

Upgrading protected areas to conserve wild biodiversity

Robert M. Pringle^{1,2,3}

International agreements mandate the expansion of Earth's protected-area network as a bulwark against the continued extinction of wild populations, species, and ecosystems. Yet many protected areas are underfunded, poorly managed, and ecologically damaged; the conundrum is how to increase their coverage and effectiveness simultaneously. Innovative restoration and rewilding programmes in Costa Rica's Área de Conservación Guanacaste and Mozambique's Parque Nacional da Gorongosa highlight how degraded ecosystems can be rehabilitated, expanded, and woven into the cultural fabric of human societies. Worldwide, enormous potential for biodiversity conservation can be realized by upgrading existing nature reserves while harmonizing them with the needs and aspirations of their constituencies.

Wild populations and species are vanishing rapidly, ushering in an anthropogenic sixth mass extinction^{1–6}. Protected areas — lands and waters that are legally designated and managed for long-term nature conservation — are the backbone of efforts to staunch this haemorrhage⁷. However, research shows that the existing global network of protected areas — despite more than tripling in size in the past 40 years^{7,8} — is insufficient to prevent the continuing depletion of biodiversity^{9–11}. There is therefore an urgent need to enlarge the protected-area estate, to increase its overlap with endangered ecosystems and at-risk species, and to reconcile these aims with projected land-use changes as Earth's human population increases to 11 billion and beyond¹².

This urgency is reflected in both international law and conservation-science research. The Convention on Biological Diversity, which is ratified by almost all nations, stipulated in its Aichi Biodiversity Target 11 that “by 2020, at least 17% of terrestrial and inland water areas, and 10% of coastal and marine areas [should be] conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures”^{9,13}. Meanwhile, conservation scientists have developed sophisticated tools for systematic conservation planning¹⁴, which seeks to prioritize new sites for protection in light of the distributions of species, ecosystems, threats, and costs^{10,11,15–23}. These efforts provide a scientific foundation — albeit not the economic and political wherewithal — for guiding the continued expansion of the global protected-area network towards the agreed targets.

The science is murkier with respect to the criterion — dictated by both common sense and Aichi Biodiversity Target 11 — that protected areas must be effectively and equitably managed. These qualities are not easily measured²⁴, and relevant data are sparse, despite a growing push to quantify the impacts of conservation measures^{25–33}. According to a 2013 study, “there remains a limited evidence base, and weak understanding of the conditions under which protected areas succeed or fail to deliver conservation outcomes”³⁴.

There is no doubt that protected areas can effectively protect populations and habitats^{35–38} and it is increasingly clear that, more often than not, they do. Global analyses show that local biodiversity is greater³⁹, rates of landscape conversion are lower⁴⁰, and wildlife population trends are generally stable or increasing⁴¹ inside protected areas. Similarly, there is mounting evidence that protected areas often reduce poverty and increase the well-being of rural populations^{26,27,42}. As the number of visitors to

protected areas has increased in many developing tropical countries⁴³, nature-based tourism has emerged as a dominant source of foreign exchange, bolstering national economies and shaping the decision-making of political leaders^{7,44}.

Yet there is also marked heterogeneity in the extent to which individual protected areas are achieving these biological and human-development aims. Protected areas in both rich and poorer countries are chronically underfunded and beset by myriad political and logistic challenges⁷, and populations of many species are declining both within individual protected areas⁴⁵ and throughout entire nations⁴⁶ and continents⁴⁷. By one estimate, roughly half of protected areas worldwide have suffered drastic deterioration and biodiversity loss during the past 20–30 years³⁸, with many functioning as little more than ‘paper parks’ — protected in law and on maps, but not in practice⁴⁸. And even successful protected areas are imperilled by eroding political support and an apparent global trend of “downgrading, downsizing and degazettement”^{49,50}.

Scientists, policymakers, and conservation investors must therefore confront a thorny question: how should we divide effort and resources between the dual imperatives of establishing new protected areas and upgrading established ones such that they are well managed, societally supported, and ecologically coherent? This question has no simple or single answer, but dodging it risks a dismal outcome: a resource-intensive scramble to meet the Aichi Biodiversity Targets by creating new protected areas that lack the financial, social, and political capital to succeed in perpetuity — and that further starve pre-existing protected areas for funds and attention. Creating a vast but dysfunctional global estate of protected areas would thwart the letter and the spirit of the Convention on Biological Diversity just as surely as failing to expand the estate.

I offer three observations. First, enormous potential for biodiversity conservation can be realized by resuscitating established-but-degraded protected areas and using them as nuclei for peripheral expansion — a strategic programme of upgrading and upsizing to counter recent trends in the opposite direction^{49,50}. Second, to illustrate the plausibility and power of this approach, I review the convergent evolution of two protected areas in radically different socio-ecological contexts: the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica and Parque Nacional da Gorongosa (PNG) in the Sofala province of Mozambique. Although the specific actions that have been undertaken to rehabilitate these protected areas are necessarily place based, context dependent, and

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA. ²Board of Directors, The Gorongosa Project, Gorongosa National Park, Sofala Province, Mozambique. ³Board of Directors, Guanacaste Dry Forest Conservation Fund, Área de Conservación Guanacaste, Costa Rica.

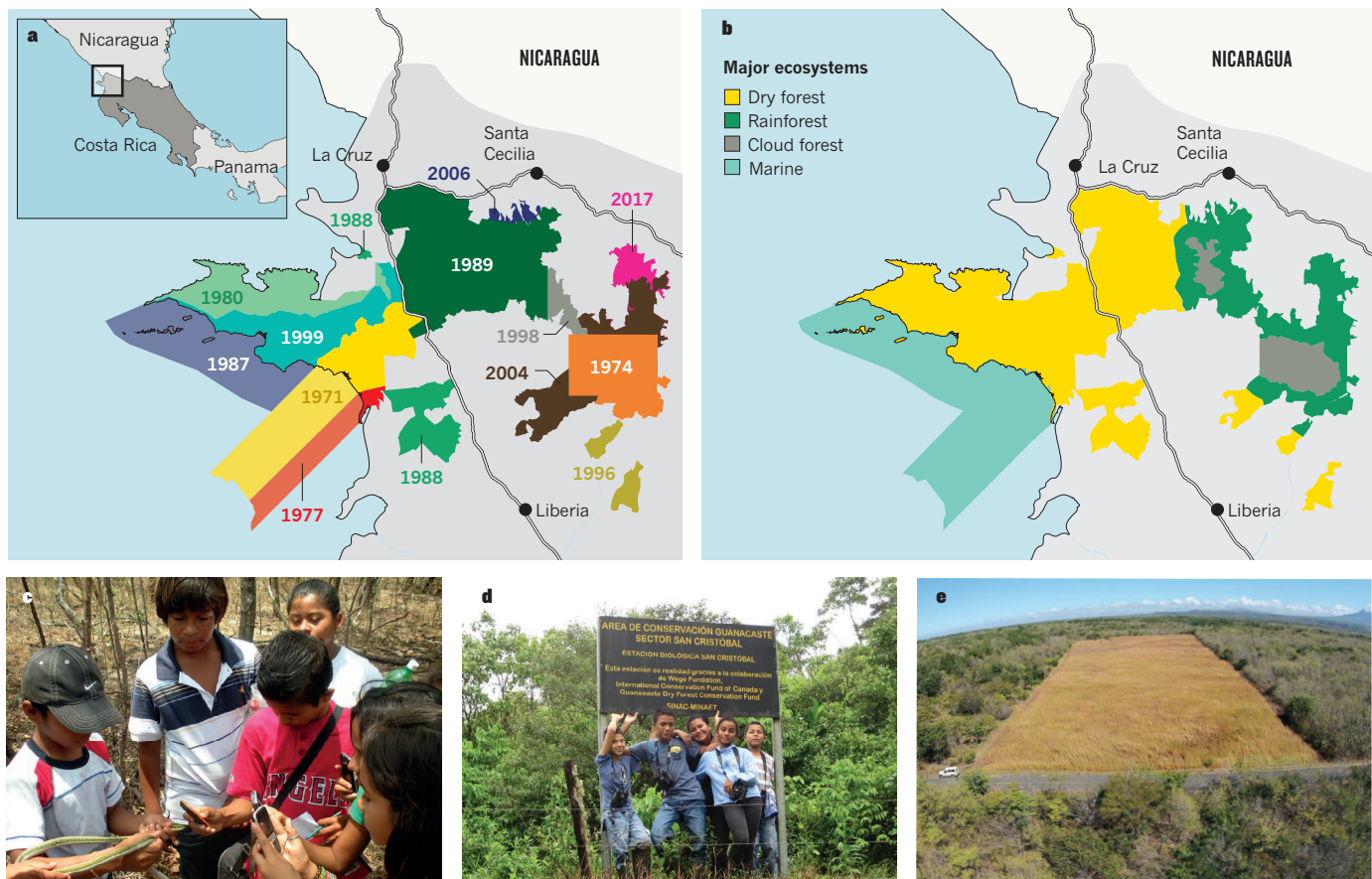


Figure 1 | Área de Conservación Guanacaste in Costa Rica. **a**, Expansion of the Área de Conservación Guanacaste (ACG) from 1971 to 2017. Each region is labelled with the approximate year in which the land was acquired. **b**, Major ecosystems of the ACG. **c**, Students from rural schools participate in the ACG's Biological Education Program. They are interviewing a harmless parrot snake (*Leptophis mexicanus*) and demonstrating how electronic devices such as mobile phones can facilitate modern bioliteracy. Image credit:

A. Jimenez. **d**, Children from the fishing village of Cuajiniquil, northwest Costa Rica, participate in the ACG's 2012 Christmas Bird Count, equipped with binoculars and cameras supplied with funds from the Guanacaste Dry Forest Conservation Fund. Image credit: M. M. Chavarría Diaz. **e**, Thirty years of tropical dry-forest restoration surrounding an experimental plot that is still burnt annually, which shows how much of the ecosystem appeared when restoration started in 1985. Image credit: J. Diaz Orias.

continuously evolving, their underlying philosophies and approaches can be generalized and applied worldwide. Third, we need a research agenda that explicitly evaluates the ledger of costs, benefits, and trade-offs — both biological and socio-economic — associated with creating new protected areas versus upgrading old ones.

Upgrading and upsizing protected areas

What can be done with protected areas that are severely degraded, under-funded, or too small and isolated to conserve viable populations and ecosystems? It has been suggested that the money saved from abandoning underperforming areas could be used to create new and better ones²⁰ — a strategy dubbed 'trade-in to trade-up'⁵¹. Although such schemes can, in theory, increase efficiency, the practical obstacles to their implementation will often be prohibitive (or prohibitively costly to overcome).

This suggests that we should not be too quick to abandon underperforming protected areas. The term 'paper park' is used as a pejorative label to describe dysfunctional protected areas, yet the mere existence of a protected area on paper is a non-trivial asset⁵². Ecological degradation can be halted and reversed, and management structures overhauled, setting ecosystems on trajectories towards recovery. Full 'recovery' may require centuries, and even then the recovered state may or may not closely resemble the pre-disturbance state; nonetheless, recovering systems rapidly yield many of the fruits that we seek to harvest from protected areas, including viable wildlife populations, aesthetic and recreational value, and utilities such as clean water^{53–55}. Moreover, even the smallest protected areas can be grown outwards and linked with others, thereby increasing

the quantity and connectivity of the conserved area and consolidating it into more-tractable management units. It is probable that expanding an established legal entity will be more politically palatable, carry lower transaction costs, and be less disruptive to human communities than the creation of a new entity from scratch.

Two case studies highlight the profound conservation gains that can be made from resuscitating damaged ecosystems and strategically growing high-functioning protected areas around them. Although these efforts are evolving independently in response to time- and place-based selective pressures, they have converged on similar guiding principles that collectively interweave diverse strands of contemporary (and not yet contemporary) thought on conservation.

The Área de Conservación Guanacaste

Costa Rica's ACG comprises 1,260 square kilometres of tropical dry forest, rainforest, and cloud forest, along with 430 square kilometres of adjacent marine protected area (Fig. 1). It is home to more than 375,000 macroscopic species, which represent approximately 65% of Costa Rica's terrestrial biodiversity and 2.4% of Earth's.

In 1966, Costa Rica decided to create a national historic site and recreation area on the Hacienda Santa Rosa, a 400-year-old mule and cattle ranch where Costa Rican armed forces had repelled several attempted invasions from Nicaragua. On the recommendation of biologists, this former battlefield became the core of a new national park, Parque Nacional Santa Rosa, in 1971 (refs 56 and 57). This park comprised roughly 100 square kilometres of old pastures with scattered clumps and strips of relictual neotropical dry forest — already an endangered ecosystem owing

to the ease with which it can be cleared for agro–pastoral use⁵⁸ — together with a 230-square-kilometre slab of marine protected area.

The pasturelands between the remnant fragments of dry forest were dominated by the exotic African savanna grass *Hyparrhenia rufa*, which was originally imported to Costa Rica for use as cattle forage⁵⁶. This patchwork of pasture and forest was created by fires lit by loggers and ranchers in the dry season, and then maintained and expanded by a mixture of regular burning, competitive suppression of tree seedlings by grasses, and consumption and trampling of some seedlings by cows⁵⁹. When the 2,000 remaining cattle were removed from the park in 1977, in a bid to increase its naturalness, grass biomass accumulated and fires raged out of control. By the mid-1980s, biologists Daniel Janzen and Winnie Hallwachs realized that these fires would soon eliminate the few remaining patches of intact forest, and sought permission from the Costa Rican government to co-implement a dry-forest restoration programme. This involved recruiting a dedicated resident firefighting force and allowing natural seed dispersal by wind and animals to plant several thousand species of forest trees, shrubs, and lianas across hundreds of square kilometres of abandoned pastures and old fields⁵⁷. The establishing woody plants increasingly excluded the grasses that had fuelled the fires, which initiated a process of successional recovery (Fig. 1).

Land surrounding Santa Rosa were acquired through open-market purchases from private landowners and were folded into what emerged as a new legal and administrative entity: the ACG^{56,57,60}. Janzen and Hallwachs secured funds for these purchases from a wide range of sources, including two-thirds of their own university salaries. In 1997, Janzen was awarded the Kyoto Prize in Basic Sciences and used the 50-million-yen (US\$430,000) prize to incorporate the Guanacaste Dry Forest Conservation Fund (GDFCF), a US non-profit organization that aims to promote the long-term survival of the ACG. GDFCF now serves as the ACG's charitable-support arm, owns and co-oversees 135 square kilometres within the ACG, and manages a growing endowment that is intended to confer financial sustainability in perpetuity. Donations and payments for ecosystem services that flow through GDFCF support biodiversity inventories, maintenance costs, and equipment purchases, adding \$1.5 million to the ACG's \$3.5-million annual allocation from the government.

When Costa Rica decreed two further national parks on the volcanic slopes that lie to the east of Santa Rosa — Parque Nacional Rincón de la Vieja in 1977 and Parque Nacional Guanacaste in 1989 — the same land-purchase approach was used to buy out the farms both inside and between all three parks. Rainforest restoration in these wetter areas was kick-started by planting the fast-growing paper-pulp plantation tree *Gmelina arborea* to shade out grasses and to provide cover for seed-dispersing animals and tree seedlings that are averse to hot, dry conditions^{56,57}. In this piecemeal fashion, the ACG was grown from the initial 100-square-kilometre mixture of degraded forest and pastureland to its present size (Fig. 1). In 1999, the area was designated a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Site; it receives 125,000 international tourists a year and supplies water to more than 200,000 people.

This progressive growth and interconnection has also enhanced the ecological coherence of the ACG, which now encompasses marine, island, coastal, freshwater, dry-forest, rainforest, and cloud-forest ecosystems, as well as many intergrades (Fig. 1). Such breadth is crucial. Thousands of the area's species migrate seasonally or inter-generationally between multiple ecosystems and require all of them for persistence. Other 'species', formerly thought to be cross-ecosystem migrants, are now known to comprise genetically differentiated dry-forest and wet-forest populations on distinct evolutionary trajectories⁶¹ — a cryptic form of biodiversity, the conservation of which requires multiple forest types. And as climate change inexorably raises temperatures, eliminates cloud forest, and disrupts seasonality throughout the ACG, lowland refugee species are increasingly moving upslope^{56,62}.

An explicit goal since its inception has been to integrate the ACG into the fabric of local, regional, national, and global society^{63,64}. It has become *de rigueur* in discussions about international biodiversity conservation

to assert the importance of engaging and serving local people⁶⁵, but this dictate is often expressed in terms of material well-being — conservation must not obstruct the alleviation of poverty⁶⁶. The ACG's 'biocultural restoration'⁶³ is distinguished by the effort not only to provide jobs (all 150 employees are citizens of Costa Rica) and to safeguard ecosystem services (for example, the water supply to the city of Liberia), but also to re-establish intellectual and emotional connections between an urbanizing society and the biodiversity with which it has increasingly lost touch^{64,67}. To promote bioliteracy⁶⁸, the ACG is extended as a classroom for around 2,000 local schoolchildren each year (Fig. 1), with the hope that children who gain such exposure are more likely to sustain the existence of conserved wild areas when they grow up into voters and tax-payers⁶⁵. Inventories of biodiversity are undertaken with a view that people will seek to keep what they can use (or what amuses them), and that the ability to sustainably use wild biodiversity (or to be entertained by its dramas, comedies and thrillers) requires at least being able to find the theatre and to identify the characters. Specimens from these inventories are preserved and catalogued with DNA barcodes (short, diagnostic sequences of DNA), with an eye towards a future in which portable devices enable *in situ* species identification and wireless access to natural-history information — and thus the democratization of knowledge that is currently confined to a small and shrinking number of biologists and hobbyists⁶⁹. And these specimens are collected and sorted by parataxonomists, providing locally recruited people with intellectually rich livelihoods while creating and empowering proud custodians of and advocates for biodiversity^{70–73}.

Parque Nacional da Gorongosa

Created by Portuguese colonial administrators in 1960, the 3,700-square-kilometre PNG was once touted as one of Africa's most spectacular national parks, owing to its picturesque savannas and woodlands and the massive herds of wildlife that roamed its Rift Valley grasslands. During Mozambique's post-colonial civil war (1977–1992), in which hundreds of thousands of people were killed, hostilities raged in and around the park⁷⁴; this conflict, and the crushing poverty that persisted after the fighting ended, extinguished more than 90% of the park's large mammals⁷⁵. Since 2004, the Gorongosa Restoration Project (now the Gorongosa Project) has sought to rehabilitate PNG and to transform it into an engine of human and economic development⁷⁶ (Fig. 2).

Even before peace was negotiated in Mozambique in 1992, its president at the time, Joaquim Chissano, was thinking about how to revitalize the country's protected areas and use nature-based tourism to leverage post-war economic recovery. With his contemporary, Nelson Mandela, Chissano helped to lay the groundwork for the creation of transfrontier conservation areas (also known as peace parks) — large protected areas that span more than one country. Chissano thought that PNG might serve as a kind of domestic peace park, given its centrality to the civil conflict and its potential to attract international tourists. However, the park's wildlife had been devastated by war^{77,78} and the decade from 1994 to 2004 saw minimal recovery: the estimated populations of most species remained in the tens or hundreds (down from thousands in the early 1970s⁷⁹), and some species, including buffalo (*Syncerus caffer*) and zebra (*Equus quagga*), were not detected at all⁸⁰. In addition, the park's roads and infrastructure had been reduced to rubble.

In 2002, Chissano met US businessman and philanthropist Gregory Carr, founder of the Carr Center for Human Rights Policy at Harvard University, and invited him to participate in the restoration of PNG. A 20-year co-management agreement between the Gregory C. Carr Foundation and the government of Mozambique was signed in 2008 (ref. 81), mandating a science-based management approach and the establishment of a sustainable tourism industry. Education, livelihoods, and neighbourliness figured prominently in this agreement: a community relations department was founded to establish contracts with community representatives, oversee the sharing of 20% of the park's revenues, recruit local employees, and guarantee local access (for example, by arranging for students from neighbouring villages to have educational field trips to the park (Fig. 3)).

Wildlife recovery has accelerated since 2004, with the total

large-mammal biomass in 2016 approaching 80% of pre-war estimates; however, species composition has shifted markedly. Several species of mid-sized antelope now exceed their pre-war population densities, whereas others remain suppressed (Fig. 2). Lion (*Panthera leo*) is now the only resident population of large carnivore, with at least 65 individuals in 2017 (compared to roughly 200 before the war). Other apex predators that are crucial for ecosystem functioning⁸², including leopard (*P. pardus*), hyena (*Crocuta crocuta*) and wild dog (*Lycaon pictus*), remain extinct locally. Yet population trajectories are increasing for almost all extant large-mammal species, mostly owing to the natural growth of remnant populations; supplementary re-introductions of buffalo, wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), and hippopotamus (*Hippopotamus amphibius*) have marginally augmented the overall numbers and may have added important genetic diversity. Scientists and parataxonomists affiliated with PNG are monitoring recovery dynamics and compiling species inventories through wildlife counts⁸³ and biodiversity surveys, and other researchers are investigating the legacies of war and restoration on species interactions and ecological processes^{75,84,85}.

As its wildlife communities reassemble, PNG has focused on establishing connections and interdependencies with local communities of people — especially the 175,000 residents of the 5,400-square-kilometre buffer zone that surrounds the park. More than 85% of the park's 500 permanent employees (and all of its 60–100 temporary employees) are recruited locally. Transportation and meals are provided for more than 2,500 local children on full-day educational visits each year (Fig. 3). Mobile teams of Mozambican health professionals, who are organized and funded by the Gorongosa Project but employed by the Mozambique Ministry of Health, implement the country's national rural healthcare strategy in the buffer zone; in 2016, these teams vaccinated more than 4,900 children, supplied more than 2,400 bed nets, treated more than 1,700 malaria cases and provided more than 1,700 prenatal consultations. Sixty-five community health workers from local villages supply information about family planning, contraceptives, and childhood-nutrition advice to thousands of households, in accordance with Mozambique's national policy. Four schools have been built. The Gorongosa Project provided agricultural and agroforestry assistance to some 4,000 smallholders in 2016, and it pays market prices to buy surplus maize and beans, which it can later sell back to farmers, if necessary, to mitigate the impacts of climatic shocks and shortages. The project has granted scholarships to at least 12 young women and men, enabling them to pursue university degrees in fields such as agriculture, wildlife management, environmental history, and journalism. Project scientists are also partnering with Mozambican universities to develop a postgraduate programme in conservation biology.

The mixed success and many failings of previous attempts to integrate conservation and human development — especially in Africa — are well documented^{86,87}. Frequent criticisms of such interventions include: that local elites tend to corral resources and opportunities; that genuinely participatory community involvement is elusive; that top-down welfare programmes are often conceived and implemented with insufficient (and sometimes grossly distorted) understanding of existing livelihoods and resource-management strategies; that conservation measures have occasionally been exclusionary or punitive, provoking local resentment and resistance; and that initiatives often lack in-built mechanisms for sustainability and are therefore short-lived^{86,87}. These problems are easy to point out but hard to solve. The Gorongosa Project's exceptionally long duration (the initial 20-year agreement was extended by 25 years in 2016 (ref. 88)) and commitment to enabling the estimated 7,500 people who reside inside the park to continue to live there (in accordance with Mozambican and international law) may help to avoid these historical missteps. Also, the Gorongosa Project is collaborating with Mozambique's government, social scientists, and public-health professionals to conduct a comprehensive survey of households in the buffer zone, which aims to inform management policy and provide a baseline for gauging future progress towards human-development goals²⁸.

Ecological surveys in the 1960s highlighted the biological and hydrological importance of Mount Gorongosa, an isolated 1,800-metre massif that supports Afromontane forests and ancient grasslands, which generates orographic rainfall that feeds streams that flow into PNG⁷⁹. As well as supplying people with fresh water, these inflows drive seasonal flooding of the park's Lake Urema, which in turn creates rich grasslands that sustain the park's wildlife. In 2010, the park was expanded to include all parts of Mount Gorongosa above an elevation of 700 metres; simultaneously, a densely settled 14-square-kilometre sliver of land in the northwest part of the park was excised. This swap — effectively, an application of the 'trade-in to trade-up' strategy^{20,51} — yielded a net expansion of 353 square kilometres, providing legal protection for regionally rare ecosystems and endemic plant, lizard, and crustacean species (and probably also for migrant species, as in the ACG). Considerable potential exists for the further growth of PNG, which could ultimately connect the park with the 1,500-square-kilometre coastal Marromeu National Reserve and the River Zambezi, by upgrading the conservation status of several sparsely populated, privately leased concessions and linking the areas with corridors (Fig. 2). Planning is already under way to upgrade Coutada 12, a 2,000-square-kilometre private hunting reserve, which would enlarge the park by 50%⁸⁹.

Although PNG's \$9-million annual budget is still supplied by a consortium of donors, the park's co-management agreement envisages a transition towards a self-sustaining financial model that is underpinned by nature-based tourism. Realizing this vision will require the continued recovery of large-mammal populations, the repatriation of the still-absent apex carnivore species, political stability, continued economic and infrastructural development and, above all, the solidification of a truly mutualistic symbiosis between the park and its human neighbours. These aims are imperilled by a number of threats, including: illegal snaring that threatens wildlife populations; current and future human-wildlife conflicts between local farmers and crop-raiding elephants; and high rates of infant mortality, childhood malnutrition, illiteracy, malaria, and other sequelae of poverty. To these ends, the Gorongosa Project harnesses financial and intellectual inputs from a diverse array of collaborators — most importantly, Mozambique's government, which recognized the crucial links between conservation and rural well-being by transferring the oversight of the national parks from the Ministry of Tourism into the Ministry of Land, Environment and Rural Development in 2015. International aid from the United States, Portugal, Norway, and Ireland has supported agriculture, healthcare, technical training, and after-school programmes that aim to sustain girls' attendance. Researchers from 36 institutions in 13 countries have channelled diverse sources of funding towards understanding the ecology of PNG, and the US Howard Hughes Medical Institute has invested \$2.4 million in science education to boost local capacity. Also, the Rizwan Adatia Foundation of India has initiated a 200-shop microfinance programme in buffer-zone communities.

The eight pillars of upgrading protected areas

Despite disparate socio-ecological contexts and challenges, the architects of restoration in the ACG and PNG have converged on common philosophies and approaches. From these similarities emerge eight general principles that can be used to guide future conservation efforts elsewhere.

Protect remaining refuges and harness nature's resilience

Nature can heal its wounds remarkably quickly once the assault has stopped — if enough remains of the original to provide a source of propagules⁵⁴. Full convalescence may take centuries, some indelible scars will remain, and some functions may be permanently impaired. Yet, just as a person who has recovered from a life-threatening injury is no less the same person, a rehabilitated ecosystem is no less the same ecosystem. Systemic recovery becomes slower and less probable the more pieces that are lost, and the loss of certain vital organisms will doom the system. But in general, restoration will be possible despite some amount of prior population extinction, and techniques for the transplantation of vital

organisms are increasingly well developed⁹⁰. In any case, the absence of some historically present species does not overly tarnish the value of a recovered ecosystem — just as the Venus de Milo, an ancient Greek statue that was reassembled from fragments, is disarmingly beautiful despite the loss of the apple she once held.

Importantly, initiating ecological recovery in both the ACG and PNG required neither aggressive micromanagement nor profound technical ingenuity, owing to the persistence of remnant population sources in the degraded matrix. Much of the toolkit for restoration ecology involves time-, labour-, and cost-intensive techniques that are prohibitive across thousands of square kilometres. At such scales, managers must act as facilitators for natural processes to do 99% of the work. Resources can therefore be conserved for crucial, surgical deployments. In the dry forest of the ACG, the restoration-enabling insight was the necessity of suppressing anthropogenic fires and reducing fuel loads, after which seed dispersal by wind and animals was sufficient to launch succession. This, in turn, reduced grass cover and attracted more seed-dispersing animals, generating a positive-feedback recovery loop. After 30 years,

the areas look, sound, and smell like forest because they are forest — not yet mature, but en route⁹¹. More laborious approaches can accelerate the restoration process⁵³; one experimental project involved dumping orange-peel waste from a nearby juice factory on abandoned pastures, which smothered grasses and decomposed into organic fertilizer, hastening succession⁵⁷.

Similarly, the act that initiated the restoration of PNG was the re-establishment of a protective human presence and the suppression of illegal hunting. The ensuing resurgence of wildlife has been driven by the natural growth of remnant populations. The considerable funds required for long-distance reintroductions of large animals can therefore be reserved for species that might not otherwise be able to re-establish — for example, zebras (Fig. 2) and the extirpated carnivore species — or to accelerate the recovery of particular functions (for example, the top-down control of herbivore populations). When little or no residual stock remains, mass rewilding can be successful: in South Africa's Madikwe Game Reserve, 23 species of large herbivore and carnivore were introduced in the mid-1990s at a cost of US\$3 million (ref. 92).

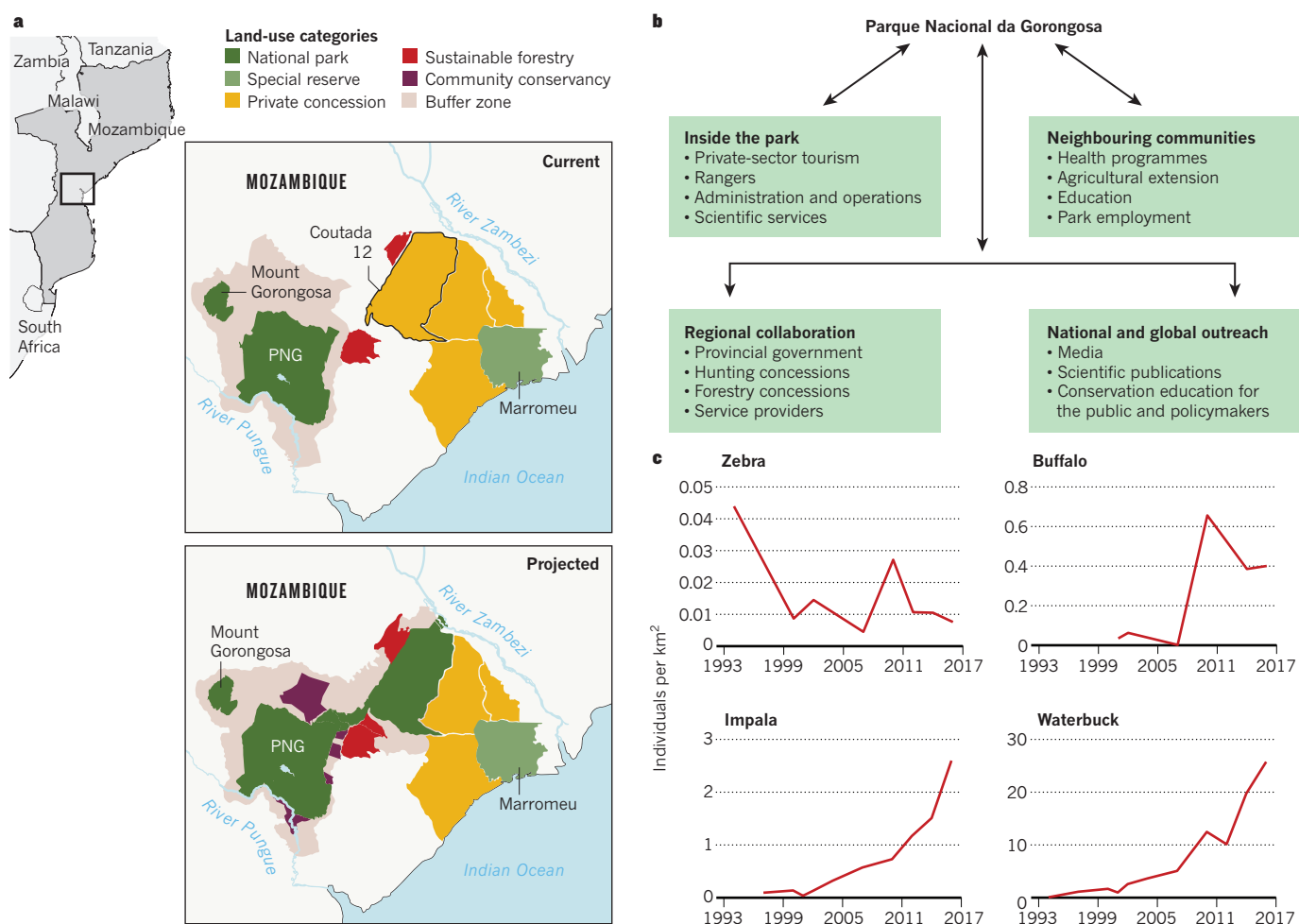


Figure 2 | Parque Nacional da Gorongosa in Mozambique. **a**, Current (top) and envisaged future (bottom) land-use scenarios in the Sofala province of Mozambique, which show the planned expansion and enhanced connectivity of Parque Nacional da Gorongosa (PNG) and various peripheral conservation and development activities. The future scenario links and embeds major ecological features (the coast, rivers Zambezi and Pungue, Rift Valley, and Mount Gorongosa) in a large mosaic of biodiversity-friendly land uses that will be more robust to increases in human population density during the coming century. **b**, Model of PNG as an engine that couples biodiversity conservation with sustainable human and economic development across scales. At the local scale (top boxes), PNG employs people to manage the park and its infrastructure, to host and guide its visitors, and to protect and study its wildlife. Most of these people are recruited from neighbouring communities

in the buffer zone, where PNG also serves its local constituencies through agricultural, health, and education programmes. At the regional scale, PNG collaborates with diverse public- and private-sector constituencies in Sofala province. At national and international scales, PNG generates media products that help to inform and inspire its global constituencies. The bidirectional arrows signify that all of these activities feed back positively to reinforce PNG and its conservation and human-development missions. **c**, Population-density trajectories for several species of wildlife since the end of the civil war in Mozambique in 1992, estimated in a 183-square-kilometre block surrounding Lake Urema in PNG. Zebra is the only large-herbivore species with a downward trend in density during this interval. Buffalo was the most abundant large-herbivore species before the war, whereas waterbuck (*Kobus ellipsiprymnus*) has increasingly dominated in the post-war era.



Figure 3 | Biological education in Gorongosa National Park. Members of the Nhamatanda Environmental Club meet a lion that was immobilized as part of the Gorongosa Lion Project's conservation programme. Image credit: P. Bouley.

Upsize and interconnect

The ACG and PNG highlight how protected areas can be grown strategically as they are restored to achieve greater ecological integrity and connectivity, as well as how boundaries can be selectively redrawn to make such expansion more politically and socially palatable. In the ACG, parcels of land purchased by GDFCF have plugged key gaps between three national parks. The result is a large and ecologically coherent whole that extends from the pelagic zone of the Pacific Ocean to the volcanic slopes that lie 50 kilometres inland (Fig. 1). In PNG, the anticipated incorporation of Coutada 12 represents a giant step towards linking the park to the Marromeu National Reserve, opening the door for a protected area that stretches more than 200 kilometres from the mangroves of the Indian Ocean to the western slopes of Mount Gorongosa (Fig. 2). Given the importance of cross-ecosystem subsidies and fluxes⁹³ and of coastal ecosystems for people's livelihoods⁹⁴, it is worth pursuing the expansion of terrestrial protected areas into the oceans and vice versa.

This approach is incremental and opportunistic; it forsakes what is optimal for what is possible. Such grassroots efforts to upsize and connect existing protected areas do not obviate top-down global prioritization methods, and may not even compete with them. A growing protected area may confront alternative routes for expansion, at which point the geospatial tools of conventional systematic conservation planning may help to reveal the best-available option. And the often-invoked fact that conservation funding is finite does not imply that the resource pool is fixed; both the ACG and PNG show how funds can be marshalled from sources that do not have biodiversity conservation as their *raison d'être*.

However, it is reasonable to suppose that the political obstacles and transaction costs associated with the piecemeal upsizing of protected areas will generally be lower than those of creating *de novo* protected areas. Existing protected areas will benefit from their established legal basis (such that expansion may require merely the amendment of laws rather than the creation of new ones), name recognition, social and political legitimacy, administrative infrastructure, and material assets. Also, expanding them requires fewer new boundaries to be established. All of these factors suggest that possibilities for the expansion of protected areas should be explicitly evaluated alongside opportunities for the creation of new reserves in efforts to prioritize conservation investments¹⁷.

Be long-term and local

The efforts in the ACG and PNG represent multidecadal commitments to single places. Such long-term monogamous marriages are necessary because meaningful large-scale ecological rehabilitation takes decades, as does the transition to institutional and financial self-reliance. Moreover, upgrading and upsizing protected areas requires persistent civic and political engagement, which in turn requires the development of sturdy social networks and trusting personal relationships. This poses a problem for large non-governmental organizations that engage in many projects in many places with transient rosters of employees. And this problem is compounded in complex charity ecosystems, in which fitness is measured in fundraising revenues and organizations with overlapping remits

must continually invent new ways to differentiate themselves from their competitors. In such cases, the survival and growth of organizations becomes an end in itself, inflating overhead costs and creating incentives that align poorly with the ostensible organizational mission. Donor fatigue and politician boredom are constant threats, and the surest way to avoid them is not to linger in one place for too long (which might suggest stagnation or, worse, failure) and to instead project dynamism and innovation by rolling out glossy new initiatives that redefine the cutting edge. Unfortunately, most conservation problems cannot be solved in five-year stands, and even long-term projects will struggle in the absence of long-term individuals. At the core of the efforts to restore the ACG and PNG are a small number of people who have made lifelong commitments to projects that will outlast them, because the success of such projects is defined as perpetuity and perpetuity is never guaranteed.

Being local is a corollary to being long-term. The director and all employees of the ACG are Costa Ricans, and the warden and most employees of the Gorongosa Project are Mozambicans. Foreign participants must earn local legitimacy through an extended physical presence, conversance in local customs and languages, kindness, humility, promise keeping, and willingness to eventually be made redundant. None of this happens overnight.

Pay the opportunity costs

It is now axiomatic that conservation cannot succeed without the cooperation, participation, and engagement of neighbouring communities and local stakeholders, although the precise meaning of these phrases is not always clear from the way they are invoked in the literature. Protected areas must try to negotiate a respected place in society, and their most important constituencies are: people living in or drawing their livelihoods from the protected area or any adjacent areas over which the protected area exerts influence (for example, the buffer zone of PNG); regional society (people living in the same district or provincial jurisdiction as the protected area); and national society. Global society also has a stake in the survival of protected areas and their biodiversity⁹⁵ and must contribute resources and expertise towards those goals, but it is not the stratum to which a protected area must ultimately justify its existence.

The opportunity costs of conservation must be paid to each of these constituencies in different currencies, and the appropriate currency for each is context dependent. Accordingly, PNG tends its local relationships with people who live in the buffer zone by providing them with access to the park, offering agricultural extension and healthcare, sharing revenues, and attempting to foster a sense of collective ownership and responsibility. At the regional level of Sofala province, the park builds support in Vila Gorongosa (the nearest town) and Beira (the nearest city) by sourcing supplies from, and routing tourists through, local businesses. And at the national level, the park pays its opportunity costs by being an internationally visible symbol of Mozambique's splendour and its government's forward-thinking approach to environmental management; politicians are encouraged to view the park's success as their own — which, of course, it is. The ACG conducts many similar activities

with and for its constituencies in Costa Rica.

None of these considerations implies that a protected area can please all of its constituents at all times. This truism bears repeating because many criticisms of conservation initiatives from the humanities and social sciences have used interviews with a handful of informants as the basis for concluding that protected areas subvert the rights and well-being of the rural poor⁹⁶. A growing body of more systematic, quantitative research suggests that protected areas generally distribute more fortune than misfortune to neighbouring people^{26,27,42,94}.

Develop creative financial strategies

Although protected areas pay their opportunity costs in diverse currencies, they must pay employees with money, and any expansion requires funds for land purchase and legal fees. The ACG and PNG show how heterogeneous and ingenious financing can drive the upgrading of protected areas. Although the specific mechanisms differ between these efforts, as well as through time within each, both were built around public–private partnerships — facultative mutualisms between governments and non-profit organizations that channel intellectual and financial capital towards the revitalization and growth of protected areas.

In the mid-1980s, the nascent ACG cobbled together its first \$1 million in donations for land purchase, management, and biological education from US-based charitable foundations and private individuals from six countries. It also accepted donations of land from local ranches, won matching funds from the government of Costa Rica under president Óscar Arias, and parlayed a \$3.5-million grant from Sweden into \$17 million of local currency through a ‘debt-for-nature’ swap — some of which was used to establish the area’s pioneering endowment⁶⁰. Since then, sources of finance have included payments for climate-change mitigation through avoided deforestation and other ecosystem services, as well as a steady stream of gifts from mostly repeat donors. Support has also come from the Japan International Cooperation Agency for biological monitoring of a geothermal development adjacent to the ACG. From 1985 to 2017, the ACG has raised a total of \$105 million, including a still-growing endowment of \$14 million that is central to the long-term self-sufficiency of essential programmes that are not covered by the government’s annual allocation.

In PNG, the Mozambique government’s appropriation is designated for equipping rangers; the rest of the budget is supplied by the Gorongosa Project, which is backed by ten major donors and scores who have made smaller contributions. Some of these backers provide general budget support, whereas others provide restricted funds for conservation, science, education, agriculture, or health programmes. In this way, the philanthropic input of the largest donor (the Carr Foundation, \$3 million in 2017) is leveraged threefold. In time, it is hoped that fees from private-sector tourism will constitute an ever-greater share of the park’s budget, contributing towards long-term fiscal sufficiency.

Public–private partnerships for the co-management of protected areas are a powerful instrument with widespread applicability, as is attested by successes elsewhere. For example, in Madikwe Game Reserve in South Africa, which was established more for socio-economic reasons than for biodiversity conservation *per se*, private-sector tourism was charged with funding management and community-development programmes⁹². Yet, like every other mechanism used for conservation, public–private partnership is a regular bullet, not a silver one — and it can be dangerous if misused. In developing countries, such partnerships introduce the risk of privatized sovereignty and extralegal abuses; in developed countries, they could provide an excuse for governments to abnegate responsibility for conservation. And tourism-based portfolios result in budget shortfalls when initial projections prove over-optimistic (as occurred in Madikwe) or when financial or geopolitical shocks dampen demand.

Know thy biodiversity

A protected area without an inventory of its resident species is like a library without a catalogue, a supermarket of unlabelled cans, and a

museum with all of its artwork piled in the basement. This condition undermines not only the ability of protected areas to provide intellectual, recreational, and material services, but also any pretence of science-based management. None of Earth’s large protected areas has a comprehensive list of its macroscopic species, but this is a long-term goal of both the ACG and PNG. Throughout the ACG, full-time parataxonomists collect and catalogue insects, plants, marine invertebrates, and other taxa. These efforts have yielded transformative scientific advances: the 35-year-long inventory of plant–caterpillar–parasitoid food webs, coordinated by Janzen and Hallwachs, was fundamental to the development and widespread adoption of DNA barcodes for species identification and ecological analysis. Incorporating DNA barcoding into this inventory has revealed thousands of cryptic species and shown that the degree of specialization in these food-web networks outstrips anything previously suggested^{97–101}.

Be adaptable

There is no one-size-fits-all recipe for upgrading protected areas. What is exportable is the game plan and the playbook (with plenty of blank pages at the end for new additions), but not the sequence of plays that should be called — the smart move depends on the context. What is the score? Who or what is the ‘opposition’? How much time remains?

Such context-dependent thinking is second nature to sports coaches, but it runs counter to the current of academic science, in which sweeping generalizations are highly prized and good ideas are therefore often overextended. In the process of adapting to continuously evolving circumstances and opportunities, the restoration architects of the ACG and PNG have blended diverse lineages of contemporary thinking on conservation (as well as pioneered new ones). Both projects exemplify the inclusive conservation that commentators have called for¹⁰². Should protected areas be conserved for their intrinsic value or their instrumental value? Leave that to the user. That protected areas deliver clean drinking water to large downstream populations⁷ does not diminish the experience of birdwatchers. Should parks be maintained to benefit people, or to benefit biodiversity? The answer is yes. The alleviation of poverty is both a motivation for resuscitating protected areas and a practical necessity for any dream of conservation in perpetuity.

Involve young people

The education programmes in the ACG and PNG recognize that the only way to create a bioliterate populace⁶⁸ and reawaken dormant biophilia¹⁰³ is to stimulate children’s interest in nature as early and as often as possible⁶⁷ (Figs 1 and 3). The need to play the long game — which only grows harder as realities grow ever-more virtual — is yet another reason why projects to upgrade protected areas require multidecadal timescales and robust biodiversity inventories.

An agenda for research and action

Given the need both to expand the coverage of protected areas and to improve the performance of existing protected areas, how and where should conservationists prioritize investment? Answering this question will require fresh research on several fronts.

First, as outlined previously, the strongest candidates for upgrading will be protected areas that are: ecologically damaged but still retain sufficient residual stock to reseed the degraded matrix; situated in landscapes or seascapes that have room for growth into relatively undeveloped and sparsely populated surroundings through the acquisition of private land or linkage with other protected areas; underfinanced or ineffectively managed but associated with governments that have the incentive to invest in protected areas. Codifying and quantifying these criteria will help to prioritize opportunities for protected-area upgrading. To achieve this, we require comprehensive data on the performance of protected areas — a periodically updated paper-park index — that includes assessments of the severity of ecological degradation, administrative capacity, and funding inputs relative to needs. Initiatives such as the Global Database of Protected Area Management Effectiveness³⁰ might ultimately serve this purpose. Reliable indicators of ecological resilience would also help, as suggested for

guiding the incorporation of degraded coral reefs into marine protected areas¹⁰⁴. Armed with such information, existing modelling frameworks and data sets used in setting conservation priorities^{11,16,20} can be adapted to rank existing protected areas according to their potential for successful interventions. Emerging technologies such as biodiversity monitoring through remote-sensing¹⁰⁵ and environmental DNA¹⁰⁶ will enable the increasingly real-time assessment of ecological integrity so that priorities can be set on the basis of current information.

Second, we need to know more about the socio-economic dimensions associated with the establishment and maintenance of successful protected areas, which are difficult to quantify at large scales²⁴. Is it true, as I have proposed in this Perspective, that the transaction costs and political hurdles associated with expanding protected areas will generally be lower than those of creating new protected areas? To what extent do these considerations compensate for the fact that already-established protected areas will typically have less latitude along which to optimize their growth with respect to the distribution of biodiversity?

Last, how can the upgrading of protected areas be implemented at a scale that is sufficient to close the gaps between the Aichi Biodiversity Targets and the forecasts of continued biodiversity decline⁵? Ultimately, the most important ingredient is the existence of willing governmental partners, which means that implementing these pillars will be heavily driven by opportunity. However, there is the potential to establish a positive-feedback cycle: as a greater number of successful case studies are pioneered, the more reference points we will have for what does and doesn't work in various socioecological contexts, the more attractive such projects will seem to risk-averse policymakers, and the more opportunities will emerge. To this end, we need to conduct more innovative experiments in protected-area rehabilitation. In an age of unprecedented accumulation of private wealth, there is also an unprecedented opportunity for creative partnership across public and private sectors to secure a future for Earth's ecosystems and biodiversity. ■

Received 24 February; accepted 9 April 2017.

- Barnosky, A. D. *et al.* Has the Earth's sixth mass extinction already arrived? *Nature* **470**, 51–57 (2012).
- Ceballos, G. *et al.* Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).
- Pimm, S. L., Jenkins, C. N., Abell, R. & Brooks, T. M. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246–1252 (2014).
- Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
- Tittensor, D. P. *et al.* A mid-term analysis of progress toward international biodiversity targets. *Science* **346**, 241–244 (2014).
- Hoffmann, M. *et al.* The impact of conservation on the status of the world's vertebrates. *Science* **330**, 1503–1509 (2010).
- Watson, J. E. M., Dudley, N., Segan, D. B. & Hockings, M. The performance and potential of protected areas. *Nature* **515**, 67–73 (2014).
This review of the history and effectiveness of protected areas proposes that conservationists should refocus on establishing large, connected, well-funded, and well-managed protected areas.
- Naughton-Treves, L., Holland, M. B. & Brandon, K. The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu. Rev. Env. Resour.* **30**, 219–252 (2005).
- Ricketts, T. H. *et al.* Pinpointing and preventing imminent extinctions. *Proc. Natl Acad. Sci. USA* **102**, 18497–18501 (2005).
- Runge, C. A. *et al.* Protected areas and global conservation of migratory birds. *Science* **350**, 1255–1258 (2015).
- Jenkins, C. N., Van Houtan, K. S., Pimm, S. L. & Sexton, J. O. US protected lands mismatch biodiversity priorities. *Proc. Natl Acad. Sci. USA* **112**, 5081–5086 (2015).
- Pouzols, F. M. *et al.* Global protected area expansion is compromised by projected land-use and parochialism. *Nature* **516**, 383–386 (2014).
- Convention on Biological Diversity (CBD). *COP 10 Decision X/2: Strategic Plan for Biodiversity 2011–2020* (CBD, 2011).
- Margules, C. R. & Pressey, R. L. Systematic conservation planning. *Nature* **405**, 243–253 (2000).
This landmark review spawned a field of research that uses geospatial tools, global data sets, and algorithmic software to prioritize conservation actions.
- Rodrigues, A. S. L. *et al.* Effectiveness of the global protected area network in representing species diversity. *Nature* **428**, 640–643 (2004).
- Wilson, K. A., McBride, M. F., Bode, M. & Possingham, H. P. Prioritizing global conservation efforts. *Nature* **440**, 337–340 (2006).
- Venter, O. *et al.* Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* **12**, e1001891 (2014).
- Joppa, L. N., Visconti, P., Jenkins, C. N. & Pimm, S. L. Achieving the convention on biological diversity's goals for plant conservation. *Science* **341**, 1100–1103 (2013).
- Wilson, K. A. *et al.* Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biol.* **5**, e223 (2007).
- Fuller, R. A. *et al.* Replacing underperforming protected areas achieves better conservation outcomes. *Nature* **466**, 365–367 (2010).
Scrapping cost-ineffective protected areas and reallocating the funds can increase the efficiency and ecological value of conserved lands without increasing overall spending.
- McCarthy, D. P. *et al.* Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. *Science* **338**, 946–949 (2012).
- Conde, D. A. *et al.* Opportunities and costs for preventing vertebrate extinctions. *Curr. Biol.* **25**, R219–R221 (2015).
- Mollanen, A., Wilson, K. A. & Possingham, H. P. *Spatial Conservation Prioritization* (Oxford Univ. Press, 2009).
- Watson, J. E. M. *et al.* Bolder science needed now for protected areas. *Conserv. Biol.* **30**, 243–248 (2016).
- Ferraro, P. J. & Pattanayak, S. K. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biol.* **4**, e105 (2006).
- Naughton-Treves, L., Alix-Garcia, J. & Chapman, C. A. Lessons about parks and poverty from a decade of forest loss and economic growth around Kibale National Park, Uganda. *Proc. Natl Acad. Sci. USA* **108**, 13919–13924 (2011).
- Ferraro, P. J., Hanauer, M. M. & Sims, K. R. E. Conditions associated with protected area success in conservation and poverty reduction. *Proc. Natl Acad. Sci. USA* **108**, 13913–13918 (2011).
- Ferraro, P. J. & Pressey, R. L. Measuring the difference made by conservation initiatives: protected areas and their environmental and social impacts. *Phil. Trans. R. Soc. B* **370**, 20140270 (2015).
- Craigie, I. D., Barnes, M. D., Geldmann, J. & Woodley, S. International funding agencies: potential leaders of impact evaluation in protected areas? *Phil. Trans. R. Soc. B* **370**, 20140283 (2015).
- Coad, L. *et al.* Measuring impact of protected area management interventions: current and future use of the Global Database of Protected Area Management Effectiveness. *Phil. Trans. R. Soc. B* **370**, 20140281 (2015).
This paper describes progress towards a worldwide evaluation of the performance of protected areas.
- Visconti, P., Bakkenes, M., Smith, R. J., Joppa, L. & Sykes, R. E. Socio-economic and ecological impacts of global protected area expansion plans. *Phil. Trans. R. Soc. B* **370**, 20140284 (2015).
- Leverington, F., Costa, K. L., Paveze, H., Lisle, A. & Hockings, M. A global analysis of protected area management effectiveness. *Environ. Manage.* **46**, 685–698 (2010).
- Geldmann, J. *et al.* Changes in protected area management effectiveness over time: a global analysis. *Biol. Conserv.* **191**, 692–699 (2015).
- Geldmann, J. *et al.* Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* **161**, 230–238 (2013).
- Bruner, A. G., Gullison, R. E., Rice, R. E. & da Fonseca, G. A. Effectiveness of parks in protecting tropical biodiversity. *Science* **291**, 125–128 (2001).
- Hilborn, R. *et al.* Effective enforcement in a conservation area. *Science* **314**, 1266 (2006).
- Joppa, L. N., Loarie, S. R. & Pimm, S. L. On the protection of “protected areas”. *Proc. Natl Acad. Sci. USA* **105**, 6673–6678 (2008).
- Laurance, W. F. *et al.* Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**, 290–294 (2012).
- Gray, C. L. *et al.* Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Commun.* **7**, 12306 (2016).
- Joppa, L. N. & Pfaff, A. Global protected area impacts. *Proc. R. Soc. B* **278**, 1633–1638 (2011).
Matching analysis of protected and unprotected areas shows that legal protection has reduced landscape conversion in 75% of 147 countries.
- Barnes, M. D. *et al.* Wildlife population trends in protected areas predicted by national socio-economic metrics and body size. *Nature Commun.* **7**, 12747 (2016).
- Andam, K. S., Ferraro, P. J., Sims, K. R. E., Healy, A. & Holland, M. B. Protected areas reduced poverty in Costa Rica and Thailand. *Proc. Natl Acad. Sci. USA* **107**, 9996–10001 (2010).
Controlled matching methods reveal that protected areas in two very different countries had net positive effects on the livelihoods of local people.
- Balmford, A. *et al.* A global perspective on trends in nature-based tourism. *PLoS Biol.* **7**, e1000144 (2009).
Although a decline in the level of outdoor recreation in some developed countries has raised concerns, this study finds an increase in visits to protected areas in most countries, especially poorer ones.
- Maekawa, M., Lanjouw, A., Rutagarama, E. & Sharp, D. Mountain gorilla tourism generating wealth and peace in post-conflict Rwanda. *Nat. Resour. Forum* **37**, 127–137 (2013).
- Ogutu, J. O. & Owen-Smith, N. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol. Lett.* **6**, 412–419 (2003).
- Western, D., Russell, S. & Cuthill, I. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE* **4**, e6140 (2009).
- Craigie, I. D. *et al.* Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228 (2010).
This continent-scale analysis shows that populations of 69 wildlife species in 78 protected areas declined by an average of 59% between 1970 and 2005.

48. Di Minin, E. & Toivonen, T. Global protected area expansion: creating more than paper parks. *Bioscience* **65**, 637–638 (2015).
49. Mascia, M. B. & Pailler, S. Protected area downgrading, downsizing, and degazettement (PADD) and its conservation implications. *Conserv. Lett.* **4**, 9–20 (2010).
50. Mascia, M. B. *et al.* Protected area downgrading, downsizing, and degazettement (PADD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol. Conserv.* **169**, 355–361 (2014).
This study of Earth's most biodiverse regions finds 543 instances in which protected areas were shrunk or defanged, most often to facilitate industrial-scale extractive industry and development.
51. Kareiva, P. Conservation science: trade-in to trade-up. *Nature* **466**, 322–323 (2010).
52. Rodríguez, J. & Rodríguez-Clark, K. M. Even 'paper parks' are important. *Trends Ecol. Evol.* **16**, 17 (2001).
53. Chazdon, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458–1460 (2008).
54. Lamb, D., Erskine, P. D. & Parrotta, J. A. Restoration of degraded tropical forest landscapes. *Science* **310**, 1628–1632 (2005).
55. McAlpine, C. *et al.* Integrating plant- and animal-based perspectives for more effective restoration of biodiversity. *Front. Ecol. Environ.* **14**, 37–45 (2016).
56. Janzen, D. H. & Hallwachs, W. in *Costa Rican Ecosystems* (ed. Kappelle, M.) Ch. 10, 290–341 (Univ. Chicago Press, 2016).
An authoritative account of conservation history in Costa Rica's ACG.
57. Janzen, D. H. Costa Rica's Area de Conservación Guanacaste: a long march to survival through non-damaging biodevelopment. *Biodiversity* **1**, 7–20 (2000).
58. Janzen, D. H. in *Biodiversity* (ed. Wilson, E. O.) 130–137 (National Academy, 1988).
59. Janzen, D. H. Management of habitat fragments in a tropical dry forest: growth. *Ann. Mo. Bot. Gard.* **75**, 105–116 (1988).
60. Allen, W. *Green Phoenix: Restoring the Tropical Forests of Guanacaste, Costa Rica* (Oxford Univ. Press, 2001).
61. Janzen, D. H. & Hallwachs, W. DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservación Guanacaste, northwestern Costa Rica. *Genome* **59**, 641–660 (2016).
62. Smith, M. A., Hallwachs, W. & Janzen, D. H. Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography* **37**, 720–731 (2014).
63. Janzen, D. H. Tropical ecological and biocultural restoration. *Science* **239**, 243–244 (1988).
64. Janzen, D. H. & Hallwachs, W. in *Man and his Environment: Tropical Forests and the Conservation of Species* (ed. Marini-Bettò, G. B.) 227–255 (Pontificae Academiae Scientiarum, 1993).
65. Ehrlich, P. R. & Pringle, R. M. Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. *Proc. Natl Acad. Sci. USA* **105**, 11579–11586 (2008).
66. Adams, W. M. *et al.* Biodiversity conservation and the eradication of poverty. *Science* **306**, 1146–1149 (2004).
67. Soga, M. & Gaston, K. J. Extinction of experience: the loss of human–nature interactions. *Front. Ecol. Environ.* **14**, 94–101 (2016).
68. Janzen, D. H. Hope for tropical biodiversity through true bioliteracy. *Biotropica* **42**, 540–542 (2010).
69. Janzen, D. H. Now is the time. *Phil. Trans. R. Soc. B* **359**, 731–732 (2004).
70. Janzen, D. H. Setting up tropical biodiversity for conservation through non-damaging use: participation by parataxonomists. *J. Appl. Ecol.* **41**, 181–187 (2004).
71. Schmiedel, U. *et al.* Contributions of paraecologists and parataxonomists to research, conservation, and social development. *Conserv. Biol.* **30**, 506–519 (2016).
72. Janzen, D. H. & Hallwachs, W. Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. *PLoS ONE* **6**, e18123 (2011).
73. Basurto, X. Bureaucratic barriers limit local participatory governance in protected areas in Costa Rica. *Conserv. Soc.* **11**, 16–28 (2013).
74. Finnegan, W. *A Complicated War: the Harrowing of Mozambique* (Univ. California Press, 1993).
75. Daskin, J. H., Stalmans, M. & Pringle, R. M. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *J. Ecol.* **104**, 79–89 (2016).
76. Pringle, R. M. How to be manipulative: intelligent tinkering is key to understanding ecology and rehabilitating ecosystems. *Am. Sci.* **100**, 30–37 (2012).
77. Cumming, D. H. M., Mackie, C. S., Magane, S. & Taylor, R. D. *Aerial Census of Large Herbivores in the Gorongosa National Park and the Marrombeu Area of the Zambezi Delta in Mozambique* (Direcção Nacional de Florestas e Fauna Bravia, 1994).
78. Dutton, P. A dream becomes a nightmare: Mozambique's ferocious 15-year bush war has devastated a once rich and abundant wildlife. *Afr. Wildlife* **48**, 6–14 (1994).
79. Tinley, K. L. *Framework of the Gorongosa Ecosystem, Mozambique*. PhD thesis, Univ. Pretoria (1977).
This exquisite 320-page study documents the ecology of PNG from 1968 to 1972, providing a benchmark for post-war restoration efforts.
80. Dunham, K. M. *Aerial Survey of Large Herbivores in Gorongosa National Park, Mozambique: 2004* (Carr Foundation, 2004).
81. Governo da República de Moçambique & Parque Nacional da Gorongosa. *Acordo de Gestão Conjunta do Parque Nacional da Gorongosa. Entre O Governo da República de Moçambique, Representado Pelo Ministério do Turismo E A Gregory C. Carr Foundation*. http://www.gorongosa.org/sites/default/files/research/acordo_gestao_conjunta_do_parque_nacional_da_gorongosa.pdf (2008).
The legal contract establishing the public–private partnership for the co-management of PNG (in Portuguese).
82. Ford, A. T. *et al.* Large carnivores make savanna tree communities less thorny. *Science* **346**, 346–349 (2014).
83. Stalmans, M. *Monitoring the Recovery of Wildlife in the Parque Nacional da Gorongosa through Aerial Surveys* http://www.gorongosa.org/sites/default/files/research/053-wildlife_count_report_2000_2012_july2012.pdf (2012).
84. Rodríguez-Echeverría, S. *et al.* Arbuscular mycorrhizal fungi communities from tropical Africa reveal strong ecological structure. *New Phytol.* **213**, 380–390 (2017).
85. Correia, M., Timóteo, S., Rodríguez-Echeverría, S., Mazars-Simon, A. & Heleno, R. Refaunation and the reinstatement of the seed-dispersal function in Gorongosa National Park. *Conserv. Biol.* **31**, 76–85 (2016).
86. West, P., Igoe, J. & Brockington, D. Parks and peoples: the social impact of protected areas. *Annu. Rev. Anthropol.* **35**, 251–277 (2006).
87. Chan, K. *et al.* When agendas collide: human welfare and biological conservation. *Conserv. Biol.* **21**, 59–68 (2007).
88. Torchia, C. Recovering from war, Mozambican park again faces conflict. *AP News* <http://bigstory.ap.org/article/0a6acdd9e6bb4080b4fe1b9586dc96a7/recovering-war-mozambican-park-again-faces-conflict> (18 December 2016).
89. Club of Mozambique. Gorongosa Park signs agreement with Entrepósito to convert game reserve into protected area. *Club of Mozambique* [http://clubofmozambique.com/news/gorongosa-park-signs-agreement-entreposto-convert-game-reserve-protected-area/](http://clubofmozambique.com/news/gorongosa-park-signs-agreement-entrepосто-convert-game-reserve-protected-area/) (1 December 2016).
90. Seddon, P. J., Griffiths, C. J., Soora, P. S. & Armstrong, D. P. Reversing defaunation: restoring species in a changing world. *Science* **345**, 406–412 (2014).
91. Powers, J. S., Becknell, J. M., Irving, J. & Pérez-Aviles, D. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *For. Ecol. Manage.* **258**, 959–970 (2009).
92. Davies, R. in *Wildlife Conservation by Sustainable Use* (eds Prins, H. H. T., Grootenhuys, J. G. & Dolan, T. T.), 439–458 (Springer, 2000).
93. Nakano, S. & Murakami, M. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl Acad. Sci. USA* **98**, 166–170 (2001).
94. McNally, C. G., Uchida, E. & Gold, A. J. The effect of a protected area on the tradeoffs between short-run and long-run benefits from mangrove ecosystems. *Proc. Natl Acad. Sci. USA* **108**, 13945–13950 (2011).
95. Pringle, R. M. The Nile perch in Lake Victoria: local responses and adaptations. *Africa* **75**, 510–538 (2005).
96. Schuetz, C. Narrative fortresses: crisis narratives and conflict in the conservation of Mount Gorongosa, Mozambique. *Conserv. Soc.* **13**, 141–153 (2015).
97. Hebert, P. D. N., Penton, E. H., Burns, J. M., Janzen, D. H. & Hallwachs, W. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Natl Acad. Sci. USA* **101**, 14812–14817 (2004).
98. Smith, M. A., Wood, D. M., Janzen, D. H., Hallwachs, W. & Hebert, P. D. N. DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera: Tachinidae) are not all generalists. *Proc. Natl Acad. Sci. USA* **104**, 4967–4972 (2007).
99. Smith, M. A., Woodley, N. E., Janzen, D. H., Hallwachs, W. & Hebert, P. D. N. DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). *Proc. Natl Acad. Sci. USA* **103**, 3657–3662 (2006).
This study integrates DNA barcoding, biodiversity inventory, and morphological taxonomic analysis to discover hundreds of undescribed cryptic species and their highly host-specific food-web interactions.
100. Smith, M. A. *et al.* Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proc. Natl Acad. Sci. USA* **105**, 12359–12364 (2008).
101. Burns, J. M., Janzen, D. H., Hajibabaei, M., Hallwachs, W. & Hebert, P. D. N. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. *Proc. Natl Acad. Sci. USA* **105**, 6350–6355 (2008).
102. Tallis, H. & Lubchenco, J. Working together: A call for inclusive conservation. *Nature* **515**, 27–28 (2014).
103. Wilson, E. O. *Biophilia* (Harvard Univ. Press, 1986).
104. Abelson, A. *et al.* Expanding marine protected areas to include degraded coral reefs. *Conserv. Biol.* **30**, 1182–1191 (2016).
105. Jetz, W. *et al.* Monitoring plant functional diversity from space. *Nature Plants* **2**, 16024 (2016).
106. Handley, L. L. How will the 'molecular revolution' contribute to biological recording? *Biol. J. Linn. Soc.* **115**, 750–766 (2015).

Acknowledgments Figs 1 and 2 were based on designs created by Terra Communications. D. Janzen, W. Hallwachs, W. Sandoval, M. Mutumucio, D. Muala, M. Stalmans, G. Carr, J. Daskin, M. Jordan, P. Naskrecki, P. Bouley and C. Tarnita supplied information, graphics, or comments that were crucial to the preparation of this article. I thank the following organizations for support: the US National Science Foundation (DEB-1355122, DEB-1457697), the Princeton Environmental Institute, Princeton's Innovation Fund for New Ideas in the Natural Sciences, and the Gorongosa Project.

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Reviewer Information Nature thanks L. Joppa and the other anonymous reviewer(s) for their contribution to the peer review of this work.