COMMENTARY

Fish extinctions and ecosystem functioning in tropical ecosystems

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The activities of modern humans have increased the extinction rate of the world's species by up to 1,000 times that observed from the fossil record (1). This extinction crisis has motivated the scientific community to understand the consequences of reduced biodiversity for the dynamics of ecosystems, especially those that provide basic services to human societies. In many cases, we are in the process of damaging ecosystems that we rely on intimately for our own livelihoods. Nevertheless, our understanding of how ecosystems respond to losses of biodiversity remains rudimentary, and ecologists are struggling to understand the implications of future species losses. In a recent issue of PNAS, McIntyre *et al.* (2) provide an ambitious attempt to understand how the cycling of limiting nutrients in species-rich aquatic ecosystems varies as species are lost from their fish communities. The results presented in that article show that the deterioration of fish biodiversity in the tropics has important consequences for the ecosystems these fish inhabit but also highlight several key points that have been underappreciated by much of biodiversity science.

The last decade has seen a flurry of research attempting to understand how ecosystems change as their taxonomic composition and diversity are compromised (3). Most of this research has worked at small spatial, temporal, and taxonomic scales where species diversity and composition can be manipulated in a tractable manner. Many of these experiments involve manipulations of ecosystems that are entirely contrived or are represented by a single trophic level. Very little of this work has attempted to estimate how the energy and nutrient cycling processes of reasonably scaled ecosystems change as their diversity declines. Although this work has attracted substantial scientific interest, the applicability of these results to understanding the implications of the extinction crisis is somewhat limiting, and the messages from these experiments are heuristic at best. We need to know how ecosystems respond to extinctions at spatial and temporal scales that are relevant to the ecosystems that humans interact with and rely on.

The majority of extinctions are occurring in the tropics where most biodiversity resides and where rapidly expanding human populations are placing exceptional pressures on ecosystems. Among ecosystem types, freshwaters are arguably the most impacted because of the concentration of human activities on them. Nonpoint source pollution, exotic species introductions, exploitation, watershed development, water withdrawals, impoundments, and climate change combine to make most aquatic ecosystems fundamentally altered in regions with even modest human populations (4–7). Because of the heavy reliance of human societies on freshwaters, this concentration of impacts on aquatic ecosystems is not surprising. However, there has been little work to explore the cumulative effects of multiple perturbations to aquatic ecosystems (but see refs. 8 and 9), and such integrative work on biodiverse tropical ecosystems is especially lacking.

Fishes represent the largest component of global vertebrate diversity, and nearly half of them are found in freshwater. The effects of fishes on ecosystem dynamics mediated through changes in trophic structure are very well described (10–12). In addition, much of this knowledge has been accomplished through modeling and experimentation at the whole ecosystem scale. Despite this wealth of information about how the addition or removal of single species alters basic ecosystem properties of lakes and rivers, little research has attempted to understand how these ecosystems respond to biodiversity loss. If we are to understand the biodiversity–ecosystem function links anywhere, it will arguably be in freshwater systems that are easily manipulated and intensively studied.

The importance of fishes to the nutrient cycles of aquatic ecosystems has been debated for decades (13). The most widely recognized roles that fish play in nutrient cycles are those by migratory species such as Pacific salmon that transport substantial quantities of nutrients from marine to freshwater ecosystems through their spawning migrations (14). Fish are also important to nutrient cycles because they control trophic structure and, therefore, affect the distribution of nutrient among various taxa in lakes and streams. Fish excretion can also be an important source of recycled nutrients readily available to nutrient-starved primary producers. Recycling of limiting nutrients from prey or detritus pools represents one of the dominant sources of nutrients to aquatic primary producers in many ecosystems (12). Thus, changes in species composition and diversity of fish communities have the potential to alter the availability of limiting nutrients to primary producers, and hence ecosystem productivity, in systems where fish excretion is an important nutrient source.

Nutrient Cycling in Tropical Ecosystems

McIntyre *et al.* (2) used computer simulations to evaluate how the recycling of nitrogen and phosphorus by fish communities responds to a variety of species-extinction scenarios in two diverse tropical ecosystems: Lake Tanganyika, Africa, and Rio Las Marias, Venezuela. The model simulations used observed patterns of species abundance and nutrient recycling rates determined from field estimates of nitrogen and phosphorus excretion by fishes (15). Abundances and nutrient excretion rates were estimated for the 36 most common fish species in Lake Tanganyika and 69 species in Rio Las Marias. McIntyre *et al.* then evaluated how nutrient recycling by the fish community was altered through a series of alternative extinction scenarios. Unlike most experimental tests of the effects of extinctions on ecosystem functioning, which assume that species extinctions occur randomly, McIntyre *et al.* considered a range of plausible extinction scenarios based on either ecological or human-related factors.

McIntyre *et al.* (2) found that most extinction scenarios led to reductions in nutrient recycling by the fish community. Simulations that allowed increased growth among surviving species to compensate for losses of extinct species offset most of this decline, until all species of a single feeding guild were extinct. At

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this point, substantial reductions in nutrient cycling rates were observed. The most interesting response was that associated with loss of a single species, *Prochilodus mariae*, which accounted for nearly half of the nutrients recycled by the fish community in Rio Las Marias, but which had only a single species capable of compensating for its extinction. Thus, only two extinctions from a diverse community produced striking changes in the ecosystem.

Other scenarios simulated the nonrandom loss of species as is expected from human exploitation of fish communities. In these cases, certain species (usually those at high trophic positions or with large body sizes) are more likely to be eliminated than is expected based on random chance. Simulations with nonrandom extinctions show that ecosystem perturbations are far more likely to be substantial than for scenarios with random extinctions. In fact, extinctions driven by fisheries exploitation produced effects that were comparable with the worst-case scenario considered in that study.

McIntyre *et al.* (2) used a simple simulation framework to scale up from estimates of nutrient recycling rates of individual fishes to the contributions from the entire community. Should we believe that such approaches reasonably capture the complexity of natural ecosystems? A parallel study by Taylor *et al.* (16) experimentally confirms some of the conclusions from this study, notably about the singular importance of *Prochilodus*. Taylor *et al.* experimentally divided Rio Las Marias to exclude *Prochilodus* from half of the stream and subsequently monitored changes in a suite of ecosystem responses. That experiment demonstrated convincingly that elimination of this single species resulted in wholesale changes in detritus accumulation and ecosystem productivity; loss of *Prochilodus* changed both ecosystem respiration and primary production, resulting in a 50% reduction in net ecosystem production. However, contrary to the predictions of McIntyre *et al.*, removal of *Prochilodus* actually increased gross primary production, but was offset by larger increases in ecosystem respiration. Thus, it appears that the importance of *Prochilodus* in ecosystem dynamics is only partially attributable to its regulation of nutrient cycles. It also controls the dynamics of detritus pools and how they are related to the decomposers in this ecosystem. Why the results of McIntyre *et al.* are not represented entirely by the ecosystem experiment presented by Taylor *et al.* is unresolved but is somewhat humbling given the extent to which this ecosystem has been studied.

What are some limitations of McIntyre *et al.*'s study (2)? Like all models, the richness of biological interactions considered is a small subset of those that govern real communities. For example, consider what happens to a community when a competitor from a specific feeding guild is driven to extinction. McIntyre *et al.* assumed either that there was no response in the remaining community or that remaining species filled the energetic void created by the loss of the extinct species. It is almost needless to say that simulations that included such compensation exhibited far more buffering from species losses than those simulations that assumed no compensatory responses. However, given the intensity of interactions among species in fish communities, we are left to wonder whether such simple models realistically capture community responses to specific extinctions. In particular, indirect effects mediated through behavioral changes in prey communities after removal of their predators can cause especially wide-ranging changes in community structure and, therefore, ecosystem processes (10, 17).

General Lessons for Biodiversity Science

What general lessons about losses of biodiversity and ecosystem functioning can we draw from McIntyre *et al.* (2)? We need to acknowledge that all species are not equally important in ecosystems; even highly diverse ecosystems may be organized around the effects of only a few keystone species (18). In fact, ecosystems may be robust to large changes in their diversity until such a keystone is eliminated, but we still lack a clear ability to identify the species and the contexts where such situations exist. Thus, studies attempting to quantify the number of species required to perform basic ecosystem functions are simply asking the wrong question. We should expect that ecosystems will respond irregularly to species losses (e.g., figure 1 in ref. 2), and identifying the causes of these irregularities seems the most logical goal for understanding ecosystem responses to biodiversity loss.

Extinctions do not occur randomly, especially for exploited species. Therefore, ecosystem responses to biodiversity loss are probably not captured by models assuming random extinctions. In the case of exploited taxa, selection certainly follows a nonrandom order whereby some species are at higher risk for extinction because they are targeted by humans. These species often occur at the top of food webs or have large body sizes. We know that the trophic structure of fish communities usually is determined by top predators or species with unique ecological attributes such as large body size or the ability to capitalize on detritus pools (e.g., *Prochilodus*). Thus, selective exploitation increases the risk of causing ecosystem changes, even those with high levels of diversity.

Considering the general messages that derive from studies such as that by McIntyre *et al.* (2), expecting that science will be able to develop a mature understanding of how ecosystems respond to biodiversity loss is possibly overly optimistic for the near future. Given the current pace of extinctions, it seems more important to develop practical conservation strategies that are robust to these uncertainties before too much damage to ecosystems accrues.

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