and motion of continental plates, to explain the geographical distribution of species. Vicariance processes have fragmented formerly continuous distributions of taxonomic groups, and the subsequent processes of dispersal, speciation, and extinction took place within each fragment (without links through long-distance dispersals among them). Supporters of the vicariance paradigm hold that dispersals over great distances are so unlikely that they never actually happen and therefore condemned dispersal biogeography as "a science of the improbable, the rare, the mysterious and the miraculous" (*3*). However, over the past two decades new discoveries and novel tools (especially molecular phylogenetic methods) have brought the dispersal-vicariance debate toward resolution. The evidence, argues de Queiroz (an evolutionary biologist at the University of Nevada, Reno), rebuts vicariance explanations and resurrects Darwin and Wallace. He thus proposes that long-distance dispersal explanations should be described with a fifth adjective: the necessary.

De Queiroz's centerpiece example is the seemingly miraculous transoceanic dispersal of monkeys. Two major taxonomic groups of monkeys—catarrhine (downward-pointing nose) monkeys of the Old World and platyrrhine (flat nose) monkeys of the New World—are closely related sister groups, which means that their disjunct distribution offers a powerful test for the dispersal-vicariance debate. Estimates from relaxed molecular clocks indicate that the platyrrhine-catarrhine split occurred about 41 million years ago (the mean of 31 million to 51 million years). That is much later than the separation of the African and South American plates as part of the breakup of Gondwana, estimated as about 110 million years ago. Thus, de Queiroz argues that monkeys must have made a highly improbable journey of at least 1450 km across the Atlantic Ocean. The immigrants eventually gave rise to the 124 extant species of monkey in the New World. Caviomorph and simodontine rodents also diversified from transoceanic-dispersed ancestors. Together, the three clades comprise 673 extant species—73% of South America's nonflying, nonaquatic mammal species—many of which play key roles in shaping the continent's ecosystems and filling its biodiversity hotspots.



Beating the odds.

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Essayist Nassim Taleb refers to rare and unpredictable random events that have a huge impact as black swans (*4*). Most discussions of black swans focus on key anthropocentric examples, such as the rise of the Internet and 9/11, but his theory can also be applied to various geophysical and biological phenomena, including extreme weather, earthquakes, wildfires, epidemics, and tumor dissemination. Such rare events are not well captured by the typical Gaussian (bell-shaped) distribution, but by fat-tailed distributions with large deviations from the mean, characterized for those systems and also for movements of organisms (*5*, *6*). De Queiroz argues that the few Eocene monkeys that completed their improbable trans-Atlantic journey merit the moniker of black swans due to the extreme rarity of their long-distance dispersal and its massive impact.

Taking readers on a tour through time and space, de Queiroz covers the key players, ideas, discoveries, and methodological advances that have occurred since Darwin and Wallace and have collectively led to a recent paradigm shift in historical biogeography. He provides fascinating examples of plants and animals from a variety of geographic locations, mostly oceanic islands. Lucidly and captivatingly written, his narrative merges snapshots from his personal perspective with detailed descriptions of key players from the past two centuries, their characters, and lives—as if the author knew them personally. Although some readers may deem it too slow or too one-sided, we found *The Monkey's Voyage* a joy to read and a great example of how a potentially dry scientific debate can be presented to attract a broad readership.

The Monkey's Voyage
How Improbable Journeys Shaped the History of Life
by Alan de Queiroz
Basic Books, New York, 2014. 368 pp. $27.99, C$31. ISBN 9780465020515.

The arguments for and against the prevalence of transoceanic long-distance dispersal in shaping the world's biota are essentially a game of very low probabilities and innumerable trials. Darwin immersed seeds in salty seawater and ran various other experiments to explore how low (some elements of) these probabilities are, and vicariance biogeographers have dismissed dispersal explanations as ridiculously improbable. Although de Queiroz strongly emphasizes and thoroughly discusses this point, *The Monkey's Voyage* lacks a basic quantitative treatment of the link between very low probabilities and big numbers. It provides only a short—but admittedly brilliant—glimpse into this core issue through a wonderful hypothetical present-day discussion among prominent biogeographers. In it, the vertebrate paleontologist George Gaylord Simpson "pulls out a pen and jots down some calculations to show that an event with a minuscule probability of occurring in any given year, such as monkeys rafting across 1800-plus miles of ocean, might yet be reasonably likely given a long enough period of time."

The probability of dispersal strongly decays as the distance from the source increases. A probability density function (commonly called the dispersal kernel) can be used to estimate the probability of a successful dispersal event after a given number of years. The calculations require estimates for the (typically fat-tailed) dispersal kernel parameters, the (huge) number of dispersers,

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and their (very low) probability of surviving the journey and establishing themselves far from the home site (*7*). Further refinements of dispersal kernels could incorporate trade winds (*8*) and other underlying mechanisms (*9*). Such a mechanistic modeling approach (*9*) is especially promising for rafting, the primary mechanism of transoceanic dispersal highlighted in *The Monkey's Voyage*—for which uncertainty can be reduced by incorporating information on the properties of the rafts as well as on the passengers, wind drifts, and oceanic currents (*10*). Furthermore, there exists a wide spectrum of dispersal-vicariance scenarios. Historical biogeography should go beyond assigning cases to these two extreme alternatives and should instead quantify their relative importance. The scope of investigation should also be expanded beyond the hallmark examples of terrestrial species moving across oceans, because long-distance movements of marine and aerial species, as well as those of terrestrial species over land, have also greatly contributed to shaping the geographical distribution of the world's biota.

Considering the probability of an explanation is essentially the common practice of nearly all aspects of our life. Yet, it is not only the histories of life and human societies that have largely been shaped by unlikely black swan events. Each of our lives is a product of an idiosyncratic chain of events, which can be considered highly improbable yet an evident reality. The central arguments of *The Monkey's Voyage* appear to be increasingly well recognized nowadays in such diverse fields as statistics, economics, engineering, computer sciences, earth sciences, chemistry, physics, and biology. It is time to proceed beyond broad awareness of the general concepts to develop quantitative frameworks to better understand the unexpected—and to cope with the high impact of rare and unpredictable "monkey's voyage" events.

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EXHIBITION

"Nature and Art Beneath One Roof"

Natural Histories
A Project

by Miguel Ángel Blanco
Museo Nacional del Prado, Madrid. Through 27 April 2014. https://www.museodelprado.es/en/exhibitions/exhibitions/at-the-museum/historias-naturales

Charles III of Spain (1716–1788) was at heart a scientist. As an Enlightenment despot, he conceived the museum of the Prado in Madrid as a place where arts and sciences would be united. Unfortunately, his death and the Peninsular War (1808–1814) intervened, and his original notion of a royal natural history cabinet was eclipsed by the magnificence of Spanish and Netherlandish paintings. Perhaps it's arrogant to try to resurrect the notion of the Prado as a cabinet of curiosities, but contemporary Spanish artist Miguel Ángel Blanco has had the temerity to insert a selection of installations of natural objects in direct response to the great paintings.

Blanco has emplaced his 22 "interventions" with delicacy, because after all most visitors come to puzzle over Velázquez's *Las Meninas* and do not want to be distracted by an albino sparrow. Or they would prefer to sorrow with Juan de Flandes' *Crucifixion* rather than inspect the gems at the foot of the cross. Nor would they want to be long deflected from Goya's stunning *Witches' Sabbath* to admire the anatomy of the hags' familiars (bat skeleton, cobra, toads, salamander, and moose hoof) displayed, many in jars of formalin, below. Although the stuffed Veragua bull staring at its feminine counterpart in Peter Paul Rubens' *Rape of Europa* certainly has presence and the wolf-whistle calls of birds of paradise giving voice to Frans Snyders' *Concert of Birds* do echo down the long gallery, maybe the intrusions are too polite. And I am not sure Blanco's approach entirely works—in part, because his pieces are so dwarfed by the splendor of the Prado's permanent collection. Nevertheless, his project succeeds in prompting visitors to look again and to notice how very often natural objects were used as props and symbols in great paintings by grand masters.

– Caroline Ash

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Miguel Ángel Blanco's *The Veragua Bull*. Rubens' *The Rape of Europa* (1628–29) and *Bos taurus*.

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