How to Be Manipulative

Intelligent tinkering is key to understanding ecology and rehabilitating ecosystems

Robert M. Pringle

"It is interesting," wrote Charles Darwin, "to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."

This sentence was part of Darwin's closing argument in *The Origin of Species* (1859). The vastly diverse soup of life does not require divine micromanagement; instead, the messy complexity of an ecosystem (such as an entangled bank) operates according to a few elegant rules of nature.

Darwin saw grandeur in this view of life. His Victorian audience saw audacity. I see excess optimism. When Darwin sketched this caricature, he did so from the enviable vantage point of having recently figured out one of those "laws acting around us"—one that helped explain how all these elaborately constructed forms came to exist in the first place. Surely other biological laws would soon be revealed.

One hundred fifty years later, ecologists like me are still working to sort out the rules that govern entangled banks and other ecosystems. We tackle questions that seem simple yet turn out to be confoundingly difficult: Why do populations occur where they do, and not somewhere else? Why are there 500 lizards in a hectare of woodland, instead of 50 or 5,000? How do the answers to these questions vary through time, or as we zoom in and out to focus on smaller or larger sections of the ecosystem?

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The textbook definition of ecology seems straightforward: the study of the interactions between organisms and their environment. Yet that simple definition is dangerously encompassing. The environment that an organism experiences is many things: individuals of the same species, individuals of other species, their spatial arrangements and movements, the temperature, the amounts of light and water, the concentrations of different chemicals. And each organism interacts with the environment in many ways: Where are nutrients, and how do I get them? How do I avoid the things that eat me and find the ones I want to copulate with? How do I keep from freezing, overheating or drying up?

The ecology of any system—entangled banks, ponds, prairies, rainforests—comprises many organisms of many types that encounter one another and react to those encounters. All those moving parts generate innumerable patterns at a variety of scales. Some are regular, easy to spot and describe, and many are not. Ecology's job is to explain why those patterns are there, and not others. Because there are always multiple processes contributing to any given pattern (and interacting with each other in intricate ways), we have to contend with a lot of hypotheses. For example, take an African grassland where there are a lot of lions, a few wildebeests and the foliage is thick. Now take a similar place where all the lions have been shot or poisoned, the wildebeests have proliferated and the grass has been chewed to stubble.

At first blush, this comparison seems to illustrate the classic "green world hypothesis" posited by Nelson Hairston, Frederick Smith and Lawrence Slobodkin in a 1960 issue of *The American Naturalist:* The world is green because predators keep herbivore numbers down, allowing plants to thrive. But wait—what if the area without lions also receives less rainfall? How much of the difference in plant biomass is attributable to wildebeest depredation and how much to the vagaries of weather? When did these two places last burn, and how fertile are their soils? And what about the other herbivores that eat these plants—how do their numbers compare in places A and B? Finally, heed Winnie the Pooh's observation that "All the good things which an animal likes have the wrong sort of swallow or too many spikes." (Or as another ecologist, Daniel Janzen, put it, almost as poetically as Pooh, "The world is not colored green; but L-Dopa, cocaine, and caffeine.") In short, maybe the plants in Place A are better defended, chemically or mechanically, than those in place B.

Explaining our simple observation—more grass here, less there—requires that we test a series of hypotheses. And once we've convinced ourselves that we understand why Place A is different from Place B, some graduate student discovers that it all works differently in Place C. Ideas scrabble for primacy in ivory towers. Clear patterns lead to much hard work and discussion, and the "why" is always complicated.

These efforts are not idle academic amusements. We really want to know—and society increasingly demands that we provide—answers to questions about how climate change, deforestation, extinction and invasive species influence things like air quality, water supply, disease dynamics and fishery yields (to pick a few from many possible examples). But we can't give good answers until we understand how the pieces fit together.

The sword of ecological complexity has two edges. The intersection of so many chemical, physical, physiological and behavioral processes creates fascinating stories that enthrall us, draw us in, enable *National Geographic* to sell magazines. But the intricacies of even the simplest ecosystems, and the contingencies of ecological interactions, tend to thwart attempts at general laws. Few of ecology's biggest riddles have been conclusively solved: to a large extent, we are still chipping away at the foundational questions of the 1960s and 1970s.

None of which is to suggest that we haven't made progress. Over the years, we have identified continent-scale patterns and explanatory rules that appear to hold for most, if not all, ecosystems. These are not quite on the order of Darwin's natural selection in terms of a conceptual scaffold for the discipline, but rules are rules—even if they're sometimes broken. Some would argue that we don't actually *need* general laws, that our compulsive search for them is a hangover from a physics-centric philosophy of science, and that we should instead be content to build an increasingly comprehensive atlas of place-based understandings. By this criterion, we've made a great deal of progress indeed.

Picking Fights with Nature

As in much of biology, the most satisfying truths in ecology derive from manipulative experimentation. Tinker with nature, and quantify how it responds. Unlike much experimental biology, however, the processes that we want to understand typically do not fit inside a Petri dish, a lab rat, or even a lab building. Of course we do experiments in the lab. But those experiments are always much-simplified abstractions of wild, hypervariable nature.

I happen to be typing this from a valley in Bhutan. Outside my window is a small mountain dotted with fir trees. The trees are sparse between the boulders at the foggy peak and get gradually denser in the red soils toward the base. This little mountain could be my study site, which in itself illustrates a central dilemma of community ecology: Many of the experiments we'd like to do are impossible. Try maintaining a colony of Bhutanese mountains in the lab.

Why would that be helpful? In 1967, Dan Janzen famously proposed that "mountain passes are higher in the tropics." Seasonal shifts in temperature increase with latitude. The mean minimum temperature in Princeton, New Jersey is –6 degrees Celsius in January and ranges to a mean maximum of 24 degrees in July, whereas in Liberia, Costa Rica, the corresponding extremes are 22 and 35 degrees. But the lapse rate—the decrease in tem-

Frank Ippolito

Figure 1. Ecology is the study of how organisms interact with the world around them. Seemingly chaotic networks of species and nutrient flows resolve, on closer inspection, into a multitude of patterns in space and time, from the population cycles of predators and their prey to the patterns of diversity observed in bounded areas like that depicted in Frank Ippolito's *Rainforest Cube* (2004). Ecologists search for consistent rules that generate these patterns. One way to find them is by tweaking the systems—adding, subtracting and perturbing components of the living web and its nonliving backdrop—and analyzing the outcomes.

perature with height—is a relatively constant 6 degrees Celsius per kilometer at all latitudes. During most of the year, therefore, an organism adapted to a temperate climate can climb quite high before temperatures drop below the winter minimum it normally experiences, whereas its tropical cousin will more quickly climb out of its comfort zone. Thus, tropical mountains are effectively "higher" for the organisms involved, and topographical variation should present a more formidable barrier to dispersal at low latitudes. The logic here is sound, the implications are profound, and components of the theory can be tested piecewise. A primary assumption—that tropical organisms have narrower thermal-tolerance ranges than their temperate cousins—can be validated by taking animals from different sources into the lab and raising or lowering the temperature while monitoring their physiological responses. A key prediction, that elevational range increases with latitude, has been corroborated by compiling 80 years of published data on the distributions of 16,500 species spanning the geographic distance from Argentina to Alberta.

But the full hypothesis is bigger, with additional assumptions and implications that are difficult to test directly—for example, that temperature, rather than some other factor that varies with altitude, determines the effectiveness of a topographic barrier to dispersal. What would a definitive experiment look like? Perhaps I could make 12 identical copies of this Bhutanese mountain and wipe them all clean of life so that they could be colonized anew. Put four of them on the equator, four in Mexico, and four in Maine. Then return annually for several decades to track the altitudinal limits and dispersal success of the colonizing species. Already, the logistical challenges seem a bit daunting.

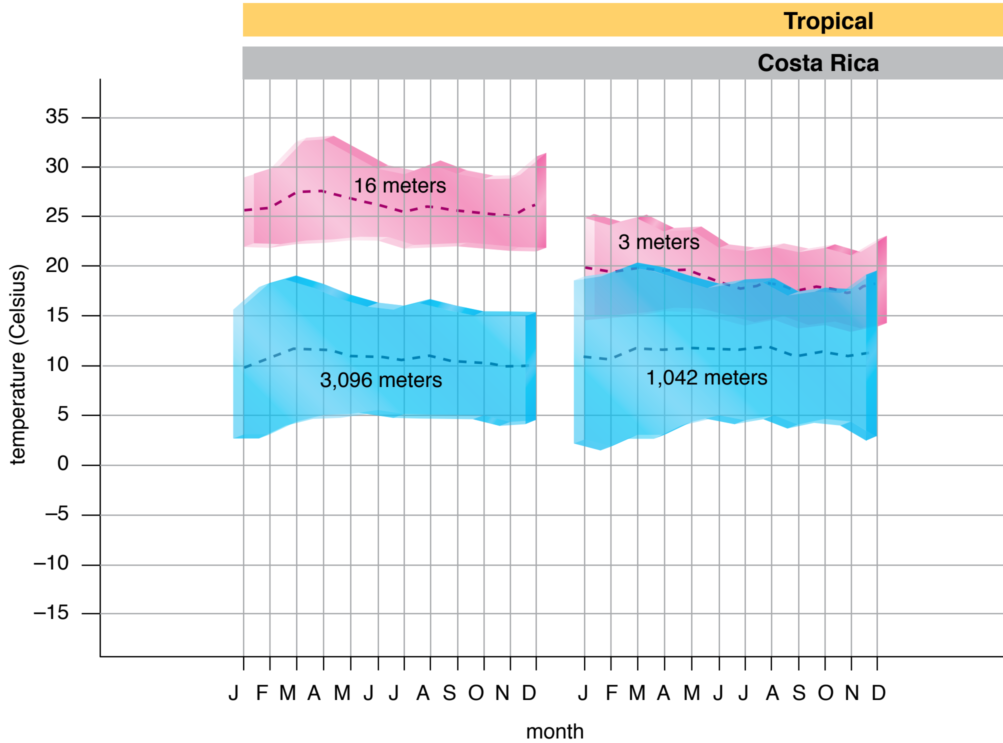


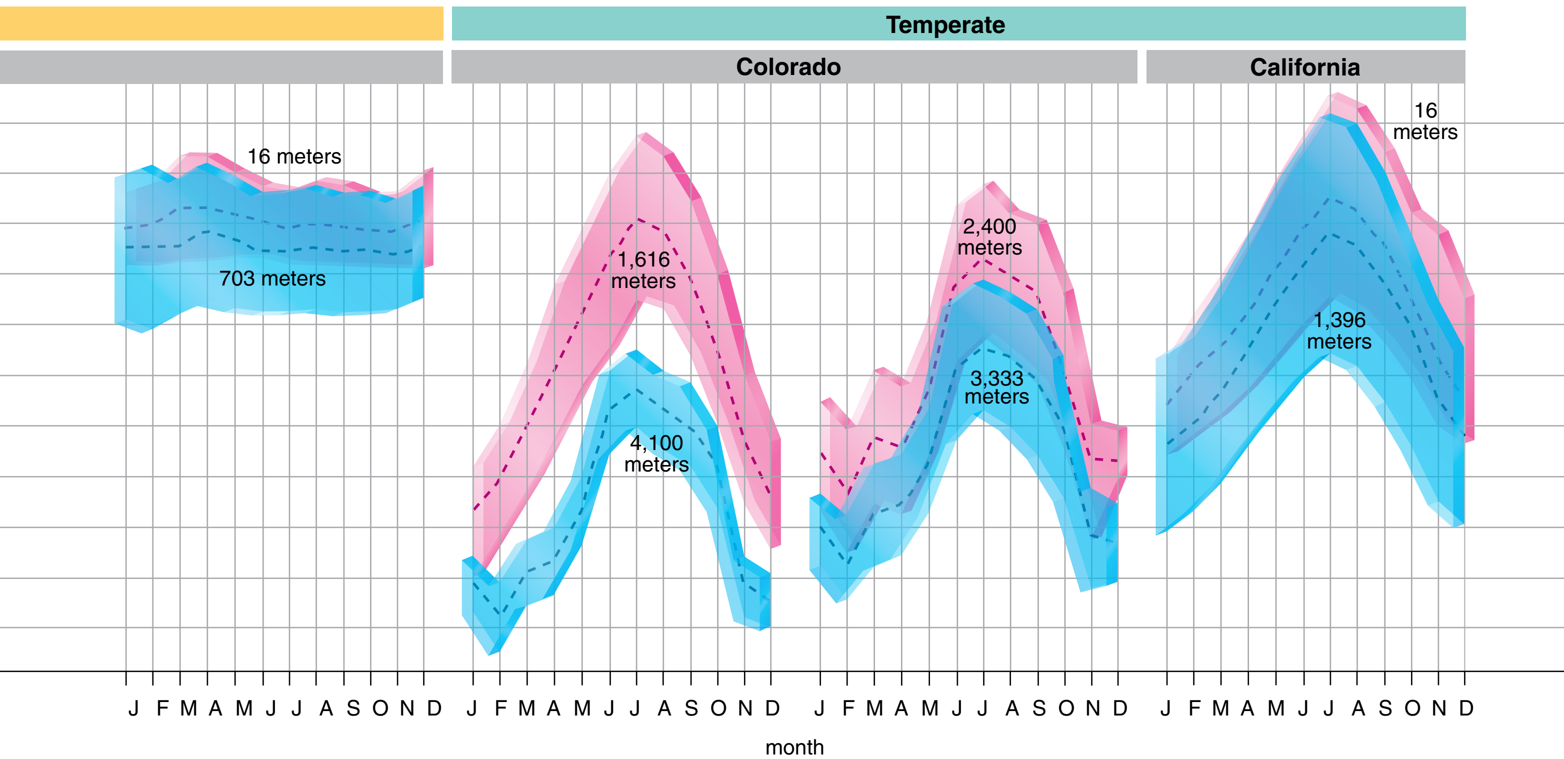
Figure 2. Are mountain passes "higher" in the tropics? In a classic 1967 paper, Daniel Janzen argued that organisms adapted to the stable temperature regimes of the tropics are more constrained in their vertical migrations than organisms at higher latitudes where temperatures fluctuate seasonally. (The decrease in temperature with altitude is relatively constant across the globe: 6 degrees Celsius per kilometer.) Using data from high and low elevations at three tropical sites in Costa Rica and three temperate ones in Colorado and California, Janzen plotted monthly means of daily maximum and minimum temperatures, along with monthly mean temperatures (dashed lines). For a given elevation range, the relative overlap in thermal regime is greater at temperate sites, suggesting that temperate organisms should more easily disperse across topographical barriers. For decades, the hypothesis remained essentially untested. Recent studies have found support for key components of the theory, but its full implications for ecology, biogeography and the biological impacts of climate change remain an active area of research. (Chart adapted from Janzen, D. H. 1967. *The American Naturalist* 101:233–246.)

Another challenge is the lack of model systems of the sort that have enabled explosive progress in genetics and cell biology. Molecular biologists have wisely concentrated on a subset of organisms that are amenable to laboratory study: single-celled prokaryotes *(E. coli)* and eukaryotes *(Saccharomyces* yeasts); fruit flies *(Drosophila);* lab mice *(Mus)*. Model systems work because many processes at the molecular and cellular levels are representative of those in other species. The biology of mouse cells is sufficiently similar to the biology of elephant cells that we learn about both by studying one. Ecologically, however, mice are not elephants. They differ in how they feed and are fed upon, and in the ways they interact among themselves and with other species. We can't assume away these differences. In fact, one of the topics my research group is currently working on is how the ecology of elephants influences the ecology of mice and other smaller species.

Simulating Extinction

Three years ago, Jacob Goheen (University of Wyoming), Todd Palmer (University of Florida) and I set out to manipulate the presence of elephants and giraffes (megaherbivores), along with two other size classes of African mammals: medium-sized mesoherbivores (such as impala and zebra), and dik-diks (diminutive but ubiquitous 5-kilogram antelopes). Our research is conducted at the Mpala Conservancy and Research Centre on the Laikipia Plateau of central Kenya. There, we constructed 36 one-hectare plots, randomly assigning 27 of them to one of three herbivore-exclusion treatments, with the remaining nine serving as controls in which all animals are allowed. By comparing plots accessible to a given class of herbivores with plots that exclude them, we can deduce the ecological roles of different-sized herbivores. We monitor a range of variables in each plot, including plant community composition and demography, rodent density and diversity, nutrient-cycling and decomposition rates, rainfall, soil composition and so forth.

Here is the shocking secret of how to manipulate the world's largest land mammals: Put up a series of 2-meter



tall posts around football-field-sized plots, string high-tensile wire around the top, and ensure that anything that touches the wire receives a 7,000-volt reminder that an experiment is in progress. Solar chargers power the fences. To exclude both mega- and meso-herbivores, string another 12 wires down to ground level. Finally, add a strip of chain-link fence around the bottom to make the last set of exclosures dik-dik proof. Voilà. You have experimentally simulated extinction the way it happens in the real world: biggest species first, then smaller ones.

Elephants quickly learn to avoid the fences, but they have their moods, and every so often one smashes a fence. Giraffes are more collision-prone and occasionally need to be chased off. Fence repair is part of the job—as is accidental contact between fence and researcher.

So is waiting, with anxious eyes on grant deadlines and tenure clocks, for results to materialize. Some effects were evident within a few months. The fences went up in September of 2008 and by November we saw consistent differences across treatments in the diversity of understory plants. Other changes will take years. Trees, for example, are slow. We hope to run this experiment for 20 years, and it may take that long before we really understand what's happening with woody plants. Other responses lie between these two extremes. By March of 2009, the density of pouched mice *(Saccostomus mearnsi)* was greater in plots from which all large herbivores had been excluded, but only in dry areas—it took another year before the same result was apparent in places where rainfall was higher. By having several replicates of each treatment in places with varying rainfall, we can begin to tease apart such localized

Figure 3. Within 27 one-hectare exclosures at the Mpala Research Centre in Kenya, different configurations of electric fencing were used to simulate the extinction of herbivores spanning three orders of magnitude in body size. The plot in the foreground excludes mammals ranging from elephants (5,000 kilograms) to impala (50 kilograms); the further plot excludes everything down to dik-diks (5 kilograms). The ecological effects of a given mammalian guild can be deduced by comparing fenced plots with unfenced controls. (Photograph courtesy of the author.)

Figure 4. Tiny islands in the Bahamas provide self-contained ecosystems in which one can study the effects of species addition and deletion. The ocean deters migration to and from the study islands, enabling researchers to experimentally measure how different combinations of predators and competitors affect biodiversity, food webs and rapid evolutionary adaptation in isolated environments. (Photograph courtesy of the author.)

idiosyncrasies, in the hope of understanding how climatic factors influence biotic interactions.

Invading Tiny Islands

Selective removal of species from plots is a common technique in field manipulations, but it is not the only one. The Kenyan work described above aims to characterize the consequences of extinction, so exclusion experiments have obvious appeal. Real ecological communities, however, reflect the interplay of species loss and species gain. Both are natural processes that today, thanks to human activity, are on fast forward. When species enter a habitat without human help—blown by the wind, say, or rafting on a piece of pelagic flotsam—we call it colonization. This is the subject of a large body of theoretical and empirical work known as island biogeography. When new populations are founded with an assist from humankind, we tend to call it invasion. Regardless of the label, ecologists need to understand how newcomers affect established populations.

In the Bahamas, my colleagues and I are trying to see this problem through the eyes of a common lizard, the brown anole *(Anolis sagrei)*. To that end, we are manipulating entire islands. Tiny ones. On some islands, we have experimentally added populations of the green anole *(A. smaragdinus)*. Green and brown anoles often occur in the same areas—greens in trees, browns on the ground. This partitioning of vertical space is thought to have arisen from competition during evolutionary history: The two species have nudged one another into slightly different niches and thus should be able to coexist on our wee islands. But what happens when we add an apex predator to the mix? Specifically, what happens when we introduce a quintet of hungry 50-gram curly-tailed lizards *(Leiocephalus carinatus)* onto islands inhabited by hitherto-complacent 5-gram brown anoles? We expect the brown anoles to flee into the shrubbery to escape the ground-patrolling predators. But there they will bump into the ghosts of competition past: green anoles better adapted to the rigors of arboreal existence. Can all three species coexist on such small islands? How will brown anoles respond behaviorally to this two-front assault? Will their populations evolve morphologically to manage life in the trees? How will the rest of the food web—plants, insects, spiders—react to this shakeup among the reptilian predators?

Figure 5. Curly-tailed lizards are voracious predators of brown anole lizards. Their introduction on Bahamian islets precipitates changes in the behavioral patterns and adaptive morphology of the anoles, which must climb up into the shrubbery to avoid being eaten. (Photograph courtesy of Robert Cox.)

The island experiment and the one in Kenya are analogous in several respects. The experimental islands in this case are analogous to fenced plots; the ocean is the "fence." Unmanipulated islands are the controls. The general objective is the same: Pick a fight with some piece of an ecosystem large enough to exhibit realistic responses. We can't shrink a wild ecosystem to fit a petri dish, but we can enlarge our conception of petri dishes.

Scientific Opportunism

How far should we go in picking these fights? One can easily imagine experiments that would be scientifically fascinating and logistically feasible, yet morally reprehensible. Different people draw that last line in different places. Is it ethical to punch the occasional elephant with 7,000 volts in light of what we stand to learn? I think so (and I've tested it on myself) but some might disagree. Is it ethical to transplant two species of anole lizards from one large island in the Bahamas to a few of the many smaller islands lying 300 meters offshore? To me, yes, but it's a matter of degree: I would never intentionally move the same lizards to regions where they did not already occur, or even to faraway places—such as Hawaii—where they do, thanks to the pet trade and international shipping. As the discussion above illustrates, our ability to predict the consequences of invasive species on native ecosystems is limited, but we do know that the effects can be catastrophic. Ecological experimentation requires weighing the scientific importance of a given manipulation against potential discomfort to the animals involved, potential effects on the conservation or sustainability of an ecosystem and potential impact on human well-being.

Many promising experiments would fail one or more of these tests, which is why ecologists keep an eye out for "natural experiments"—scenarios in which quasiexperimental conditions have been created haphazardly. These are often conditions that ecologists have neither the inclination, the funds nor the societal blessing to create themselves. Clearing rainforest, damming rivers and introducing invasive species can all produce natural experiments.

Such opportunities have generated some of the most influential studies in modern ecology. When 1,000 square kilometers of the Brazilian Amazon were to be cleared for cattle in the early 1980s, far-sighted investigators persuaded ranchers to leave behind replicated forest patches of 1, 10 and 100 hectares. This led to the Biological Dynamics of Forest Fragments Project, which has shaped our understanding of many important questions surrounding habitat fragmentation, edge effects, metapopulations and island-biogeography theory. We might mourn the lost flora and fauna, but the 500-plus publications from this project have bolstered our ability to forecast the effects of deforestation, and the training of hundreds of Brazilian and international students has created a new cadre of environmentally sensitive citizens and scientists.

Mark Moffett/Minden Pictures/National Geographic Stock

Figure 6. The Biological Dynamics of Forest Fragments Project, near Manaus, Brazil, is an archetypal example of a "natural experiment." This large-scale manipulation of the environment—the razing of rainforest for pasture—would never have been sanctioned in the name of science alone. Via an agreement with ranchers, however, forest fragments of various sizes were preserved, enabling a unique and highly productive long-term study.

A similar opportunity arose in Venezuela when, in 1986, a 4,300-square kilometer hydroelectric impoundment created a series of forest fragments isolated by water. The smaller of these newborn islands lacked large carnivores, enabling John Terborgh of Duke University and colleagues to document what they famously called "ecological meltdown in predator-free forest fragments." Minus large predators, rodents, monkeys, iguanas and leaf-cutter ants ran amok, decimating the vegetation.

Rewilding

In both of these cases, habitat degradation and species loss were the price of augmenting ecological knowledge—a bittersweet trade-off. However, it is sometimes possible to augment nature and knowledge at the same time. What if, for example, we tried the inverse of our exclusion experiment: Repatriate African megafauna to places where they've been extirpated, and study that instead?

An ambitious rewilding project is doing exactly this in Mozambique's Parque Nacional da Gorongosa, at the southern terminus of the Great Rift Valley. Gorongosa has been home to modern humans for more than 100,000 years. It was declared a hunting reserve by Portuguese colonists in the 1920s and became a much-visited safari park in the 1960s. Throughout most of the 20th century, Gorongosa supported 29 species of large herbivores—tens of thousands of individuals—ranging from savanna icons such as elephants, hippos, zebras and wildebeests, to less familiar but even more stunning animals such as nyala, kudu and sable. Carnivores numbered about 20, from lions to striped polecats. Then came guerillas. A campaign for independence against the Portuguese, followed by a gruesome 15-year civil war, wiped out the large mammals, ended tourism and crippled Mozambique.

The human suffering was immense. But Gorongosa's unraveling was tragic in its own right, in part because ecotourism represented one of the few pathways to sustainable development in a decidedly underdeveloped country. Early efforts to revitalize the park faltered. Ecological rehabilitation was not the greatest challenge involved. Gorongosa needed to start over—create physical and administrative infrastructure, entice nervous tourists to tinguish the mammoths, camels, horses and other megafauna that populated the continent until 11,000 years ago.

The historical baseline used by early environmentalists such as John Muir was, implicitly, nature prior to the invasion of industrialized Europeans. As modern researchers dismantle the myth of virgin preindustrial Edens, many conservationists nonetheless cling to this Muirian reference point, consciously or subconsciously. That choice, once it is acknowledged as one, can be persuasively argued. After all, preindustrial people didn't have strip mines, strip malls, offshore rigs or bulldozers, and there were never seven billion of them. But any baseline is arbitrary, and the ones we favor reflect culturally determined ideas about what is "natural" and what constitutes degradation. You could say that the fall began with the invention of the steam engine; I could counter that it began with the invention of the spear, the taming of fire or even the descent of man.

It might seem obvious that a pre-European baseline for North American wildlands is more sensible than a pre-Clovis one, since we have scant knowledge of what prehuman North America actually looked like, other than that many of the species that were present then are now extinct. But not everyone would agree. One group of biologists, for example, made headlines in 2005 by recommending that North America be rewilded using African and Asian megafauna in lieu of their extinct New World counterparts. Their rationale was that many species in North America today are anachronistic. Why are pronghorn so fast? So that they can escape American cheetahs, which no longer exist. Why are some New World fruits so big? To entice long-gone megaherbivores that once dispersed their seeds. Introducing analogs from other continents would, these authors argued, functionally revive these dead interactions.

Don't hold your breath for cheetahs in Wyoming. But consider some of the immediate practical questions facing the Gorongosa Restoration Project. Choosing a baseline by which to define success in restoration requires decisions that affect both people and wildlife. For logistical reasons, 1975 would represent a plausible baseline: That was the year Mozambique gained independence, and we have excellent quantitative data about the

Figure 7. Philanthropist Gregory Carr, in collaboration with the Mozambican government, local community leaders, and other institutional partners, is working to rehabilitate Gorongosa National Park. An iconic ecosystem of Africa's Great Rift Valley, Gorongosa became a casualty of civil war and postcolonial poverty. When hostilities ended in 1992, little remained of its fauna. The park is now undergoing an astonishing transformation; ecologists hope to study the unique biological dynamics of large-scale rewilding and contribute knowledge to the restoration effort. (Photograph courtesy of the author.)

visit, and most importantly, negotiate new relationships with the people living in and around the park. Rebuilding requires resources, and relationships require trust. Both were scarce in postwar Mozambique.

Things began to change in 2004, when the Mozambican government invited American philanthropist Gregory Carr to oversee the restoration of Gorongosa. A 20-year agreement signed in 2007 laid the foundation for a vast restoration effort, facilitating the recovery of many—although not yet all—wildlife species.

The reinvention of Gorongosa National Park is ecological manipulation on a grand scale. Its primary aims are humanitarian and environmental, not scientific, but the potential for synergy is great. As of late 2011, plans for a biological field station are taking shape. The questions to be addressed are endless and fascinating. How will vegetation and small-mammal communities, as well as crucial processes such as nutrient and hydrological cycles, respond to the resurgence of large herbivores and their predators? Why are some species recovering rapidly, others slowly? What are the genetic and potential evolutionary consequences for the species that passed through severe population bottlenecks prior to recovery—will they suffer from inbreeding depression, and might this influence recovery dynamics? How will intensifying herbivory interact with the dynamics of fire, and with what consequences for ecosystem structure and function? The questions and the system are there, awaiting ecologists to take up the challenge.

But What Is "Restoration"?

Restoration ecology is now an established discipline allied to conservation biology, with its own society, journal and specialists. But what does it mean to "restore" a natural space? When we talk about restoring an ecosystem like Gorongosa, we raise questions that are deeply interwoven with values and aesthetics—subjective qualities that make many scientists squirm.

From the outset, the conservation movement grew around a fiction that today seems as misguided as it is difficult to abandon: that there is such a thing as "pristine wilderness." In the Americas, for example, indigenous peoples left a major footprint—they hunted, burned, farmed and helped exstate of the ecosystem in the late 1960s and early 1970s. But if we choose 1975, we confront difficult questions. As of late 2011, there are several thousand people living within the park. Should they stay? If so, how many, and on what terms? Human settlements are anathema to many old-school conservationists, but others are quick to point out that an African savanna sans *Homo sapiens* is a very artificial thing indeed. Humans have inhabited Gorongosa for almost as long as there have been humans, hunting, gathering, farming and fishing. It was the Portuguese who imported the notion of a national park without people, transforming hunters into poachers and farmers into squatters. The humanitarian implications of forcibly re-evicting a large population of poor people from the reborn national park demands serious scrutiny (and is in fact against park policy). Then again, for better and worse, nothing is as it was prior to European imperialism. Mozambique's population has tripled since the park's establishment in 1960; it remains hungry and has unprecedented access to guns, snare wire and nets that our prehistoric ancestors lacked. Whatever the evidence for human-wildlife coexistence prior to imperial conquest, there is little reason to assume that it would be stable today in the absence of limits on population growth and livelihood activities. What limits are sustainable? Are they ethical? How should the government weigh the access rights of today's population against anticipated economic growth and the quality of life of future generations?

Likewise for wildlife: What composition of species and configuration of habitats should the park engineer, and how actively and aggressively must the landscape be managed to obtain that outcome? If we plan a return to 1975, do we then write off two antelopes—roan and tsessebe—that went extinct prior to 1970 (with an assist from European hunters)? White rhinos were extirpated around 1940, but reintroduced in 1970, and cheetahs were reintroduced in 1973. Theoretically, moving our baseline forward or backward a few years would dictate whether these spectacular species should be re-reintroduced or not.

And then there is the brain-bending question of zebras. The park needs zebras for several reasons: They are a tourist draw; they are food for lions, which are an even bigger tourist draw; and they are bulk grazers that would help open up the rank and overgrown grasslands, which in turn would likely increase plant productivity and diversity and reduce the heat and intensity of dry-season fires. The problem is that Gorongosa lies at the biogeographical interface of what some authorities consider two distinct subspecies of zebra: *Equus quagga crawshayi* to the north, and *E. q. chapmani* to the south. A recent molecular analysis revealed strikingly little genetic divergence among these putative races, but they look a bit different—something in the stripes. Strict adherence to a recent historical baseline would demand repopulating the park starting with the handful of zebras still in the park, but these are scarce and vulnerable; left alone, the remnant Gorongosa population would take decades to recover, if it did at all. The alternative would be to count these zebras among the other casualties of war and modernity, and instead augment Gorongosa's zebra population with individuals of a slightly different stripe, which can be obtained from neighboring countries. This is a problem with no optimal solution. Resolution hinges on the relative values assigned to an ostensibly unique subspecies, on the one hand, and the urgency of restoring ecosystem function and touristic viability on the other. Again, we are forced to ask: What exactly are we trying salvage, and what are we trying to restore? In a world of limited resources, limited time and limited zebras, what are our priorities? Opinions differ, and emotions run strong.

The upshot is this: Restoration in any rigid and consistent sense of the word is impossible. The best we can do is approximate some prior state of any given ecosystem, and the approximation we work toward will reflect both the values of the people directing the effort and the inevitable limitations of knowledge and capacity. On top of all that, there is no guarantee of getting what we aim for. Our predictive tools are not sophisticated enough to forecast the long-term results of any process set in motion today. Some species will be winners, some will be casualties, and there will be surprises.

We must recognize that restoration is really reimagination. Creation. Gardening. Not only are we unable to reconstruct Pompeii and populate it with ancient Pompeians, we have no reason to think that we should try. This is liberating. If what we're doing is imagining and creating, then we can be imaginative and creative. And that's exciting. How should our gardens grow? Ask first what any architect asks before ground is broken: Who are the clients, what do they need, what do they want, and which blueprints fuse needs and wants into something truly beautiful?

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