PRIMATOLOGY

Impending extinction crisis of the world's primates: Why primates matter

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Nonhuman primates, our closest biological relatives, play important roles in the livelihoods, cultures, and religions of many societies and offer unique insights into human evolution, biology, behavior, and the threat of emerging diseases. They are an essential component of tropical biodiversity, contributing to forest regeneration and ecosystem health. Current information shows the existence of 504 species in 79 genera distributed in the Neotropics, mainland Africa, Madagascar, and Asia. Alarmingly, ~60% of primate species are now threatened with extinction and ~75% have declining populations. This situation is the result of escalating anthropogenic pressures on primates and their habitats—mainly global and local market demands, leading to extensive habitat loss through the expansion of industrial agriculture, large-scale cattle ranching, logging, oil and gas drilling, mining, dam building, and the construction of new road networks in primate range regions. Other important drivers are increased bushmeat hunting and the illegal trade of primates as pets and primate body parts, along with emerging threats, such as climate change and anthroponotic diseases. Often, these pressures act in synergy, exacerbating primate population declines. Given that primate range regions overlap extensively with a large, and rapidly growing, human population characterized by high levels of poverty, global attention is needed immediately to reverse the looming risk of primate extinctions and to attend to local human needs in sustainable ways. Raising global scientific and public awareness of the plight of the world's primates and the costs of their loss to ecosystem health and human society is imperative.

INTRODUCTION

Nonhuman primates (primates hereafter) are of central importance to tropical biodiversity and to many ecosystem functions, processes, and services. They are our closest living biological relatives, offering critical insights into human evolution, biology, and behavior and playing important roles in the livelihoods, cultures, and religions of many societies. Unsustainable human activities are now the major force driving primate species to extinction. Here, we combine the most frequently used standard for species conservation status [the International Union for Conservation of Nature (IUCN) Red List] with data from peer-reviewed scientific literature and from the United Nations databases to evaluate human-induced threats to primate survival. We examine trends in forest loss resulting from regional and global economic pressures and discuss the impacts of hunting, illegal trade, and other anthropogenic threats on primate populations. We also model agricultural expansion into the 21st century and identify expected spatial conflict within primate range areas. We assess the current level of scientific knowledge available for individual primate taxa, and we highlight the ecological, social, cultural, economic, and scientific importance of primates, as well as the global consequences of their population declines. We also consider future research needs and advances in technology for monitoring human-induced environmental changes that affect primate populations. Finally, we propose a conceptual

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model to guide the development of global, regional, and local approaches to promote primate conservation while at the same time attending to human needs. The goal of this review is not to produce a list of threats but rather to urge attention to the multiple global and regional anthropogenic factors that imperil primates worldwide and to encourage the development of sustainable and effective solutions that enhance primate survival in the medium and long term.

IMPENDING DEFAUNATION OF THE WORLD'S PRIMATES

The order Primates is one of the most species-rich groups of mammals, surpassed only by the orders Chiroptera (bats, 1151 species) and Rodentia (rodents, 2256 species) (*1*, *2*). The most recent taxonomic compilation (April 2016) lists 701 extant taxa belonging to 504 species from 79 genera and 16 families (tables S1 to S4 and Supplementary Text) (*2*–*5*). Primates occur in four regions—the Neotropics (171 species), mainland Africa (111 species), Madagascar (103 species), and Asia (119 species) (Fig. 1)—and are present naturally in 90 countries; however, two-thirds of all species occur in just four countries—Brazil, Madagascar, Indonesia, and the Democratic Republic of the Congo (DRC) (figs. S1 and S2A). These countries represent high-priority areas for primate conservation. The large majority of primates inhabit tropical moist lowland forests, but they also occur in tropical dry forests, mangrove vegetation above high-tide levels, moist montane forests, high-elevation (from 1000 to >4000 m) deciduous and broadleaf temperate forests, savannas, grasslands, inland wetlands, rocky areas, and even deserts (*2*, *4*). The body mass of living primates ranges from 30 g in Madame Berthe's mouse lemur (*Microcebus berthae*) to about 200 kg in male western and eastern gorillas (*Gorilla gorilla* and *Gorilla beringei*, respectively) (Supplementary Text) (*2*, *4*, *5*).

Using information from the IUCN and our current assessment, we estimate that ~60% of primate species, from all 16 extant families, are threatened with extinction because of unsustainable human activities (Figs. 1 and 2 and tables S1 to S4). Threats to primates are widespread: 87% of species in Madagascar are threatened, as are 73% in Asia, 37% in mainland Africa, and 36% in the Neotropics (Fig. 1 and figs. S2B and S3A). The populations of 75% of primate species are decreasing globally (Fig. 1 and fig. S3B). Considering the large number of species currently threatened and experiencing population declines, the world will soon be facing a major extinction event if effective action is not implemented immediately.

FACTORS THAT THREATEN PRIMATE POPULATIONS

The IUCN indicates that the main threats to primate species are loss of habitat due to agriculture (76% of species), logging and wood harvesting (60%), and livestock farming and ranching (31%), as well as direct loss due to hunting and trapping (60%) (fig. S4A). Other threats, such as habitat loss due to road and rail construction, oil and gas drilling, and mining, affect 2 to 13% of primate species, and there are also emerging threats, such as pollution and climate change (fig. S4B and table S5). Globally, agriculture is the principal threat, but secondary threats vary by region. For example, livestock farming and ranching negatively affect 59% of primate species in the Neotropics. In contrast, in mainland Africa, Madagascar, and Asia, hunting and trapping affect 54 to 90% of the

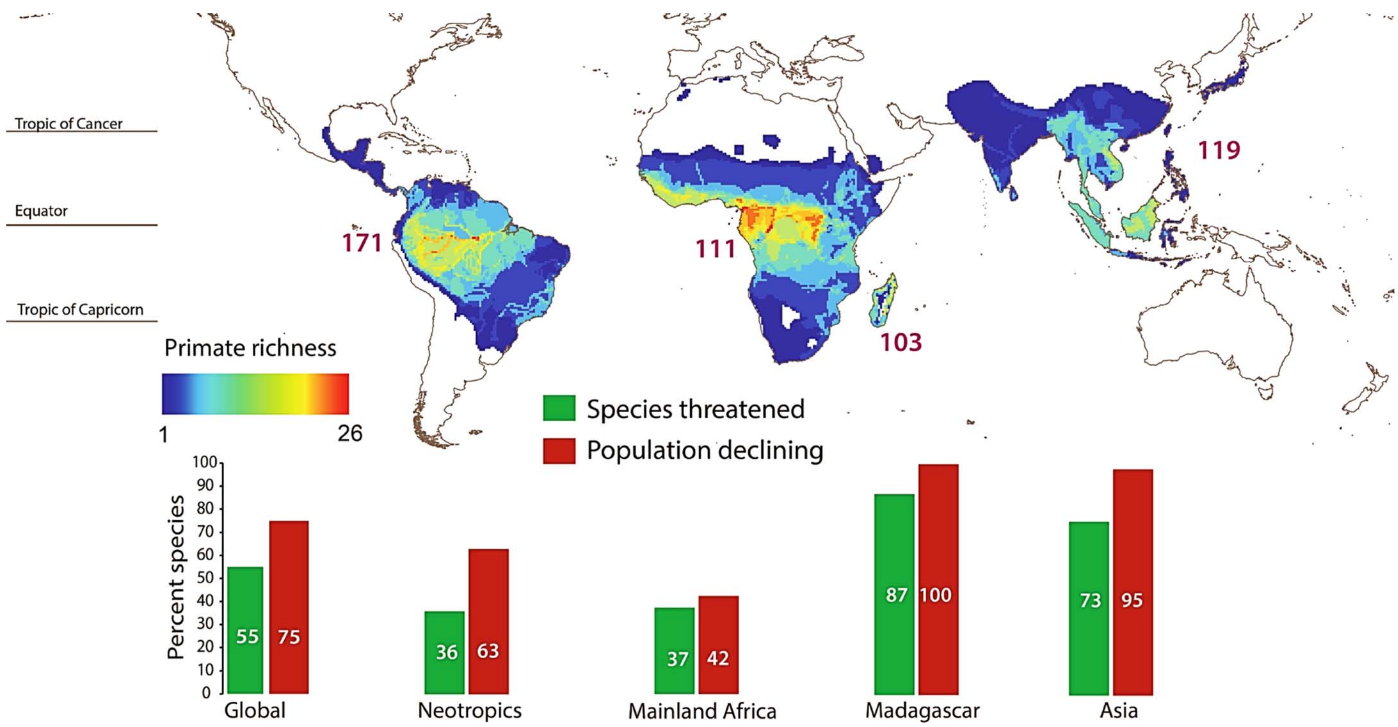

Fig. 1. Global primate species richness, distributions, and the percentage of species threatened and with declining populations. Geographic distribution of primate species. Numbers in red by each region refer to the number of extant species present. The bars at the bottom show the percent of species threatened with extinction and the percent of species with declining populations in each region. Percentage of threatened species and percentage of species with declining populations in each region from tables S1 to S4. Geographical range data of living, native species from the IUCN Red List (www.iucnredlist.org) are overlaid onto a 0.5° resolution equal-area grid. In cases in which a species' range was split into multiple subspecies, these were merged to create a range map for the species. Mainland Africa includes small associated islands.

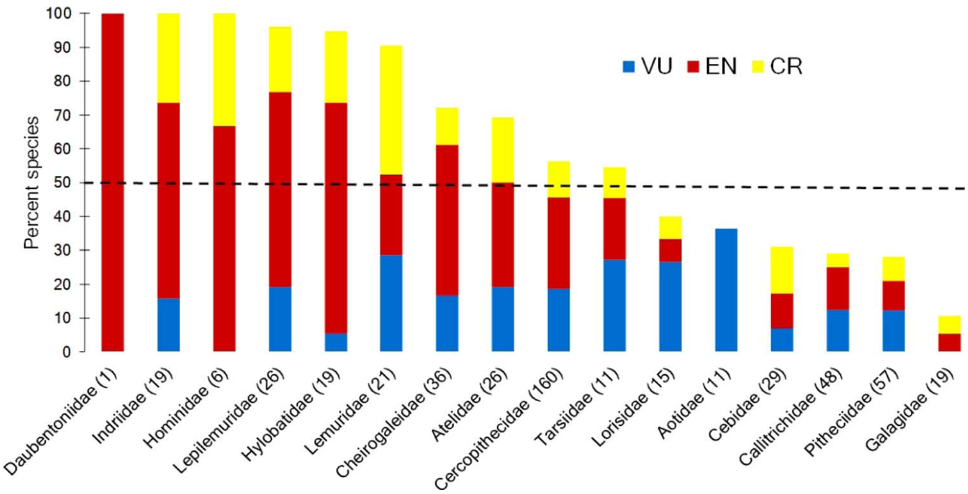

Fig. 2. Percent of species threatened with extinction in each primate family. Assessment of threat level is according to the IUCN Categories and Criteria VU (Vulnerable), EN (Endangered), and CR (Critically Endangered). Number in parentheses after each family indicates the number of species recognized in the family. Data for each species are indicated in tables S1 to S4. Notably, there are threatened species in all 16 primate families. Ten families have more than 50% of their species threatened (broken line at 50%). Note that the graph is only for the Threatened IUCN categories. Families not showing 100% values may have some species classified as Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE) (see tables S1 to S3). Upon revision of the taxonomy of Malagasy lemurs, a number of taxa once thought to be widespread are now highly threatened; a similar scenario is envisioned for the galagids, where there appears to be a large number of newly recognized species with limited ranges. Taxonomy is based on previous works (*1*–*3*).

species. Logging is the third greatest threat to primates in all regions (fig. S4A).

Land-cover changes, global market demands, and industry-driven deforestation

Global market demands for nonarboreal (for example, soybeans, sugar cane, and rice) and arboreal crops (for example, oil palm and natural rubber), livestock (particularly cattle), and tropical hardwoods have resulted in a process of rapid and widespread industry-driven deforestation in the Neotropics, mainland Africa, Madagascar, and Asia (Supplementary Text and fig. S5, A to F) (*6*). For example, between 1990 and 2010, agricultural expansion in primate range regions was estimated at 1.5 million km^2 (an area three times that of France) and forest cover loss at 2 million km^2 (Fig. 3 and fig. S6, A to C). Increasing global demand for oil palm products is a major driver of recent severe declines in Sumatran and Bornean orangutan (*Pongo abelii* and *Pongo pygmaeus*, respectively) numbers and a serious risk for African apes because large segments of existing populations occur outside protected areas (*7*–*10*). Moreover, future oil palm development is likely to threaten forested areas in South America and Africa (*10*), which is projected to result in severe negative consequences for primate populations in those regions (fig. S5C). The expansion of rubber plantations in southwest China has caused the near extinction of the northern white-cheeked crested gibbon (*Nomascus leucogenys*) and the Hainan gibbon (*Nomascus hainanus*) (*11*). Similarly, deforestation due to the establishment of rubber plantations in India is reported to have severely affected the Bengal slow loris (*Nycticebus bengalensis*), the western hoolock gibbon (*Hoolock hoolock*), and Phayre's langur (*Trachypithecus phayrei*) (*11*, *12*). Modeling the overlap between primate species' distributions and forecasted future agricultural production for the 21st century indicates that regions predicted to undergo the greatest agricultural expansion over the next decades comprise 68% of the global area currently occupied by primates (Fig. 4). This will result in unprecedented spatial conflict with 75% of primate species worldwide (Supplementary Text). Therefore, the implementation of policies to divert agricultural expansion to areas where it is likely to result in the least environmental impacts is essential to reduce spatial conflicts between primate-rich areas and the expanding agricultural frontier (*13*).

Logging, mining, and fossil fuel extraction

Globalized financial markets and a worldwide commodity boom have led to an ever-growing demand for tropical timber and a concomitant expansion of industrial logging, resulting in deforestation and creating a potent economic impetus for road building in forested areas (Supplementary Text) (*14*). Countries in primate range regions are responding to global market demands by expanding logging activities to increase economic growth. In 2010, the Neotropics accounted for 48% of the production of industrial hardwood, followed by Southeast Asia (23%), sub-Saharan Africa (16%), and South Asia (13%) (fig. S5E). In Madagascar, the large-scale harvesting of rosewood (*Dalbergia*) since 2009 has negatively affected several protected areas (*15*). The immediate and long-term effects of legal and illegal logging are a reduction of canopy cover, the destruction of forest undergrowth, and the decline of large tree species important to primates as sources of food and shelter (*16*).

Mining for minerals and diamonds is also a growing threat to tropical ecosystems and their primates. Although it involves relatively small areas, mining contributes to deforestation, forest degradation, and the pollution and poisoning of streams and soil (*17*). In central Africa, the population densities of apes in mined forests [75.7 (45.35 to 126.33) nests/km^2] are markedly lower than in forested sites where mining is absent [234 (185 to 299) nests/km^2] (*18*). In Madagascar, illicit gold and sapphire mining by itinerant miners has affected many forests, including protected ones (*19*). Mining of gold, nickel, and copper on Dinagat island, in the Philippines, is endangering the survival of the Philippine tarsier (*Carlito syrichta*) (*20*). Bushmeat hunting associated with the mining of coltan, tin, gold, and diamonds in the DRC is the main threat

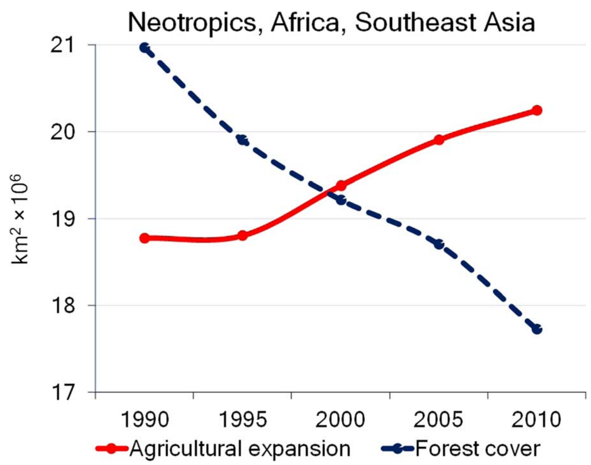

Fig. 3. Agricultural expansion and declines in forest cover for the period 1990–2010 in primate range regions. A rapid expansion of agriculture in primate range regions has been paralleled by a sharp decline in forest cover in the 20-year period considered. Trends for each individual region are shown in fig. S6 (A to C). Data for Africa include Madagascar (source of raw data, FAOSTAT: faostat.fao.org/site/377/DesktopDefault.aspx?PageID=377#ancor. Consulted June 2016).

to Grauer's gorilla (*G. beringei graueri*) (*21*); recent surveys indicate a 77% decline in its numbers, from 17,000 in 1995 to just 3800 in 2014/2015 (*22*). In Perú, the mining of zinc and copper threatens the endemic and Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*) (*23*). Development associated with fossil fuel extractions also jeopardizes primate survival. By 2035, global demand for oil and natural gas is projected to increase by >30 and 53% respectively, and primate-rich areas, such as the western Amazon and the western Pacific Ocean (Malaysia, Borneo) will be adversely affected. It is estimated that oil and gas concessions in the western Amazon, and in remote forested areas of Colombia, Ecuador, Brazil, Perú, and Bolivia, already cover about 733,414 km^2 (twice the size of Germany) (*24*).

Other anthropogenic stressors

The expansion of industrialized agriculture, logging, mining, oil/gas extraction, and the building of dams and power-line corridors in tropical forest areas is expected to increase human transportation road networks by some 25 million km by 2050 (Supplementary Text) (*25*). Consequences of the unrestricted road and rail building include increased forest losses from human population migration, illegal colonization, and logging; increased bushmeat hunting; and the illegal wildlife trade (Supplementary Text) (*26*). The construction of conventional dams and megadams for generating electricity to attract energy-intensive industry and stimulate local productivity in the world's most biodiverse river basins—the Amazon, Congo, and Mekong—also poses a severe threat to local primate persistence (*27*). For example, the development of 12 megadams in the state of Sarawak, Malaysia, is expected to result in the loss of at least 2425 km^2 of forest cover, affecting populations of the Endangered Müller's gibbon (*Hylobates muelleri*) (*28*).

Currently, primates feeding on crops (commonly termed "crop raiding") is not considered a major cause of global primate population declines by the IUCN because much of the conflict is local in its occurrence, impact, and the types of crops and primate species affected (*9*, *29*–*33*). There are areas of the world, such as parts of North Africa and Asia, where humans tolerate primates as crop pests because of religious beliefs, cultural traditions, and economic benefit (*29*). For example, in the Lindu highlands and Buton island of Sulawesi, humans are tolerant of crop feeding macaques due to the role the macaques hold in the local folklore and because they can help in the harvesting of certain crops, such as cashews, where the monkeys eat only the fruit and let the nut fall to the ground to be collected by farmers (*29*). In other cases, crop feeding by primates (for example, howler monkeys) is tolerated without any economic reward (*30*). Where human and nonhuman primates come into more severe conflict due to crop raiding [for example, chimpanzees (*Pan troglodytes*), gorillas (*Gorilla* spp.), and baboons (*Papio* spp.) in Africa and orangutans (*Pongo* spp.) in Southeast Asia] (*9*, *31*–*33*), culturally and economically appropriate management interventions can mitigate the impact (*9*, *33*). Human-primate conflict due to primates feeding on crops remains a persistent problem and is likely to increase because primate-suitable habitat is converted into agricultural fields or gardens in response to local and global market demands (Fig. 4).

Civil unrest also affects primate populations because of saturation bombing, the use of defoliating chemicals (*34*, *35*), and the increase in bushmeat hunting. Poaching of bonobos (*Pan paniscus*) and gorillas, for example, markedly increased in the DRC and Rwanda as a result of ongoing civil wars (*34*). In Cambodia, armed conflicts have severely affected populations of the black-shanked douc (*Pygathrix nigripes*) (*35*). Land mines, the legacy of wars in the 1960s and 1970s, continue to endanger apes in Southeast Asia and Africa (*34*, *36*).

Forest fragmentation and degradation and the limited resilience of primates

Long-term deforestation has resulted in the fragmentation of 58% of subtropical and 46% of tropical forests (*37*, *38*), forcing primates to live in isolated forest patches, including protected areas. This has led to decreasing numbers, population restructuring, and the loss of genetic diversity, as shown for pied tamarins (*Saguinus bicolor*), northern muriquis (*Brachyteles hypoxanthus*), Udzungwa red colobus monkeys (*Piliocolobus gordonorum*), several species of Chinese colobines (*Rhinopithecus* and *Trachypithecus*), Cross River gorillas (*G. gorilla diehli*), and Bornean orangutans (*39*–*45*). Edge effects predominate in many areas of disturbed forests, exacerbating habitat degradation (*37*). Agricultural expansion as well as legal and illegal logging cause further desiccation of vegetation, and human-induced forest fires devastate large areas in primate range regions yearly, resulting in increased tree mortality and losses of up to one-third of canopy cover (*46*, *47*). Although the effects of habitat loss, fragmentation, and degradation upon primates are mediated by variations in species-specific traits (rarity, trophic levels, dispersal mode, reproductive biology, life history, diet, and ranging behavior), the common response across taxa is population decline (Fig. 1).

Some primates are more behaviorally and ecologically resilient than others when faced with habitat loss, fragmentation, and degradation. Bornean orangutans, for example, can survive, at least temporarily, in logged forests, *Acacia* plantations, and oil palm plantations (*48*). Baboons (*Papio*), Hanuman langurs (*Semnopithecus*), and macaques (*Macaca*) are particularly adaptable and can survive even in urban areas (*49*). Chimpanzees appear to evaluate risks when crop-foraging and adjust their foraging patterns in deciding whether to exploit fragmented forests near humans (*50*). Bonobos tend to avoid areas of high human activity, fragmented forests, or both, and although this may suggest flexibility, the presence of humans appears to significantly reduce their access to potentially available habitat (*51*). Still, persistence in isolated

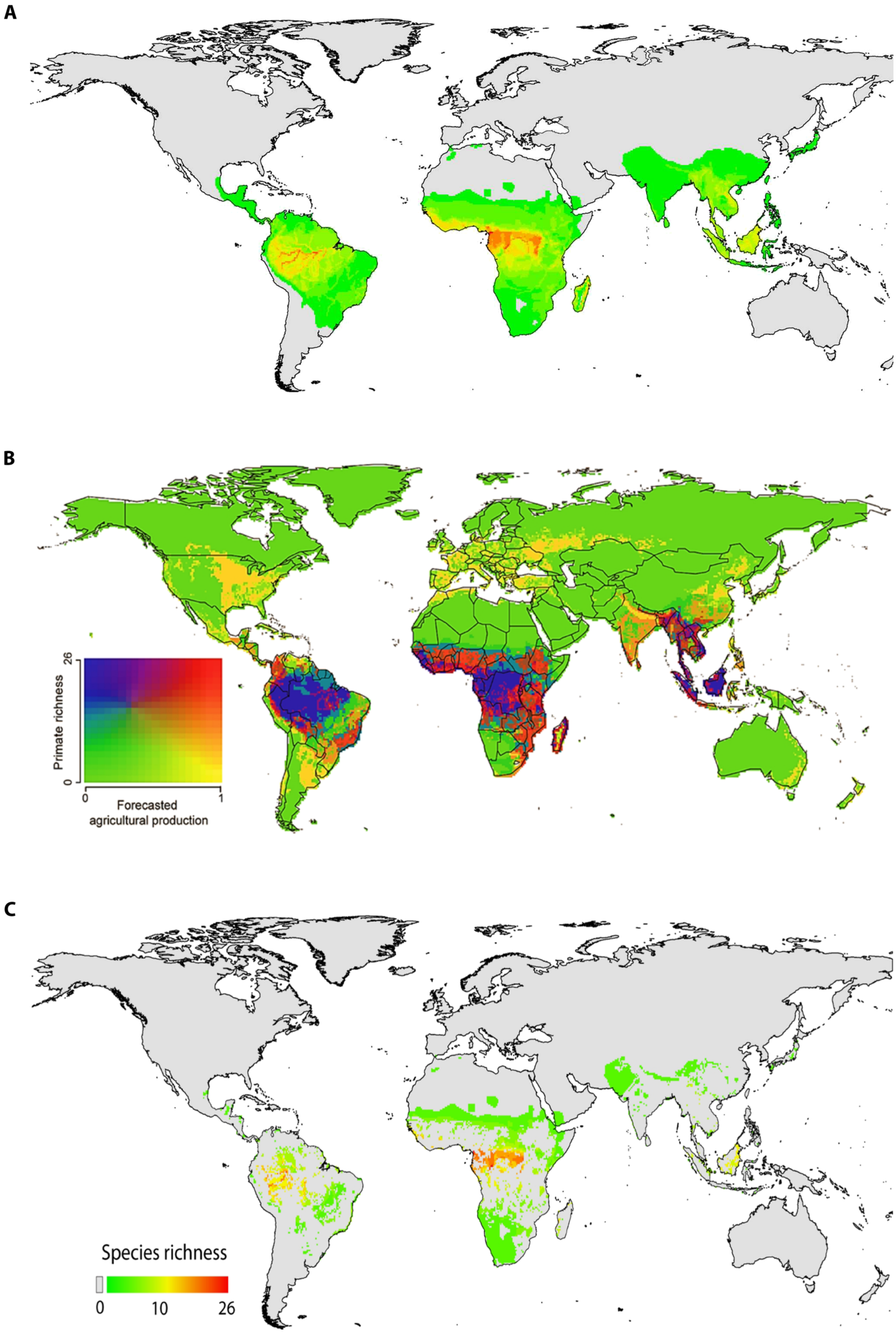

Fig. 4. Global patterns of forecasted agricultural expansion for the 21st century in primate range regions and estimated range contraction. (**A**) Estimated current global primate distributions. (**B**) The predicted 21st century expansion of agriculture estimates a spatial overlap with about 75% of primate species habitat worldwide. Red areas indicate higher spatial overlap between agricultural expansion and primate habitat. Blue areas indicate limited spatial conflict. Agricultural expansion represents a synthesis of the expected increase in the location and area devoted to agricultural production, according to the land-cover map produced by the Integrated Model to Assess the Global Environment and potential productivity obtained from the Global Agro-Ecological Zones (Supplementary Text) (*13*). (**C**) Estimated range contraction in primate distributions by the end of the 21st century under a worst-case scenario of agricultural expansion. See Supplementary Text for methods.

forest fragments, logged forests, agroecosystems, and urban areas is unlikely to be a sustainable option for most species due to hunting, further habitat reduction and fragmentation, reduced carrying capacity, parasite and disease transmission from humans and domestic animals, dog predation, human-primate conflict due to crop raiding, isolation, and continued changes in land use (*52*).

Primates in degraded forests face nutritional shortfalls and lower gut microbial diversity (*53–55*). They also show an increased prevalence of parasites and pathogens. For example, the increased exposure of lemurs (*Avahi laniger*, *Eulemur rubriventer*, *Hapalemur aureus*, *Microcebus rufus*, *Propithecus edwardsi*, and *Prolemur simus*) and chimpanzees (*P. troglodytes*) to human populations has increased their risk of infection by diarrhea-causing enteric pathogens (*56*, *57*). The close phylogenetic relationship between humans and other primates also creates an exceptionally high potential for pathogen exchange (*58*), as evidenced by disease emergence in humans as an unintentional effect of the hunting and butchering of wild primates (for example, human outbreaks of Ebola and the global HIV/AIDS pandemic) (*59*). In addition, exponential human population growth (fig. S7, A and B) and associated human-induced forest loss increase opportunities for wild primates to become exposed to human and domesticated animal pathogens (*60*). Primates escaping or released from the pet trade or sanctuaries can carry pathogens with a potential of transmission to resident populations (*61*). Moreover, ecotourism and research, despite contributing in positive ways to primate conservation, have the unintended consequence of exposing wild primates to human pathogens (*62*, *63*).

Hunting

Human population growth and increasing per capita wealth have led to an increase in commercialized bushmeat hunting relative to subsistence hunting in many parts of the world. This has become a major driving force for primate population decline, especially in Africa and Southeast Asia (*45*, *64*). Although bushmeat hunting is difficult to track, reports indicate that about 150,000 primate carcasses from 16 species were traded annually as bushmeat in urban and rural markets at 89 sites in Nigeria and Cameroon (Supplementary Text) (*64*). In Borneo, between 1950 and 3100 orangutans are estimated to be killed annually (including 375 to 1550 females), a level that far exceeds the maximum sustainable offtake for population viability (*45*). Because only a relatively small number of primates live inside protected areas [for example, 21 to 27.5% of all great apes (*51*, *65*)], populations outside protected areas are declining rapidly; the consequent increase in rarity raises the price of primate meat, making it more worthwhile for poachers to risk encroaching into protected areas to hunt (*66*).

Legal and illegal trade

Many primate species are increasingly threatened by legal and illegal unsustainable trade. Primates are traded for consumption, biomedical research, and zoo and wildlife collections; as pets; for the sale of body parts (bodies, skins, hair, and skulls) used in traditional medicine; as talismans and trophies; and for magical purposes (*67*, *68*). The Convention on International Trade in Endangered Species (CITES) database for 2005–2014 reported a global primate trade of some 450,000 live individuals plus an additional 11,000 individuals in the form of body parts. Asian species accounted for 93% of this trade (12 genera), Neotropical species for 4% (13 genera), and African species for 3% (33 genera) (table S6 and fig. S8, A to C). However, these figures are conservative because CITES only reports statistics formally provided by each country. For example, although CITES reported fewer than 400 night monkeys (*Aotus*) traded internationally between 2005 and 2014 (table S6), in the tri-border area between Perú, Brazil, and Colombia, it was estimated that ~4000 night monkeys (*Aotus nancymaae*, *Aotus vociferans*, and *Aotus nigriceps*) were traded to a single biomedical research facility between 2007 and 2008 alone, for a price of approximately $100,000 (*69*). The expansion of road networks in frontier forests facilitates the extraction and trade of primates to cities and beyond borders (*25*). Together with increasing opportunities from e-commerce, this has given suppliers and smugglers unprecedented access to new markets (*70*, *71*). Wildlife laundering (mixing protected species with legal shipments of similar species) also occurs when wild-collected primates are passed off as captive bred (Supplementary Text) (*72*).

Climate change

Although empirical evidence for the impact of climate change on primates is scarce, a recent global assessment suggests that numerous primates will experience changing climatic conditions during the 21st century, with the Amazon, the Atlantic Forest of Brazil, Central America, and East and Southeast Asia being considered hotspots of climate change–induced primate vulnerability (*73*). Primate taxa with limited geographic distributions and species characterized by slow life history traits (for example, late age at first reproduction and long interbirth intervals) are highly vulnerable to shifting ecological conditions and are likely to be most affected (*74*, *75*). Although some species may cope with these changes either by migrating to more suitable conditions or by adapting in situ, dispersal or range shift is not always possible and may have highly negative consequences (Supplementary Text) (*76*). Forest fragmentation induced by climate change can affect the availability of dispersal routes (*77*). Climate change may also force individuals out of protected areas, making them more vulnerable to hunting and other anthropogenic impacts (*78*), and range shifts among interacting species can affect food supplies and introduce new predators, pathogens, and/or competitors (*79*). Interactions between climate change and other extinction drivers also need to be considered. For instance, projections of land-cover change show that the Bornean orangutan might lose 15 to 30% of its habitat by 2080, mainly due to deforestation and oil palm agriculture, but when coupled with climate change, even more habitat is likely to become unsuitable (*80*). Additionally, more frequent and severe climate change can induce floods, droughts, fires, hurricanes, and El Niño–Southern Oscillation events (*81*) that can affect the food supply available to primate populations, with negative impacts on health, fertility, and mortality (*82*).

Extinction risk and phylogenetic signal

The effect of anthropogenic threats on primates may be compounded by phylogenetic relatedness. Multispecies analyses have shown that extinction risk is not spread randomly across mammalian taxa. Rather, the prevalence of threatened taxa in some clades but not in others implies a strong phylogenetic pattern in susceptibility (*83*, *84*). Our own comparative analysis of 340 primate species suggests that closely related species are more likely to face the same threat status relative to species selected randomly from the phylogeny (Fig. 5, fig. S9, A to C, and Supplementary Text). This result is likely due to the fact that related taxa share intrinsic aspects of their biology, such as body mass, life history, reproductive physiology, geographical distribution, dietary requirements, and behaviors (*85–87*). For example, several colobines (*Trachypithecus*, *Presbytis*, and *Simias*) in Southeast Asia are highly threatened island endemics and share biological traits known to increase their exposure and vulnerability to threats and extinction risks, such as relatively large body mass, diurnal behavior, and restricted geographic ranges.

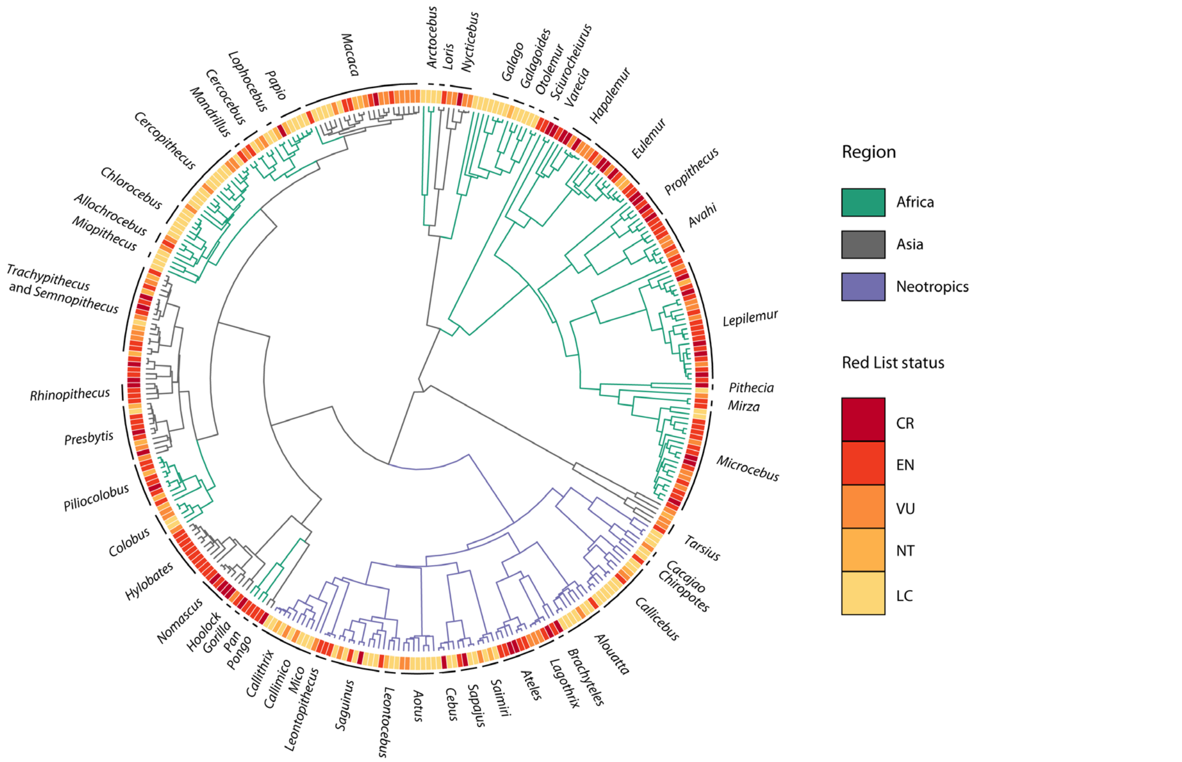

Fig. 5. Phylogenetic signal as a predictor of extinction risk in the world's primates. Distribution of threat values (IUCN Red List categories) for 340 primate species. Representative genera labeled. After taxonomic updates, our working phylogeny included 350 of the 367 species considered in the molecular supertree (*73*), of which 340 are not Data Deficient. Closely related species are more likely to have the same threat status than species taken randomly from the phylogeny [$D = 0.31$; $P (D < 1) < 0.001$], supporting a strong phylogenetic signal (see Supplementary Text for details of methodology). Data for Africa include Madagascar. IUCN Red List Categories: CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern).

WHY PRIMATES MATTER

Social and cultural importance

Beyond sharing a close evolutionary history with humans, primates contribute importantly to the biological and cultural richness and the natural heritage of the countries in which they occur. Many primates play key roles in ecosystem dynamics and sustainability and are central figures in local and regional traditional knowledge, folklore, history, and even economies (*88*). For example, throughout South and Southeast Asia, monkeys figure strongly in Hindu and Buddhist mythology (for example, the Hanuman langur is the monkey god Hanuman in the Ramayana) and have centuries-old sympatric relationships with humans at temples and holy shrines. Today, many of these "monkey temples" are tourist sites, where the monkeys are protected, and provide an important source of income for local populations (*88*). Many traditional societies protect or tolerate primates and have integrated them into their historical narratives as sacred cultural figures and persons, as pets, and as food. For example, the Amazonian Guajá people integrate monkeys into their kinship and religious systems while also relying on primates as a sustainable food source (*89*). As primates become locally rare or extinct, we risk losing complex ecological, social, and cultural relationships that have developed between humans and primates over millennia (Supplementary Text) (*88*, *90*).

Ecological importance

Primates are prey, predator, and mutualist species in food webs and thereby influence ecosystem structure, function, and resilience. Their evolution, feeding ecology, and geographic distribution are closely linked to the diversification of angiosperms, a principal source of food (pollen, nectar, fruits, and seeds) (*91*) for many animals and humans (*92*–*94*). Many primates have been identified or suspected as important pollinators due to their opportunistic nondestructive feeding on flowers and nectar (*94*, *95*). As consumers of different plant parts (for example, fruits, flowers, seeds, gums, and leaves), primates can affect plant propagule dissemination, cause tree mortality, and may negatively affect the reproductive investment of some plants (*95*). However, numerous primates are highly frugivorous, and their relatively large size enables them to disperse small and large seeds over long distances, enhancing forest regeneration (*95*). In the absence of zoochorous seed dispersal by primates, plant populations can experience decreased genetic heterozygosity and increased genetic subpopulation differentiation, increased negative density dependence, and decreased recruitment (*96*–*99*). For example, Madagascar's lemurs display complex relationships with large seed–producing trees, and lemur extinction may be facilitating a decline in the viability of certain Malagasy tree species (*100*). The population collapse of large atelids and cebids in heavily hunted forests of Amazonia has severely degraded long-term forest dynamics and the sustainability of many hardwood tree species with implications for the carbon-storing potential of forests (*101*, *102*). Similarly, the hunting of gibbons in northern Thailand has had a negative effect on the demography of the lapsi tree (*Choerospondias axillaris*), which depends on gibbons to disperse its seeds into light gaps (*103*). The loss of primate seed dispersers has demonstrable impacts on human populations in the same ecosystems. For example, 48% of the plants whose seeds are dispersed by primates in the western regions of Côte d'Ivoire and 42% in Uganda have economic or cultural utility to local human inhabitants (*92*). In southern Nigeria, rural people rely on gathering primate-dispersed fruit and seed species (*104*), suggesting the considerable importance of primate conservation to local human food security.

Primates as model animals

Primates are highly valued model animals, advancing our understanding of the evolutionary history of our species and providing insight into human behavior, cognition, parenting, cooperation, adult social bonds, forms of social conflict and resolution, learning and memory, and the evolution of tool use and language (*105*–*108*). Although there exist important ethical issues that need to be considered when using primates in medical research (*109*), primate models have furthered our understanding of atherosclerosis, respiratory diseases, HIV/AIDS, treatment responses to psychoactive drugs, psychopathologies, sociality, mental health disorders, communication, immunology, brain functioning, pharmacology, endocrine regulation of reproduction, genetics and genomics, and disease risk and parasite dynamics, among many other subjects (*109*). Wild primate populations may hold valuable clues to the origins and evolution of important pathogens and processes of natural disease transmission by serving as sentinels for early disease detection, identification, and surveillance, thus benefiting humans. Because emerging infectious diseases also pose serious threats to both endangered and nonendangered primate species, studies of these diseases in one primate population may benefit conservation efforts for others (*59*).

ADDRESSING CONSERVATION NEEDS

Deforestation, hunting, illegal trade, and wood extraction are leading to a worldwide impoverishment of primate fauna. Drivers of primate loss are dynamic and interact with each other at local, regional, and global scales, leading to a trajectory of biosimplification that is most keenly felt as marked reductions in population sizes and, all too soon, extinctions (Fig. 6). The global scale of primate population declines and the predicted increase in the intensity of major anthropogenic threats (Fig. 1) suggest that conserving wild primates is an immediate but daunting challenge. Without widespread systemic changes in human behavior, populations will continue to decline over the next few decades, with species currently listed by the IUCN as Threatened becoming extinct and species now classified as Near Threatened or Least Concern facing increased extinction risk. Many primates are iconic (for example, gorillas, chimpanzees, orangutans, spider monkeys, and lemurs; Fig. 7), but given the scale of their decline, it is clear that neither their charisma nor their flagship status is sufficient to safeguard them from the threat of human-induced extirpation throughout their native ranges. Extinction rarely results from deficient scientific knowledge of the steps required to protect the species. Instead, it is embedded in political uncertainty, socioeconomic instability, organized criminality, corruption, and policies that favor short-term profits over long-term sustainability (*110*). Meaningful primate conservation will require a major revolution in commitment and policy. Alleviating pressures upon primate habitats requires decreasing the per capita demand of industrialized nations for tropical hardwoods, beef, palm oil, soy, rubber, minerals, and fossil fuels, among other goods, while simultaneously promoting sustainable resource-use practices (Fig. 6) (*111*).

Improving the human condition

The human capital in primate range localities is of utmost importance to primate conservation. High rates of human population growth (5.1 billion people in 2010 to 7.3 billion in 2050 in primate range countries), high levels of poverty and inequality, the loss of natural capital due to extensive and rapid land-cover changes driven by global market demands, poor governance, and the need for food security, health, and literacy are key factors to consider (Supplementary Text and fig. S7, A to C). Solutions to the challenge of primate conservation must include reducing human birth rates and population growth, improving health, reducing poverty and gender biases in education, developing sustainable land-use initiatives, and preserving traditional livelihoods (Fig. 6) (*112*). Locally, people and governments need to become stakeholders in this effort and perceive that they can benefit from protecting primate populations and their forests while at the same time satisfying their basic needs. This will require education, rethinking, and investment from government, nongovernmental organizations (NGOs), and the private sector. There is no single solution to this global problem. Primate ecotourism may be an effective approach in some localities (for example, gorilla ecotourism in Rwanda, DRC, and Uganda) (*113*). In others, mini-livestock breeding may be a productive route to improve food security (*114*). Because bushmeat is an important source of food and income for inhabitants from poverty-ridden primate range countries, as well as an important aspect of indigenous culture, in some countries, nonprimate game ranching and game farming may contribute to food security and indirectly to primate conservation (*115*).

Expansion of protected areas

Although the percentage of the land surface devoted to protected areas has steadily increased in primate range countries (fig. S7D), highlighting protected areas as the only plausible conservation tool may contribute to local poverty by denying poor people power over and access to the natural resources that support their livelihoods (*116*). Protected areas must be sufficiently large and provide suitable primate habitats, and species of concern must be present in sufficient numbers within those areas (*117*). Unfortunately, countries in the Neotropics, Africa, and Asia are currently downgrading, downsizing, and degazetting protected areas due to growing industrial-scale natural resource extraction, and a significant number of protected areas are experiencing substantial deforestation (*118*, *119*). Despite these trends, protected areas can and do provide long-term sanctuary for wildlife. For example, a study in the Udzungwa mountains of Tanzania showed that colobine primate populations were stable in the protected areas but declined severely in the unprotected forests (*120*). An 8-year study (2007–2014) using camera traps to annually monitor terrestrial mammals and birds in 15 protected areas in the Neotropics, Africa, and Southeast Asia showed strong evidence of stability and even increases in populations, including those of 23 primate species (19 cercopithecines in Africa and Asia, 3 African apes, and 1 lemur) (*121*). A complementary conservation approach is the REDD+ program, where payments are made to tropical countries to reduce emissions from deforestation and forest degradation (*122*). REDD+ could be a productive approach to increasing primate habitat and connectivity via reforestation and to providing important economic and ecological value for local populations. However, as of yet, no examples of implemented programs and their success on primate conservation are available (*123*).

Land-sharing and land-sparing

Because forests are among the few economic assets available to the rural poor in the tropics, securing their ownership and sustainable commercial use can help poor families cope with and move out of poverty (*124*). In a land-sharing approach (mixing protection and production in an agroecological matrix), community-managed forests are one option to integrate forest management into national poverty reduction programs in

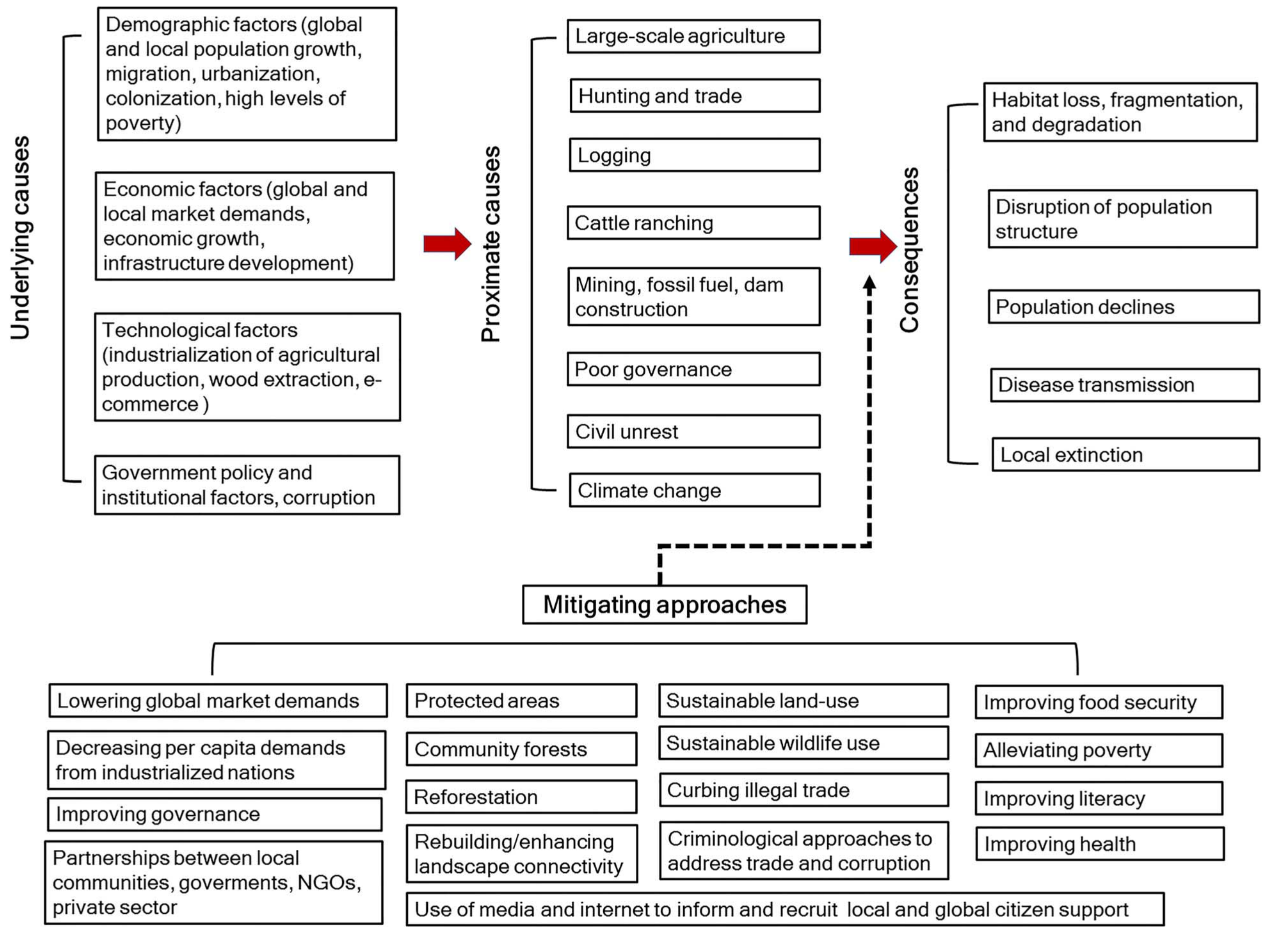

Fig. 6. Factors driving primate population declines and possible mitigating approaches. Four broad social and economic processes drive the proximate causes of threat to primates and human actions that directly affect primate habitats and populations. Mitigating approaches aim at lowering the impact of proximate causes of primate declines. Infrastructure development also includes road and rail expansion.

rural areas, favoring primate species with small area requirements. These forests also have lower and less variable annual deforestation rates than protected ones (*124*). In both land-sparing (favoring species with large area requirements) and land-sharing approaches, promoting biodiversity and the use of lattice-work corridors to connect landscapes along latitudinal and elevational gradients may promote a diversity of habitats for the long-term persistence of primate species that differ in their ecological requirements and may mitigate some of the deleterious effects of climate change (*125*, *126*). A recent study of the fauna, including lemurs, of a 90-km-long biodiversity corridor connecting two national parks in Madagascar showed the need to differentiate among passive dispersers (species that settle randomly around the source population), active dispersers (species that settle only in favorable habitats), and gap-avoiding dispersers (species that avoid dispersing across nonhabitat areas). Thus, a better understanding of the natural history of different primates is critical to identify which taxa might be sustained within forested corridors and those for which no substitute or alternative habitat exists (*127*).

Use of new and traditional technology to monitor primate population vulnerability

A new science of monitoring primate habitats, population status, and anthropogenic threats is currently emerging. It includes taking advantage of global telecommunication systems and wireless Internet, satellite- and airborne-based imagery, drone technology, ever more powerful handheld devices (for example, smart phones and tablets), and camera traps (Supplementary Text) (*120*, *128*). Combined with geographic information system and ground surveys, some of this technology has been used in evaluating sustainable land-use spatial planning and human-primate conflicts [for example, Javan gibbons (*Hylobates moloch*)] (*129*) and in providing case-by-case assessments of species vulnerability to climate change, as shown for Borneo's orangutans (Supplementary Text) (*80*). These same technologies can also be used by local citizen scientists for species and habitat monitoring, thus enhancing the effectiveness of mitigation measures (*128*). Recent technological advances in molecular biology—particularly high-throughput sequencing of DNA extracted from noninvasive samples (for example, feces, urine, and hair)—can accelerate assessments of population size and structure, genetic diversity and evidence of outbreeding, diet (plant, vertebrate, and invertebrate DNA consumption), and parasite and gut microbial diversity for wild primates (*130*–*134*). These advances have allowed researchers to identify species and origins of primate parts confiscated in the illegal bushmeat or pet trade (*135*) and are helpful in the genetic assessment and management of captive populations designed to establish viable, hybrid-free, "backup" populations to refresh the genetic pool of wild populations via reintroduction (*136*, *137*).

Fig. 7. Photos of selected primates from each major world region. Conservation status and photo credits include the following: (**A**) Golden snub-nosed monkey (*Rhinopithecus roxellana*), Endangered, P. A. Garber. (**B**) Ring-tailed lemur (*Lemur catta*), Endangered, R. A. Mittermeier. (**C**) Udzungwa red colobus (*P. gordonorum*), Endangered (Photo Credit: Thomas Struhsaker, Duke University). (**D**) Javan slow loris (*Nycticebus javanicus*), Critically Endangered (Photo Credit: Andrew Walmsley, Andrew Walmsley Photography). (**E**) Sumatran orangutan (*P. abelii*), Critically Endangered (Photo Credit: Perry van Duijnhoven). (**F**) Azara's night monkey (*Aotus azarae*), Least Concern [Photo Credit: Claudia Valeggia (Yale University)/Owl Monkey Project, Formosa-Argentina].

Although these innovations open new avenues for primate study, successful, long-term programs that monitor primate population abundance also rely on simpler and less expensive methods that engage students and local research assistants, such as traditional census methods. There are relatively few multigeneration studies of primate population dynamics, largely because primates are long-living animals and population changes occur over time periods longer than the duration of most studies and research grants. However, a recent study from the Udzungwa Mountains of Tanzania combined locally based monitoring routines and advanced statistical approaches to investigate population abundance, even when information was missing for some monitoring periods (*120*). Another study showed the value of basic field procedures (transect surveys) in monitoring Sumatran orangutan populations, with results that doubled the estimated population from 6600 to 14,613, even though the population was still assessed as declining rapidly due to deforestation (*138*).

Mitigating illegal trade

It has been noted that to mitigate wildlife poaching, interventions need to go beyond regulation by encouraging capacity building in local communities to conserve wildlife, reexamining sustainable offtake mechanisms, such as regulated trade, ranching, and wildlife farming (*139*), and to use social media and the Internet to reduce demand and, ultimately, to curb trade (Supplementary Text and Fig. 6) (*71*, *140*). Although the use of social media to raise local, regional, and global awareness of the plight of the world's primate fauna and of the ecological, social, cultural, and economic importance of primates is, no doubt, essential, it is just as important to develop local, action-oriented conservation education programs, especially those targeting young people and community decision makers. These are powerful conservation tools, combining knowledge and action acquired from successful ongoing programs in Madagascar (*141*), West Java, Indonesia (*142*), and Colombia (*143*) (see details in Supplementary Text). Criminological investigation that focuses on bushmeat trade and the trafficking of primates for pets, body parts, and trophies is also important for tracing the supply chains and criminal networks involved in illegal trade (see the "Focus of future research efforts" section).

Reintroductions and long-term forest protection as conservation tools

Where primate species are locally extinct, reintroductions are an option but can be expensive, and long-term protection of forests is arguably a more cost-effective means of preserving primates than reintroduction (*144*). Nonetheless, reintroductions raise public and political awareness and provide placement solutions for rescued animals in line with welfare concerns. The use of wild-born, rescued, and rehabilitated primates instead of captive-bred animals in reintroduction programs reduces costs and can increase success (*145*). A range of primate species have been successfully introduced in some places, including orangutans, lar gibbons (*Hylobates lar*), southern yellow-cheeked gibbons (*Nomascus gabriellae*), Indonesian slow lorises (*Nycticebus*), Delacour's langurs (*Trachypithecus delacouri*), western gorillas, woolly monkeys (*Lagothrix lagotricha*), golden lion tamarins (*Leontopithecus rosalia*), and pygmy marmosets (*Cebuella pygmaea*) (*146–150*). Still, evidence of outbreeding and introgression in, for example, Bornean orangutan populations due to the reintroduction of rescued animals of different species and subspecies into wild populations highlights the care that must be taken using these kinds of conservation interventions (*151*).

Reducing the urban footprint on primate habitats

Worldwide, urban policies need to be targeted at reducing people's ecological footprints in primate range regions. For instance, promoting the recycling of cell phones, laptops, and other electronic devices could diminish the demand for coltan mining from the Congo Basin in Central Africa, which threatens primates in the region, including gorillas and chimpanzees (*22*, *152*). Decreasing the world's per capita demand for tropical hardwoods, food and nonfood products, minerals, and fossil fuels, among other goods, from primate range regions would help alleviate pressures on primate habitats (*112*).

FOCUS OF FUTURE RESEARCH EFFORTS

The scientific research effort on primates, as measured by the number of published articles on individual primate species on the Web of Science from January 1965 to March 2016, yielded ~47,000 records pertaining to both wild and captive primates. Overall, 16% involve studies of Neotropical monkeys, 36% of African primates, and 48% of Asian primates. Sixty-six percent of the publication records focused on a single family, the Cercopithecidae, principally *Macaca* in Asia and *Papio* in Africa (fig. S10). These results reflect the important role of some taxa in this family (for example, *Macaca mulatta* and *Papio anubis*) as models for studies of human health, behavior, and physiology. Studies of primates in the African Hominidae (chimpanzees, bonobos, and gorillas) constituted another 10% of the total records, and species in the Neotropical families Callitrichidae, Cebidae, and Atelidae combined constituted 13%. Species in the remaining 11 primate families accounted for only 11% of the total records (fig. S10). Thus, despite considerable research efforts over the past 40 years, scientific data for a great majority of primate species are still limited. Moreover, decade-long studies have been conducted on very few species, and studies spanning several generations are even fewer. Such paucity of knowledge suggests that there is an urgent need to generate species- and habitat-specific knowledge about population size, life history and ecology, habitat loss, forest fragmentation, climate change, potential for disease transmission, and human-primate interactions, including detailed population/species recovery plans.

Cultural mapping and the fostering of mutually beneficial partnerships with government and people in local communities, coupled with ethnoprimatological field work, are effective tools to identify specific problems and workable in situ solutions for primate conservation (*153*). For example, a decade-long study in the Central African Republic revealed that traditional forest uses (for example, hunting and gathering) have been replaced by new activities, such as logging, bushmeat hunting, and even conservation programs, and that local human populations are both materially and culturally impoverished by animal declines (*153*). Another study showed that the use of lorises (*Nycticebus* and *Loris*) in traditional medicine and the pet trade in Sri Lanka, Cambodia, and Indonesia followed culturally specific patterns (*154*), and therefore, a deep understanding of local customs is required to develop effective conservation policies.

Because the unprecedented market globalization of the illegal wildlife, bushmeat, and amulet trade is rapidly depleting natural primate populations (*110*), criminological intelligence network analyses, within and outside range states, is critically needed. To be effective, this effort needs to integrate local and global attitudes about environmental insecurity and biodiversity exploitation. For example, local people's perceptions of the risk associated with illegal lemur hunting in Madagascar do not reflect the perception of policy makers (*155*). Attention to poaching as a serious conservation crime will yield a better understanding of whether local people engage in such activities to ensure food security and/or to generate income and may illuminate how best to incentivize sustainable alternatives, such as food subsidies or employment as rangers and conservation guards (*156*). Given the severity of this problem, the social and organized crime contexts of primate bushmeat and live trade need to be included in an integrated model (*157*) that also addresses corruption in supervising government entities in charge of monitoring and prosecuting illegal trade (Fig. 6) (*110*).

Finally, studies that document the interactions of anthropogenic drivers of environmental change with species-specific biological and behavioral traits (for example, body mass, reproductive rate, dietary flexibility, and nutritional needs) within a phylogenetic comparative framework are needed to further our understanding of the imminent threats faced by individual taxa, especially for species that have few close taxonomic relatives. Over the past two decades, a resynthesis and reorganization of new and previously collected data have increased the number of recognized primate species from 180 to 376 in 2005 and from 376 to 504 in 2016 (*158–161*). The recognition of the urgent need to understand the diversity of threatened primates inspired a workshop in 2000 in Orlando, Florida, sponsored by Disney's Animal Kingdom. This workshop gave rise to landmark conservation assessments and action plans for each of the major primate regions (*162–166*).

CONCLUDING COMMENTS

Despite the impending extinction facing many of the world's primates, we remain adamant that primate conservation is not yet a lost cause, and we are optimistic that the environmental and anthropogenic pressures leading to population declines can still be reversed. However, this is contingent on implementing effective scientific, political, and management decisions immediately. Unless we act, human-induced environmental threats in primate range regions will result in a continued and accelerated reduction in primate biodiversity. Primate taxa will be lost through a combination of habitat loss and degradation, population isolation in fragmented landscapes, population extirpation by hunting and trapping, and rapid population decline due to human and domestic animal-borne diseases, increasing human encroachment, and climate change. Perhaps the starkest conclusion of this review is that collectively—as researchers, educators, administrators, and politicians—we are failing to preserve primate species and their habitats. We face a formidable challenge moving forward, as success requires that sustainable solutions address the social, cultural, economic, and ecological interdependencies that are the basis of primate conservation. Our review suggests that by refocusing and publicizing our efforts to academics, government agencies, NGOs, businesses, and the public at large, we can build a comprehensive understanding of the consequences of primate population declines and encourage urgent and effective conservation policies. These policies will differ among countries, regions, habitats, and primate species based on the site-specific nature of each problem. We have one last opportunity to greatly reduce or even eliminate the human threats to primates and their habitats, to guide conservation efforts, and to raise worldwide awareness of their predicament. Primates are critically important to humanity. After all, they are our closest living biological relatives.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/1/e1600946/DC1
fig. S1. Primate habitat countries ranked by the number of species present.
fig. S2. Countries with primate species in the Neotropics, Africa (including Madagascar), and Asia and percent of countries with threatened species.
fig. S3. IUCN threat categories and population status of primate species.
fig. S4. Percent of primate species listed under each proximate threat, according to the IUCN.
fig. S5. Growth trends in cattle stock, agricultural activity, and deforestation in primate range regions.
fig. S6. Agricultural expansion and declines in forest cover for the period 1990–2010 in the Neotropics, Africa, and Asia.
fig. S7. Human population growth in primate range regions.
fig. S8. Global primate trade for the period 2005–2014, as reported by parties to the CITES Secretariat.
fig. S9. Phylogenetic patterns associated with extinction risk for primate species in the Neotropics, Africa, and Asia.
fig. S10. Number of published articles found in the Web of Science for primate species in each family.
table S1. Primate species in the Neotropics grouped by family.
table S2. Primate species in mainland Africa grouped by family.
table S3. Primate species in Madagascar grouped by family.
table S4. Primate species in Asia grouped by family.
table S5. Summary of sources of threat and the number of primate species affected, according to the IUCN Red List.
table S6. Global international trade in primates for the period 2005–2014, as reported by parties to the CITES Secretariat.
Supplementary Text
References (*167–209*)

REFERENCES AND NOTES

1. D. E. Wilson, D. M. Reeder, Eds., *Mammal Species of the World* (Johns Hopkins Univ. Press, ed. 3, 2005).
2. International Union for Conservation of Nature, IUCN Red List of threatened species. Version 2015–4; www.iucnredlist.org [accessed 20 January 2016].
3. Integrated Taxonomic Information System (ITIS), Order Primates; www.itis.gov.
4. R. A. Mittermeier, A. B. Rylands, D. E. Wilson, Eds., *Handbook of the Mammals of the World: 3. Primates* (Lynx Edicions, 2013).
5. C. Campbell, A. Fuentes, K. MacKinnon, S. Bearder, R. Stumpf, Eds., *Primates in Perspective* (Oxford Univ. Press, ed. 2, 2010).
6. W. F. Laurance, J. Sayer, K. G. Cassman, Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* **29**, 107–116 (2014).
7. H. S. Nantha, C. Tisdell, The orangutan–oil palm conflict: Economic constraints and opportunities for conservation. *Biodivers. Conserv.* **18**, 487–502 (2009).
8. S. A. Wich, J. Garcia-Ulloa, H. S. Kühl, T. Humle, J. S. H. Lee, L. P. Koh, Will oil palm's homecoming spell doom for Africa's great apes? *Curr. Biol.* **24**, 1659–1663 (2014).
9. A. Lanjouw, H. Rainer, A. White, Apes overview, in *State of the Apes: Industrial Agriculture and Ape Conservation*, H. Rainer, A. White, A. Lanjouw, Eds. (Arcus/Cambridge Univ. Press, 2015), pp. 164–192.
10. V. Vijay, S. L. Pimm, C. N. Jenkins, S. J. Smith, The impacts of oil palm on recent deforestation and biodiversity loss. *PLOS ONE* **11**, e0159668 (2016).
11. P.-F. Fan, H.-L. Fei, A.-D. Luo, Ecological extinction of the critically endangered northern white-cheeked gibbon *Nomascus leucogenys* in China. *Oryx* **48**, 52–55 (2014).
12. M. K. Mazumder, Diversity, habitat preferences, and conservation of the primates of southern Assam India: The story of a primate paradise. *J. Asia Pac. Biodivers.* **7**, 347–354 (2014).
13. R. Dobrovolski, R. Loyola, G. A. B. Da Fonseca, J. A. F. Diniz-Filho, M. B. Araújo, Globalizing conservation efforts to save species and enhance food production. *Bioscience* **64**, 539–545 (2014).
14. Y. Malhi, T. A. Gardner, G. R. Goldsmith, M. R. Silman, P. Zelazowski, Tropical forests in the Anthropocene. *Annu. Rev. Environ. Resour.* **39**, 125–159 (2014).
15. M. A. Barrett, J. L. Brown, M. K. Morikawa, J.-N. Labat, A. D. Yoder, CITES designation for endangered rosewood in Madagascar. *Science* **328**, 1109–1110 (2010).
16. S. L. Lewis, D. P. Edwards, D. Galbraith, Increasing human dominance of tropical forests. *Science* **349**, 827–832 (2015).
17. N. L. Alvarez-Berríos, T. Mitchell Aide, Global demand for gold is another threat for tropical forests. *Environ. Res. Lett.* **10**, 014006 (2015).
18. A. Lanjouw, in State of the Apes: Extractive Industries and Ape Conservation, H Rainer, A. White, A. Lanjouw, Eds. (Arcus/Cambridge Univ. Press, 2014), pp. 127–161.
19. R. Duffy, Gemstone mining in Madagascar: Transnational networks, criminalisation and global integration. *J. Mod. Afr. Stud.* **45**, 185–206 (2007).
20. R. M. Brown, J. A. Weghorst, K. V. Olson, M. R. Duya, A. J. Barley, M. V. Duya, M. Shekelle, I. Neri-Arboleda, J. A. Esselstyn, N. J. Dominy, P. S. Ong, G. L. Moritz, A. Luczon, M. L. Diesmos, A. C. Diesmos, C. D. Siler, Conservation genetics of the Philippine tarsier: Cryptic genetic variation restructures conservation priorities for an island archipelago primate. *PLOS ONE* **9**, e104340 (2014).
21. P. T. Mehlman, Current status of wild gorilla populations and strategies for their conservation, in *Conservation in the 21st Century: Gorillas as a Case Study*, T. S. Stoinski, H. D. Steklis, P. T. Mehlman, Eds. (Springer, 2008), pp. 3–54.
22. A. J. Plumptre, S. Nixon, R. Critchlow, G. Vieilledent, R. Nishuli, A. Kirkby, E. A. Williamson, J. S. Hall, D. Kujirakwinja, *Status of Grauer's Gorilla and Chimpanzees in Eastern Democratic Republic of Congo: Historical and Current Distribution and Abundance* (Wildlife Conservation Society, Fauna & Flora International and Institut Congolais pour la Conservation de la Nature, 2015).
23. N. Shanee, S. Shanee, Yellow-tailed woolly monkey (*Lagothrix flavicauda*): Conservation status, anthropogenic threats, and conservation initiatives, in *The Woolly Monkey: Behaviour, Ecology, Conservation and Systematics*, T. R. Defler, P. R. Stevenson, Eds. (Springer, 2014), pp. 283–299.
24. M. Finer, B. Babbitt, S. Novoa, F. Ferrarese, S. E. Pappalardo, M. De Marchi, M. Saucedo, A. Kumar, Future of oil and gas development in the western Amazon. *Environ. Res. Lett.* **10**, 024003 (2015).
25. W. F. Laurance, G. R. Clements, S. Sloan, C. S. O'Connell, N. D. Mueller, M. Goosem, O. Venter, D. P. Edwards, B. Phalan, A. Balmford, R. Van Der Ree, I. B. Arrea, A global strategy for road building. *Nature* **513**, 229–232 (2014).
26. W. F. Laurance, S. Sloan, L. Weng, J. A. Sayer, Estimating the environmental costs of Africa's massive "development corridors". *Curr. Biol.* **25**, 3202–3208 (2015).
27. K. Winemiller, P. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, S. Nam, I. Baird, W. Darwall, N. Lujan, I. Harrison, M. L. Stiassny, R. A. Silvano, D. B. Fitzgerald, F. M. Pelicice, A. A. Agostinho, L. C. Gomes, J. S. Albert, E. Baran, M. Petrere Jr., C. Zarfl, M. Mulligan, J. P. Sullivan, C. C. Arantes, L. M. Sousa, A. A. Koning, D. J. Hoeinghaus, M. Sabaj, J. G. Lundberg, J. Armbruster, M. L. Thieme, P. Petry, J. Zuanon, G. Torrente Vilara, J. Snoeks, C. Ou, W. Rainboth, C. S. Pavanelli, A. Akama, A. van Soesbergen, L. Saenz, Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351**, 128–129 (2016).
28. J. Kitzes, R. Shirley, Estimating biodiversity impacts without field surveys: A case study in northern Borneo. *Ambio* **45**, 110–119 (2016).
29. E. P. Riley, N. E. C. Priston, Macaques in farms and folklore: Exploring the human-nonhuman primate interface in Sulawesi Indonesia. *Am. J. Primatol.* **72**, 848–854 (2010).
30. Ó. M. Chaves, J. C. Bicca-Marques, Crop-feeding by brown howler monkeys (*Alouatta guariba clamitans*) in forest fragments: The conservation value of cultivated species. *Int. J. Primatol.* **11**, e0145819 (2016).
31. K. J. Hockings, M. R. McLennan, S. Carvalho, M. Ancrenaz, R. Bobe, R. W. Byrne, R. I. M. Dunbar, T. Matsuzawa, W. C. McGrew, E. A. Williamson, M. L. Wilson, B. Wood, R. W. Wrangham, C. M. Hill, Apes in the Anthropocene: Flexibility and survival. *Trends Ecol. Evol.* **30**, 215–222 (2015).
32. N. Seiler, M. M. Robbins, Factors influencing ranging on community land and crop raiding by mountain gorillas. *Anim. Conserv.* **19**, 176–188 (2015).
33. G. Fehlmann, M. J. O'Riain, C. Kerr-Smith, A. J. King, Adaptive space use by baboons (Papio ursinus) in response to management interventions in a human-changed landscape. *Anim. Conserv.* (2016).
34. L. R. Douglas, K. Alie, High-value natural resources: Linking wildlife conservation to international conflict, insecurity, and development concerns. *Biol. Conserv.* **171**, 270–277 (2014).
35. C. Loucks, M. B. Mascia, A. Maxwell, K. Huy, K. Duong, N. Chea, B. Long, N. Cox, T. Seng, Wildlife decline in Cambodia, 1953–2005: Exploring the legacy of armed conflict. *Conserv. Lett.* **2**, 82–92 (2009).
36. J. A. McNeely, Conserving forest biodiversity in times of violent conflict. *Oryx* **37**, 142–152 (2003).
37. N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
38. B. Mercer, Tropical Forests: A Review (The Prince's Charities' International Sustainability Unit, 2015).
39. I. P. Farias, W. G. Santos, M. Gordo, T. Hrbek, Effects of forest fragmentation on genetic diversity of the Critically Endangered primate, the pied tamarin (*Saguinus bicolor*): Implications for conservation. *J. Hered.* **106**, 512–521 (2015).
40. P. B. Chaves, C. S. Alvarenga, C. B. Possamai, L. G. Dias, J. P. Boubli, K. B. Strier, S. L. Mendes, V. Fagundes, Genetic diversity and population history of a critically

endangered primate, the northern muriqui (Brachyteles hypoxanthus). *PLOS ONE* **6**, e20722 (2011).
41. M. J. Ruiz-Lopez, C. Barelli, F. Rovero, K. Hodges, C. Roos, W. E. Peterman, N. Ting, A novel landscape genetic approach demonstrates the effects of human disturbance on the Udzungwa red colobus monkey (*Procolobus gordonorum*). *Heredity* **116**, 167–176 (2016).
42. Z. Liu, G. Liu, C. Roos, Z. Wang, Z. Xiang, P. Zhu, B. Wang, B. Ren, F. Shi, H. Pan, M. Li, Implications of genetics and current protected areas for conservation of 5 endangered primates in China. *Conserv. Biol.* **29**, 1508–1517 (2015).
43. R. A. Bergl, B. J. Bradley, A. Nsubuga, L. Vigilant, Effects of habitat fragmentation, population size and demographic history on genetic diversity: The Cross River gorilla in a comparative context. *Am. J. Primatol.* **70**, 848–859 (2008).
44. R. Sharma, N. Arora, B. Goossens, A. Nater, N. Morf, J. Salmona, M. W. Bruford, C. P. van Schaik, M. Krützen, L. Chikhi, Effective population size dynamics and the demographic collapse of Bornean orang-utans. *PLOS ONE* **7**, e49429 (2012).
45. E. Meijaard, D. Buchori, Y. Hadiprakarsa, S. S. Utami-Atmoko, A. Nurcahyo, A. Tjiu, D. Prasetyo, L. C. Nardiyono, M. Ancrenaz, F. Abadi, I. N. G. Antoni, D. Armayadi, A. Dinato, P. G. Ella, T. P. Indrawan, C. M. Kussaritano, C. W. P. Priyono, Y. Purwanto, D. Puspitasari, M. S. W. Putra, A. Rahmat, H. Ramadani, J. Sammy, D. Siswanto, M. Syamsuri, N. Andayani, H. Wu, J. A. Wells, K. Mengersen, Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLOS ONE* **6**, e27491 (2011).
46. J. M. Silveira, J. Louzada, J. Barlow, R. Andrade, L. Mestre, R. Solar, S. Lacau, M. A. Cochrane, A multi-taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon forest. *Biotropica* **48**, 170–180 (2016).
47. S. F. Gouveia, F. Villalobos, R. Dobrovolski, R. Beltrão-Mendes, S. F. Ferrari, Forest structure drives global diversity of primates. *J. Anim. Ecol.* **83**, 1523–1530 (2014).
48. E. Meijaard, S. Wich, M. Ancrenaz, A. J. Marshall, Not by science alone: Why orangutan conservationists must think outside the box. *Ann. N. Y. Acad. Sci.* **1249**, 29–44 (2012).
49. M. F. Jaman, M. A. Huffman, The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates* **54**, 49–59 (2013).
50. S. Krief, M. Cibot, S. Bortolamiol, A. Seguya, J.-M. Krief, S. Masi, Wild chimpanzees on the edge: Nocturnal activities in croplands. *PLOS ONE* **9**, e109925 (2014).
51. J. R. Hickey, J. Nackoney, N. P. Nibbelink, S. Blake, A. Bonyenge, S. Coxe, J. Dupain, M. Emetshu, T. Furuichi, F. Grossmann, P. Guislain, J. Hart, C. Hashimoto, B. Ikembelo, O. Ilambu, B.-I. Inogwabini, I. Liengola, A. L. Lokasola, A. Lushimba, F. Maisels, J. Masselink, V. Mbenzo, N. M. Mulavwa, P. Naky, N. M. Ndunda, P. Nkumu, V. Omasombo, G. E. Reinartz, R. Rose, T. Sakamaki, S. Strindberg, H. Takemoto, A. Vosper, H. S. Kühl, Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. *Biodivers. Conserv.* **22**, 3085–3104 (2013).
52. A. Estrada, B. E. Raboy, L. C. Oliveira, Agroecosystems and primate conservation in the tropics: A review. *Am. J. Primatol.* **74**, 696–711 (2012).
53. K. Amato, C. J. Yeoman, A. Kent, N. Righini, F. Carbonero, A. Estrada, H. Rex Gaskins, R. M. Stumpf, S. Yildirim, M. Torralba, M. Gillis, B. A. Wilson, K. E. Nelson, B. A. White, S. R. Leigh, Habitat degradation impacts black howler monkey (*Alouatta pigra*) gastrointestinal microbiomes. *ISME J.* **7**, 1344–1353 (2013).
54. C. Barelli, D. Albanese, C. Donati, M. Pindo, C. Dallago, F. Rovero, D. Cavalieri, K. M. Tuohy, H. C. Hauffe, C. De Filippo, Habitat fragmentation is associated to gut microbiota diversity of an endangered primate: Implications for conservation. *Sci. Rep.* **5**, 14862 (2015).
55. A. Gomez, K. Petrzelkova, C. J. Yeoman, K. Vlckova, J. Mrázek, I. Koppova, F. Carbonero, A. Ulanov, D. Modry, A. Todd, M. Torralba, K. E. Nelson, H. R. Gaskins, B. Wilson, R. M. Stumpf, B. A. White, S. R. Leigh, Gut microbiome composition and metabolomic profiles of wild western lowland gorillas (*Gorilla gorilla gorilla*) reflect host ecology. *Mol. Ecol.* **24**, 2551–2565 (2015).
56. D. C. Bublitz, P. C. Wright, F. T. Rasambainarivo, S. J. Arrigo-Nelson, J. R. Bodager, T. R. Gillespie, Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *Am. J. Primatol.* **77**, 330–337 (2015).
57. M. B. Parsons, D. Travis, E. V. Lonsdorf, I. Lipende, D. M. A. Roellig, S. Kamenya, H. Zhang, L. Xiao, T. R. Gillespie, Epidemiology and molecular characterization of *Cryptosporidium* spp. in humans, wild primates, and domesticated animals in the greater Gombe ecosystem, Tanzania. *PLOS Neglected Trop. Dis.* **9**, e0003529 (2015).
58. N. Cooper, C. L. Nunn, Identifying future zoonotic disease threats: Where are the gaps in our understanding of primate infectious diseases? *Evol. Med. Public Health* **2013**, 27–36 (2013).
59. S. Calvignac-Spencer, S. A. J. Leendertz, T. R. Gillespie, F. H. Leendertz, Wild great apes as sentinels and sources of infectious disease. *Clin. Microbiol. Infect.* **18**, 521–527 (2012).
60. T. R. Gillespie, C. L. Nunn, F. H. Leendertz, Integrative approaches to the study of primate infectious disease: Implications for biodiversity conservation and global health. *Am. J. Phys. Anthropol.* **137**, 53–69 (2008).
61. W. B. Karesh, R. A. Cook, E. L. Bennett, J. Newcomb, Wildlife trade and global disease emergence. *Emerg. Infect. Dis.* **11**, 1000–1002 (2005).
62. F. Schaumburg, L. Mugisha, B. Peck, K. Becker, T. R. Gillespie, G. Peters, F. H. Leendertz, Drug-resistant human *Staphylococcus aureus* in sanctuary apes pose a threat to endangered wild ape populations. *Am. J. Primatol.* **74**, 1071–1075 (2012).
63. K. Gilardi, T. Gillespie, F. Leendertz, E. Macfie, D. Travis, C. Whittier, E. Williamson, *Best Practice Guidelines for Health Monitoring and Disease Control in Great Ape Populations* (IUCN/SSC Primate Specialist Group, 2015); www.primate-sg.org/best_practice_disease.
64. J. E. Fa, J. Olivero, M. Farfán, A. L. Márquez, J. Duarte, J. Nackoney, A. Hall, J. Dupain, S. Seymour, P. J. Johnson, D. W. Macdonald, R. Real, J. M. Vargas, Correlates of bushmeat in markets and depletion of wildlife. *Conserv. Biol.* **29**, 805–815 (2015).
65. International Union for Conservation of Nature, *Regional Action Plan for the Conservation of Western Lowland Gorillas and Central Chimpanzees 2015–2025* (IUCN SSC Primate Specialist Group, 2014), 56 pp; www.primate-sg.org/WEA2014.pdf.
66. F. Rovero, A. S. Mtui, A. S. Kitegile, M. R. Nielsen, Hunting or habitat degradation? Decline of primate populations in Udzungwa Mountains, Tanzania: An analysis of threats. *Biol. Conserv.* **146**, 89–96 (2012).
67. V. Nijman, K. A. I. Nekaris, G. Donati, M. W. Bruford, J. Fa, Primate conservation: Measuring and mitigating trade in primates. *Endanger. Species Res.* **13**, 159–161 (2011).
68. R. R. N. Alves, W. M. S. Souto, R. R. D. Barboza, Primates in traditional folk medicine: A world overview. *Mamm. Rev.* **40**, 155–180 (2010).
69. A. M. Maldonado, V. Nijman, S. K. Bearder, Trade in night monkeys *Aotus* spp. in the Brazil–Colombia–Peru tri-border area: International wildlife trade regulations are ineffectively enforced. *Endanger. Species Res.* **9**, 143–149 (2009).
70. N. Shanee, A. P. Mendoza, S. Shanee, Diagnostic overview of the illegal trade in primates and law enforcement in Peru. *Am. J. Primatol.* **2015** (2015).
71. K. A.-I. Nekaris, N. Campbell, T. G. Coggins, E. J. Rode, V. Nijman, Tickled to death: Analysing public perceptions of 'cute' videos of threatened species (slow lorises—*Nycticebus* spp.) on Web 2.0 sites. *PLOS ONE* **8**, e69215 (2013).
72. UNODC, *Transnational Organized Crime in East Asia and the Pacific. A Threat Assessment* (United Nations Office on Drugs and Crime, Regional Office for Southeast Asia and the Pacific, 2013).
73. T. L. Graham, H. D. Matthews, S. E. Turner, A global-scale evaluation of primate exposure and vulnerability to climate change. *Int. J. Primatol.* **37**, 158–174 (2016).
74. R. G. Pearson, J. C. Stanton, K. T. Shoemaker, M. E. Aiello-Lammens, P. J. Ersts, N. Horning, D. A. Fordham, C. J. Raxworthy, H. Y. Ryu, J. McNees, H. R. Akçakaya, Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Change* **4**, 217–221 (2014).
75. P. R. Sesink Clee, E. E. Abwe, R. D. Ambahe, N. M. Anthony, R. Fotso, S. Locatelli, F. Maisels, M. W. Mitchell, B. J. Morgan, A. A. Pokempner, M. K. Gonder, Chimpanzee population structure in Cameroon and Nigeria is associated with habitat variation that may be lost under climate change. *BMC Evol. Biol.* **15**, 2 (2015).
76. A. Schloss, T. A. Nuñez, J. J. Lawler, Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8606–8611 (2012).
77. S. F. Gouveia, J. P. Souza-Alves, L. Rattis, R. Dobrovolski, L. Jerusalinsky, R. Beltrão-Mendes, S. F. Ferrari, Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. *Glob. Chang. Biol.* **22**, 2003–2012 (2016).
78. M. B. Araújo, M. Cabeza, W. Thuiller, L. Hannah, P. H. Williams, Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Chang. Biol.* **10**, 1618–1626 (2004).
79. J. M. Tylianakis, R. K. Didham, J. Bascompte, D. A. Wardle, Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363 (2008).
80. M. J. Struebig, M. Fischer, D. L. Gaveau, E. Meijaard, S. A. Wich, C. Gonner, R. Sykes, A. Wilting, S. Kramer-Schadt, Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans. *Glob. Chang. Biol.* **21**, 2891–2904 (2015).
81. Y. Malhi, J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, C. A. Nobre, Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172 (2008).
82. R. Wiederholt, E. Post, Tropical warming and the dynamics of endangered primates. *Biol. Lett.* **6**, 257–260 (2010).
83. S. A. Fritz, A. Purvis, Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042–1051 (2010).
84. M. S. Springer, R. W. Meredith, J. Gatesy, C. A. Emerling, J. Park, D. L. Rabosky, T. Stadler, C. Steiner, O. A. Ryder, J. E. Janečka, C. A. Fisher, W. J. Murphy, Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLOS ONE* **7**, e49521 (2012).
85. L. D. Verde Arregoitia, K. Leach, N. Reid, D. O. Fisher, Diversity, extinction, and threat status in Lagomorphs. *Ecography* **38**, 1155–1165 (2015).

86. L. D. Verde Arregoitia, S. P. Blomberg, D. O. Fisher, Phylogenetic correlates of extinction risk in mammals: Species in older lineages are not at greater risk. *Proc. Biol. Sci.* **280**, 20131092 (2013).
87. A. C. Lootvoet, J. Philippon, C. Bessa-Gomes, Behavioral correlates of primates conservation status: Intrinsic vulnerability to anthropogenic threats. *PLOS ONE* **10**, e01135538 (2015).
88. A. Fuentes, Ethnoprimatology and the anthropology of the human-primate interface. *Annu. Rev. Anthropol.* **41**, 101–117 (2012).
89. L. Cormier, A preliminary review of neotropical primates in the subsistence and symbolism of indigenous lowland South American peoples. *Ecol. Environ. Anthropol.* **2**, 14–32 (2006).
90. M. Haslam, L. V. Luncz, R. A. Staff, F. Bradshaw, E. B. Ottoni, T. Falótico, Pre-Columbian monkey tools. *Curr. Biol.* **26**, R521–R522 (2016).
91. R. W. Sussman, D. T. Rasmussen, P. H. Raven, Rethinking primate origins again. *Am. J. Primatol.* **75**, 95–106 (2013).
92. I. Koné, J. E. Lambert, J. Refisch, A. Bakayoko, Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: Implications for the conservation of forest fragments. *Trop. Conserv. Sci.* **1**, 293–306 (2008).
93. J. Lambert, Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *Afr. J. Ecol.* **36**, 234–240 (1998).
94. E. W. Heymann, Florivory, nectarivory, and pollination—A review of primate-flower interactions. *Ecotropica* **17**, 41–52 (2011).
95. C. A. Chapman, T. R. Bonnell, J. F. Gogarten, J. E. Lambert, P. A. Omeja, D. Twinomugisha, M. D. Wasserman, J. M. Rothman, Are primates ecosystem engineers? *Int. J. Primatol.* **34**, 1–14 (2013).
96. T. T. Caughlin, J. M. Ferguson, J. W. Lichstein, P. A. Zuidema, S. Bunyavejchewin, D. J. Levey, Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. Biol. Sci.* **282**, 20142095 (2015).
97. L. F. Pacheco, J. A. Simonetti, Genetic structure of a mimosoid tree deprived of its seed disperser, the spider monkey. *Conserv. Biol.* **14**, 1766–1775 (2000).
98. G. Nunez-Iturri, O. Olsson, H. F. Howe, Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biol. Conserv.* **141**, 1536–1546 (2008).
99. C. Bello, M. Galetti, M. A. Pizo, L. F. S. Magnago, M. F. Rocha, R. A. F. Lima, C. A. Peres, O. Ovaskainen, P. Jordano, Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105 (2015).
100. S. Federman, A. Dornburg, D. C. Daly, A. Downie, G. H. Perry, A. D. Yoder, E. J. Sargis, A. Richard, M. J. Donoghue, A. L. Baden, Implications of lemuriform extinctions for the Malagasy flora. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 5041–5046 (2016).
101. C. A. Peres, T. Emilio, J. Schietti, S. J. M. Desmoulière, T. Levi, Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 892–897 (2016).
102. P. R. Stevenson, A. M. Aldana, Potential effects of ateline extinction and forest fragmentation on plant diversity and composition in the western Orinoco Basin, Colombia. *Int. J. Primatol.* **29**, 365–377 (2008).
103. J. F. Brodie, O. E. Helmy, W. Y. Brockelman, J. L. Maron, Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol. Appl.* **19**, 854–863 (2009).
104. E. Efiom, thesis, Consequences of bushmeat hunting in tropical forests, Lund University (2013).
105. B. Hare, From hominoid to hominid mind: What changed and why? *Annu. Rev. Anthropol.* **40**, 293–309 (2011).
106. M. E. Thompson, Comparative reproductive energetics of human and nonhuman primates. *Annu. Rev. Anthropol.* **42**, 287–304 (2013).
107. H. Pontzer, Energy expenditure in humans and other primates: A new synthesis. *Annu. Rev. Anthropol.* **44**, 169–187 (2015).
108. E. Fernandez-Duque, C. R. Valeggia, S. P. Mendoza, The biology of paternal care in human and nonhuman primates. *Annu. Rev. Anthropol.* **38**, 115–130 (2009).
109. K. A. Phillips, K. L. Bales, J. P. Capitanio, A. Conley, P. W. Czoty, B. A. t'Hart, W. D. Hopkins, S.-L. Hu, L. A. Miller, M. A. Nader, P. W. Nathanielsz, J. Rogers, C. A. Shively, M. L. Voytko, Why primate models matter. *Am. J. Primatol.* **76**, 801–827 (2014).
110. United Nations Office on Drugs and Crime, *World Wildlife Crime Report: Trafficking in Protected Species* (United Nations Office on Drugs and Crime, 2016); www.unodc.org/documents/data-and-analysis/wildlife/World_Wildlife_Crime_Report_2016_final.pdf.
111. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Synthesis* (Island Press, 2005).
112. F. Dalerum, Identifying the role of conservation biology for solving the environmental crisis. *Ambio* **43**, 839–846 (2014).
113. C. B. Stanford, *Planet Without Apes* (Harvard Univ. Press, 2012), 272 pp.
114. J. Hardouin, É. Thys, V. Joiris, D. Fielding, Mini-livestock breeding with indigenous species in the tropics. *Livestock Res. Rural Dev.* **15**, 4 (2003).
115. N. van Vliet, D. Cornelis, H. Beck, P. Lindsey, R. Nasi, S. LeBel, J. Moreno, J. Fragoso, F. Jori, Meat from the wild: Extractive uses of wildlife and alternatives for sustainability, in *Current Trends in Wildlife Research*, R. Mateo, B. Arroyo, J. T. García, Eds. (Springer International Publishing, 2016), pp. 225–265.
116. W. A. Adams, J. Hutton, People, parks and poverty: Political ecology and biodiversity conservation. *Conserv. Soc.* **5**, 147–183 (2007).
117. R. Hill, C. Miller, B. Newell, M. Dunlop, I. J. Gordon, Why biodiversity declines as protected areas increase: The effect of the power of governance regimes on sustainable landscapes. *Sustainability Sci.* **10**, 357–369 (2015).
118. M. B. Mascia, S. Pailler, R. Krithivasan, V. Roshchanka, D. Burns, M. J. Mlotha, D. R. Murray, N. Peng, Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol. Conserv.* **169**, 355–361 (2014).
119. B. D. Spracklen, M. Kalamandeen, D. Galbraith, E. Gloor, D. V. Spracklen, A global analysis of deforestation in moist tropical forest protected areas. *PLOS ONE* **10**, e0143886 (2015).
120. F. Rovero, A. Mtui, A. Kitegile, P. Jacob, A. Araldi, S. Tenan, Primates decline rapidly in unprotected forests: Evidence from a monitoring program with data constraints. *PLOS ONE* **10**, e0118330 (2015).
121. L. Beaudrot, J. A. Ahumada, T. O'Brien, P. Alvarez-Loayza, K. Boekee, A. Campos-Arceiz, D. Eichberg, S. Espinosa, E. Fegraus, C. Fletcher, K. Gajapersad, C. Hallam, J. Hurtado, P. A. Jansen, A. Kumar, E. Larney, M. G. M. Lima, C. Mahony, E. H. Martin, A. McWilliam, B. Mugerwa, M. Ndoundou-Hockemba, J. C. Razafimahaimodison, H. Romero-Saltos, F. Rovero, J. Salvador, F. Santos, D. Sheil, W. R. Spironello, M. R. Willig, N. L. Winarni, A. Zvoleff, S. J. Andelman, Standardized assessment of biodiversity trends in tropical forest protected areas: The end is not in sight. *PLOS Biol.* **14**, e1002357 (2016).
122. O. Venter, L. P. Koh, Reducing emissions from deforestation and forest degradation (REDD+): Game changer or just another quick fix? *Ann. N. Y. Acad. Sci.* **1249**, 137–150 (2012).
123. J. García-Ulloa, L. P. Koh, Payment for ecosystem services the role of REDD+ in primate conservation, in An Introduction to Primate Conservation, S. A. Wich, A. J. Marshal, Eds. (Oxford Univ. Press, 2016), pp. 257–268.
124. L. Porter-Bolland, E. A. Ellis, M. R. Guariguata, I. Ruiz-Mallén, S. Negrete-Yankelevich, V. Reyes-García, Community managed forests and forest protected areas: An assessment of their conservation effectiveness across the tropics. *Forest Ecol. Manag.* **268**, 6–17 (2012).
125. P. A. Townsend, K. L. Masters, Lattice-work corridors for climate change: A conceptual framework for biodiversity conservation and social-ecological resilience in a tropical elevational gradient. *Ecol. Soc.* **20**, 1 (2015).
126. P. A. Stephens, Land sparing, land sharing, and the fate of Africa's lions. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 14753–14754 (2015).
127. T. Ramiadantsoa, O. Ovaskainen, J. Rybicki, I. Hanski, Large-scale habitat corridors for biodiversity conservation: A forest corridor in Madagascar. *PLOS ONE* **10**, e0132126 (2015).
128. S. L. Pimm, S. Alibhai, R. Bergl, A. Dehgan, C. Giri, Z. Jewell, L. Joppa, R. Kays, S. Loarie, Emerging technologies to conserve biodiversity. *Trends Ecol. Evol.* **30**, 685–696 (2015).
129. M. A. Reisland, J. E. Lambert, Sympatric apes in sacred forests: Shared space and habitat use by humans and Endangered Javan gibbons (*Hylobates moloch*). *PLOS ONE* **11**, e014689 (2016).
130. E. K. Mallott, R. S. Malhi, P. A. Garber, High-throughput sequencing of fecal DNA to identify insects consumed by wild Weddell's saddleback tamarins (*Saguinus weddelli*, Cebidae, Primates) in Bolivia. *Am. J. Phys. Anthropol.* **156**, 474–481 (2015).
131. L. Moore, L. Vigilant, A population estimate of chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic capture–recapture methods. *Am. J. Primatol.* **76**, 335–346 (2014).
132. S. Köndgen, S. Schenk, G. Pauli, C. Boesch, F. H. Leendertz, Noninvasive monitoring of respiratory viruses in wild chimpanzees. *Ecohealth* **7**, 332–341 (2010).
133. B. J. Bradley, M. Stiller, D. M. Doran-Sheehy, T. Harris, C. A. Chapman, L. Vigilant, H. Poinar, Plant DNA sequences from feces: Potential means for assessing diets of wild primates. *Am. J. Primatol.* **69**, 699–705 (2007).
134. T. Minhós, E. Wallace, M. J. F. da Silva, R. M. Sá, M. Carmo, A. Barata, M. W. Bruford, DNA identification of primate bushmeat from urban markets in Guinea-Bissau and its implications for conservation. *Biol. Conserv.* **167**, 43–49 (2013).
135. W. Liu, C. Huang, C. Roos, Q. Zhou, Y. Li, F. Wei, Identification of the species, origin and sex of smuggled douc langur (Pygathrix sp.) remains. *Vietnamese J. Primatol.* **1–2**, 63–69 (2008).
136. C. Hvilsom, P. Frandsen, C. Børsting, F. Carlsen, B. Sallé, B. T. Simonsen, H. R. Siegismund, Understanding geographic origins and history of admixture among chimpanzees in European zoos, with implications for future breeding programmes. *Heredity* **110**, 586–593 (2013).

137. J. Pastorini, M. L. Sauther, R. W. Sussman, L. Gould, F. P. Cuozzo, P. Fernando, C. M. Nievergelt, N. I. Mundy, Comparison of the genetic variation of captive ring-tailed lemurs with a wild population in Madagascar. *Zoo Biol.* **34**, 463–472 (2015).
138. S. A. Wich, I. Singleton, M. G. Nowak, S. S. Utami Atmoko, G. Nisam, S. M. Arif, R. H. Putra, R. Ardi, G. Fredriksson, G. Usher, D. L. A. Gaveau, H. S. Kühl, Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Sci. Adv.* **2**, e1500789 (2016).
139. D. W. S. Challender, D. C. MacMillan, Poaching is more than an enforcement problem. *Conserv. Lett.* **7**, 484–494 (2014).
140. E. F. Daut, D. J. Brightsmith, M. J. Peterson, Role of non-governmental organizations in combating illegal wildlife—Pet trade in Peru. *J. Nat. Conserv.* **24**, 72–82 (2015).
141. F. L. Dolins, A. Jolly, H. Rasamimanana, J. Ratsimbazafy, A. T. Feistner, F. Ravoavy, Conservation education in Madagascar: Three case studies in the biologically diverse island-continent. *Am. J. Primatol.* **72**, 391–406 (2010).
142. J. Supriatna, A. Ario, Primates as flagships for conserving biodiversity and parks in Indonesia: Lessons learned from West Java and North Sumatra. *Primate Conserv.* **29**, 123–131 (2015).
143. A. Savage, R. Guillen, I. Lamilla, L. Soto, Developing an effective community conservation program for cotton-top tamarins (*Saguinus oedipus*) in Colombia. *Am. J. Primatol.* **72**, 379–390 (2010).
144. H. B. Wilson, E. Meijaard, O. Venter, M. Ancrenaz, H. P. Possingham, Conservation strategies for orangutans: Reintroduction versus habitat preservation and the benefits of sustainably logged forest. *PLOS ONE* **9**, e102174 (2014).
145. M. C. M. Kierulff, C. R. Ruiz-Miranda, P. P. de Oliveira, B. B. Beck, A. Martins, J. M. Dietz, D. M. Rambaldi, A. J. Baker, The golden lion tamarin *Leontopithecus rosalia*: A conservation success story. *Int. Zoo Yearb.* **46**, 36–45 (2012).
146. P. Osterberg, P. Samphanthamit, O. Maprang, S. Punnadee, W. Y. Brockelman, Gibbon (*Hylobates lar*) reintroduction success in Phuket, Thailand, and its conservation benefits. *Am. J. Primatol.* **77**, 492–501 (2015).
147. R. S. Moore, Wihermanto, K. A. I. Nekaris, Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. *Endang. Species Res.* **26**, 93–102 (2014).
148. G. Le Flohic, P. Motsch, H. DeNys, S. Childs, A. Courage, T. King, Behavioural ecology and group cohesion of juvenile western lowland gorillas (*Gorilla g. gorilla*) during rehabilitation in the Batéké Plateaux National Park, Gabon. *PLOS ONE* **10**, e0119609 (2015).
149. D. Car, V. L. Queirogas, M. A. Pedersoli, Translocation and radio-telemetry monitoring of pygmy marmoset, Cebuella pygmaea (Spix, 1823), in the Brazilian Amazon. *Braz. J. Biol.* **75**, 91–97 (2015).
150. J. F. Millán, S. E. Bennett, P. R. Stevenson, Notes on the behavior of captive and released woolly monkeys (Lagothrix lagothricha): Reintroduction as a conservation strategy on Colombian southern Amazon, in *The Woolly Monkey: Behavior, Ecology, Systematics, and Captive Research*, T. R. Defler, P. R. Stevenson, Eds. (Springer, 2014), pp. 249–266.
151. G. L. Banes, B. M. F. Galdikas, L. Vigilant, Reintroduction of confiscated and displaced mammals risks outbreeding and introgression in natural populations, as evidenced by orang-utans of divergent subspecies. *Sci. Rep.* **6**, 22026 (2016).
152. D. Moran, M. Petersone, F. Verones, On the suitability of input–Output analysis for calculating product-specific biodiversity footprints. *Ecol. Indic.* **60**, 192–201 (2016).
153. N. Malone, A. H. Wade, A. Fuentes, E. P. Riley, M. Remis, C. J. Robinson, Ethnoprimatology: Critical interdisciplinarity and multispecies approaches in anthropology. *Crit. Anthropol.* **34**, 8–29 (2014).
154. A. I. Nekaris, C. R. Shepherd, C. R. Starr, V. Nijman, Exploring cultural drivers for wildlife trade via an ethnoprimatological approach: A case study of slender and slow lorises (*Loris* and *Nycticebus*) in South and Southeast Asia. *Am. J. Primatol.* **72**, 877–886 (2010).
155. M. L. Gore, M. L. Lute, J. H. Ratsimbazafy, A. Rajaonson, Local perspectives on environmental insecurity and its influence on illegal biodiversity exploitation. *PLOS ONE* **11**, e0150337 (2016).
156. M. L. Gore, J. Ratsimbazafy, A. Rajaonson, A. Lewis, J. S. Kahler, Public perceptions of poaching risks in a biodiversity hotspot: Implications for wildlife trafficking interventions. *J. Trafficking Organ. Crime Secur.* **2**, 1–20 (2016).
157. J. S. Brashares, B. Abrahms, K. J. Fiorella, C. D. Golden, C. E. Hojnowski, R. A. Marsh, D. J. McCauley, T. A. Nuñez, K. Seto, L. Withey, Wildlife decline and social conflict. Policies aimed at reducing wildlife-related conflict must address the underlying causes. *Science* **345**, 376–378 (2014).
158. A. B. Rylands, R. A. Mittermeier, Primate taxonomy: Species and conservation. *Evol. Anthropol.* **23**, 8–10 (2014).
159. C. P. Groves, Order Primates, in Mammal Species of the World: A Taxonomic and Geographic Reference, D. E. Wilson, D. M. Reeder, Eds. (Smithsonian Institution Press, ed. 2, 1993), pp. 243–277.
160. C. P. Groves, *Primate Taxonomy* (Smithsonian Institution Press, 2001).
161. C. P. Groves, Order Primates, in *Mammal Species of the World: A Taxonomic and Geographic Reference*, D. E. Wilson, D. M. Reeder, Eds. (Johns Hopkins Univ. Press, ed. 3, 2005), pp. 111–184.
162. A. B. Rylands, H. Schneider, A. Langguth, R. A. Mittermeier, C. P. Groves, E. Rodríguez-Luna, An assessment of the diversity of New World primates. *Neotrop. Primates* **8**, 61–93 (2000).
163. P. Grubb, T. M. Butynski, J. F. Oates, S. K. Bearder, T. R. Disotell, C. P. Groves, T. T. Struhsaker, Assessment of the diversity of African primates. *Int. J. Primatol.* **24**, 1301–1357 (2003).
164. D. Brandon-Jones, A. A. Eudey, T. Geissmann, C. P. Groves, D. J. Melnick, J. C. Morales, M. Shekelle, C.-B. Stewart, Asian primate classification. *Int. J. Primatol.* **25**, 97–164 (2004).
165. R. A. Mittermeier, J. U. Ganzhorn, W. R. Konstant, K. Glander, I. Tattersall, C. P. Groves, A. B. Rylands, A. Hapke, J. Ratsimbazafy, M. I. Mayor, E. E. Louis Jr., Y. Rumpler, C. Schwitzer, R. Rasoloarison, Lemur diversity in Madagascar. *Int. J. Primatol.* **29**, 1607–1656 (2008).
166. M. E. Blair, E. J. Sterling, M. M. Hurley, Taxonomy and conservation of Vietnam's primates: A review. *Am. J. Primatol.* **73**, 1093–1106 (2011).
167. I. Tattersall, Cathemeral activity in primates: A definition. *Folia Primatol.* **49**, 200–202 (1987).
168. D. A. Burney, L. P. Burney, L. R. Godfrey, W. L. Jungers, S. M. Goodman, H. T. Wright, A. J. T. Hull, A chronology for late prehistoric Madagascar. *J. Hum. Evol.* **47**, 25–63 (2004).
169. E. F. Lambin, P. Meyfroidt, Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3465–3472 (2011).
170. P. K. Thornton, Livestock production: Recent trends, future prospects. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2853–2867 (2010).
171. A. S. Cohn, A. Mosnier, P. Havlík, H. Valin, M. Herrero, E. Schmid, M. O'Hare, M. Obersteiner, Cattle ranching intensification in Brazil can reduce global greenhouse gas emissions by sparing land from deforestation. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 7236–7241 (2014).
172. A. Casson, *Oil Palm, Soybeans and Critical Habitat Loss: A Review* (WWF Forest Conversion Initiative, 2003).
173. F. Danielsen, H. Beukema, N. D. Burgess, F. Parish, C. A. Brühl, P. F. Donald, D. Murdiyarso, B. E. N. Phalan, L. Reijnders, M. Struebig, E. B. Fitzherbert, Biofuel plantations on forested lands: Double jeopardy for biodiversity and climate. *Conserv. Biol.* **23**, 348–358 (2009).
174. L. P. Koh, J. Ghazoul, Spatially-explicit scenario analysis for reconciling agricultural expansion, forest protection, and carbon conservation in Indonesia. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 11140–11144 (2010).
175. J. M. Linder, African primate diversity threatened by "new wave" of industrial oil palm expansion. *Afr. Primates* **8**, 25–38 (2013).
176. Z. Li, J. M. Fox, Mapping rubber tree growth in mainland Southeast Asia using time-series MODIS 250m NDVI and statistical data. *Appl. Geogr.* **32**, 420–432 (2012).
177. E. Warren-Thomas, P. M. Dolman, D. P. Edwards, Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conserv. Lett.* **8**, 230–241 (2015).
178. J. Clay, *World Agriculture and the Environment: A Commodity-by-Commodity Guide to Impacts and Practices* (Island Press, 2004).
179. A. Ahrends, P. M. Hollingsworth, A. D. Ziegler, J. M. Fox, H. Chen, Y. Su, J. Xu, Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. *Glob. Environ. Chang.* **34**, 48–58 (2015).
180. Forestry Economics and Policy Division, Planted Forests. A Statement of Principles (Food and Agriculture Organization of the United Nations, 2010); www.fao.org/forestry/plantedforests.
181. Forestry Economics and Policy Division, *State of the World's Forests 2011* (Food and Agriculture Organization of the United Nations, 2011); (www.fao.org/docrep/013/i2000e/i2000e00.htm.
182. M. C. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
183. P. J. Fashing, N. Nguyen, P. Luteshi, W. Opondo, J. F. Cash, M. Cords, Evaluating the suitability of planted forests for African forest monkeys: A case study from Kakamega forest, Kenya. *Am. J. Primatol.* **74**, 77–90 (2012).
184. R. Bshary, Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behav. Ecol. Sociobiol.* **50**, 251–256 (2001).
185. R. Noë, R. Bshary, The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proc. Biol. Sci.* **264**, 253–259 (1997).
186. L. A. Isbell, Predation on primates: Ecological patterns and evolutionary consequences. *Evol. Anthropol.* **3**, 61–71 (1994).

187. M. J. Remis, C. A. Jost Robinson, Reductions in primate abundance and diversity in a multiuse protected area: Synergistic impacts of hunting and logging in a Congo Basin forest. *Am. J. Primatol.* **74**, 602–612 (2012).
188. J. F. Ranaivoarisoa, J. R. Zaonarivelo, R. Lei, S. E. Johnson, T. M. Wyman, R. A. Mittermeier, E. E. Louis Jr., Rapid survey and assessment of the northern sportive lemur, *Lepilemur septentrionalis*, in northern Madagascar. *Primate Conserv.* **27**, 23–31 (2013).
189. N. F. Kümpel, E. J. Milner-Gulland, J. M. Rowcliffe, G. Cowlishaw, Impact of gun-hunting on diurnal primates in continental Equatorial Guinea. *Int. J. Primatol.* **29**, 1065–1082 (2008).
190. J. F. Oates, *Primates of West Africa: A Field Guide and Natural History* (Conservation International, 2011).
191. C. R. Shepherd, Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in North Sumatra. *Endang. Spec. Res.* **11**, 201–205 (2012).
192. V. Nijman, D. Spaan, E. J. Rode-Margono, Wirdateti, K. A. I. Nekaris, Changes in the primate trade in Indonesian wildlife markets over a 25-year period: Fewer apes and langurs, more macaques, and slow lorises. *Am. J. Primatol.* 10.1002/ajp.22517 (2015).
193. C. Starr, K. A. I. Nekaris, U. Streicher, L. Leung, Traditional use of slow lorises *Nycticebus bengalensis* and *N. pygmaeus* in Cambodia: An impediment to their conservation. *Endang. Spec. Res.* **12**, 17–23 (2010).
194. A. L. S. Meyer, M. R. Pie, F. C. Passos, Assessing the exposure of lion tamarins (*Leontopithecus spp.*) to future climate change. *Am. J. Primatol.* **76**, 551–562 (2014).
195. S. Shanee, Predicting future effects of multiple drivers of extinction risk in Peru's endemic primate fauna, in *Ethnoprimatology: Primate Conservation in the 21st Century*, M. Waller, Ed. (Springer, 2016), pp. 315–349.
196. J. M. Rothman, C. A. Chapman, T. T. Struhsaker, D. Raubenheimer, D. Twinomugisha, P. G. Waterman, Long-term declines in nutritional quality of tropical leaves. *Ecology* **96**, 873–878 (2015).
197. M. A. Barrett, J. L. Brown, R. E. Junge, A. D. Yoder, Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and conservation in Madagascar. *Biol. Conserv.* **157**, 409–422 (2013).
198. United Nations Population Fund, State of World Population 2011 (United Nations Population Fund, 2011), www.unfpa.org/sites/default/files/pub-pdf/EN-SWOP2011-FINAL.pdf [accessed September 2015].
199. R. I. McDonald, P. Green, D. Balk, B. M. Fekete, C. Revenga, M. Todd, M. Montgomery, Urban growth, climate change, and freshwater availability. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 6312–6317 (2011).
200. United Nations Development Programme, Human Development Report (United Nations Development Programme, 2014); http://hdr.undp.org/en/content/human-development-report-2014 [accessed 4 September 2015]
201. R. W. Kates, P. Dasgupta, African poverty: A grand challenge for sustainability science. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 16747–16750 (2007).
202. S. Shanee, N. Shanee, Measuring success in a community conservation project: Local population increase in a Critically Endangered primate, the yellow-tailed woolly monkey (Lagothrix *flavicauda*) at la Esperanza, northeastern Peru. *Trop. Conserv. Sci.* **8**, 169–186 (2015).
203. I. Koné, K. Ouattara, A. D. Koffi, A top priority site for primate conservation in Côte d'Ivoire soon designated as a protected area? *Afr. Primates* **10**, 59–60 (2015).
204. R. H. Horwich, R. Das, A. Bose, Conservation and the current status of the golden langur in Assam, India, with reference to Bhutan. *Primate Conserv.* **27**, 77–83 (2013).
205. A. C. van Andel, S. A. Wich, C. Boesch, L. P. Koh, M. M. Robbins, J. Kelly, H. S. Kuehl, Locating chimpanzee nests and identifying fruiting trees with an unmanned aerial vehicle. *Am. J. Primatol.* **77**, 1122–1134 (2015).
206. K. Kakaes, F. Greenword, M. Lippincott, S. Dosemagen, P. Meier, S. A. Wich, Drones and Aerial Observation: New Technologies for Property Rights, Human Rights, and Global Development: A Primer (New America, 2015); http://drones.newamerica.org/primer/DronesAndAerialObservation.pdf
207. K. M. Fornace, C. J. Drakeley, T. William, F. Espino, J. Cox, Mapping infectious disease landscapes: Unmanned aerial vehicles and epidemiology. *Trends Parasitol.* **30**, 514–519 (2014).
208. M. B. Parsons, T. R. Gillespie, E. V. Lonsdorf, D. Travis, I. Lipende, B. Gilagiza, S. Kamenya, L. Pintea, G. M. Vazquez-Prokopec, Global positioning system data-loggers: A tool to quantify fine-scale movement of domestic animals to evaluate potential for zoonotic transmission to an endangered wildlife population. *PLOS ONE* **9**, e110984 (2014).
209. P. O'Donoghue, C. Rutz, Real-time anti-poaching tags could help prevent imminent species extinctions. *J. Appl. Ecol.* **53**, 5–10 (2016).

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