PERSPECTIVES: ECOLOGY

Caribbean Catastrophes

Thomas Brooks and Michael Leonard Smith

Human destruction of populations, species, and habitats in the hot spots of biodiversity is causing an extinction crisis (*1*). To quantify this crisis, we must estimate how often extinctions happen in the absence of human pressures. Although aggregated studies of the fossil record reveal rates of 0.1 to 1 extinction per year per million species (*2*), there is not really any "normal" extinction rate. Rather, the severity of background extinction events is inversely proportional to how often they occur; major catastrophic events are rare (*3*). Thus, a plot of magnitude versus frequency has the form of a hollow curve (see the figure). For life to persist, the processes that generate biodiversity—speciation and, locally, colonization—must keep pace with these extinctions. The archipelago of Caribbean islands called the West Indies has always been a fertile testing ground for those who study these processes, because of the islands' complex geographic history and propensity for catastrophe. Two elegant studies in this issue (*4*, *5*), carried out at opposite ends of the Caribbean island arc, throw new light on extinction (and hence conservation) at opposite ends of the magnitude-frequency curve.

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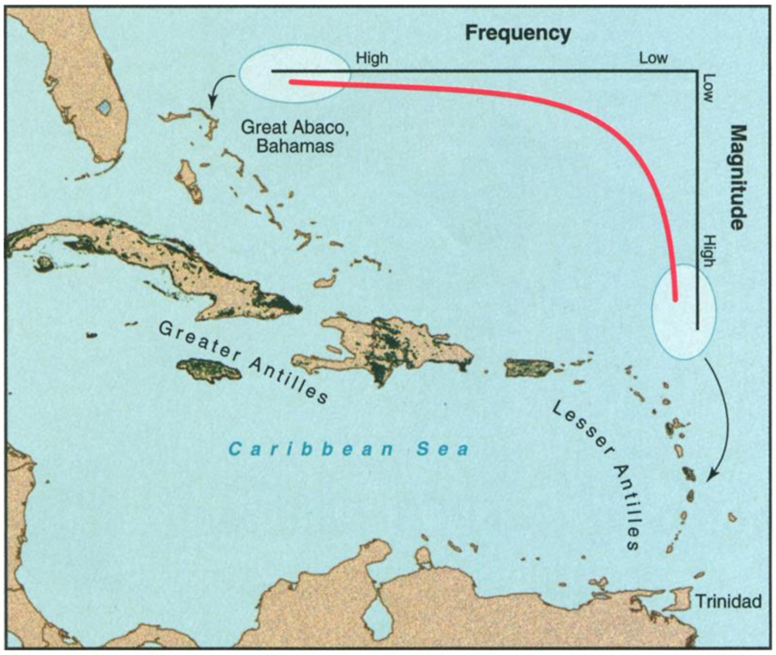

Recovering from catastrophe. Map of the Caribbean showing forest cover on islands from the Bahamas to the Lesser Antilles (*9*). The inset is an example plot of magnitude versus frequency of species extinctions. One end of the plot is mapped to the Bahamas, where rapid recovery after a low-magnitude but high-frequency catastrophe has been assessed (*5*). The other end is mapped to the Lesser Antilles, where slow recovery after a high-magnitude, low-frequency catastrophe has been demonstrated (*4*).

On page 1522 of this issue, Ricklefs and Bermingham examine mitochondrial DNA sequences from 161 island populations of 37 small land bird species in the Lesser Antilles (*4*). From these, they estimate the average genetic divergence from the closest sister populations on Trinidad (and South America) or the Greater Antilles. To assess the pattern of colonization over time, they plot the cumulative number of lineages against increasing genetic divergence. Strikingly, whereas around half of the lineages differed only slightly from their presumed sister stock, with genetic divergence of 2% or less, the other half showed high genetic divergence values from 2% up to 15%. Assuming that genetic divergence increases uniformly over time, and calibrating this molecular clock from the literature, Ricklefs and Bermingham found that a dramatic change in the mean age of the Lesser Antillean avifauna apparently occurred a little over half a million years ago. The authors suggest two possible causes for this change. One would be a mass extinction event (perhaps due to a tsunami or the impact of a meteorite) superimposed on a background of high colonization. Alternatively, a sudden increase from a low to a high colonization rate (perhaps due to increased exposure of land during periods of lowered sea levels) would have had the same effect. They conclude that the existing Lesser Antillean avifauna is primarily a product of such historical events, with little post-catastrophic recovery.

On a much finer scale, the work of Schoener *et al.* on page 1525 reveals a very different story (*5*). They tracked the fate of a single lizard species, the Cuban brown anole *Anolis sagrei*, on 66 individual islands in the Bahamas, ranging in size from 10 to 10,000 m^2. Initially, island area was the single determinant of presence or absence of the species. Then, in September 1999, Hurricane Floyd extirpated lizards from 37 of the 49 islands that they had inhabited before the catastrophe. Elevation proved to be the determinant of adult survival through the hurricane and especially through the associated 3-m storm surge. On islands lower than 3 m, all hatched lizards perished. As a fascinating aside, the authors discovered recently hatched lizards soon after the hurricane on 10 islands from which all adults were eliminated. Subsequent experimentation revealed that eggs of *A. sagrei* can in fact survive for 6 hours submerged in seawater—a surprising physiological result as well as a key factor in allowing such a rapid recovery rate. Crucially, however, Schoener *et al.* then found that island area progressively increased in importance as a predictor of the presence of this lizard species. Within only 2 years, a species-area relationship—similar to that before the hurricane—was reestablished on the islands.

What might explain these apparently contradictory results? The obvious possibility is scale (see the figure). Although the time lag for recolonization has yet to be shown to be related to area, the converse situation—that of extinction after habitat loss—is certainly scale dependent (*6*). It therefore appears likely that the impact of catastrophes involving relatively simple communities and covering relatively small areas, such as Simberloff's classic fumigation of islets in the Florida Keys (*7*), can be experimentally observed to decrease in importance over time. On the other hand, huge, very rare catastrophes affecting entire regions are likely to remain imprinted in local community structure for millennia (*8*).

The conservation implications of these studies are clear. The Caribbean is already one of the world's hottest hot spots, retaining only just over 10% of its original forest cover (*1*). Habitat across the archipelago has been reduced to tiny patches—islands within islands

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(*9*)—aggravating the vulnerability to catastrophes inherent in the region's geographic subdivision. Species extinctions resulting from human pressures have already struck the West Indies on a massive scale. Of the 197 endemic mammals and birds across the islands (*1*), at least 43 have become extinct over the last 500 years (*10*). This equates to nearly 500 extinctions per year per million species, three orders of magnitude higher than expected given species' lifetimes in the fossil record (*2*). Worse yet, 84 more Caribbean endemic mammals and birds are classified on the Red List as threatened with a high probability of extinction in the medium-term future (*10*). Seen from a gloomy perspective, these species represent an extinction debt—losses already under way after habitat destruction. Worst of all, the remaining habitat patches of the Caribbean are small (and getting smaller), and so, given that the rate of extinction after habitat loss is scale dependent (*6*), these extinctions will probably occur soon.

The studies of Schoener *et al.* and of Ricklefs and Bermingham do, however, cast one ray of hope for conservation of the Caribbean's unique biodiversity. Imagine a conservation vision across the region, with the land- and seascape of surviving habitat fragments connected within a matrix of benign land use by "corridors" (*11*). Such corridors would consist not only of restored habitat and zones of low-impact human activity, but also, as Schoener *et al.* indicate, interdependent systems of tiny, largely pristine, islands. Recall that to reconcile the two studies, we invoke scale dependence in the persistence of the impact of historical catastrophe. If this is correct, then surely the recolonization of tiny habitat fragments across the conservation landscape would be rapid, analogous to the situation illustrated by Schoener *et al.* Obviously, it is too late for groups such as the West Indian macaws, already forced into catastrophic extinction (*12*). For the large portion of Caribbean biodiversity currently threatened with extinction, though, these studies suggest that all is not yet lost—as long as conservation can be implemented on an unprecedented scale across the region.

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PERSPECTIVES: SURFACE SCIENCE

Catalysts Under Pressure

Charles T. Campbell

From car catalysts to petroleum refining, chemical reactions catalyzed by solid surfaces play a major role in our lives today. This knowledge has fostered intensive research in catalysis for many decades, but the need for basic and applied research is stronger than ever. Improved catalysts may, for example, help to reduce the use of fossil fuels by enhancing reaction yields and fuel conversion efficiencies. "Greener" industrial and automotive chemical processes that minimize undesirable side products may be achieved by modifying existing catalysts or developing new ones. Given the correlation between areas with high cancer death rates and those with high densities of pollution sources, this may also help to reduce cancer incidence rates.

To modify existing catalysts or develop new ones, it helps to understand how existing catalysts work. On page 1508 of this issue, Hansen *et al.* (*1*) beautifully demonstrate that structural characterization of a catalyst's surface in the presence of reactive gases can help to clarify how a catalyst modifier—in this case, a barium promoter for ammonia synthesis—promotes the catalyst's activity. The results may help to discover other catalyst promoters.

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The authors study the ammonia synthesis reaction

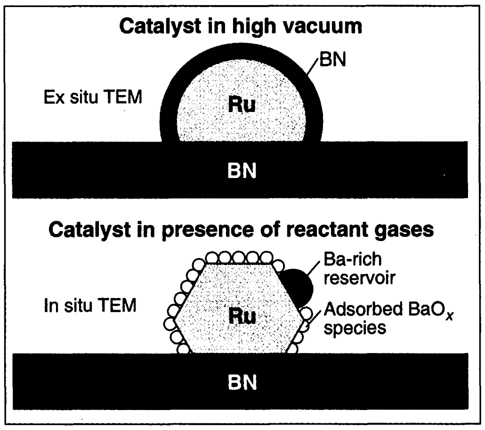
$$N_2 + 3H_2 \rightarrow 2NH_3$$

which provides the essential ingredient for the manufacture of fertilizer. Ever since Haber and Bosch developed the first synthetic process for making ammonia in the early 20th century, this reaction has helped to diminish famine worldwide. It has also been an important prototype reaction for fundamental studies of catalysis.

The difficulty with this reaction is that dinitrogen, N_2, is very unreactive. A transition metal catalyst is therefore required to activate the N_2 reactant. In the best catalysts, the transition metal surfaces are decorated with alkali and/or alkaline earth elements, which promote the reaction, possibly by facilitating N_2 dissociation (*2*).

Many studies have aimed to elucidate the action of the promoters as well as the steps of the reaction mechanism that occur directly on the transition metal surface (*2–5*). Many approaches (both experimental and theoretical) widely used today in catalytic research were first developed when studying this prototype reaction (*2–4*, *6*). Still, the role of the alkali and alkaline earth promoters has remained elusive.

Hansen *et al.* (*1*) reveal why this has been so and provide important new insights into the role of the barium promoter in enhancing the activity of boron nitride–supported Ru catalysts for ammonia synthesis. The Ba promoter/Ru catalyst system studied by the authors is perhaps the most active catalyst currently known for the ammonia synthesis reaction. Furthermore, ammonia synthesis has long served as a prototype reaction for understanding promotion of catalysts by alkali and alkaline earth elements, which plays an important role in many catalytic reactions.



The value of in situ characterization. The surface structure of a catalyst can change when the gases that make up the reaction mixture are removed, as shown by Hansen *et al.* (*1*) for a BN-supported Ru catalyst with a Ba promoter. At high vacuum, no Ba-rich phases are identified, and the Ru particles seem to be covered with a BN multilayer film. In the presence of reactant gases, this film is not present. Instead, two Ba-rich phases are formed: an adsorbed BaOx species, which acts to electronically promote the Ru surface sites, and Ba-rich particles, which probably act as a reservoir to maintain the surface coverage of BaOx over time.