Animals are rapidly disappearing from forests in Borneo and across the world.

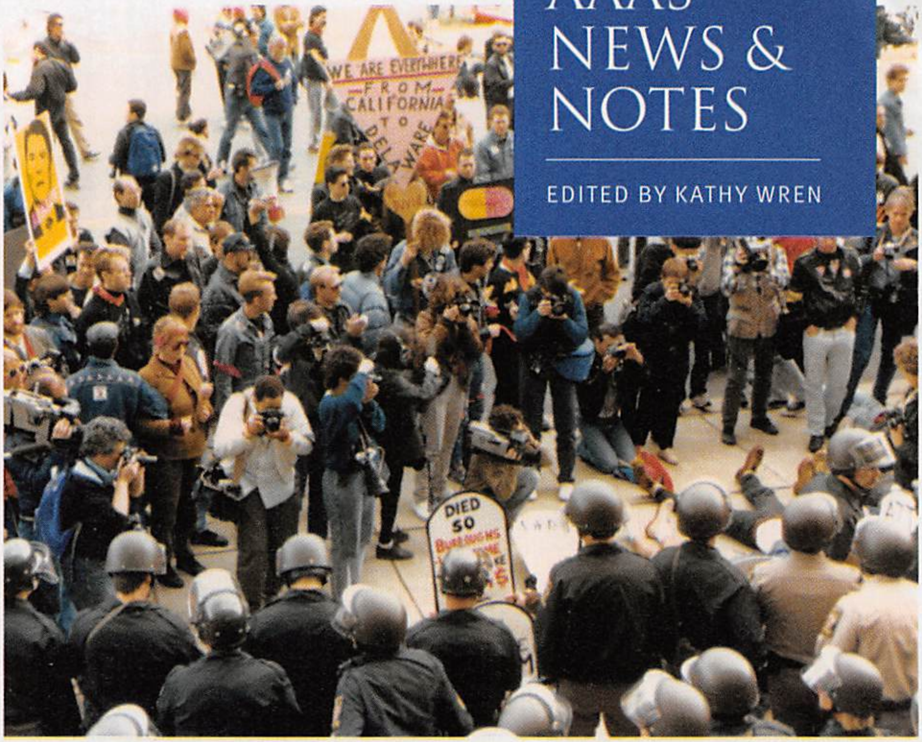
PHOTO: CHRISTIAN ZIEGLER

AAAS NEWS & NOTES

EDITED BY KATHY WREN

At FDA, speedier approval could add uncertainty over risks

By **Kathy Wren**



In 1988, days after AIDS activists protested at the FDA for greater access to experimental drugs, the agency announced new regulations to speed up approval for certain medical products.

Officials at the Food and Drug Administration (FDA) must wrestle with a difficult paradox. Since the early 1960s, after the thalidomide tragedy, the agency has been charged with protecting the public from unsafe and ineffective medical products. At the same time, across society, the demand for faster access to new therapies has risen. As patients exhaust treatment options for serious or life-threatening conditions, their tolerance for risk may grow.

In an effort to balance prudence and innovation, the FDA has implemented a variety of new regulatory pathways to expedite the approval of new drugs and medical devices that meet certain conditions. But the benefits of these accelerated approaches must be weighed against their drawbacks, speakers cautioned at a 13 June event at AAAS headquarters in Washington, DC. The meeting was cosponsored by AAAS; the Program on Regulation, Therapeutics, and Law within the Division of Pharmacoepidemiology and Pharmacoeconomics of Brigham and Women's Hospital/Harvard Medical School; and the National Center for Health Research.

Scientific evidence is paramount to balancing the multiple demands on the Obama Administration, according to FDA Commissioner Margaret Hamburg. "At the end of the day, we have to be guided by science in everything we do. It has to be our compass," she said in a keynote address.

Several of these speedier approval pathways are specifically designed to allow FDA validation based on studies measuring "surrogate end points." Certain cholesterol levels, for example, have been proven to adequately reflect a patient's risk of having a heart attack, so a drug that reduces those levels may be presumed to lower cardiovascular mortality.

Forty-nine percent of the drug approvals by the FDA from 2005 to 2012 were based on surrogate end points, according to a study by Joseph Ross, an assistant professor of medicine and of public health at the Yale University School of Medicine. The numbers varied by medical specialty, with a full 80% of cancer drug approvals relying on these measurements.

As speedier approval pathways allow the use of surrogate measures in a wider variety of conditions, fewer of these measures are subject to the rigorous validation required of earlier FDA-authorized surrogates such as cholesterol levels or systolic blood pressure.

"We need to do better studies to validate whether these surrogates are as good as we think, and not just assume things about them," said Jerry Avorn, a professor of medicine at Harvard Medical School and chief of the Division of Pharmacoepidemiology and Pharmacoeconomics at Brigham and Women's Hospital.

Speakers at the meeting cited study design as another area of concern. While randomized, controlled clinical trials are the gold standard in medical research, this type of study is not always used when testing new medical products for FDA approval. And it is particularly rare for new devices, which are subject to different regulatory procedures from prescription drugs.

More than 90% of all new medical devices are not tested in clinical trials at all, according to Diana Zuckerman, president of the National Center for Health Research. And, when Rita Redberg, a cardiologist at the University of California, San Francisco, School of Medicine, investigated the approval of cardiovascular devices in the highest-risk category over an 8-year period, she found that only one-third were approved on the basis of a randomized clinical trial.

In some cases, bypassing a controlled trial may cost lives. An intracranial stent called the Wingspan Stent System was approved for use in stroke prevention on the basis of a 45-person study, according to Redberg. Instead of using a randomized control group, the researchers compared the patients' outcomes to those in a previous study. The FDA approved the Wingspan stent via the "humanitarian device exemption," which is intended to encourage the development of devices for treating rare diseases.

Later, a larger, randomized, controlled trial known as the SAMPRISS trial determined that 1 out of every 11 patients who received the Wingspan stent experienced a stroke or died. An FDA committee agreed that these data did not support the stent's use for stroke, and the agency recommended narrowing the official list of ways that the device should be used.

The SAMPRISS trial was able to gather data effectively because it required anyone using the device to be enrolled in the trial, and it may thus be a good model for future postmarket studies, Redberg suggested.

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Vanishing fauna

By **Sacha Vignieri**

During the Pleistocene epoch, only tens of thousands of years ago, our planet supported large, spectacular animals. Mammoths, terror birds, giant tortoises, and saber-toothed cats, as well as many less familiar species such as giant ground sloths (some of which reached 7 meters in height) and glyptodonts (which resembled car-sized armadillos), roamed freely. Since then, however, the number and diversity of animal species on Earth have consistently and steadily declined. Today we are left with a relatively depauperate fauna, and we continue to lose animal species to extinction rapidly. Although some debate persists, most of the evidence suggests that humans were responsible for extinction of this Pleistocene fauna, and we continue to drive animal extinctions today

INSIDE

through the destruction of wild lands, consumption of animals as a resource or a luxury, and persecution of species we see as threats or competitors.

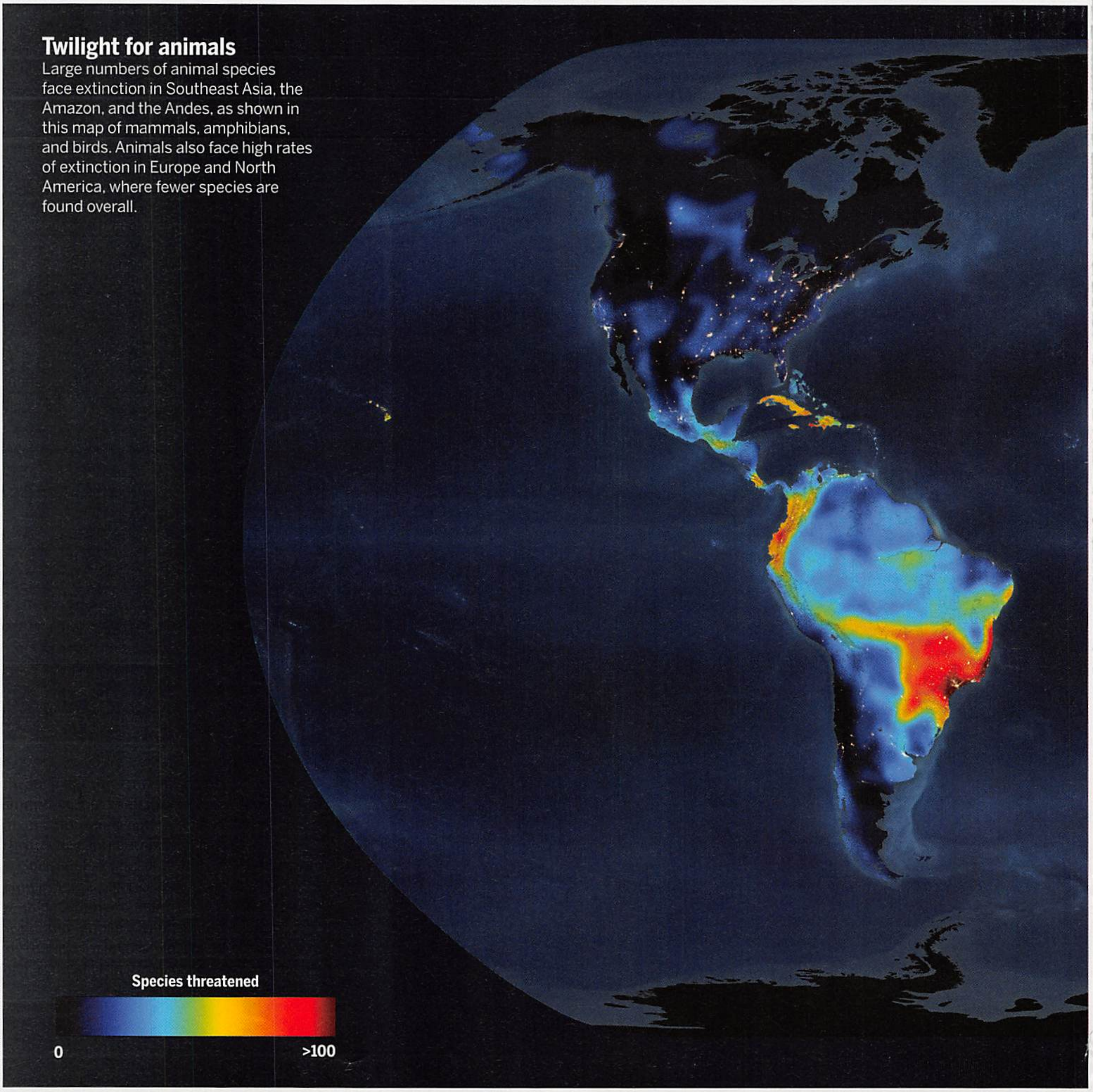
Such global loss of animal species, or defaunation, is increasingly recognized as a problem akin to deforestation in terms of scale and impact. Though for emotional or aesthetic reasons we may lament the loss of large charismatic species, such as tigers, rhinos, and pandas, we now know that loss of animals, from the largest elephant to the smallest beetle, will also fundamentally alter the form and function of the ecosystems upon which we all depend (see Dirzo *et al.*, p. 401).

Identifying the drivers of these extinctions is straightforward, but stemming the loss is a daunting challenge. Animal species continue to decline in, and disappear from, even large, long-protected reserves, due both to direct impacts, such as poaching, and indirect ecological feedbacks, such as habitat fragmentation. Though hunting and poaching might seem obvious candidates for targeted policy and management interventions, there are complex social issues underlying these activities that will require coordinated and cooperative actions by nations (see Brashares *et al.*, p. 376).

While stemming this loss remains a chal-

Twilight for animals

Large numbers of animal species face extinction in Southeast Asia, the Amazon, and the Andes, as shown in this map of mammals, amphibians, and birds. Animals also face high rates of extinction in Europe and North America, where fewer species are found overall.



MAP: FÉLIX PHARAND-DESCHÊNES (VISUALIZATION), CLINTON JENKINS (DATA PROCESSING), IUCN/BIRDLIFE INTERNATIONAL (DATA)

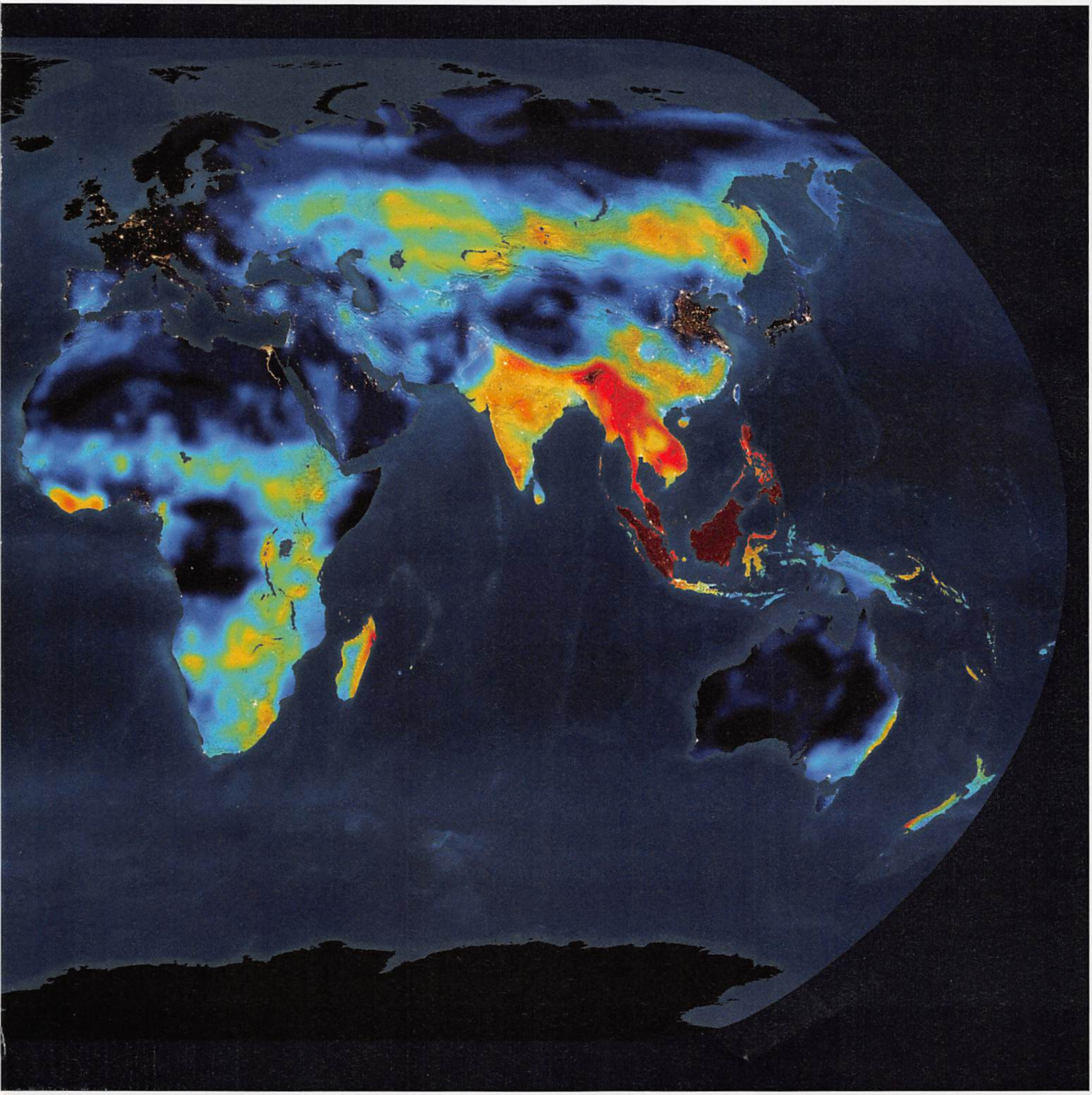
lenging goal, attempts to reverse the extinction trend are increasing. Such "refaunation" efforts involve a variety of approaches, including breeding animals in captivity, with the hope of reintroducing them to the wild, and assisting recolonization of areas where species have become locally extinct (see Seddon *et al.*, p. 406). Active reversal of animal extinctions is proving just as challenging as preventing extinctions in the first place, but a few success stories provide some hope.

Many note and mourn the loss of animals but have not recognized that the impacts of this loss go beyond an aesthetic and emotional need to maintain animals as a part of nature. Current research reveals startling rates of animal declines and extinctions and confirms the importance of these species to ecosystems (see Stokstad, p. 396). Further, and more broadly, it suggests that if we are unable to end or reverse the rate of their loss, it will mean more for our own future than a broken heart or an empty forest. ■

ONLINE

View slideshow at sciencemag.org/special/vanishing

This special issue has been edited by Sacha Vignieri, Andrew M. Sugden, and Elizabeth Pennisi.



A suspension bridge helps researchers study changes to the forest in Lambir Hills National Park.

PHOTO: CHRISTIAN ZIEGLER

The empty forest

A beleaguered national park in Borneo hints at what can happen when animals disappear

By **Erik Stokstad**

Darkness comes quickly at Lambir Hills National Park in western Borneo. The cicadas fall silent, and tree frogs start to chirp softly. Tourists and day hikers have left the ancient forest, so it is a good time to look for the slow loris, a shy arboreal primate. But one night, while ecologist Rhett Harrison was searching for wildlife, a man stepped out of the shadows. The hunter scowled; he knew he wasn't allowed to shoot the animals in the park. No one spoke. The man raised his bakakuk, a homemade shotgun. Unarmed and helpless, Harrison slowly backed away.

The encounter was a rare, heart-stopping event in several years of research at the park in the mid-1990s. Usually, Harrison only heard distant gunshots echoing through the forest or came across snares. But the cost of the hunting became clear with time. In Lambir—one of the most diverse forests in the world—the richness of animals has declined precipitously over the last 3 decades, work by Harrison and others has shown. Flying foxes, sun bears, gibbons, rhinoceros hornbills. All gone. "It's empty of large wildlife," says Richard Corlett of the Xishuangbanna Tropical Botanical Garden in Menglun, China. "There's been dramatic and rapid change."

PHOTO: KAREN KASMAUSKI

Deer and pigs are primary targets of hunters looking for meat to sell or eat.

Lambir is not alone in its defaunation, a process in which an ecosystem loses animals. Much of Asia, Africa, and Latin America also suffers from poaching and overhunting. In some places, the quarry are elephants, tigers, or other high-value species for the international black market. Elsewhere, hunters are just trying to put meat on the dinner table. "It's an epidemic that's going through tropical forest reserves," says Harrison, who works for the World Agroforestry Centre in Kunming, China.

In 1992, Kent Redford, then of the University of Florida, brought widespread attention to the potential fallout from this epidemic, arguing that the forest itself could not survive without the animals that help plants reproduce. "We must not let a forest full of trees fool us into believing that all is well," he wrote in *BioScience*. "An empty forest is a doomed forest."

Since then, researchers have been documenting animal losses and their consequences for a wide range of species and ecosystems including pollinators in farm fields and sharks on coral reefs. Lambir is a key case study. Long-term research on its vegetation is revealing how a forest changes when it loses the herbivores that once thinned saplings and the fruit eaters that dispersed seeds. Borneo is also the scene of more hopeful developments, as researchers and nongovernmental organizations seek ways to stem the damage. "Overhunting is bad for both people and wildlife," says Jedediah Brodie of the University of British Columbia, Vancouver, in Canada. "If we can make hunting sustainable, then it's a win-win."

What is not sustainable is the millions of metric tons of meat harvested in central Africa and the Amazon each year, or the impact of China's burgeoning demand for bear gallbladders and other animal parts used in traditional medicine. In the forests of Laos and Vietnam, few animals heavier than 80 grams can now be found. "There is deafening silence," says Carlos Peres of the University of East Anglia in Norwich, U.K.

Researchers exploring the impacts of defaunation consistently find that it favors plants with wind-dispersed seeds over those that rely on animals to disperse their seeds. In Panama, S. Joseph Wright of the Smithsonian Tropical Research Institute and colleagues have linked hunting to an increase

While some researchers study insects in the park, others have probed the fate of plants based on their fruit or seed.

in woody vines called lianas, which cast their seeds into the wind. Other studies in Peru, Thailand, and Nigeria have also shown changing patterns of plant distributions. But long-term studies in Lambir offered researchers a closer look at what happens to a forest as ever more animals disappear.

BORNEO'S INDIGENOUS NOMADS, the Penan, long made a living by hunting, but their impact was minimal. They would move their forest camps when the sago palm became scarce and game, as they put it, turned shy. In addition, their communities were small relative to the forest.

Life for the Penan and other peoples began to change rapidly in the 1970s. Loggers carved roads into previously isolated areas, making it easier for outsiders and migrants to hunt deep in the forest. They would take game back to village markets or sell it to the work camps. Although the Indonesian government had long since banned guns, dangerous homemade shotguns proliferated. Even more devastating has been the use of snares, which indiscriminately kill animals.

Yet well into the 1980s, Lambir (established in 1975) was reachable only by a dirt logging road. It would wash out in the rainy season, giving the park some protection. Helmeted hornbills filled the sky with the whoosh of their wings. Hunters covet these magnificent birds, because artisans carve the casque, a large, ivorylike protrusion on its upper beak. "It was as near to an undisturbed forest you could have had at that time," Harrison says.

Now, after decades of logging, the park is a lonely island in a sea of oil palm plantations. The road to the park was paved in 1987, easing access by tourists and nearby residents of Miri, the center of Borneo's petroleum industry. Its 6952 hectares contain waterfalls and sparkling pools. The trees growing on the clay soil are gargantuan, dwarfing those of the Amazon. "It's like being in a gothic cathedral," says Peter Ashton, a retired botanist who set up research plots there in 1964. The warm, moist air, smelling a bit like cigars, buzzes with insects. To many, especially newcomers, the park looks pristine.

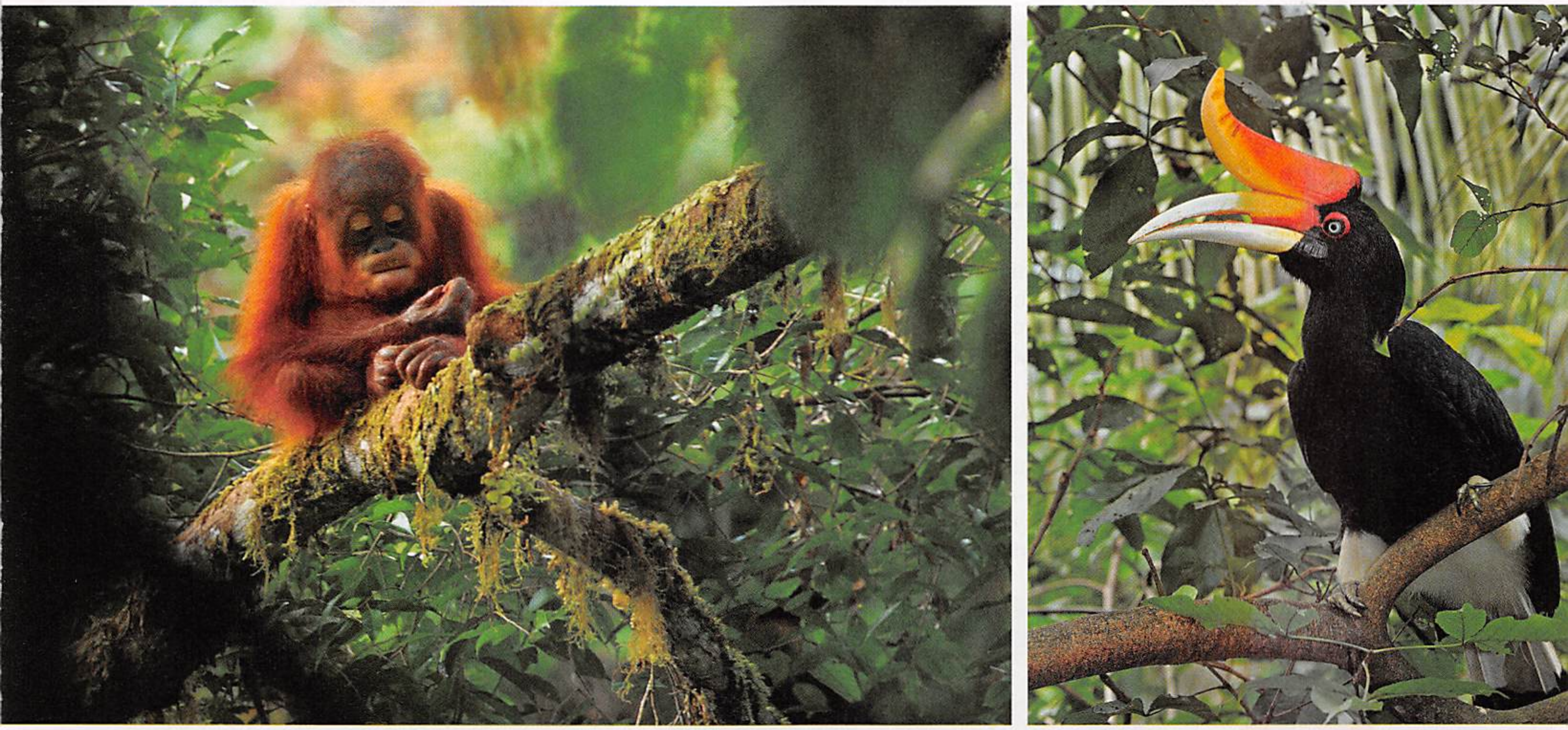
But the forest is not what it was. The helmeted hornbill was long gone by the time Harrison arrived in 1994 to start his doctoral research on fig trees. And other species, such as the swan-sized rhinoceros hornbill and the gibbon, seemed rarer than they should have been. "I felt there was something wrong," Harrison recalls. It wasn't a big leap to suspect hunting. In addition to hearing the blasts of shotguns, he came across snares and evidence of hunters' camps.

In the evening, when Harrison and his colleagues drove to Miri, they would sometimes see sport hunters parked in large four-wheel-drive vehicles, shining spotlights into the forest to catch reflections of wild eyes. In the city, curio shops sold earrings made from hornbill casques. Vendors in the open-air market hawked small mammals in cages, ready to be cooked or taken home as pets.

Years later, Harrison decided to pull together the data about the decline in animal species. He went through previous records, interviewed older researchers, and walked his own surveys. The situation appeared grim: A camera-trap survey in 2004 detected only one bearded pig in 8 months. And when Harrison spent 6 months in the park in 2007, he couldn't find a single animal that weighed more than a kilogram. Not all animals are gone; small birds, rodents, and geckos persist, for example.

Harrison decided to explore the consequences of these losses, taking advantage of the data that the Smithsonian has collected at Lambir since 1991. Every 5 years, researchers and staff members spend about 9 months measuring each and every one of the 370,000 trees and saplings in a

PHOTOS: CHRISTIAN ZIEGLER (3)



Orangutans and rhinoceros hornbills are gone from Lambir, leaving only small creatures such as geckos (*lower left*).

52-hectare plot. Harrison and colleagues pored over books and museum records to figure out how these trees disperse their seeds. Then they analyzed how common each species was across the plant surveys.

The changes were dramatic. For all species, they found that the density of the saplings had increased by 25%, likely from the paucity of deer and other herbivores that thin new growth. The higher density of saplings could be a problem, as overcrowding can promote the spread of plant diseases. Even though there were more saplings, their diversity has fallen by 1.9% since 1992, they reported online in March 2013 in *Ecology Letters*.

This is large and rapid change for a rainforest, Harrison says, and it's due to the loss of seed dispersal by animals. Another impact: Compared with wind-dispersed species, saplings of fruit trees became more clustered around the adults, especially tightly so for species with large fruit. Eventually, the distribution of adult trees may shift, and some species could disappear.

A FIRM CONCLUSION ABOUT THE FATE of the forest is still elusive, as much is unknown about the demography of trees. "It can be overwhelming to go into a rainforest and try to understand anything," Brodie says. "There's just so much going on." Even Redford, who in 2011 established Archipelago Consulting in Portland, Maine, doesn't want to oversell the risk. "It's my suspicion that there is a lot more hype than data about how everything goes to hell once the big animals are gone," he says. It could be that small, reclusive animals will take over the role of dispersing seeds, for example.

Lisa Curran of Stanford University, an anthropologist who studies land use change and biodiversity in Borneo, even questions how big a role hunting has played in Lambir's loss of fauna. The park may be simply too small to support many large animals, she says. And because it's surrounded by plantations, animals emigrating from other areas can't easily replenish the population.

Some officials and activists in various parts of Borneo are nevertheless taking action against overhunting and illegal trade, with mixed success. Enforcing hunting bans can be a challenge. This past December, wildlife rangers raided an open-air market in the state of Sabah. They confiscated 160 kilograms of unlicensed meat from sambar and barking deer. Angry villagers then hurled stones and machetes, damaging vehicles and injuring an officer. Many conservation groups shy away from confronting overhunting, because they don't want to be seen as hurting local livelihoods.

But some groups are helping head off poaching and illegal logging. For example, staff with the HUTAN-Kinabatangan Orang-utan Conservation Project patrol part of a 26,000-hectare wildlife sanctuary in northeast Borneo. And some local communities have stepped up as well. Sungai Wain Protection Forest, an upland reserve on the east side of Borneo, was protected after the nearby city of Balikpapan realized its importance for providing water for the local petroleum refinery. It retains abundant wildlife, including many rare birds and mammals. "You don't need a really great forest," Harrison says. "What you need is protection from hunting."

As for Lambir, many think the outlook is gloomy, at least in the short term. But not long ago, rhinoceros hornbills—the state emblem of Sarawak—were spotted in a nearby park. "I think the significance is huge," Harrison says. "It suggests that if hunting is controlled, at least some species like the hornbills that can fly substantial distances could reestablish." The hornbills might become an emblem of hope, a testament to the capacity of nature to heal. ■

PHOTOS: (LEFT TO RIGHT) CHRISTIAN ZIEGLER; © THOMAS MARENT/MINDEN PICTURES/CORBIS

OPINION

An animal-rich future

The rate at which animals are vanishing from this planet is one of the signatures of this age, as sure a sign of human dominance as our impact on Earth's nitrogen, phosphorus, and carbon cycles. This disappearance of animals from the world's ecosystems is generally a by-product of human activity, not an intentional act. Animals do matter to people, but on balance, they matter less than food, jobs, energy, money, and development. As long as we continue to view animals in ecosystems as irrelevant to these basic demands, animals will lose.

If we accept that humans now shape the future of this planet, the future for existing and extirpated fauna will depend on vision as much as on science. What type of world do we want to pass on, and what role do animals have in that world?

A responsible vision must include the dominating influence of people on the planet. The near future is likely to include 8 to 9 billion people, 3 billion more people in the middle class, a doubling of the terrestrial footprint of cities, and a transformation of global food and energy systems. A vision that includes a vital future for animals requires thinking beyond "restoration" and even beyond "rewilding." To maintain the animal diversity of the present and restore the animal abundance of the past, we must place animals squarely in a world where human systems are integrated with functioning natural systems. We cannot focus on recreating the ecosystems of the past—our impacts are making this untenable in most places—but we must not give up on nature or wildness, either.

> ***"A vision that includes a vital future for animals requires thinking beyond 'restoration' and even beyond 'rewilding.'"***

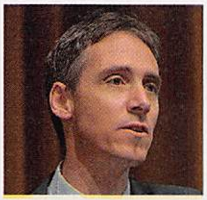
To begin, we need to recognize the importance of animals in all socioecological systems, pristine and human-dominated, terrestrial and marine. When we consider the benefits of a world rich with animals, we should shift some of our focus to systems where many people depend on animals. As an example, 2.6 billion people depend on ocean animals for protein.

In addition, we will have to grapple with tricky issues, such as those associated with the management of novel ecosystems and species substitution. There is also the potential application of synthetic biology, but the positive and negative impacts must be fully explored. How do we reduce the risks of ecosystem-level experimentation? When considering whether to introduce a new species into a system to replace the loss of another, for example, we must weigh the consequences of no intervention against the consequences of actions taken to recover ecological function. This is not a trivial exercise, as the ecological, economic, and cultural impact of an animal within an ecosystem is dynamic, and often obscured by complex ecological dynamics, shifting baselines (what a natural system "should" be like), and changing cultural norms. A full understanding of the relevant natural history, as well as the values of the people with a stake in the outcome, will be essential to any path forward. This is not entirely new territory, as our successes and failures in biological control can serve as a guide.

We cannot give up on the difficult species—the species that do not coexist well with people and require large areas for their survival. Conservation of these animals will hinge on recognition of their full value—ecological, economic, and cultural—by those with the power to protect them. A country with many large animals has as much right to development as a country without, and thus the global community must find pathways that would allow communities sharing their land with these animals to benefit from their presence.

Defaunation is a global issue. A world without animals represents a loss to humanity as much as a loss to ecology.

– Joshua J. Tewksbury and Haldre S. Rogers



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PHOTOS: (LEFT) PAUL ROLLISON/FLICKR; (TOP RIGHT) NEXUS 2014/WATER FOOD CLIMATE AND ENERGY CONFERENCE; (BOTTOM RIGHT) SUSANNAH BARR

REVIEW

Defaunation in the Anthropocene

Rodolfo Dirzo,[1]* Hillary S. Young,[2] Mauro Galetti,[3] Gerardo Ceballos,[4] Nick J. B. Isaac,[5] Ben Collen[6]

We live amid a global wave of anthropogenically driven biodiversity loss: species and population extirpations and, critically, declines in local species abundance. Particularly, human impacts on animal biodiversity are an under-recognized form of global environmental change. Among terrestrial vertebrates, 322 species have become extinct since 1500, and populations of the remaining species show 25% average decline in abundance. Invertebrate patterns are equally dire: 67% of monitored populations show 45% mean abundance decline. Such animal declines will cascade onto ecosystem functioning and human well-being. Much remains unknown about this "Anthropocene defaunation"; these knowledge gaps hinder our capacity to predict and limit defaunation impacts. Clearly, however, defaunation is both a pervasive component of the planet's sixth mass extinction and also a major driver of global ecological change.

In the past 500 years, humans have triggered a wave of extinction, threat, and local population declines that may be comparable in both rate and magnitude with the five previous mass extinctions of Earth's history (*1*). Similar to other mass extinction events, the effects of this "sixth extinction wave" extend across taxonomic groups, but they are also selective, with some taxonomic groups and regions being particularly affected (*2*). Here, we review the patterns and consequences of contemporary anthropogenic impact on terrestrial animals. We aim to portray the scope and nature of declines of both species and abundance of individuals and examine the consequences of these declines. So profound is this problem that we have applied the term "defaunation" to describe it. This recent pulse of animal loss, hereafter referred to as the Anthropocene defaunation, is not only a conspicuous consequence of human impacts on the planet but also a primary driver of global environmental change in its own right. In comparison, we highlight the profound ecological impacts of the much more limited extinctions, predominantly of larger vertebrates, that occurred during the end of the last Ice Age. These extinctions altered ecosystem processes and disturbance regimes at continental scales, triggering cascades of extinction thought to still reverberate today (*3*, *4*).

The term defaunation, used to denote the loss of both species and populations of wildlife (*5*), as well as local declines in abundance of individuals, needs to be considered in the same sense as deforestation, a term that is now readily recognized and influential in focusing scientific and general public attention on biodiversity issues (*5*). However, although remote sensing technology provides rigorous quantitative information and compelling images of the magnitude, rapidity, and extent of patterns of deforestation, defaunation remains a largely cryptic phenomenon. It can occur even in large protected habitats (*6*), and yet, some animal species are able to persist in highly modified habitats, making it difficult to quantify without intensive surveys.

Analyses of the impacts of global biodiversity loss typically base their conclusions on data derived from species extinctions (*1*, *7*, *8*), and typically, evaluations of the effects of biodiversity loss draw heavily from small-scale manipulations of plants and small sedentary consumers (*9*). Both of these approaches likely underestimate the full impacts of biodiversity loss. Although species extinctions are of great evolutionary importance, declines in the number of individuals in local populations and changes in the composition of species in a community will generally cause greater immediate impacts on ecosystem function (*8*, *10*). Moreover, whereas the extinction of a species often proceeds slowly (*11*), abundance declines within populations to functionally extinct levels can occur rapidly (*2*, *12*). Actual extinction events are also hard to discern, and International Union for Conservation of Nature (IUCN) threat categories amalgamate symptoms of high risk, conflating declining population and small populations so that counts of threatened species do not necessarily translate into extinction risk, much less ecological impact (*13*). Although the magnitude and frequency of extinction events remain a potent way of communicating conservation issues, they are only a small part of the actual loss of biodiversity (*14*).

The Anthropocene defaunation process

Defaunation: A pervasive phenomenon

Of a conservatively estimated 5 million to 9 million animal species on the planet, we are likely losing ~11,000 to 58,000 species annually (*15*, *16*). However, this does not consider population extirpations and declines in animal abundance within populations.

Across vertebrates, 16 to 33% of all species are estimated to be globally threatened or endangered (*17*, *18*), and at least 322 vertebrate species have become extinct since 1500 (a date representative of onset of the recent wave of extinction; formal definition of the start of the Anthropocene is still being debated) (table S1) (*17*, *19*, *20*). From an abundance perspective, vertebrate data indicate a mean decline of 28% in number of individuals across species in the past four decades (fig. S1, A and B) (*14*, *21*, *22*), with populations of many iconic species such as elephant rapidly declining toward extinction (*19*).

Loss of invertebrate biodiversity has received much less attention, and data are extremely limited. However, data suggest that the rates of decline in numbers, species extinction, and range contraction among terrestrial invertebrates are at least as severe as among vertebrates (*23*, *24*). Although less than 1% of the 1.4 million described invertebrate species have been assessed for threat by the IUCN, of those assessed, ~40% are considered threatened (*17*, *23*, *24*). Similarly, IUCN data on the status of 203 insect species in five orders reveal vastly more species in decline than increasing (Fig. 1A). Likewise, for the invertebrates for which trends have been evaluated in Europe, there is a much higher proportion of species with numbers decreasing rather than increasing (*23*). Long-term distribution data on moths and four other insect orders in the UK show that a substantial proportion of species have experienced severe range declines in the past several decades (Fig. 1B) (*19*, *25*). Globally, long-term monitoring data on a sample of 452 invertebrate species indicate that there has been an overall decline in abundance of individuals since 1970 (Fig. 1C) (*19*). Focusing on just the Lepidoptera (butterflies and moths), for which the best data are available, there is strong evidence of declines in abundance globally (35% over 40 years) (Fig. 1C). Non-Lepidopteran invertebrates declined considerably more, indicating that estimates of decline of invertebrates based on Lepidoptera data alone are conservative (Fig. 1C) (*19*). Likewise, among pairs of disturbed and undisturbed sites globally, Lepidopteran species richness is on average 7.6 times higher in undisturbed than disturbed sites, and total abundance is 1.6 times greater (Fig. 1D) (*19*).

Patterns of defaunation

Although we are beginning to understand the patterns of species loss, we still have a limited understanding of how compositional changes in communities after defaunation and associated disturbance will affect phylogenetic community structure and phylogenetic diversity (*26*). Certain lineages appear to be particularly susceptible to human impact. For instance, among vertebrates, more amphibians (41%) are currently considered

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threatened than birds (17%), with mammals and reptiles experiencing intermediate threat levels (27).

Although defaunation is a global pattern, geographic distribution patterns are also decidedly nonrandom (28). In our evaluation of mammals (1437 species) and birds (4263 species), the number of species per 10,000 km^2 in decline (IUCN population status "decreasing") varied across regions from a few to 75 in mammals and 125 in birds (Fig. 2), with highest numbers in tropical regions. These trends persist even after factoring in the greater species diversity of the tropics (29, 30). Similarly, most of 177 mammal species have lost more than 50% of their range (9).

The use of statistical models based on life history characteristics (traits) has gained traction as a way to understand patterns of biodiversity loss (31). For many vertebrates, and a few invertebrates, there has been excellent research examining the extent to which such characteristics correlate with threat status and extinction risk (32–34). For example, small geographic range size, low reproductive rates, large home range size, and large body size recur across many studies and diverse taxa as key predictors of extinction risk, at least among vertebrates. However, these "extinction models" have made little impact on conservation management, in part because trait correlations are often idiosyncratic and context-dependent (31).

We are increasingly aware that trait correlations are generally weaker at the population level than at the global scale (31, 35). Similarly, we now recognize that extinction risk is often a synergistic function of both intrinsic species traits and the nature of threat (32, 34–37). For example, large body size is more important for predicting risk in island birds than mainland birds (34) and for

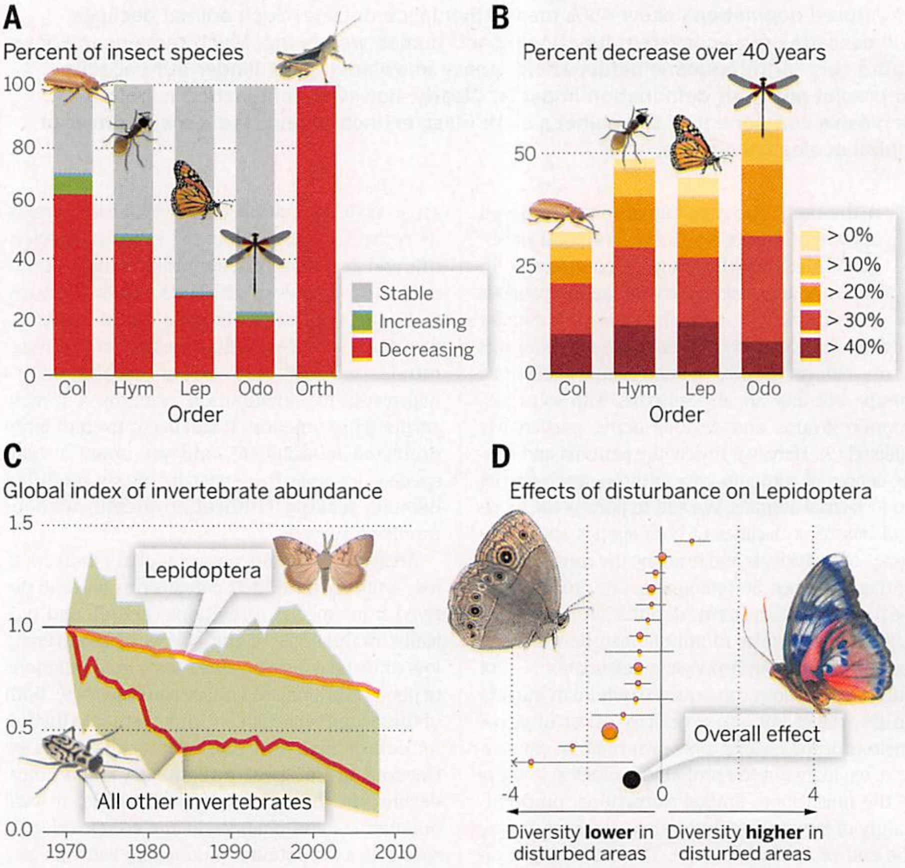

Fig. 1. Evidence of declines in invertebrate abundance. (**A**) Of all insects with IUCN-documented population trends, 33% are declining, with strong variation among orders (19). (**B**) Trends among UK insects (with colors indicating percent decrease over 40 years) show 30 to 60% of species per order have declining ranges (19). (**C**) Globally, a compiled index of all invertebrate population declines over the past 40 years shows an overall 45% decline, although decline for Lepidoptera is less severe than for other taxa (19). (**D**) A meta-analysis of effects of anthropogenic disturbance on Lepidoptera, the best-studied invertebrate taxon, shows considerable overall declines in diversity (19).

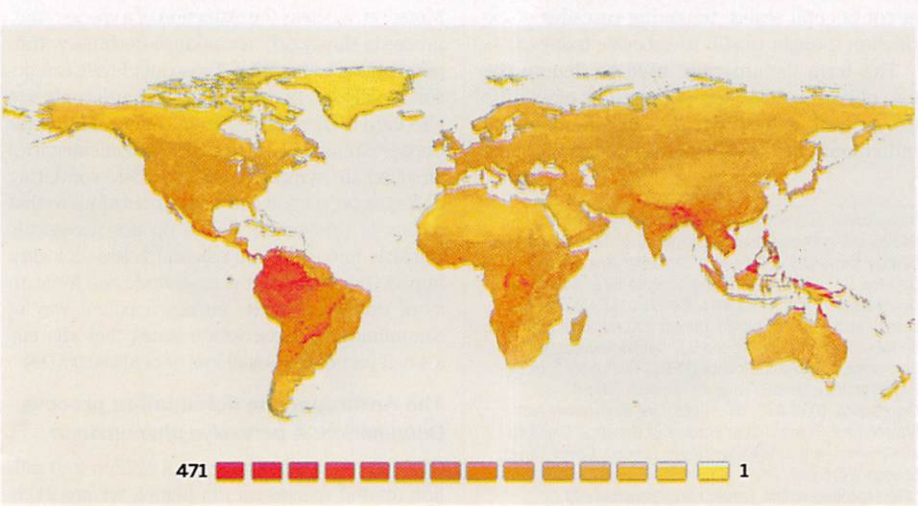

Fig. 2. Global population declines in mammals and birds. The number of species defined by IUCN as currently experiencing decline, represented in numbers of individuals per 10,000 km^2 for mammals and birds, shows profound impacts of defaunation across the globe.

tropical mammals than for temperate ones (*36*). However, increasingly sophisticated approaches help to predict which species are likely to be at risk and to map latent extinction risk (*38*), holding great promise both for managing defaunation and identifying likely patterns of ecological impact (*39*). For instance, large-bodied animals with large home ranges often play specific roles in connecting ecosystems and transferring energy between them (*40*). Similarly, species with life history characteristics that make them robust to disturbance may be particularly competent at carrying zoonotic disease and therefore especially important at driving disease emergence (*41, 42*).

The relatively well-established pattern of correlation between body size and risk in mammals creates a predictable size-selective defaunation gradient (Fig. 3) (*19, 36, 43*). For instance, there are strong differences in body mass distributions among mammals that (i) became extinct in the Pleistocene [<50,000 years before the present (B.P.)], (ii) went recently extinct (<5000 years B.P., Late Holocene and Anthropocene), (iii) are currently threatened with extinction (IUCN category "threatened" and above), and (iv) extant species not currently threatened (Fig. 3), all showing greater vulnerability of larger-bodied species. The myriad consequences of such differential defaunation have been quantified via the experimental manipulation of the large wildlife in an African savanna (Fig. 4 and table S3), revealing substantial effects on biodiversity, ecological processes, and ecosystem functioning.

Multiple unaddressed drivers of defaunation

The long-established major proximate drivers of wildlife population decline and extinction in terrestrial ecosystems—namely, overexploitation, habitat destruction, and impacts from invasive species—remain pervasive (*18*). None of these major drivers have been effectively mitigated at the global scale (*14, 18*). Rather, all show increasing trajectories in recent decades (*14*). Moreover, several newer threats have recently emerged, most notably anthropogenic climate disruption, which will likely soon compete with habitat loss as the most important driver of defaunation (*44*). For example, ~20% of the landbirds in the western hemisphere are predicted to go extinct because of climate change by 2100 (*45*). Disease, primarily involving human introduced pathogens, is also a major and growing threat (*46*).

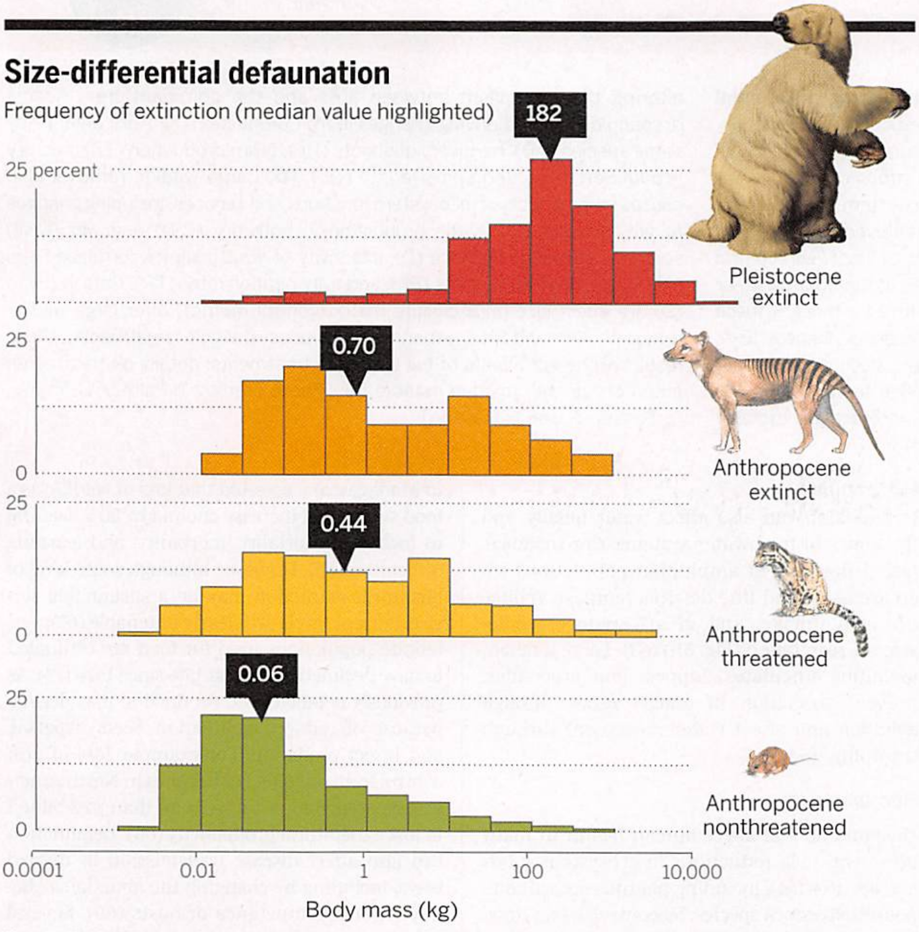

Fig. 3. Extinction and endangerment vary with body size. Comparing data on body size of all animals that are known to have gone extinct in Pleistocene or are recently extinct (<5000 years B.P.) shows selective impact on animals with larger body sizes (median values denoted with black arrow). Differences in body masses between distributions of currently threatened and nonthreatened species suggest ongoing patterns of size-differential defaunation (Kolmogorv-Smirnov test, $K = 1.3$, $P < 0.0001$) (*19*). [Animal image credits: giant sloth, C. Buell; others, D. Orr]

Although most declining species are affected by multiple stressors, we still have a poor understanding of the complex ways in which these drivers interact and of feedback loops that may exist (*7, 11*). Several examples of interactions are already well documented. For example, fragmentation increases accessibility to humans, compounding threats of reduced habitat and exploitation (*47*). Similarly, land-use change is making it difficult for animals to expand their distributions into areas made suitable by climate change (*25, 48*). Feedbacks among these and other drivers seem more likely to amplify the effects of defaunation than to dampen them (*11*).

Consequences of defaunation

Because animal loss represents a major change in biodiversity, it is likely to have important effects on ecosystem functioning. A recent meta-analyses of biodiversity-ecosystem function studies suggests that the impact of biodiversity losses on ecosystem functions is comparable in scale with that of other global changes (such as pollution and nutrient deposition) (*9*). However, most efforts to quantify this relationship have focused largely on effects of reduced producer diversity, which may typically have much lower functional impacts than does consumer loss (*49, 50*). Efforts to quantify effects of changes in animal diversity on ecosystem function, particularly terrestrial vertebrate diversity, remain more limited (*19, 51*).

Impacts on ecosystem functions and services

We examined several ecosystem functions and services for which the impacts of defaunation have been documented that are either a direct result of anthropogenic extirpation of service-providing animals or occur indirectly through cascading effects (Fig. 5).

Pollination

Insect pollination, needed for 75% of all the world's food crops, is estimated to be worth ~10% of the economic value of the world's entire food supply (*52*). Pollinators appear to be strongly declining globally in both abundance and diversity (*53*). Declines in insect pollinator diversity in Northern Europe in the past 30 years have, for example, been linked to strong declines in relative abundance of plant species reliant on those pollinators (*54*). Similarly, declines in bird pollinators in New Zealand led to strong pollen limitation, ultimately reducing seed production and population regeneration (Fig. 5H) (*55*).

Pest control

Observational and experimental studies show that declines in small vertebrates frequently lead to multitrophic cascades, affecting herbivore abundance, plant damage, and plant biomass (*56*).

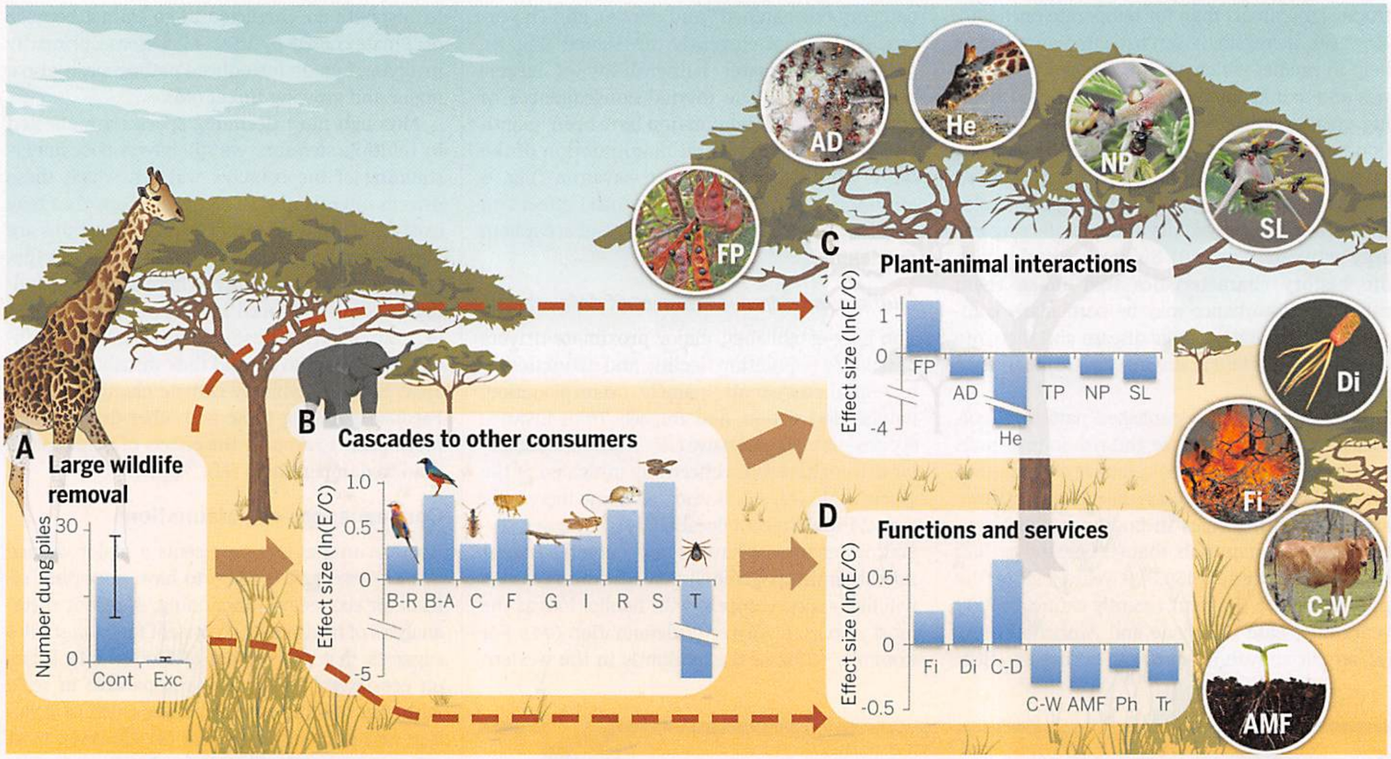

Fig. 4. Results of experimental manipulation simulating differential defaunation. As a model of the pervasive ecosystem effects of defaunation, in just one site (the Kenya Long Term Exclosure Experiment), the effects of selective large-wildlife (species >15 kg) removal drive strong cascading consequences on other taxa, on interactions, and on ecosystem services (*81*). (**A**) In this experiment, large wildlife are effectively removed by fences, as evidenced by mean difference in dung abundance (±1 SE) between control and exclosure plots. (**B**) This removal leads to changes in the abundance or diversity of other consumer groups. Effects were positive for most of these small-bodied consumers—including birds (B-R, bird species richness; B-A, granivorous bird abundance), Coleoptera (C), fleas (F), geckos (G), insect biomass (I), rodents (R), and snakes (S)—but negative for ticks (T). (**C**) Experimental defaunation also affects plant-animal interactions, notably altering the mutualism between ants and the dominant tree, *Acacia drepanolobium* and driving changes in fruit production (FP), ant defense by some species (AD), herbivory of shoots (He), thorn production (TP), nectary production (NP), and spine length (SL). (**D**) Large-wildlife removal also causes major effects on ecosystem functions and services, including changes to fire intensity (Fi), cattle production in both dry (C-D) and wet (C-W) seasons, disease prevalence (D), infectivity of arbuscular mycorrhizae fungi (AMF), photosynthetic rates (Ph), and transpiration rates (TR). Data in (B) to (D) are effect size [ln(exclosure metric/control metric)] after large-wildlife removal. Although this experiment includes multiple treatments, these results represent effects of full exclosure treatments; details on treatments and metrics are provided in table S3. [Photo credits: T. Palmer, H. Young, R. Sensenig, and L. Basson]

Cumulatively, these ubiquitous small-predator trophic cascades can have enormous impacts on a wide variety of ecological functions, including food production. For example, arthropod pests are responsible for 8 to 15% of the losses in most major food crops. Without natural biological control, this value could increase up to 37% (*57*). In the United States alone, the value of pest control by native predators is estimated at $4.5 billion annually (*58*).

Nutrient cycling and decomposition

The diversity of invertebrate communities, particularly their functional diversity, can have dramatic impacts on decomposition rates and nutrient cycling (*59*–*61*). Declines in mobile species that move nutrients long distances have been shown to greatly affect patterns of nutrient distribution and cycling (*62*). Among large animals, Pleistocene extinctions are thought to have changed influx of the major limiting nutrient, phosphorus, in the Amazon by ~98%, with implications persisting today (*3*).

Water quality

Defaunation can also affect water quality and dynamics of freshwater systems. For instance, global declines in amphibian populations increase algae and fine detritus biomass, reduce nitrogen uptake, and greatly reduce whole-stream respiration (Fig. 5E) (*63*). Large animals, including ungulates, hippos, and crocodiles, prevent formation of anoxic zones through agitation and affect water movement through trampling (*64*).

Human health

Defaunation will affect human health in many other ways via reductions in ecosystem goods and services (*65*), including pharmaceutical compounds, livestock species, biocontrol agents, food resources, and disease regulation. Between 23 and 36% of all birds, mammals, and amphibians used for food or medicine are now threatened with extinction (*14*). In many parts of the world, wild-animal food sources are a critical part of the diet, particularly for the poor. One recent study in Madagascar suggested that loss of wildlife as a food source will increase anemia by 30%, leading to increased mortality, morbidity, and learning difficulties (*66*). However, although some level of bushmeat extraction may be a sustainable service, current levels are clearly untenable (*67*); vertebrate populations used for food are estimated to have declined by at least 15% since 1970 (*14*). As previously detailed, food production may decline because of reduced pollination, seed dispersal, and insect predation. For example, loss of pest control from ongoing bat declines in North America are predicted to cause more than $22 billion in lost agricultural productivity (*68*). Defaunation can also affect disease transmission in myriad ways, including by changing the abundance, behavior, and competence of hosts (*69*). Several studies demonstrate increases in disease prevalence after defaunation (*41*, *42*, *70*). However, the impacts of defaunation on disease are far from straightforward (*71*), and few major human pathogens seem to fit the criteria that would make such a relationship pervasive (*71*). More work is

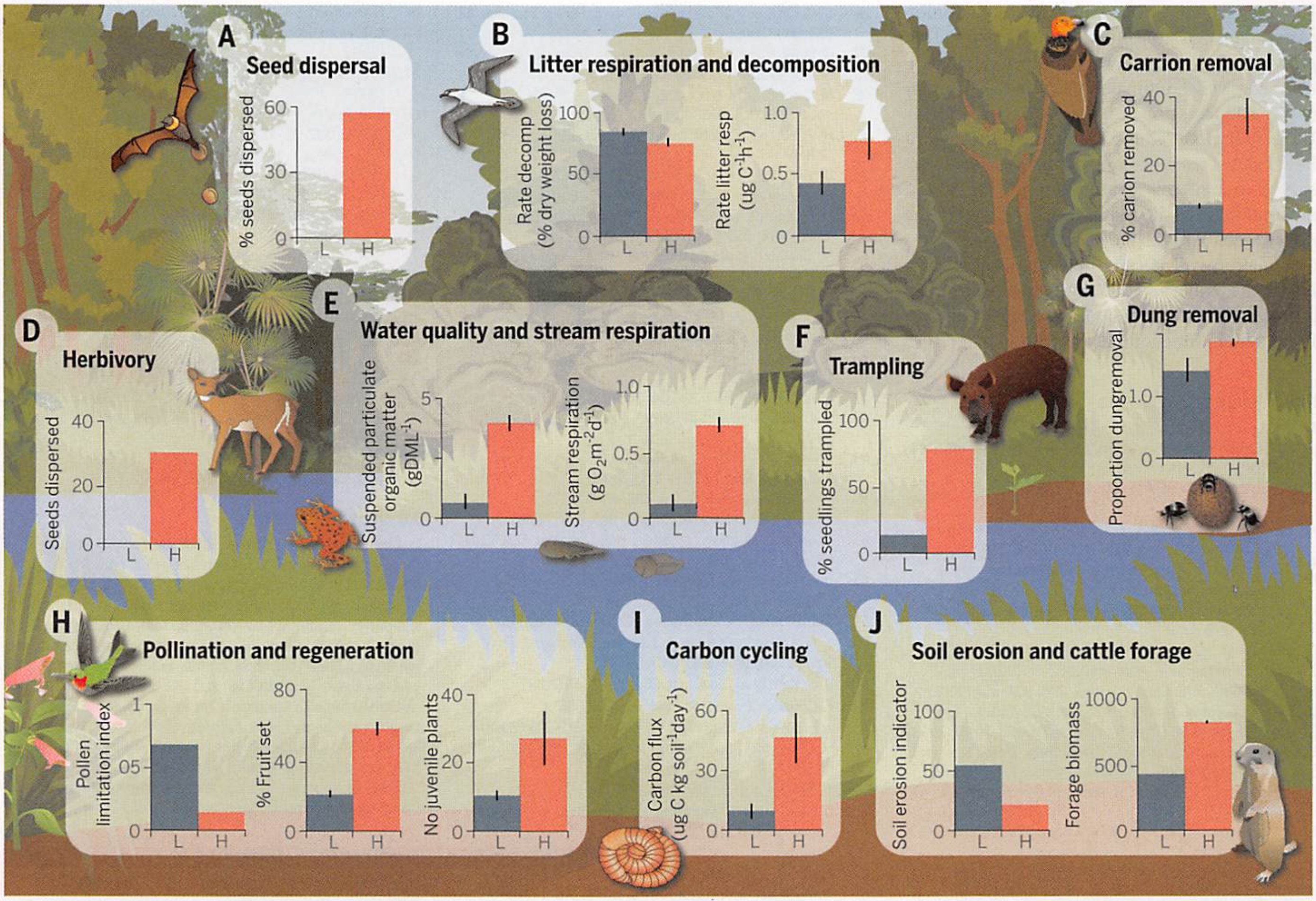

Fig. 5. Consequences of defaunation on ecosystem functioning and services. Changes in animal abundance from low (blue, L) to high (red, H) within a region have been shown to affect a wide range of ecological processes and services (*19*), including (**A**) seed dispersal (flying foxes), (**B**) litter respiration and decomposition (seabirds), (**C**) carrion removal (vultures), (**D**) herbivory (large mammals), (**E**) water quality and stream restoration (amphibians), (**F**) trampling of seedlings (mammals), (**G**) dung removal (dung beetles), (**H**) pollination and plant recruitment (birds), (**I**) carbon cycling (nematodes), and (**J**) soil erosion and cattle fodder (prairie dogs).

urgently needed to understand the mechanisms and context-dependence of defaunation-disease relationships in order to identify how defaunation will affect human disease.

Impacts on evolutionary patterns

The effects of defaunation appear not to be merely proximally important to the ecology of affected species and systems but also to have evolutionary consequences. Several studies have detected rapid evolutionary changes in morphology or life history of short-lived organisms (*72*) or human-exploited species (*73*). Because defaunation of vertebrates often selects on body size, and smaller individuals are often unable to replace fully the ecological services their larger counterparts provide, there is strong potential for cascading effects that result from changing body-size distributions (*74*). Still poorly studied are the indirect evolutionary effects of defaunation on other species, not directly affected by human defaunation. For example, changes in abundance or composition of pollinators or seed dispersers can cause rapid evolution in plant mating systems and seed morphology (*75*, *76*). There is a pressing need to understand the ubiquity and importance of such "evolutionary cascades" (*77*).

Synthesis and ways forward

This Review indicates that a widespread and pervasive defaunation crisis, with far-reaching consequences, is upon us. These consequences have been better recognized in the case of large mammals (*78*, *79*). Yet, defaunation is affecting smaller and less charismatic fauna in similar ways. Ongoing declines in populations of animals such as nematodes, beetles, or bats are considerably less evident to humans yet arguably are more functionally important. Improved monitoring and study of such taxa, particularly invertebrates, will be critical to advance our understanding of defaunation. Ironically, the cryptic nature of defaunation has strong potential to soon become very noncryptic, rivaling the impact of many other forms of global change in terms of loss of ecosystem services essential for human well-being.

Although extinction remains an important evolutionary impact on our planet and is a powerful social conservation motivator, we emphasize that defaunation is about much more than species loss. Indeed, the effects of defaunation will be much less about the loss of absolute diversity than about local shifts in species compositions and functional groups within a community (*80*). Focusing on changes in diversity metrics is thus unlikely to be effective for maintaining adequate ecological function, and we need to focus on predicting the systematic patterns of winners and losers in the Anthropocene and identify the traits that characterize them because this will provide information on the patterns and the links to function that we can then act on.

Cumulatively, systematic defaunation clearly threatens to fundamentally alter basic ecological functions and is contributing to push us toward global-scale "tipping points" from which we may not be able to return (*7*). Yet despite the dramatic rates of defaunation currently being observed, there is still much opportunity for action. We must more meaningfully address immediate drivers of defaunation: Mitigation of animal overexploitation and land-use change are two feasible, immediate actions that can be taken (*44*). These actions can also buy necessary time to address the other critical driver, anthropogenic climate disruption.

However, we must also address the often nonlinear impacts of continued human population growth and increasingly uneven per capita consumption, which ultimately drive all these threats (while still fostering poverty alleviation efforts). Ultimately, both reduced and more evenly distributed global resource consumption will be necessary to sustainably change ongoing trends in defaunation and, hopefully, eventually open the door to refaunation. If unchecked, Anthropocene defaunation will become not only a characteristic of the planet's sixth mass extinction, but also a driver of fundamental global transformations in ecosystem functioning.

REFERENCES AND NOTES

1. A. D. Barnosky *et al.*, *Nature* **471**, 51–57 (2011).
2. M. Cardillo *et al.*, *Philos. R. Soc. London B. Biol.* **275**, 1441–1448 (2008).
3. C. E. Doughty, A. Wolf, Y. Malhi, *Nat. Geosci.* **6**, 761–764 (2013).
4. J. L. Gill, J. W. Williams, S. T. Jackson, K. B. Lininger, G. S. Robinson, *Science* **326**, 1100–1103 (2009).
5. R. Dirzo, in *Global Biodiversity in a Changing Environment: Scenarios for the 21st Century*, F. S. Chapin, O. E. Sala, E. Huber-Sannwald, Ed. (Springer, New York, 2001), pp. 251–276.
6. C. A. Peres, E. Palacios, *Biotropica* **39**, 304–315 (2007).
7. A. D. Barnosky *et al.*, *Nature* **486**, 52–58 (2012).
8. G. Ceballos, P. R. Ehrlich, *Science* **296**, 904–907 (2002).
9. D. U. Hooper *et al.*, *Nature* **486**, 105–108 (2012).
10. K. J. Gaston, R. A. Fuller, *Trends Ecol. Evol.* **23**, 14–19 (2008).
11. B. W. Brook, N. S. Sodhi, C. J. Bradshaw, *Trends Ecol. Evol.* **23**, 453–460 (2008).
12. T. Säterberg, S. Sellman, B. Ebenman, *Nature* **499**, 468–470 (2013).
13. A. Ø. Mooers, D. P. Faith, W. P. Maddison, *PLOS One* **3**, e3700 (2008).
14. S. H. M. Butchart *et al.*, *Science* **328**, 1164–1168 (2010).
15. C. Mora, A. Rollo, D. P. Tittensor, *Science* **443**, 295 (2013).
16. B. R. Scheffers, L. N. Joppa, S. L. Pimm, W. F. Laurance, *Trends Ecol. Evol.* **27**, 501–510 (2012).
17. IUCN, The IUCN Red List of Threatened Species (2013); available at www.iucnredlist.org.
18. M. Hoffmann *et al.*, *Science* **330**, 1503–1509 (2010).
19. Materials and methods are available as supplementary materials on *Science* Online.
20. G. Ceballos, A. García, P. R. Ehrlich, *J. Cosmol.* **8**, 1821 (2010).
21. B. Collen *et al.*, *Conserv. Biol.* **23**, 317–327 (2009).
22. Living Planet Rport, "Living Planet Report 2012: Biodiversity, biocapacity and better choices" (WWF, Zoological Society of London, Global Footprint Network, European Space Agency, London, 2012).
23. B. Collen, M. Böhm, R. Kemp, J. Baillie, *Spineless: Status and Trends of the World's Invertebrates* (Zoological Society of London, London, 2012).
24. B. Collen, J. E. M. Baillie, *Science* **329**, 140 (2010).
25. R. Fox *et al.*, *J. Appl. Ecol.* 10.1111/1365-2664.12256 (2014).
26. J. Cavender-Bares, K. H. Kozak, P. V. Fine, S. W. Kembel, *Ecol. Lett.* **12**, 693–715 (2009).
27. J. Schipper *et al.*, *Science* **322**, 225–230 (2008).
28. S. L. Pimm *et al.*, *Science* **344**, 1246752 (2014).
29. R. Dirzo, P. H. Raven, *Annu. Rev. Environ. Resour.* **28**, 137–167 (2003).
30. C. N. Jenkins, S. L. Pimm, L. N. Joppa, *Proc. Natl. Acad. Sci. U.S.A.* **110**, E2602–E2610 (2013).
31. M. Cardillo, E. Meijaard, *Trends Ecol. Evol.* **27**, 167–171 (2012).
32. A. D. Davidson, M. J. Hamilton, A. G. Boyer, J. H. Brown, G. Ceballos, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10702–10705 (2009).
33. E. Öckinger *et al.*, *Ecol. Lett.* **13**, 969–979 (2010).
34. T. M. Lee, W. Jetz, *Philos. R. Soc. London B. Biol.* **278**, 1329–1338 (2011).
35. M. J. Pocock, P. Roy, *Philos. R. Soc. London B. Biol.* **278**, 1532–1538 (2011).
36. S. A. Fritz, O. R. P. Bininda-Emonds, A. Purvis, *Ecol. Lett.* **12**, 538–549 (2009).
37. G. Cowlishaw, R. A. Pettifor, N. J. Isaac, *Philos. R. Soc. London B. Biol.* **276**, 63–69 (2009).
38. M. Cardillo, G. M. Mace, J. L. Gittleman, A. Purvis, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 4157–4161 (2006).
39. H. Hillebrand, B. Matthiessen, *Ecol. Lett.* **12**, 1405–1419 (2009).
40. D. J. McCauley *et al.*, *Ecol. Appl.* **22**, 1711–1717 (2012).
41. F. Keesing *et al.*, *Nature* **468**, 647–652 (2010).
42. P. T. Johnson, D. L. Preston, J. T. Hoverman, K. L. Richgels, *Nature* **494**, 230–233 (2013).
43. M. Di Marco *et al.*, *Conserv. Biol.* 10.1111/cobi.12249 (2014).
44. O. E. Sala *et al.*, *Science* **287**, 1770–1774 (2000).
45. C. H. Sekercioglu, S. H. Schneider, J. P. Fay, S. R. Loarie, *Conserv. Biol.* **22**, 140–150 (2008).
46. K. F. Smith, D. F. Sax, K. D. Lafferty, *Conserv. Biol.* **20**, 1349–1357 (2006).
47. C. A. Peres, *Conserv. Biol.* **14**, 240–253 (2000).
48. S. T. Jackson, D. F. Sax, *Trends Ecol. Evol.* **25**, 153–160 (2010).
49. J. Reiss, J. R. Bridle, J. M. Montoya, G. Woodward, *Trends Ecol. Evol.* **24**, 505–514 (2009).
50. B. J. Cardinale *et al.*, *Nature* **486**, 59–67 (2012).
51. B. J. Cardinale *et al.*, *Nature* **443**, 989–992 (2006).
52. N. Gallai, J.-M. Salles, J. Settele, B. E. Vaissière, *Ecol. Econ.* **68**, 810–821 (2009).
53. S. G. Potts *et al.*, *Trends Ecol. Evol.* **25**, 345–353 (2010).
54. J. C. Biesmeijer *et al.*, *Science* **313**, 351–354 (2006).
55. S. H. Anderson, D. Kelly, J. J. Ladley, S. Molloy, J. Terry, *Science* **331**, 1068–1071 (2011).
56. D. S. Karp *et al.*, *Ecol. Lett.* **16**, 1339–1347 (2013).
57. E.-C. Oerke, *J. Agric. Sci.* **144**, 31–43 (2006).
58. J. E. Losey, M. Vaughan, *Bioscience* **56**, 311–323 (2006).
59. M. O. Gessner *et al.*, *Trends Ecol. Evol.* **25**, 372–380 (2010).
60. T. B. Atwood *et al.*, *Nat. Geosci.* **6**, 191–194 (2013).
61. D. Hawlena, M. S. Strickland, M. A. Bradford, O. J. Schmitz, *Science* **336**, 1434–1438 (2012).
62. H. S. Young, D. J. McCauley, R. B. Dunbar, R. Dirzo, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2072–2077 (2010).
63. M. Whiles *et al.*, *Ecosystems (N.Y.)* **16**, 146–157 (2013).
64. J. P. Wright, C. G. Jones, A. S. Flecker, *Oecologia* **132**, 96–101 (2002).
65. S. S. Myers *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18753–18760 (2013).
66. C. D. Golden, L. C. Fernald, J. S. Brashares, B. J. Rasolofoniaina, C. Kremen, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 19653–19656 (2011).
67. J. E. Fa, C. A. Peres, J. Meeuwig, *Conserv. Biol.* **16**, 232–237 (2002).
68. J. G. Boyles, P. M. Cryan, G. F. McCracken, T. H. Kunz, *Science* **332**, 41–42 (2011).
69. R. S. Ostfeld, F. Keesing, *Annu. Rev. Ecol. Evol. Syst.* **43**, 157–182 (2012).
70. H. S. Young *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* 10.1073/pnas.1404958111 (2014).
71. C. L. Wood *et al.*, *Ecology* **95**, 817–832 (2014).
72. S. R. Palumbi, *Science* **293**, 1786–1790 (2001).
73. C. T. Darimont *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 952–954 (2009).
74. M. Galetti, C. I. Donatti, M. A. Pizo, H. C. Giacomini, *Biotropica* **40**, 386–389 (2008).
75. S. A. Bodbyl Roels, J. K. Kelly, *Evolution* **65**, 2541–2552 (2011).
76. M. Galetti *et al.*, *Science* **340**, 1086–1090 (2013).
77. J. A. Estes, J. S. Brashares, M. E. Power, *Am. Nat.* **181** (suppl. 1), S76–S99 (2013).
78. J. A. Estes *et al.*, *Science* **333**, 301–306 (2011).
79. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/345/6195/401/suppl/DC1
Materials and Methods
Figs. S1 to S6
Tables S1 to S3
References (*80–167*)

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REVIEW

Reversing defaunation: Restoring species in a changing world

Philip J. Seddon,[1]* Christine J. Griffiths,[2] Pritpal S. Soorae,[3] Doug P. Armstrong[4]

The rate of biodiversity loss is not slowing despite global commitments, and the depletion of animal species can reduce the stability of ecological communities. Despite this continued loss, some substantial progress in reversing defaunation is being achieved through the intentional movement of animals to restore populations. We review the full spectrum of conservation translocations, from reinforcement and reintroduction to controversial conservation introductions that seek to restore populations outside their indigenous range or to introduce ecological replacements for extinct forms. We place the popular, but misunderstood, concept of rewilding within this framework and consider the future role of new technical developments such as de-extinction.

Recent analyses have shown that the rate of biodiversity loss has not slowed despite global commitments made through the 2002 Convention on Biological Diversity (*1*). Projected future extinction rates for terrestrial species might exceed current rates of extinction (*2*). A key component of biodiversity loss is defaunation, the loss or depletion of animal species from ecological communities (*3*, *4*). Such losses can reduce the stability of ecological communities (5), with cascading effects (3).

In situ conservation measures—including the creation and management of protected areas, increasing connectivity between wildlife populations, and reduction of the impacts of predation and hunting—can achieve some success where the amount of habitat remaining is sufficient for viable populations (6). Increasingly, however, more intensive forms of threatened species management are required to address local extinctions and impending threats to critical areas of habitat. Progress in reversing defaunation is emerging from conservation translocations—the intentional movement of animals to restore populations (7) (Fig. 1).

Population restoration: Reintroduction and reinforcement

The intentional movement and release of animals has occurred for millennia, but the use of translocations to address conservation objectives is barely 100 years old (8). In recent decades, there has been an increase in the number of species that are the focus of conservation translocations to restore and enhance populations; for vertebrates alone, at least 124 species were translocated during 1900-1992, and this had risen to 199 species by 1998 and to 424 species by 2005 (9). Two types of translocation for population restoration are recognized: (i) reinforcements, involving the release of an organism into an existing population of conspecifics to enhance population viability, and (ii) reintroductions, where the intent is to reestablish a population in an area after local extinction (7) (Fig. 1). The critical feature of these translocations is the release of animals into their indigenous range, the known or inferred distribution derived from historical records or other evidence (7).

Previous work has shown that conservation translocation projects, as with other types of conservation management, show a marked taxonomic bias toward birds (33% of projects, whereas birds make up 18% of species represented in nature) and mammals (41% of projects versus 8% of species), particularly the larger, more charismatic species, almost irrespective of the degree of threat or vulnerability (10). Recent data on reinforcements show that this bias toward birds and mammals is continuing (11). For conservation translocations in general, relatively few invertebrate, reptile, amphibian, or fish species are represented relative to their prevalence in nature (Fig. 2). The global distribution of species' translocations suggests a geographic bias also, with most activity in developed regions (Fig. 2).

The ultimate objective of any reintroduction is the establishment of a self-sustaining population and, using this definition, reviews of reintroduction outcomes have indicated generally low success rates (12), as low as 23% (13). Concern over high failure rates prompted analyses of the factors associated with translocation success. In 1989, the first comprehensive review looked at the reintroduction and reinforcement of 93 species of native birds and mammals (12). This data set was updated, and 181 mammal and bird programs were reanalyzed in 1998 (14). Both studies identified habitat quality at the release site, release into the core of a species range, and total numbers released as determinants of success (12, 14). An independent analysis of a broader taxonomic range of animal translocations over 20 years highlighted the greater likelihood of success associated with the release of wild versus captive animals and confirmed the importance of larger founder group sizes (13).

Reintroduced populations go through a period of relatively small population size where the risks of inbreeding and loss of genetic variation is high; the challenge, therefore, is to minimize loss of genetic variation by creating large effective population sizes (15). The key determinants of the genetic diversity retained in a reintroduction will be the total number of founders and the proportion contributing genetically to the next generations (16). Thus, even when a large population results, there might be considerable loss of genetic diversity during the early stages of population establishment (17), and the number of founders necessary for preservation of genetic diversity might be substantially greater than that required for population establishment and growth (18). Low initial population sizes might also make reintroduced populations vulnerable to Allee effects, which might have contributed to past reintroduction failures, although this link has not been shown (19). Reinforcement of existing populations can increase population size, prevent Allee effects, and increase genetic diversity, but also carries a risk of loss of local adaptation and the introduction of pathogens, particularly from captive breeding programs (11).

Simple classification of any reintroduction as success or failure to result in a self-sustaining population is of limited use because the time scale for success evaluation is important, and there are examples of successful projects failing at a later stage (13). The International Union for Conservation of Nature (IUCN) guidelines advocate that projects make clear definitions of success in relation to three phases of any reintroduction: establishment, growth, and regulation, with future population persistence assessed through population viability analysis (7). Assessment of success or of the causes of failure can be made only through adequate postrelease monitoring (20). Monitoring is needed also to facilitate meta-analyses (13), to track genetic diversity (16), and to evaluate the performance of reintroduced populations and the possible impacts on recipient ecosystems (21).

Conservation introductions

Perhaps the greatest challenge facing practitioners of species or ecosystem restoration is the definition of a target state (22). Attempts to return a system to some historical condition make somewhat arbitrary decisions about how far back in time to go. Historical restoration reference states vary according to the history of human occupation, with pre-European settlement conditions often held up as the baseline (23). However, a desire to return to some past state makes some assumptions, including the implication that near-pristine conditions existed in pre-European times and that historical restoration targets will be sustainable with changing climate (22). It is now recognized that past species distributions do not indicate current suitability and that current species' distribution does not guarantee future suitability (24). Climate change, in tandem with human-facilitated species invasions and land transformation, contribute to the creation of novel ecosystems: systems that differ in composition and function from past systems (25).

If we acknowledge that restoration and maintenance of species within their indigenous ranges will remain a foundation of conservation efforts, the realization that a return to a completely natural world is not achievable frees us to think about more radical types of conservation translocation. Conservation introductions involve the movement and release of an organism outside its indigenous range (7). Two types of conservation introduction are recognized by the IUCN: assisted colonization and ecological replacement (Fig. 1).

Assisted colonization

In 1985, Peters and Darling (26) suggested that climate change might alter habitat suitability for species confined within protected areas, effectively stranding them in increasingly unsuitable sites. They proposed the translocation of individuals into new reserves encompassing habitat that was or would become appropriate. Possibly because of the low profile of global climate change, the unreliability of early predictive models of climate, and the radical nature of the proposal, the idea of proactive translocation initially gained little traction (27). However, there is growing acknowledgment that conservation managers could take action to address climate-induced changes in species' habitats where individuals of affected species are unable to naturally colonize new areas as habitat suitability shifts (28-30). Understandably, given the devastating ecological impact wrought by invasive species, assisted colonization has been greeted with extreme skepticism, which has promoted a vigorous debate in the literature (31, 32). The 2013 IUCN guidelines define assisted colonization in broad terms as the intentional movement of an organism outside its indigenous range to avoid extinction of populations due to current or future threats (7). Under this definition, far from being a radical new translocation approach, assisted colonization is already being applied as a conservation tool in Australasia to protect, on predator-free islands, populations of species, such as the kakapo

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(*Strigops habroptilus*), threatened by predation from exotic mammalian predators in mainland habitat (*24*). The creation of a disease-free population of Tasmanian devils (*Sarcophilus harrisii*) outside the species' indigenous range in Tasmania (*33*) also fits this definition.

The 2013 IUCN guidelines place great emphasis on feasibility and risk analysis as essential components of any conservation translocation. Given the uncertainties involved in moving species outside their range, assisted colonization is inherently more risky than "traditional" translocations such as reintroductions. New approaches for understanding and managing risk under uncertainty are being applied to conservation introduction planning, including quantitative risk analysis (*34*), active adaptive management (*35*), and structured decision-making (*36*). Where protection from threats in the indigenous range is unfeasible and where appropriate habitat can be identified elsewhere, application of carefully planned assisted colonizations might become more acceptable (*37*).

A critical aspect in planning for assisted colonization is selection of suitable release sites that match the biotic and abiotic needs of the focal species (*7*) under future climate scenarios. Climate-envelope models have been used to determine species' future habitat suitability to guide some of the first experimental assisted colonizations of two butterfly species to sites ~35 and ~65 km beyond their indigenous range in northern England (*38*). But static bioclimatic envelope models might not adequately account for species' ability to disperse or for changing demographic processes as habitat quality shifts. More complex integrative climate suitability models will be required (*39*), although these too can never be perfect predictors of complex environments. Improved approaches to predict future habitat suitability explicitly integrate species distribution data with population dynamics or physiology. For example, stochastic population modeling combined with habitat suitability models predict how the vital rates of hihi (*Notiomystis cincta*), a New Zealand endemic passerine, could be influenced by climate change, with at least two populations potentially at risk of extinction (*40*). Ecoenergetic and hydrological models were integrated to evaluate the long-term suitability of habitat for the Western swamp tortoise (*Psuedemydura umbrina*) and extended to identify new regions that would meet the tortoise's thermodynamic requirements under a range of warmer and drier climates predicted by 2030 (*41*). Future developments around assisted colonization planning will include the

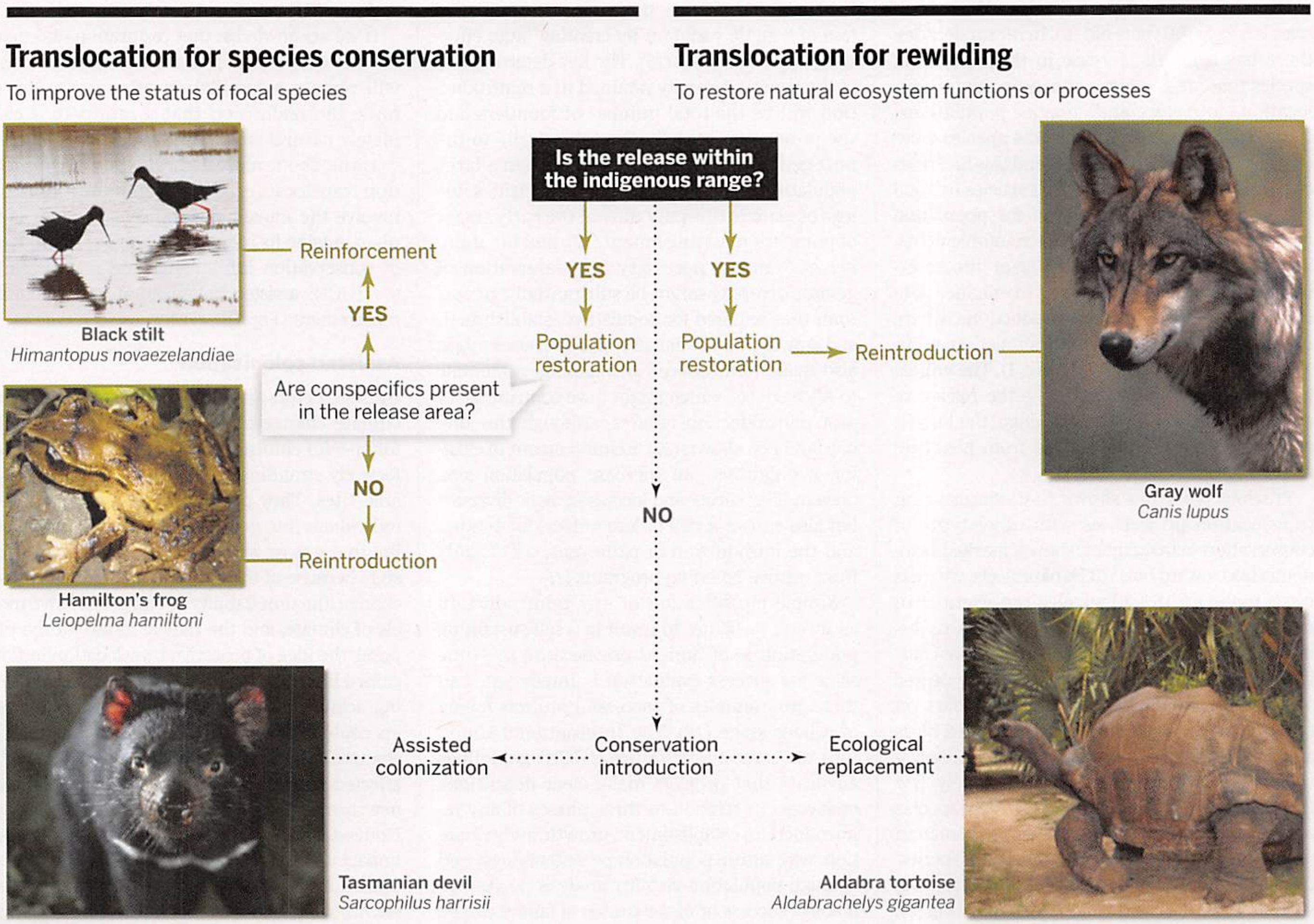


Fig. 1. The conservation translocation spectrum [based on (*7*)]. Translocations with the primary objective of improving the status of the focal species are a species conservation tool, and releases can take place inside or outside the indigenous range. Releases inside the indigenous range may be for reinforcements, as illustrated by the black stilt (*68*), or reintroductions, for example, of amphibians, such as Hamilton's frog (*69*). Releases outside the indigenous range for species conservation are assisted colonizations, e.g., Tasmanian devil (*33*). Translocations with the primary objective of restoring ecosystem functions are a component of rewilding and may include reintroductions, e.g., gray wolf (*46*). Rewilding releases outside the indigenous range might be justified if an ecological function has been lost due to extinction, e.g., dispersal of large-seeded plants by giant tortoises (*70*). Releases may have both objectives, but these should be explicitly stated as each will require specific targets and outcome monitoring. [Photo credits: black stilt (P. Guilford), Hamilton's frog (P. Bishop), Tasmanian devil (G. King), gray wolf (B. Quayle), Aldabra giant tortoise (M. Whittaker)]

application of fully integrated models that combine climatic suitability, habitat availability, population dynamics, and mechanistic movement models of dispersal (*39*, *42*). These may involve a single species or two or more interacting species.

Ecological replacements

Biodiversity can increase ecosystem stability by buffering the effects of environmental change, resisting species invasions, and preventing secondary extinctions after species losses (*43*). Species extinctions reduce interaction network diversity (*44*) and can lead to cascading effects, including the loss of other species and their biotic interactions (*45*). Where only local extinction occurs, critical ecosystem functions might be reinstated through reintroductions; for example, the reintroduction of wolves into Yellowstone National Park in 1995–1996 restored direct effects on their prey and a range of indirect effects (*46*). The global extinction of a species, however, means that restoration of functions might be achieved only through introduction of functionally similar exotic species.

The 2013 IUCN guidelines define ecological replacement as a form of conservation introduction involving the release of an appropriate substitute species to reestablish an ecological function lost through extinction. Although the rationale for ecological replacement is different from that of assisted colonization, the two terms have often been used interchangeably in the literature [e.g., (*47*)]. Although, in some situations, an assisted colonization to prevent extinction of the focal species could serve in parallel to restore an ecosystem function outside the indigenous range (*47*), in many cases, the most appropriate ecological replacements might not be endangered species. Recognition of ecological replacement as a valid conservation tool represents a departure from the single-species focus that once characterized conservation translocations and conforms more closely to the current global conservation emphasis on restoring natural processes rather than addressing only extinction risk (*48*).

There has been interest in the replacement of ecological functions once performed by extinct

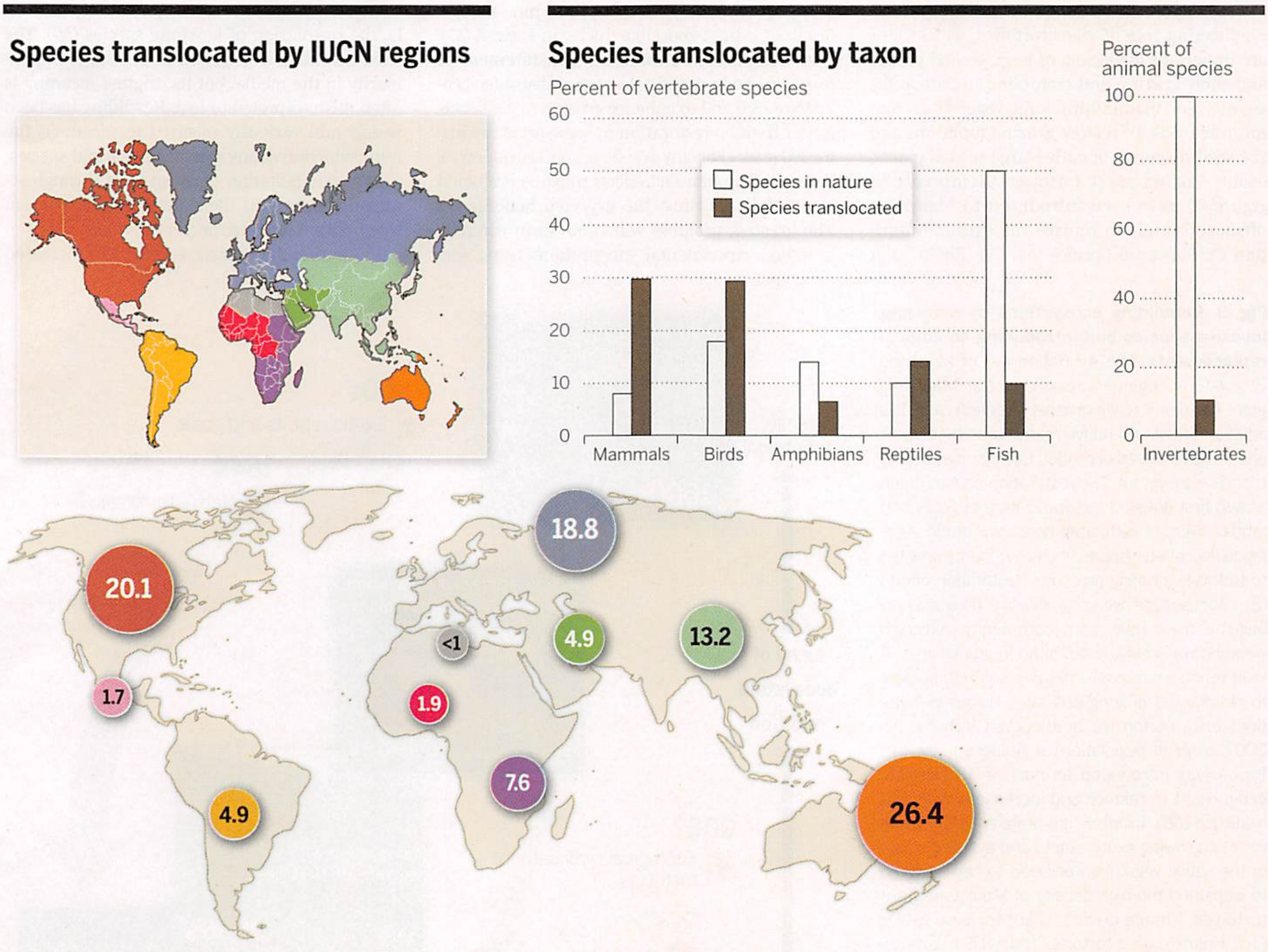


Fig. 2. Global and taxonomic range of conservation translocations. The proportions of 303 species that have been translocated for conservation purposes, by IUCN region (main map—the larger the circle the greater the proportion of species), and by taxon (inset bar chart: shaded bars are proportions of species translocated out of the total of 303; unshaded bars are proportions of species in nature. Because invertebrate species are estimated to be >99% of all animal species in nature, for clarity, the relative proportion of invertebrates in nature and the proportion of invertebrate species that have been translocated out of the total of 303 animal species are presented on the right; the proportions relative to vertebrate species only are on the left. [Data from (*10*).] The color inset map shows the 10 IUCN regions; west to east, these are North America and Caribbean, Meso-America, South America, North Africa, Central and West Africa, East and Southern Africa, West Asia and the Middle East, Europe and the Mediterranean, Asia, and Oceania (source iucn.org). Data on the 303 species was derived from downloadable project summaries available at iucnsscrsg.org. Base map source: commons.wikimedia.org

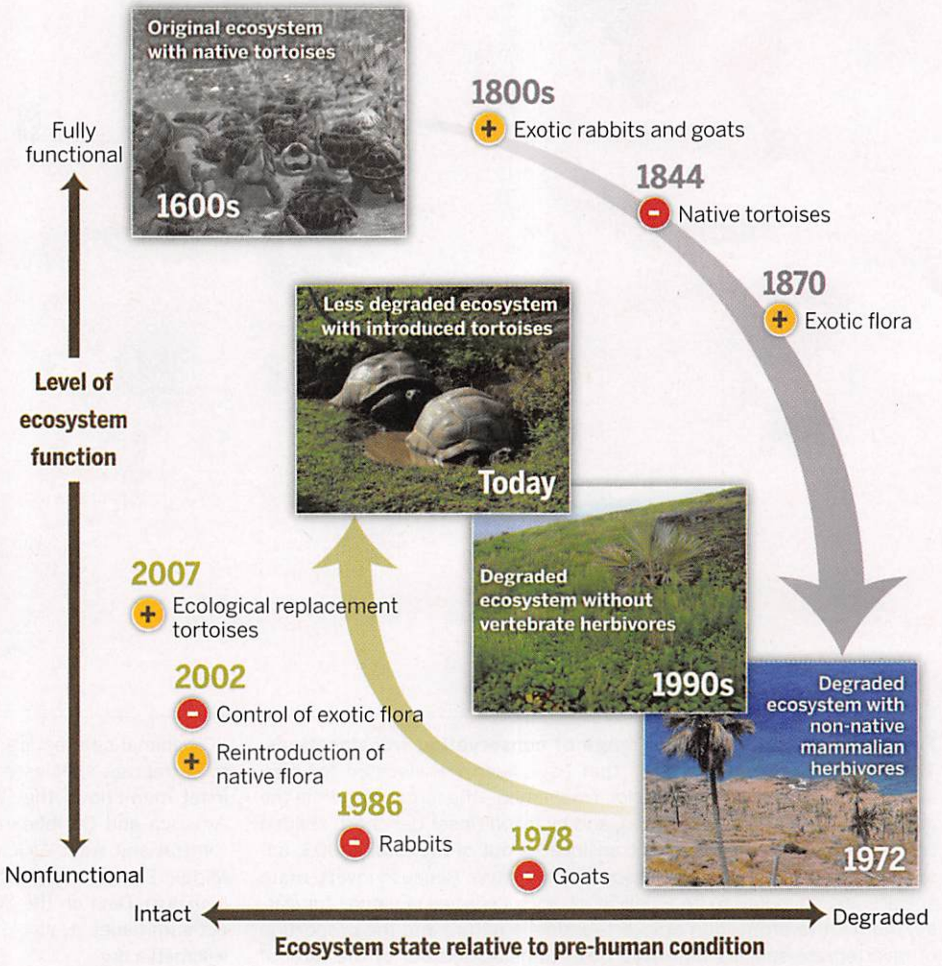
megafauna, because they would have had large ecosystem impacts in relation to their abundance (*49, 50*). The megafaunal concept must, however, be viewed as context-dependent, because in island ecosystems, the largest native frugivore may be an order of magnitude lighter than those in continental systems, yet loss of large island frugivores can result in more sizable cascading effects owing to the lower functional redundancy on islands (*51*). The most important application of ecological replacements to date has been in the restoration of herbivory and seed dispersal functions in island ecosystems. Extinction of large frugivores can disrupt seed dispersal, interrupt recruitment, and reduce genetic variation of large-seeded fleshy-fruited plants (*52*); it can also drive rapid evolutionary reduction in seed size, affecting seed survival (*45*). There is evidence of the ecosystem-engineering role of giant tortoises, as tortoises are important dispersers of large-seeded plants, and their grazing and trampling is critical for creating and maintaining some vegetation communities (*53*). To restore grazing functions and the seed dispersal of native large-seeded plants, exotic Aldabra giant tortoises (*Aldabrachelys gigantea*) have been introduced to Mauritian offshore islands to replace the extinct Mauritian *Cylindraspis* species (*54, 55*) (Fig. 3). Not only has seed dispersal resumed, but passage through the tortoise gut also improves seed germination success (*55*). Further projects are planned or under way to use ecologically similar species of giant tortoise to reinstate processes lost with the extinction of endemic giant tortoises in the islands of Madagascar, the Galapagos, the Mascarenes, the Seychelles, and the Caribbean (*56*).

The future challenge is the identification of suitable replacements to perform the desired ecosystem functions within a given system. The longer the time since the extinction of the original form, the greater the uncertainty about the best substitute. The best replacements might not be closely related taxa. If and when risk and uncertainty are adequately evaluated, radical substitutions could be considered, such as the use of tortoises as replacements for moa-nalo, a group of extinct gooselike ducks, in Hawaii (*57*). The focus must be more on reinstatement of functions and processes to restore degraded ecosystems (*58*) and to enhance ecosystem resilience, rather than on restoration to some arbitrary historical state. For any conservation introduction, the risk of unintended effects must be evaluated and weighed against the expected benefits (*7*). The greatest progress will come from carefully designed experimental substitutions using species that can be readily monitored and managed (*58*) and easily removed should the manifestation of unwanted effects reach some predetermined threshold.

Rewilding

In 1998, the concept of "rewilding" was proposed as a "fourth current in the modern conservation movement" that would complement the protection of representative biotic elements (*59*). The original concept of rewilding was built around the keystone role played by wide-ranging, large animals—particularly carnivores—able to maintain ecosystem structure, resilience, and diversity through top-down trophic interactions (*46, 59*). Rewilding would entail restoration of "big wilderness" through the creation and management of large, strict, core protected areas, enhanced connectivity between core reserves, and critically, the restoration of keystone species (*59*). The term rewilding is going through a surge in popularity in the media, but its original meaning is often misinterpreted or lost. Rewilding has been widely and variously misused to mean: (i) the reintroduction of any recently extirpated species; (ii) the rehabilitation of ecosystems through reintroductions; (iii) the return of an ecosystem to a prehuman state; or (iv) the release of non-native, rather than native, species. The increased

Fig. 3. Rebuilding ecosystems by removing invasive species and introducing ecological replacements. The extinction (–) of keystone ecosystem engineers, such as the Mauritian giant tortoises (*Cylindraspis* species), and the addition (+) of non-native mammalian herbivores and invasive plants degraded (gray arrow) Round Island's ecosystem. The restoration phase (green arrow) first entailed the eradication of goats and rabbits. Without vertebrate herbivory, exotic vegetation flourished, suppressing native plants adapted to tortoises' grazing pressure. Restoration efforts then focused on weeding invasive flora and rebuilding the native plant community, although weeding was costly and limited in spatial area. A long-term, more cost-effective solution sought to restore the grazing and seed dispersal functions once performed by the giant tortoises. In 2007, a small population of Aldabra giant tortoises was introduced as part of a reversible experiment to restore and increase ecosystem resilience (*68*). Tortoises are preferentially grazing the fast-growing exotic plants and avoiding much of the native vegetation believed to have evolved to withstand the high density of Mauritian giant tortoises. [Image credits: Giant tortoise 1600s (J. P. Hulme), giant tortoises today (Z. Ahamud), 1990s (C. Griffiths), 1972 (C. Jouanin)]



use and misuse of the term rewilding has been perhaps due to controversy around the proposed introduction of megafauna to North America to replace species lost 13,000 years ago (*60*). Pleistocene rewilding is at its core true to the original concept of rewilding, as it recognizes the important ecosystem-shaping role of large vertebrates, but made a major departure by arguing for the ecological replacement of long-extinct species. The radical nature of the Pleistocene rewilding concept spawned other, similarly controversial suggestions—such as the introduction of elephants to Australia to control invasive plants (*61*)—but also usefully reenergized the debate on ecological replacements as a valid conservation tool.

Where does this leave rewilding as a concept? The most valuable redefinition of rewilding replaces the "keystone species restoration" component with "species reintroduction to restore ecosystem functioning" (*50*). More broadly though, the restoration of ecosystem function could also involve the introduction of ecological replacements (*50*). This harmonizes rewilding with the current conservation translocation framework (Fig. 1). There is a distinction between translocation for species conservation—where the primary objective is to improve the status of the focal species through reinforcement, reintroduction, or assisted colonization—and translocation for rewilding—where the objective is to restore natural ecosystem functions or processes. Translocation for rewilding could entail population restoration through reintroduction, where releases occur in the indigenous range with the primary aim of restoring some ecological function. A rewilding translocation could also take the form of a conservation introduction through ecological replacement using suitable substitute species.

In its original form, rewilding was seen as a way to restore wilderness, the implication being that there would be large areas of land where human influence was minimal and ongoing management interventions unnecessary. The restoration of keystone species would facilitate the recovery of other "habitat-creating" species and the recovery of natural disturbance regimes (*59*). Oostvaardersplassen (OVP) is a 6000-ha state-owned polder 40 km north of Amsterdam, Netherlands. In the 1980s, the ecologist Frans Vera began to recreate an ecosystem shaped by grazing of large ungulates (*62*), unregulated by large predators. Red deer (*Cervus elaphus*) were released, along with back-bred Konik horses (*Equus ferus caballus*), and the domestic descendants of the Auroch, Heck cattle, as replacements for extinct Auroch (*Bos primigenius*) and Tarpan (*Equs przewalski gmelini*). Rather than seeking the preservation or restoration of indigenous biodiversity, OVP is one manifestation of a European vision of rewilding, as the restoration of ecological processes to create untamed landscapes reminiscent of ecological conditions at the end of the Pleistocene (*63*). The challenge is uncertainty over the emergent properties and climax equilibrium vegetation of the area, but the emphasis is on minimizing human interventions.

However, restoration that aspires to exclude human influence and activity has been challenged as being unobtainable or unsustainable. The positive average annual population growth rates for the larger carnivores, the golden jackal (*Canis aureus*), gray wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), Iberian lynx (*Lynx pardinus*), and wolverine (*Gulo gulo*), in Europe between 1961 and 2005 (*64*), for example, has shifted emphasis away from preventing extinctions and prompted thinking toward future planning under a new model of coexistence between predators and humans over large spatial scales (*65*). This reshaping of rewilding acknowledges that humans are an integral part of, not apart from, nature and recasts the retrospective goals of restoring "wilderness" as future-oriented visions of creating "wildness" in which ecological processes, such as predator-prey interactions, are managed within landscapes shared by humans and wildlife (*65*).

Future prospects and implications

With official IUCN recognition of a spectrum of conservation translocation tools, the emphasis has now shifted to how best to apply these approaches to maximize conservation benefit while minimizing the risk of unintended consequences. Particularly for the inherently more uncertain conservation introductions, the focus needs to be on development and application of rigorous methods to match species to habitats while evaluating risk. The IUCN guidelines (*7*) provide a framework for dealing with the complexities of conservation translocations and are sufficiently comprehensive to be able to accommodate new developments. The prospect of species de-extinction, the resurrection of extinct species using selective breeding or the clonal technologies of synthetic biology potentially broadens the range of species and associated processes we might seek to restore. De-extinction of multiple species will occur at some future time, but one question that must be addressed is which species? Because the goals of de-extinction relate to ecological enrichment, selection of de-extinction candidates should be guided by the feasibility and risks of their release into suitable habitat (*66*).

Daniel Pauly (*67*) called attention to "shifting baselines" in fisheries—a concept extended to encompass the gradual attrition in people's expectations of what the natural world around them should look like, whereby each generation grows up within a slightly more impoverished natural biodiversity. Defaunation is a major contributing factor to this extinction of experience. Translocations for the restoration of populations of threatened species, for reestablishment of ecological functions and processes, and for the re-creation of wildness provide a foundation for resetting public aspirations for biodiversity. Conservation translocation projects provide a powerful means to reconnect people with their natural heritage, to engage them as conservation partners, and to make them stewards of the wild animals and habitats around them.

Part of this reconnection with nature will entail a new appreciation of the concept of wild, moving away from increasingly unobtainable concepts of self-sustaining wildlife populations within pristine landscapes untouched by human influence. We are moving instead toward understanding the value of restoring and sustaining species and their habitats, possibly in novel configurations, with ongoing management, and with the needs of humans both acknowledged and integrated.

REFERENCES AND NOTES

1. S. H. M. Butchart *et al.*, *Science* **328**, 1164–1168 (2010).
2. H. M. Pereira *et al.*, *Science* **330**, 1496–1501 (2010).
3. R. Dirzo *et al.*, *Science* **345**, 401–406 (2014).
4. H. C. Giacomini, M. Galetti, *Biol. Conserv.* **163**, 33–41 (2013).
5. B. J. Cardinale *et al.*, *Nature* **486**, 59–67 (2012).
6. M. E. Soulé, G. H. Orians, Eds., *Conservation Biology: Research Priorities for the Next Decade* (Society for Conservation Biology, Island Press, Washington, DC, 2001).
7. IUCN, *Guidelines for Reintroductions and Other Conservation Translocations* (IUCN SSC, Gland, Switzerland, ed. 1.0, 2013).
8. J. G. Ewen, D. P. Armstrong, K. A. P. Parker, P. J. Seddon, Eds, *Reintroduction Biology: Integrating Science and Management* (Wiley-Blackwell, West Sussex, UK, 2012).
9. P. J. Seddon, D. P. Armstrong, R. F. Maloney, *Conserv. Biol.* **21**, 303–312 (2007).
10. P. J. Seddon, P. S. Soorae, F. Launay, *Anim. Conserv.* **8**, 51–58 (2005).
11. J. Champagnon, J. Elmberg, M. Guillemain, M. Gauthier-Clerc, J.-D. Lebreton, *J. Nat. Conserv.* **20**, 231–241 (2012).
12. B. Griffith, J. M. Scott, J. W. Carpenter, C. Reed, *Science* **245**, 477–480 (1989).
13. J. Fischer, D. B. Lindenmayer, *Biol. Conserv.* **96**, 1–11 (2000).
14. C. M. Wolf, T. Garland Jr., B. Griffith, *Biol. Conserv.* **86**, 243–255 (1998).
15. L. F. Keller *et al.*, in *Reintroduction Biology: Integrating Science and Management*, J. G. Ewen, D. P. Armstrong, K. A. P. Parker, P. J. Seddon, Eds. (Wiley-Blackwell, West Sussex, UK, 2012), pp. 360–394.
16. J. J. Groombridge *et al.*, in *Reintroduction Biology: Integrating Science and Management*, J. G. Ewen, D. P. Armstrong, K. A. P. Parker, P. J. Seddon, Eds. (Wiley-Blackwell, West Sussex, UK, 2012), pp. 395–440.
17. I. G. Jamieson, R. C. Lacy, in *Reintroduction Biology: Integrating Science and Management*, J. G. Ewen, D. P. Armstrong, K. A. P. Parker, P. J. Seddon, Eds. (Wiley-Blackwell, West Sussex, UK, 2012), pp. 441–475.
18. L. N. Tracy, G. P. Wallis, M. G. Efford, I. G. Jamieson, *Anim. Conserv.* **14**, 439–446 (2011).
19. A. Deredec, F. Courchamp, *Ecoscience* **14**, 440–451 (2007).
20. W. J. Sutherland *et al.*, *Conserv. Lett.* **3**, 229–235 (2010).
21. D. P. Armstrong, P. J. Seddon, *Trends Ecol. Evol.* **23**, 20–25 (2008).
22. S. T. Jackson, R. J. Hobbs, *Science* **325**, 567–569 (2009).
23. A. S. Thorpe, A. G. Stanley, *J. Appl. Ecol.* **48**, 275–279 (2011).
24. C. D. Thomas, *Trends Ecol. Evol.* **26**, 216–221 (2011).
25. R. J. Hobbs, E. S. Higgs, C. Hall, Eds., *Novel Ecosystems: Intervening in the New Ecological World Order* (Wiley-Blackwell, West Sussex, UK, 2013).
26. R. L. Peters, J. D. S. Darling, *Bioscience* **35**, 707–717 (1985).
27. N. E. Heller, E. S. Zavaleta, *Biol. Conserv.* **142**, 14–32 (2009).
28. J. S. McLachlan, J. J. Hellmann, M. W. Schwartz, *Conserv. Biol.* **21**, 297–302 (2007).
29. M. L. Hunter Jr., *Conserv. Biol.* **21**, 1356–1358 (2007).
30. O. Hoegh-Guldberg *et al.*, *Science* **321**, 345–346 (2008).

31. S. R. Loss, L. A. Terwilliger, A. C. Peterson, *Biol. Conserv.* **144**, 92–100 (2010).
32. N. Hewitt *et al.*, *Biol. Conserv.* **144**, 2560–2572 (2011).
33. B. Nogardy, *Ecos* **25**, 13036 www.ecosmagazine.com/?paper=EC13036 (2013).
34. T. M. Lee, W. Jetz, *Proc. Biol. Sci.* **278**, 1329–1338 (2011).
35. E. McDonald-Madden, M. C. Runge, H. P. Possingham, T. G. Martin, *Nat. Climate Change* 1, 261–265 (2011).
36. M. W. Schwartz, T. G. Martin, *Ann. N. Y. Acad. Sci.* **1286**, 15–28 (2013).
37. B. M. H. Larson, C. Palmer, *Ethics. Policy Environ.* **16**, 16–18 (2013).
38. S. G. Willis *et al.*, *Conserv. Lett.* **2**, 46–51 (2009).
39. B. Huntley *et al.*, *Ecography* **33**, 621–626 (2010).
40. A. L. M. Chauvenet, J. G. Ewen, D. Armstrong, N. Pettorelli, *J. Appl. Ecol.* **50**, 1330–1340 (2013).
41. N. Mitchell *et al.*, *Biology* 2, 1–25 (2012).
42. L. M. J. Travis *et al.*, *Oikos* **122**, 1532–1540 (2013).
43. A. S. MacDougall, K. S. McCann, G. Gellner, R. Turkington, *Nature* **494**, 86–89 (2013).
44. J. M. Tylianakis, E. Laliberté, A. Nielsen, J. Bascompte, *Biol. Conserv.* **143**, 2270–2279 (2010).
45. M. Galetti *et al.*, *Science* **340**, 1086–1090 (2013).
46. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).
47. I. D. Lunt *et al.*, *Biol. Conserv.* **157**, 172–177 (2013).
48. M. W. Cadotte, K. Carscadden, N. Mirotchnick, *J. Appl. Ecol.* **48**, 1079–1087 (2011).
49. M. Pedrono *et al.*, *Biol. Conserv.* **159**, 501–506 (2013).
50. C. Sandom *et al.*, in *Key Topics in Conservation Biology 2*, D. W. MacDonald, K. J. Willis, Eds. (Wiley-Blackwell, West Sussex, UK, 2013), pp. 430–451.
51. D. M. Hansen, M. Galetti, *Science* **324**, 42–43 (2009).
52. P. R. Guimarães, M. Galetti, P. Jordano, *PLOS ONE* 3, e1745 (2008).
53. J. P. Gibbs, C. Marquez, E. J. Sterling, *Restor. Ecol.* **16**, 88093 (2008).
54. C. J. Griffiths *et al.*, *Restor. Ecol.* **18**, 1–7 (2010).
55. C. J. Griffiths, D. M. Hansen, C. G. Jones, N. Zuël, S. Harris, *Curr. Biol.* **21**, 762–765 (2011).
56. D. M. Hansen, C. J. Donlan, C. J. Griffiths, K. J. Campbell, *Ecography* **33**, 272–284 (2010).
57. S. Reardon, *New Sci.* **221**, 40–43 (2014).
58. R. T. Corlett, *Biol. Conserv.* **163**, 13–21 (2013).
59. M. Soulé, R. Noss, *Wild Earth* **1998** (Fall), 1-11 (1998).
60. J. Donlan, *Nature* **436**, 913–914 (2005).
61. D. Bowman, *Nature* **482**, 30 (2012).
62. F. W. M. Vera, *Br. Wildlife* **20** (suppl.), 28–36 (2009).
63. J. Lorimer, C. Driessen, *Trans. Inst. Br. Geogr.* **3**, 169–181 (2013).
64. S. Deinet et al., 2013. *Wildlife Comeback in Europe: The Recovery of Selected Mammal and Bird Species* (Final report to Rewilding Europe by ZSL, Birdlife International, and the European Bird Census Council, London, UK; Zoological Society of London, London, 2013).
65. L. Boitani, L. D. C. Linnell, in *Rewilding European Landscapes*, H. Periera, L. Navarro, Eds. (Springer Science, Dordrecht, 2014).
66. P. J. Seddon, A. Moehrenschlager, J. Ewen, *Trends Ecol. Evol.* **29**, 140–147 (2014).
67. D. Pauly, *Trends Ecol. Evol.* **10**, 430 (1995).
68. R. J. Keedwell, R. F. Maloney, D. P. Murray, *Biol. Conserv.* **105**, 369–374 (2002).
69. J. M. Germano, P. J. Bishop, *Conserv. Biol.* **23**, 7–15 (2009).
70. C. J. Griffiths, N. Zuël, C. G. Jones, Z. Ahamud, S. Harris, *Conserv. Biol.* **27**, 690–700 (2013).

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