

MASS EVOLUTION EVENTS

island
biogeography
inspires
a new
perspective
on mass
extinctions



By Susan De Wolf

Although the contentious concept of extinction emerged in 1796, the evolution of jargon for the study of extinction has continued to provoke novel controversy. Within the past 50 years, biologists have identified a distinction between “mass extinction”, the disappearance of a proportionally high percentage of species from a broad diversity of taxa throughout the planet within a condensed period of geological time (1), and “background

extinction”, the inevitable fate of species unable to compete in Darwin’s evolutionary battle of the survival of the fittest. The term “mass extinction” itself, however, is currently under attack. Rigorous analysis of the fossil record reveals that there have indeed been five moments in the natural history of the earth in which 75 percent or more of the existing species suddenly disappeared: the End Ordovician, End Devonian, End Permian, End Triassic,

and End Cretaceous extinctions. While all five events certainly represent unprecedented times of global crisis and loss of biological diversity, “they share little else in common,” Bambach, Knoll, and Wang contend in a 2004 publication (2). This team therefore has coined the term “mass depletions” in an attempt to re-characterize these periods of tremendous biological loss, claiming that two of the five were not in fact mass extinctions but merely intervals lacking

dramatically in the origination of new taxa (2).

While the name of these distinctive events remain in question, another title to consider is mass evolution events. While “mass extinctions” are responsible for the loss of less than 10 percent of extinct species (3), they have certainly had a disproportionate effect on evolutionary history of life of earth. The sudden disappearance of the majority of incumbent taxa, taxa that already existed, inherently leaves an abundance of unoccupied environmental niches or ecospace for the diversification of new taxa. Focusing on the extreme biological vacancy resulting from “mass extinction” events, one can begin to identify a striking parallel between mass extinctions and the entirely distinct subject of island biogeography. Oceanic islands, islands that arise as land masses physically independent from any mainland, present a completely unoccupied ecospace for any organism that can colonize it. While currently biologists’ understanding of the recovery of global ecosystems from “mass extinction” events stems exclusively from the fossil record, perhaps the study of evolution on oceanic islands can provide a new perspective on the evolutionary significance of “mass extinctions”—or “mass evolutions”.

The first remarkable correspondence between post-extinction recovery and islands is that the mathematical models most often used to illustrate the evolutionary dynamics after “mass extinction” events are based on MacArthur and Wilson’s 1967 equilibrium model published in *The Theory of Island Biogeography* (3). While the 1967 model sought to define the equilibrium popu-

“There have indeed been five moments in the natural history of the earth in which 75 percent or more of the existing species suddenly disappeared: the End Ordovician, End Devonian, End Permian, End Triassic, and End Cretaceous extinctions.”

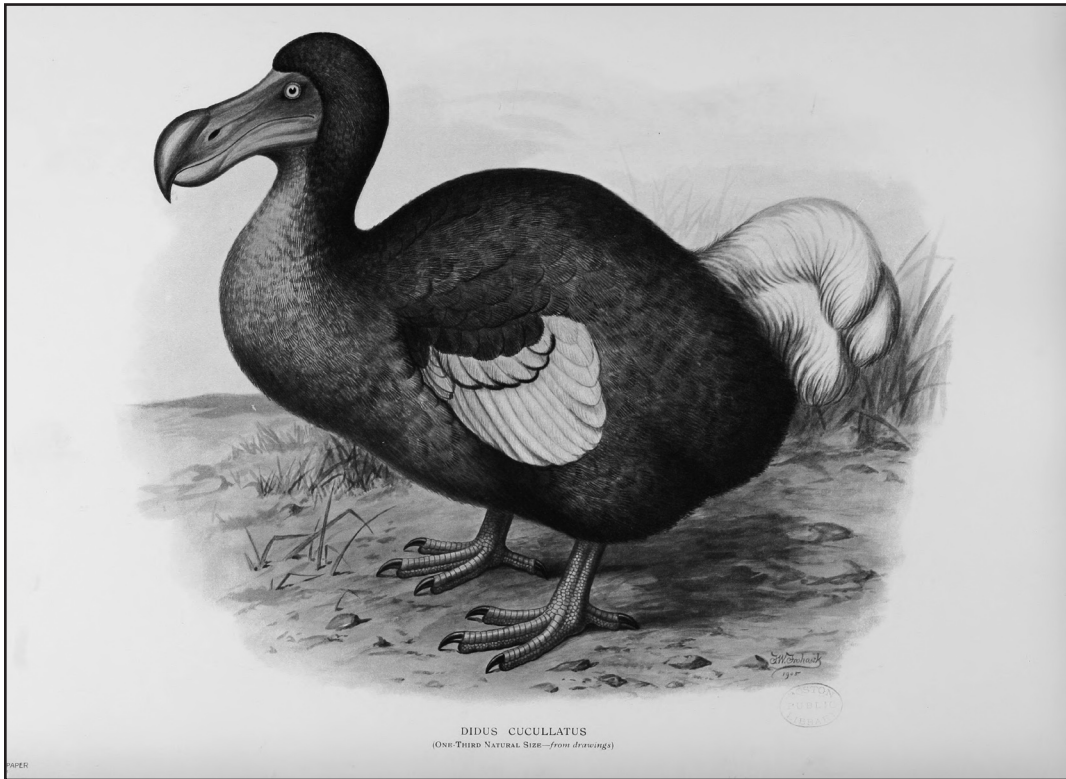
lation size of an island a specific size and distance from the main land (4), it has since served as the foundation for curves predicting the re-establishment of a stable density of taxa after an extinction event. One of the most successful features of these curves is their sigmoidal or s-like shape, predicting a substantial lag time before dramatic exponential growth. Remarkably, a distinctive feature of many “mass extinctions” is this significant delay in the onset of biological recovery of about five million years, with the classic example of the seven to eight million year gap in reef fossils after the End Permian Extinction (5).



▲ A revolution in biology began on January 21, 1796 when Georges Cuvier, right, a 27 year old naturalist, presented to the National Institute of Sciences and Arts in Paris virtually indisputable evidence for the validity of extinction.

Beyond mathematical models, there are specific trends in the evolutionary development of islands that seem relevant for understanding “mass extinctions” as well. The first is the phenomenon of disharmony, in both species that colonize a new island and taxa that endure a “mass extinction” event. When an oceanic island forms, it is entirely open for settlement, but hardly many creatures have the dispersal mechanism to get there. Arriving at an island in the middle of the ocean requires wings, like birds or bats, the ability to swim, like elephants, or another means of traveling long distances in the water or air. Although islands may be diverse in location and geography, the type of species on islands is noticeably conserved, in large part because of the distinctive subset of species that originally populate them (6).

One of the most unique aspects of islands is that entire taxa of familiar, widespread organisms with limited dispersal abilities are surprisingly ab-



◀ An extinct Dodo bird.

variety of specific causes, from glaciation to massive volcanic activity, the biased survival of generalists or taxa with other key capabilities leads to the disharmonious nature of the taxa initiating a post-extinction recovery.

The extraordinary amount of open ecological habitats for species diversification is a fundamental feature of both island and post-extinction environments, regardless of what species are there to diversify into those niches. On the island of Santa Cruz in the Galapagos, two species of finches have evolved on

sent. Hawaii is an island without ants (6). Madagascar is an island without cats. New Zealand is an island without rodents (4). An archetypical story for understanding the exceptional biological character of islands is that of Rakata in the Malay Archipelago. An explosion in 1883 led to the complete obliteration of all life on the island. After nine months, naturalists identified a lone spider on the island, but after three years mosses, algae, grasses, and flowering plants, specifically the airborne disperser dandelions, had arrived. Six years later, there was even a large monitor lizard on the island. Not only was the type of lizard known for its swimming abilities, but it was also a generalist carnivore, ready to eat anything from crabs to eggs, and a reptile, intrinsically able to eat less frequently than a mammal (4).

This idea of the survival of the gener-

alist is one that links directly to the disharmony of “mass extinction”: not only are there specific factors that decrease a taxon’s vulnerability to extinction, but being a widely-dispersed, generalist renders a taxon most secure of survival.

“While currently biologists’ understanding of the recovery of global ecosystems from “mass extinction” events stems exclusively from the fossil record, perhaps the study of evolution on oceanic islands can provide a new perspective on the evolutionary significance of “mass extinctions”—or “mass evolutions”.

David Jablonski’s analysis of gastropods in the fossil record established the model for the finding, but the trend has since been observed in all five “mass extinctions” (Powell 530). Other traits strongly correlated with survival of “mass extinctions” include the ability to withstand low oxygen conditions (5) and taxa lacking calcareous skeletons (Knoll 295), along with a diversity of other qualities. Although individual “mass extinction” events may have an

the same small island, an extremely rare occurrence in evolution as there is no physical separation on the island preventing the two evolving species from interbreeding: one has specialized to eat small seeds and the other large seeds (6). This phenomenon is exacerbated in light of disharmony as not only do the exceptional colonizers face little competition in their own adaptive zone evolved on the mainland, but suddenly there are a myriad of novel niches for that species to exploit. Because there are no ants in Hawaii, both a genus of herbivorous moths and a species of aquatic dragon flies have adapted to become terrestrial carnivores, the typical role of ants in an ecosystem (6). In New Zealand with no rodents, a species of bat, the short-tailed bat, has become a ground-loving, foraging creature (6). Islands are the evolutionary sources of flightless birds like the dodo, giant komodo dragons, and pygmy elephants (4). The island of Hawaii alone, lacking not only ants, but also amphibians, reptiles, land mammals, and freshwater fish, has produced almost 10,000 types of insects from approximately

only 400 initial species: with so few competitors, insects have dominated the evolutionary battle in an unparalleled range of ecospace (6).

This observation translates directly to “mass extinctions”: “mass extinctions” have consistently led to dramatic biotic transitions. Major global diversification followed all five major “mass extinctions”, from the Ordovician radiation of bivalves in which the number of genera and families tripled (7), to the post-Devonian radiation of ray-finned fish (5), to the End Permian radiation of semi-aquatic tetrapods and weed-like plants (5), to the notorious demise of the dinosaurs in the End Cretaceous leading to the ascendancy of mammals. An important point to consider is that during these periods of biological turnover, the diversifying taxa did not simply reoccupy vacant niches, but evolved to thrive in the potentially new environmental conditions of the post-extinction planet while also constrained by intrinsic biological factors (8).

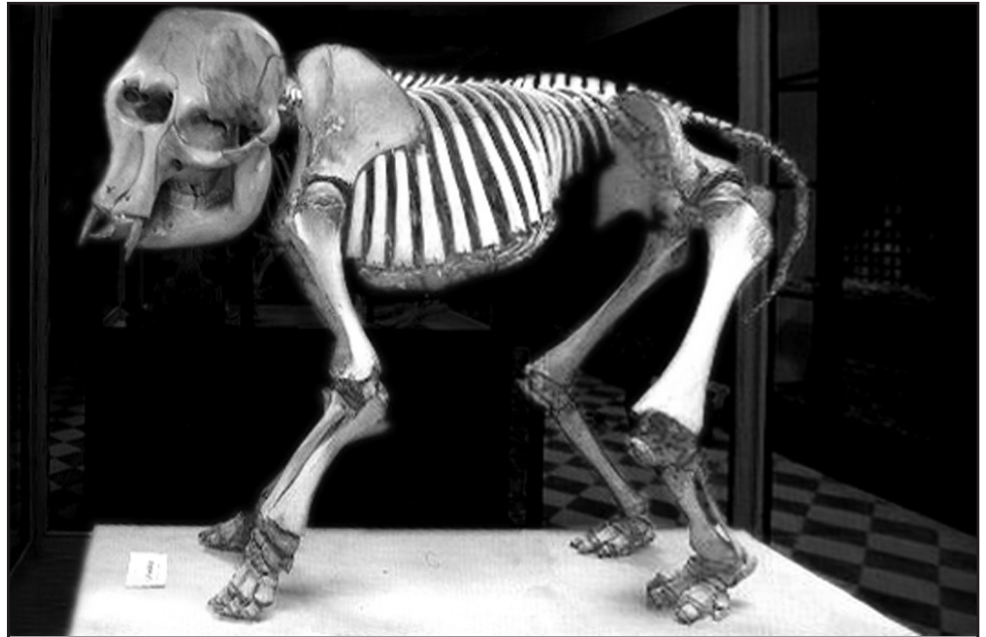
Furthermore, studies of both the semi-aquatic terrestrial tetrapods (four-legged animals) and mollusks that thrived after the End Permian and End Cretaceous

extinctions respectively have led to the classification of these groups as “bloom”(5) or “disaster” taxa—species that developed rapidly into a tremendous variety of specialists, but were ultimately “evolutionary dead-ends,” out-competed by other taxa over 20-50 million years after the extinction event (5). This discovery from the fossil record may have pertinent implications for the modern field of conservation biology. A distinctive feature of the 21st century earth is the fluidity of transportation around the planet.

“Ecosystems like islands that maybe have been virtually isolated for millennia are suddenly becoming part of the global dialog.”

Ecosystems like islands that maybe have been virtually isolated for millennia are suddenly becoming part of the global dialog, experiencing directly the perpetual buzz and chatter of planes, boats, and everything those human inventions carry with them. Although on islands species like flightless birds and foraging bats may have been able to flourish, just like the “bloom”(5) taxa of the fossil record, they too may soon be replaced by creatures newly arriving from the mainland.

Perhaps the most important aspect of recovery from “mass extinctions” that can be extrapolated from a comparison with island biogeography is that whether or not the precise cause, magnitude, or effect of distinct extinction events are similar or different, there are specific trends in the evolutionary patterns that follow these episodes of stark biological catastrophe, just as there are convergent aspects of life of island despite the inherent diversity among island environments themselves. Islands and “mass extinctions” fuel essential evolutionary change—for only did the disap-



▲ An extinct pygmy elephant skeleton.

pearance of the dinosaurs in the End Cretaceous extinction allow birds to take over the ecospace of pterodactyls and other fierce avian creatures—and only did the isolated island environment of Mauritius engender the transition of those the soaring pigeon into the flightless dodo. “Mass extinctions”, this juxtaposition with island biogeography underlines, are “mass evolution” events. **[1]**

—Susan De Wolf *‘10 is a Neurobiology concentrator in Lowell House.*

References

1. Kemp, T.S. *Fossils and Evolution*. Oxford University Press, New York: 1999.
2. Bambach, Richard et al. “Origination, extinction, and mass depletion of marine diversity”. *Paleobiology*, 30(4): 522-542. 2004.
3. Erwin, Douglas. “Lessons from the past: Biotic recoveries from mass extinctions”. *PNAS*, 98(11): 5399-5403. 2001.
4. Quammen, David. *The Song of the Dodo*. Scribner, New York: 1996.
5. Hallam, A. and P.B. Wignall. *Mass Extinctions and their Aftermath*. Oxford University Press, New York: 2000.
6. Berry, Andrew. “Evolution on Islands” in *A World of Islands*, Godfrey Baldacchino, Ed. Institute of Island Studies, Prince Edward Island: 2007.
7. Foote, Michael and Arnold Miller. *Principles of Paleontology* 3rd Edition. W.H. Freeman and Company, New York: 2007.
8. Jablonski, David. “Lessons from the past: Evolutionary impacts of mass extinctions”. *PNAS*, 98(10): 5393-5393. 2001.