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Perspective

Future coexistence with great apes will require major changes to policy and practice

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John C. Mitani (1,2), Ekwoge Abwe^{3,4}, Genevieve Campbell⁵, Tamara Giles-Vernick (6, Tony Goldberg (7, Matthew R. McLennan (8,9, Signe Preuschoft¹⁰, Jatna Supriatna (1,12,13,14,15)

The great apes—bonobos, chimpanzees, gorillas and orangutans—are critically threatened by human activities. We have destroyed their habitats, hunted them and transmitted fatal diseases to them. Yet we also conduct research on them, try to protect them and live alongside them. They are endangered, and time is running out. Here we outline what must be done to ensure that future generations continue to share this planet with great apes. We urge dialogue with those who live with great apes and interact with them often. We advocate conservation plans that acknowledge the realities of climate change, economic drivers and population growth. We encourage researchers to use technology to minimize risks to great apes. Our proposals will require substantial investment, and we identify ways to generate these funds. We conclude with a discussion of how field researchers might alter their work to protect our closest living relatives more effectively.

The nonhuman great apes (hereafter, great apes)-bonobos, chimpanzees, gorillas, and orangutans (Fig. 1)-are humankind's closest living relatives. There are compelling reasons to protect them. Great apes live in tropical habitats and protecting them safeguards other threatened species in areas of high biodiversity. As keystone species¹, they can have a role in preserving ecosystems², which must be maintained to ensure human well-being and survival³. Great ape tourism can also provide income that improves the lives of people in some range countries⁴. The similarities between great apes and humans generate considerable scientific and media interest, making them flagship species that support the conservation of other species⁵. These similarities also raise scientific^{6,7}, moral^{8,9}, ethical and legal¹⁰ considerations that underscore our responsibility to protect them. Recognition of these matters has fuelled substantial investment in great ape conservation¹¹. For example, over one billion US dollars was spent to protect orangutans between 2000 and 2019¹². Nevertheless, populations of all seven currently recognized great ape species—bonobos; chimpanzees; eastern and western gorillas; and Bornean, Sumatran and Tapanuli orangutans—continue to decline, and their 'endangered' and 'critically endangered' designations reflect their high risk of extinction in the wild¹³. Time is running out to save these extraordinary animals, and we need more effective conservation strategies. In this Perspective, we make some proposals designed to ensure that great apes continue to survive now and into the future (Fig. 2). The views expressed here draw on prior research and an extensive literature, but also derive from our personal experience. Collectively, we have spent over 200 years working with great apes. We begin by briefly reviewing their status in the wild.

The current situation

The threats to wild great apes are well known and primarily include habitat loss, hunting and disease (Fig. 3). Consequently, prior efforts to conserve them and their ecosystems have focused on creating areas

¹Department of Anthropology, University of Michigan, Ann Arbor, MI, USA. ²Ngogo Chimpanzee Project, Phoenix, AZ, USA. ³San Diego Zoo Wildlife Alliance, Escondido, CA, USA. ⁴Cameroon Biodiversity Association, Douala, Cameroon. ⁵Re:wild, Austin, TX, USA. ⁶Anthropology and Ecology of Disease Emergence Unit, Institut Pasteur/Université Paris Cité, Paris, France. ⁷Department of Pathobiological Sciences, School of Veterinary Medicine, University of Wisconsin, Madison, WI, USA. ⁸Bulindi Chimpanzee and Community Project, Hoima, Uganda. ⁹Faculty of Humanities and Social Sciences, Oxford Brookes University, Oxford, UK. ¹⁰Ape Protection Unit, Four Paws, Hamburg, Germany. ¹¹Department of Biology, Faculty of Mathematics and Sciences, University of Indonesia, Depok, West Java, Indonesia. ¹²Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA. ¹³Program in the Environment, University of Michigan, Ann Arbor, MI, USA. ¹⁵Program in Computing for the Arts and Sciences, University of Michigan, Ann Arbor, MI, USA. ¹⁵Program in Computing for the Arts and Sciences, University of Michigan, Ann Arbor, MI, USA.

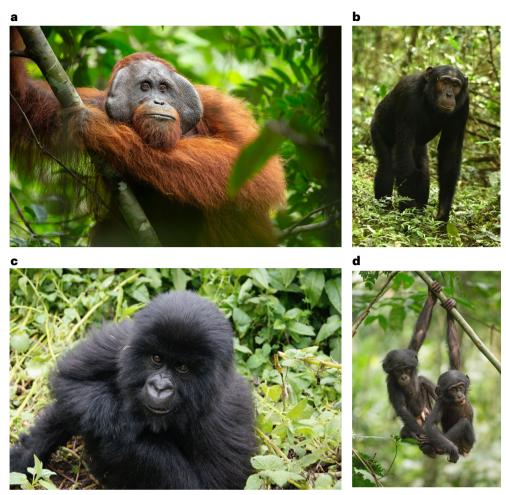


Fig. 1 | The great apes, like humans, develop over distinct life-history stages and have long lives. a, An adult male Bornean orangutan (*Pongo pygmaeus*). b, An adolescent male chimpanzee (*Pan troglodytes*). c, A juvenile male eastern

gorilla (*Gorilla beringei*). **d**, Female and male infant bonobos (*Pan paniscus*). Credits: **a**, Time Laman; **b**, Kevin C. Lee; **c**, Stacy Rosenbaum/The Dian Fossey Gorilla Fund; **d**, Takeshi Furuichi.

to protect intact natural habitats. These efforts have been successful in some areas, especially in situations where researchers have conducted long-term fieldwork on great apes habituated to human presence¹⁴. Fieldworkers intervene to protect great apes and their habitats, and the presence of researchers can deter activities that negatively impact them¹⁵. Nevertheless, some protected areas harbouring great apes are not managed effectively. This can often be attributed to scarce resources. Great apes live in countries that may not have the financial capability to invest in conservation and require great ape habitats to produce immediate economic returns. Failure to involve local people, whose lives are affected by conservation interventions, further reduces the efficacy of protected areas to conserve great apes¹⁶.

Complicating this situation, most great apes now reside in unprotected areas^{17,18} where conflicts between them and humans inevitably arise. Not long ago, considerable habitat outside of protected areas was available to great apes in many range countries^{19,20}, but these areas have disappeared owing to human population growth, the concomitant spread of human economic activities and rapid changes in land use. When great apes are forced to live in human-altered habitats, they feed on cultivated foods, use agricultural and village areas, navigate roads and build nests in exotic trees^{21,22} (Fig. 4). They can also behave aggressively owing to repeated and deleterious interactions with people. Chimpanzees and gorillas can attack people, and chimpanzees have killed small children, albeit rarely. These interactions have tragic consequences not only for the families and communities of victims but also because they create negative perceptions of great apes²³. Finding ways for great apes and humans to coexist outside protected areas is a central challenge for their conservation in the future.

Great ape numbers do not always decline during coexistence with humans. Many people who live in proximity to great apes depend on forest and wildlife products, and, historically, this relationship has been sustainable in some places for some animals²⁴. But when humans hunt great apes, even using rudimentary techniques, offtake rates can exceed natural population growth rates, resulting in population declines^{25,26}. Nowhere is the damaging effect of hunting more evident than in the commercial wild-meat trade (Fig. 3b). Hunting and the trade of wildlife products, including infant great apes taken for pets, generate millions of US dollars annually, especially in Central Africa and West Africa²⁷. Logging and other commercial activities that make large areas of remote forest accessible (Fig. 3a)²⁸ exacerbate the unsustainable offtake of great apes driven by demand in urban areas with increasing human populations^{29,30}. Although laws exist to protect great apes against hunting in most countries, they are often poorly enforced for several reasons. These include unfamiliarity with existing laws, inadequate resources, a paucity of wildlife personnel, lack of prosecution, corruption, political and social instability, and armed conflict³¹.

Disease compounds these problems. Human immunodeficiency virus, the severe acute respiratory syndrome (SARS) coronaviruses, and other recent cases of pathogen spillover from animals to humans are well known. The opposite, pathogen transmission from humans to a

a		–	Stakeholder groups							
		Benefits beyond apes		Great ape researchers	Conservation NGOs	Local government	National government	International community		Extractive industries
а	Enforce existing laws, integrating locally appropriate approaches	٠				•	•	•		•
b	Engage and partner with local people; respect their perspectives and needs	•		•	•	•				
с	Acknowledge the expertise of local people; elevate them to key leadership positions	٠		•	•		•	•		
d	Conduct basic and applied research outside protected areas			•						
е	Provide tangible benefits linked to conservation outcomes	•				•	•	•		
f	Reduce demand for products derived from ape habitats							•	•	
g	Promote recycling, circular economies and deforestation-free supply chains	•				•	•	•		•
h	Collaborate with stakeholders in extractive activities and infrastructure projects	٠		•	•		•			•
i	Transparently evaluate and report outcomes of conservation interventions	•		•	•	•	•			
j	Reduce demand by furnishing reasons to protect instead of hunt apes						•			
k	Promote the historical and cultural importance of apes among local people						•			
ι	Promote local people as ambassadors for great ape conservation			•		•	•	•		
m	Investigate and prosecute individuals involved in killing and capturing apes				•	•	•	•		
n	Facilitate efforts to keep apes and people apart			•	•					
0	Provide healthcare to people who come into contact with apes	•		•		•	•			
р	Assess the efficacy of existing measures and revise them as necessary			•						•
q	Ensure existing and future guidelines are followed			•		•	•			
r	Reconsider the role of direct observation of apes			•				•		
S	Identify and develop novel funding streams	•		•	•	•	•	•	•	•

b

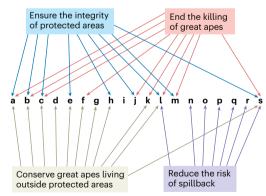


Fig. 2 | Synopsis of our proposals. a, Specific strategies for great ape conservation. Strategies that will provide conservation benefits beyond great apes are indicated, as are the key stakeholders for each. b, Four general approaches to great ape conservation (boxes) and their links to the strategies in a (arrows).

animals (spillback, reverse zoonosis or anthroponosis), is an increasingly important problem that threatens great apes, especially in Africa³² The disease risk posed by humans has been documented at long-term chimpanzee research sites where many individuals have died due to spillback³³⁻³⁶ (Fig. 3c). This has led field researchers to implement protocols to protect the great apes they study following recommendations of the International Union for the Conservation of Nature (IUCN). Measures are revised as conditions change and currently include: (1) quarantining before initiating field observations; (2) wearing face masks when following great apes; (3) maintaining a minimum distance of 7–10 metres from subjects; (4) requiring observers to sanitize their hands regularly; (5) banning sick people from accessing great apes; and (6) ensuring the vaccination status of all researchers and field staff. A few of these practices have been implemented at some, but not all,







Fig. 3 | Threats to great apes in the wild. a, Habitat destruction. Great ape habitat is lost due to human economic activities, including agriculture, logging and extractive industry. The latter includes mining as illustrated here by an open pit coal mine in East Kalimantan, Indonesia. These coal mines destroy large tracts of habitat occupied by Bornean orangutans. b, Hunting. The wild-meat trade has decimated some populations of great apes. These two infant bonobos were orphaned after their mothers fell victim to hunters. The bonobo on the left was severely malnourished following her ordeal. The bonobos were rescued and cared for at Lola ya Bonobo, a sanctuary in the Democratic Republic of Congo. c, Disease. Veterinarians collect clinical samples from a deceased chimpanzee in the wild. Subsequent laboratory analyses revealed that the chimpanzee succumbed to respiratory illness caused by human metapneumovirus, a common and deadly reverse zoonotic pathogen. Credit: a, Nanang Sujana; b, Lola ya Bonobo Sanctuary; c, Ronan Donovan. sites where tourists visit great apes in the wild³⁷, and we need to promote compliance with and improve upon these measures³⁸. Most places where people and great apes come into contact, however, are neither research nor tourism sites, so these measures cannot be applied.

A way forward

Waning great ape numbers despite extensive efforts to protect them indicate an urgent need for more effective approaches. The task is challenging because it requires addressing multiple issues at many levels. These include reducing or reversing habitat loss due to large- and small-scale human economic activity, finding alternatives to hunting and lowering the risk of reverse zoonoses that threaten great apes inside and outside protected areas. Although some of the ideas we propose apply specifically to great apes, others do so more broadly and will contribute to positive conservation outcomes for many endangered organisms (Fig. 2). We begin by acknowledging three guiding principles. First, humans control the means to protect great apes, so we must devise ways to coexist now and in the future. Second, the multiple reasons for conserving them demand that we value their lives on par with our own. This means that we must commit to saving every individual great ape in the wild today. Third, implemented policies require empirical evaluation and transparent reporting of successes and failures as well as testing to ascertain the conditions for success³⁹. With these principles in mind, what can be done?

Ensuring the integrity of protected areas

We believe that safeguarding great apes in protected areas is an effective strategy and will remain a cornerstone of future efforts to conserve them (Fig. 5). Protection must include effective law enforcement 40,41 . Such enforcement, however, is currently lacking in many protected areas^{42,43}, leading to declines in resident great ape populations⁴⁴⁻⁴⁶. In some areas, substantial changes from current practices will be required if laws are to be adequately enforced^{47,48}. Here we advocate several measures, including increasing funding⁴⁹; fighting corruption⁵⁰; using forensic genetics to identify illegally trafficked animals⁵¹; strengthening legal systems to raise conviction rates and impose sentences that deter wildlife crimes⁵²; providing law enforcement officers with rapid information on population trends⁵³; and increasing the use of technology⁵⁴ such as real-time remote sensing, micro-light aircraft, protected area management software and camera traps to improve patrolling efficacy. The latter will be enhanced by advances in computational methods and analysis.

We acknowledge that focusing solely on law enforcement is unlikely to adequately protect wildlife^{55,56}, particularly where laws prohibit local people from accessing lands over which they have historically held customary rights¹⁶. History, logic and modelling suggest that integrating evidence-based, locally appropriate and complementary approaches can achieve better outcomes than law enforcement alone^{11,57,58}. A good example is tourism, which when successfully implemented, can have dramatic, positive effects on the success of protected areas. Mountain gorilla tourism in the Volcanoes National Park, Rwanda⁵⁹ generates millions of US dollars every year, furnishing a powerful incentive to safeguard gorillas and their habitat⁶⁰. Remarkably, only one mountain gorilla succumbed due to the hostilities during the 1990-1994 Rwandan civil war and genocide^{61,62}. Our experience there during the civil war indicated that both sides involved in the conflict stayed away from areas inhabited by the gorillas. It is likely that this was because the victors would obtain the revenue from gorilla tourism. Tourism is unlikely to work in all-perhaps most-protected areas, however63, emphasizing the need for a diverse portfolio of conservation tactics.

Conservation practitioners have long discussed the moral and practical necessity of engaging local people so that the costs of protecting great apes do not rest solely with under-resourced communities. Consequently, successful conservation efforts depend crucially on effective partnerships with local communities¹¹, and there has been





Fig. 4 | **Great apes in human-modified environments.** Great apes who live outside of protected areas interact with humans in several contexts. **a**, A juvenile chimpanzee feeds on maize in a farmer's field. **b**, Male chimpanzees look at their reflections in the window of a village house. **c**, Chimpanzees cross a road that

divides their territory. **d**, An adult male chimpanzee rests in a nest built in an exotic *Eucalyptus* tree. Credit: **a**, **d**, Matthew McLennan/Bulindi Chimpanzee and Community Project; **b**, Ronan Donovan; **c**, Jacqueline Rohen/Bulindi Chimpanzee and Community Project.

extensive discussion of building capacity, raising awareness among local people about the importance of protecting great apes and their habitats, and ensuring that they alone do not bear the burden of protection⁶⁴⁻⁶⁶. Although these efforts are essential, the expertise of these people has not been properly acknowledged. Some local people possess extensive knowledge about the habitats and behaviour of great apes that relies, in part, on rich cultural and historical belief systems. We suggest that this represents a heretofore underutilized opportunity that could promote great ape conservation. Valorization of local expertise in all of its forms can be accomplished using traditional and social media, elevating local people to key leadership roles, providing opportunities to pursue higher education and creating national and international awards, such as the Whitley Award (https://whitleyaward.org). Recognizing the knowledge that local people have about great apes can build pride and deeper engagement with these experts, as both participants and leaders in research and conservation, and promote attempts to safeguard their habitat^{67,68}. Developing this expertise, in turn, promises to generate interest in and raise concern about great apes among people whose communities border protected areas or who share land with them.

In summary, preservation of great apes in protected areas will require management strategies that are multifaceted, context-specific, flexible and responsive to local knowledge and needs^{12,43,69}. Enacting these strategies will require diverse expertise^{70,71}, greater acknowledgement of the expertise of people who live with great apes and adequate resources requiring substantial investment (see 'Identifying and promoting novel funding mechanisms').

Addressing conservation of great apes outside protected areas

As noted above, most great apes live outside protected areas and ensuring their survival will depend on sustainable management of these



Fig. 5 | **Protected areas safeguard great ape habitat.** Gunung Palung National Park in West Kalimantan, Indonesia covers 1,080 km² and harbours one of the largest remaining populations of Bornean orangutans in Southeast Asia. Credit: Gene Estrada.

populations and their habitats. Thus, much conservation work in the future must be conducted outside formally protected areas in heterogeneous, multi-use landscapes⁷². Fortunately, generalized adaptations and behavioural flexibility make some great apes ecologically resilient and able to persist in habitats that are very different from the intact, pristine ecological conditions that we generally consider to be ideal^{18,21}. In fact, when great apes are not hunted or harassed, they can survive in human-dominated and modified landscapes^{22,67,69}, as orangutans appear to have done for thousands of years, albeit under conditions in which the impact of humans was less intense than most areas today⁷³. Few long-term studies of great apes, however, have been conducted

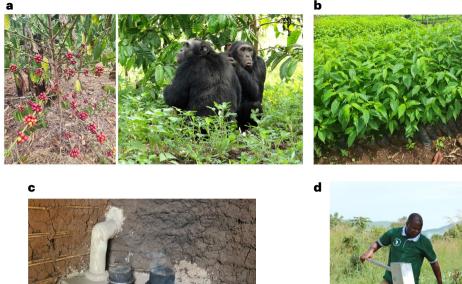




Fig. 6 | **Conserving great apes outside protected areas.** Protecting apes in these regions depends on ensuring humans benefit when sharing land with them. The Bulindi Chimpanzee and Community Project in Uganda provides incentives to promote chimpanzee–human coexistence. **a**, Growing coffee (left) is economically viable for local farmers and planted on existing farmland. Although chimpanzees (right) use gardens, they ignore the coffee berries. **b**, Seedlings of fast-growing tree species are given to landowners and reduce

outside protected areas⁷⁴, and we have limited understanding of their ecology and behaviour in the marginal habitats where most future conservation management will occur. This gap in knowledge is particularly acute for bonobos and gorillas, for whom research is even more biased towards protected areas⁷⁴. A key question is how do we configure and allocate shared habitat to ensure that great apes continue to survive in multi-use landscapes. We endorse more basic and applied research conducted outside of protected areas to address this question⁷⁵⁻⁷⁷.

Great apes suffer and their numbers fall when their presence conflicts with human interests. Because of this, efforts to protect them must create ways for humans to benefit as well. As with attempts to conserve great apes in protected areas, we advocate strategies and tactics that are diverse, context-specific⁷⁰, and engage multiple stakeholders, including local communities and leaders, policymakers, scientists, conservationists, government experts and representatives from extractive industries⁷⁸. At the local level, conservation efforts will be most effective if they place people in key leadership positions to navigate conflicts between great apes and humans sensitively, incorporate culturally appropriate education to promote conservation values and awareness of laws, and foster positive attitudes about great apes that reinforce cultural identities and a sense of pride in them^{65,79}. Above all, it is imperative that local stakeholders, primarily government officials and people who directly interact with great apes, regard their conservation as beneficial. Because long-term coexistence between people and great apes will depend on creating conditions in which their presence is a net benefit, we must develop programmes to help the mostly under-resourced people who live alongside great apes. Specifically, initiatives must furnish tangible benefits, such as

reliance on local forests. These trees provide an alternative source of wood for cooking, construction and income from timber sales. **c**, Energy-efficient cook stoves reduce fuelwood consumption and curb the destruction of chimpanzee habitat. **d**, Water wells supply clean water away from forest streams and the areas chimpanzees frequent. Credit: **a**-**c**, Matthew McLennan/Bulindi Chimpanzee and Community Project; **d**, Jacqueline Rohen/Bulindi Chimpanzee and Community Project.

livelihood opportunities, healthcare, education and funding for local councils, that are directly tied to great ape conservation outcomes (Fig. 6). Local people will have ideas about the kinds of incentives most valuable to them, so they must be involved in the development of conservation initiatives from the outset. We propose options such as provision of healthcare at reduced costs for people contributing positively to great ape conservation⁸⁰; carbon payments for tree planting or forest conservation on private or community land⁸¹; tourism⁵⁷; and subsidies for crops that are economically viable but unpalatable to great apes⁸².

Novel approaches will also be required to combat larger-scale threats associated with industrial mining, oil and gas, and logging. First, reducing the demand for products derived from these industries, primarily driven by non-great-ape-range countries, is critical⁸³. Second, the promotion of recycling and circular economies⁸⁴ will decrease the impact of large-scale industry on great ape habitat. Third, many companies have already adopted deforestation-free supply chains⁸⁵, and considerations must be given to avoid great ape habitat when decisions are made about where to develop large-scale projects. Over time, this should become the norm. Finally, additional steps must be taken for projects that continue to be established in great ape habitat. For these, their design and effective mitigation measures require direct, collaborative engagement between companies, lending institutions, nongovernmental organizations (NGOs) as well as governments responsible for developing and regulating extractive industries and infrastructure projects where great apes occur⁸⁶⁻⁸⁸. Specifically, we support certification of great-ape-friendly timber concessions, industrial pulp and paper estates, and oil palm and rubber plantations to reward

companies that develop land in ways that are compatible with the long-term preservation of wild great ape populations^{89,90}.

End the killing of great apes

It is illegal to kill, capture and trade great apes¹³, and eliminating these demands action on two fronts at different scales. In places where they are hunted for food, limiting dependence on them is necessary. The key will be to find alternative, but realistically obtainable and affordable sources of food, particularly protein, for people who consume great apes⁹¹. As emphasized above, implementing successful programmes depends on the specific economic, social and political conditions where great apes reside. This requires genuine exchange with local hunters and others in their communities, and not simply suppression of hunting imposed from the outside. Again, harnessing the knowledge local hunters have about great apes, valuing their expertise and involving them in wildlife management efforts may strengthen the motivation to protect, instead of hunt, great apes^{92,93}.

Strategies to curb hunting of great apes for large commercial and international markets must target the entire supply chain, starting with specialist hunters in local communities. More importantly, it will be necessary to stop those who transport great apes to markets for consumption and traffic them for the pet trade and other reasons. The demand for great apes in these markets exists because people value them, as their consumption⁹⁴ and use are important to their lives⁹⁵. Changing consumer preferences here will require understanding the multiple reasons great apes are prized, including the belief that their meat is organic and healthy and its symbolic value to enhance social status and masculinity⁹⁶. Programmes designed to reduce demand must be carefully crafted to address these issues and consider that the cultural values and interests of those who hunt great apes are not likely to be congruent with those of conservationists⁹⁷. Although behaviour change will be difficult, we believe it can be facilitated through widespread, locally adapted media campaigns to inform the public of the value of local wildlife, the ecosystem services they provide and the imminent threat of extinction that lies on the horizon for great apes. It will be essential to promote the perspectives of local community experts, who will have insights about the historical and cultural importance of great apes. Harnessing the power of social media and traditional means of communication, including television, radio and newspapers, promises to sensitize people to these issues. Some NGOs have launched effective campaigns using celebrity 'conservation ambassadors', for example, WildAid (https://wildaid.org),

We advocate additional measures to curb the trade of great apes as pets. Sanctuaries and rehabilitation centres can have an important role in this regard because they furnish refuges to care for great apes confiscated from traders and can work effectively with law enforcement officials⁹⁸. Their efforts should be encouraged, expanded and supported by sustainable funding. Our experience indicates that local people employed at these facilities become effective conservation ambassadors. They learn about great apes while taking care of them and share the knowledge and respect they have for them with others in their communities. Finally, halting hunting and trafficking domestically and abroad depend on renewed efforts to deter and prosecute those involved and strengthening and enforcing existing laws designed to protect great apes and their habitats (Fig. 7).

Reducing the risk of spillback

Recognition of the risks that human pathogens pose to great apes has led to the adoption of protocols designed to limit this threat at research and tourist sites (see 'The current situation'). Nevertheless, the effectiveness of these measures, such as wearing face masks and maintaining a safe distance from great apes remains unknown, as they usually rely on reasonable assumptions about transmission rather than empirical evidence. In addition, protocols implemented to stop the spread of one pathogen may not prove effective against others. For example, steps



Fig. 7 | Protecting great apes against the threat of hunting. The Cross River gorilla is a critically endangered great ape found along the Nigeria– Cameroon border. Rangers, who patrol their habitat, are equipped with rugged smartphones loaded with SMART (Spatial Monitoring And Reporting Tool) software. Using SMART, rangers record their locations and activities in real time, resulting in more efficient and effective patrols. Implementation of SMART technology has led to a substantial reduction in hunting pressure on these gorillas. Credit: Richard Bergl.

taken to reduce transmission of respiratory viruses are unlikely to stop the spread of soil-transmitted helminths. Given these considerations, several approaches will be required to mitigate the disease risk humans pose to great apes. One strategy guaranteed to reduce risk is keeping people and great apes apart. Reducing the time that people spend in great ape habitats, their proximity to them, and the frequency with which great apes enter human settlements will reduce disease risk for pathogens across a spectrum of modes of transmission. Maintaining separate areas for great apes and people should also decrease indirect, environmental transmission, such as from contamination of soil and water with human faeces or the introduction of urban, vector-borne diseases into forests.

We recognize that creating entirely separate spaces for great apes apart from humans is impractical and that additional steps must be taken to reduce the possibility of great apes succumbing to human disease⁹⁹. People who share habitats with great apes in remote areas do not have ready access to medical facilities. Improving their health and access to healthcare will enhance their lives and decrease the potential for spillback. Funding to create and maintain local and mobile clinics and healthcare teams will produce the kind of win-win situation necessary for both great apes and humans to thrive (Fig. 8). Additional initiatives focusing on human sanitation and health promise to mitigate cases of spillback. For example, human litter and faeces can harbour environmentally persistent pathogens, and people deposit both in open trash pits and defecation sites in spaces shared with great apes. This can result in cases of spillback involving great apes who frequent these areas and can be reduced by building alternative waste cache systems and latrines for people who need them. Such strategies demand additional investment, but also outreach efforts to increase awareness about how steps taken to enhance human well-being and



Fig. 8 | **Providing healthcare to reduce the threat of spillback.** This mobile clinic was developed and supported by the Kibale Monkey Project and the Uganda Wildlife Authority in Kibale National Park, Uganda, home to one of the largest populations of chimpanzees in East Africa. The clinic provided healthcare services to people in communities surrounding the park and who may come into contact with chimpanzees. By ensuring that people stay healthy, these services help to reduce the threat of spillback. The programme is currently maintained by the Kasiisi Project. Credit: The Kasiisi Project (photo); Uganda Wildlife Authority (logo).

health will have additional positive consequences for great apes and many other animals.

It will be difficult to prevent spillback in situations where great apes come into proximity or physical contact with humans, but we can prevent it in some situations that are under our control. In keeping with the idea that every great ape's life has value, we call on researchers to take the lead in finding novel ways to mitigate spillback. In this context, we ask fieldworkers to consider a difficult question: is it necessary to conduct direct observations of great apes? Primate field research relies on an established tradition that involves collecting data on animals at close range^{100,101}. Now that we know that the presence of humans creates the potential for spillback, we should re-evaluate how we do our work. When the presence of an observer is not essential, we propose adopting technology to minimize contact with great apes. Camera traps¹⁰², passive acoustic monitors¹⁰³, capture recapture using genetic samples collected non-invasively¹⁰⁴, next-generation telemetry¹⁰⁵, and drones¹⁰⁶ have been increasingly used to study wildlife, including great apes. Advances in technology will make these techniques increasingly affordable, thus facilitating their widespread implementation and potential to furnish new insights into great ape behaviour and ecology while minimizing the probability they will succumb due to spillback.

Identifying and promoting novel funding mechanisms

The measures we propose to protect great apes require additional funds to make conservation a more economically viable option than competing extractive alternatives^{107,108} and need to address inequities regarding who bears the costs of conservation⁸¹. Although we applaud the aims of programmes that seek to protect biodiversity and the entire planet by fundamentally altering present economic systems¹⁰⁹, it is unclear whether implementing them will have a positive impact on great ape conservation, at least in the short to medium term over which action is urgently needed¹¹⁰. Moreover, our experience suggests that effective strategies must accept the world as it is, and we base our proposals in light of current economic and political realities. Here, we suggest that tourism⁵⁷, carbon payments¹¹¹ and wildlife credits^{112–114} can compensate local communities in range countries foregoing extractive activities that are detrimental to great apes. Efforts to assess and publicize the monetary value of the ecosystem services provided by great apes will probably increase the funding available for such initiatives¹¹⁵. In this context, we support initiatives that turn permits that would typically be issued to extractive industries into sustainable biodiversity conservation programmes. These programmes value nature and its long-term benefits to local communities, instead of the short-term economic gains derived from exploiting the environment¹¹⁶. We advocate these nature-based investment schemes recognizing that other conservationists may hold differing views on this matter¹⁰⁹.

Philanthropic foundations provide the major source of funding for great ape conservation. Despite their substantial efforts, we lack a long-term vision and plan to ensure a recurrent funding stream to support great ape conservation activities in perpetuity. Industries could support such initiatives. Some already help to fund conservation through the payment of offsets. These payments are temporary, however, and we suggest that this money could be better used to support biodiversity trust funds that finance conservation activities with a clear long-term vision¹¹⁷. Specifically, we propose establishing a great ape trust fund that could, for example, finance the conservation activities detailed in the IUCN Action Plans for the different great ape taxa (https://www.iucngreatapes.org/action-planning). It will take time to generate a sufficiently large endowment required for this purpose. More dialogue and collaboration between NGOs, industry, governments and private donors will be necessary.

Reconsidering the role of field research

Research on great apes has revolutionized our understanding of our place in nature and how humans evolved¹¹⁸⁻¹²¹. These findings derive from observing individual great apes that have often taken years to habituate to human presence¹²². As noted previously, an important benefit of long-term fieldwork is that the presence of researchers helps protect great apes in the wild. Nevertheless, there are trade-offs¹²³. We have discussed how researchers pose a threat to great apes owing to the risk of disease transmission. In addition, habituation can stress animals¹²⁴, increase their vulnerability to poaching¹²⁵ and negatively impact conspecifics. For instance, habituated chimpanzees possess an advantage during intergroup encounters with unhabituated neighbours because the latter fear humans (J.C.M. personal observation). This increases the probability of unhabituated chimpanzees becoming victims of coalitionary attacks by conspecifics who are accustomed to human observers. The deleterious consequences of habituating great apes for research can thus compromise data used to address long-standing questions about their behaviour, life history and evolution.

Taken together, the preceding issues force us to reconsider how we carry out research. This has led to our proposal to limit direct observation of great apes and to employ technology when possible. There are additional advantages of adopting technology. First, it will create new opportunities for individuals in range countries to study great apes without creating large carbon footprints and incurring the expense of field research. This will diversify the discipline and promote study that is environmentally sustainable. For example, the Pan African Programme has utilized camera traps to integrate African scientists into the study of great apes (http://panafrican.eva.mpg.de). Findings from this project have furnished new insights into great ape biological and behavioural variation^{126,127}. Second, collecting behavioural observations is inexpensive, but time consuming. Implementing technology will give the next generation of field researchers more time to work with members of local communities and government officials in range countries, a critical element of many successful conservation efforts^{11,128}. In the future, we envision other uses of technology and additional immersive digital tools, including 'virtual safaris' where tourists can track great apes in real time on their own devices and eventually through the metaverse¹²⁹. Virtualizing tourism is not a substitute for traditional tourism, but a supplement that promises to furnish

additional revenue to range countries while expanding the potential pool of tourists to include those who do not have the ability to travel to great ape habitats. Despite their potential, we recognize that such programmes must be implemented carefully to protect the well-being of great apes, and we suggest that a set of best practices be developed and strictly adhered to for this purpose.

Although compelling reasons exist to embrace technology, there are limitations. Currently available technologies suffer in their ability to document the diversity and subtlety of great ape behaviour^{120,130,131}. Telemetric methods require affixing electronic devices to individuals, necessitating the close contact we seek to minimize. Habituating animals to drones, equipping them with batteries to ensure they fly for long, uninterrupted periods, and maintaining radio and video links to them in the forest habitats occupied by great apes represent major challenges. Despite these problems, we can envision a future where miniaturized autonomous machines follow and film great apes, who have become accustomed to them, throughout the day and in real time. Using different technologies together will also open new areas of enquiry into great ape behaviour. In summary, we urge fieldworkers to think outside the box. Remarkable progress has been made during the brief history of great ape research, and methods once unimaginable have already led to revolutionary findings.

We understand that the implementation of these technologies will not occur immediately, as there are formidable technical and financial challenges to overcome. In the meantime, we must think creatively and implement safeguards that challenge existing paradigms in places that we can control such as research and tourism sites. We must also redouble our commitment to protect the habituated animals that we continue to observe for these purposes. If great ape populations continue to decline owing to spillback, it may become necessary to consider a moratorium on new habituation efforts for research and tourism and restrict close contact with them. Finally, establishing a governing body to oversee great ape field research as well as tourism warrants discussion. The goal would be to confirm that health and safety measures are based on evidence and reported transparently and accurately. This governing body might also be given the authority to renew permits to conduct field research on great apes and regulate tourist sites.

Recognition that the great apes are our closest living relatives furnished the impetus to initiate long-term field research investigating their behaviour and ecology^{132,133}. Many of these studies continue to this day, with the goal of providing insights into human evolution and contemporary human behaviour. This tradition has led researchers to establish their study sites in remote, protected habitats thought to be relatively unaltered by human activity. Many of us, who continue to devote our lives to this research programme, have benefited greatly. Spending time with great apes in the wild is a privilege that is hard to repay, but now is the time to do so. As they continue to perish, it will be necessary to commit more time, energy and resources to stop their decline. If we fail to do so, then humanity is certain to face a bleak and depauperate future, not only one devoid of our closest living relatives but many other organisms as well. With this in mind, we ask members of the research community to shift more attention to the study of great apes who live outside protected areas. This will be particularly important to improve our understanding of the impending threats to great apes posed by large-scale industrial projects and to devise effective mitigation strategies.

Conclusions

To make a meaningful difference, we must be more inventive, flexible and ambitious. We will also need to be practical, resilient and prepared for substantial challenges ahead. It is unrealistic to expect ape range countries to develop without utilizing their natural resources, and it would be unethical and hypocritical to make such a request¹³⁴. This highlights some of the thorniest problems we outline above: how do Intensified development of natural resources, even when done in the least harmful way possible, will further degrade and fragment ape habitats. We should therefore anticipate future declines in many, perhaps most, ape populations inside and outside protected areas. This should not prevent action, but as noted previously, it does require conservation plans that acknowledge the world as it is. We must prepare for the reality of climate change and heighten mitigation efforts¹³⁵, effectively integrate uncertainty and risk in our conservation planning, and acknowledge that we are already engaging in ape conservation triage¹³⁶. Wise, clear-eyed policy decisions we make now could meaningfully curtail the rates of great ape population decline¹¹⁰ and reduce the probability that any ape species will go extinct.

The world will look very different a century from now, perhaps in just a few decades. People's attitudes towards great apes or their approaches to resource consumption may change in a positive direction. Human population growth is likely to stabilize and even decrease¹³⁷, thereby reducing the threats and problems reviewed here. Economies may stabilize at more socially conscious and environmentally sustainable optima. Governments could make additional commitments to conserve threatened habitats. For example, Indonesia has placed a moratorium on developing new plantations on peatlands and primary forests¹³⁸. New multinational initiatives will also improve the prospects for long-term ape persistence. At the recent fifteenth meeting of the Conference of Parties (COP15), 188 countries agreed to place 30% of the planet under protection by 2030, and the European Union has just passed legislation prohibiting the import and export of products produced on deforested land¹³⁹. Technological advances might present novel solutions to some of the problems we have discussed. Incentive structures may change to favour more sustainable land uses. These changes would all result in markedly improved conservation outcomes for great apes. But great apes will only rebound if they are prevented from going extinct in the meantime. So, every individual we save now is crucial to guarantee that future generations will continue to share our planet with great apes.

References

- 1. Paine, R. T. A note on trophic complexity and community stability. *Am. Nat.* **103**, 91–93 (1969).
- Tutin, C. E. G., Williamson, E. A., Rogers, M. E. & Fernandez, M. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *J. Trop. Ecol.* 7, 181–199 (1991).
- 3. Millennium Ecosystem Assessment Program. *Ecosystems and Human Well-being: Synthesis* (Island Press, 2005).
- 4. Macfie, E. J. & Williamson, E. A. Best Practice Guidelines for Great Ape Tourism (IUCN/SSC Primate Specialist Group, 2010).
- Clucas, B., McHugh, K. & Caro, T. Flagship species on covers of US conservation and nature magazines. *Biodivers. Conserv.* 17, 1517–1528 (2008).
- 6. McGrew, W. C., Marchant, L. F. & Nishida, T. Great Ape Societies (Cambridge Univ. Press, 1996).
- 7. Tuttle, R. H. Apes and Human Evolution (Harvard Univ. Press, 2014).
- 8. Cavalieri, P. & Singer, P. The Great Ape Project: Equality Beyond Humanity (St. Martin's Press, 1994).
- 9. Nussbaum, M. C. Justice for Animals: Our Collective Responsibility (Simon & Schuster, 2023).

- 10. Wise, S. M. Rattling the Cage: Toward Legal Rights for Animals (Perseus Books, 2000).
- 11. Bettinger, T., Cox, D., Kuhar, C. & Leighty, K. Human engagement and great ape conservation in Africa. *Am. J. Primatol.* **83**, e23216 (2021).
- Santika, T. et al. Effectiveness of 20 years of conservation investments in protecting orangutans. *Curr. Biol.* 32, 1754–1763.e6 (2022).
- 13. The IUCN Red List of Threatened Species v.2022-2 (IUCN, 2022).
- Campbell, G., Kuehl, H., Diarrassouba, A., N'Goran, P. K. & Boesch, C. Long-term research sites as refugia for threatened and over-harvested species. *Biol. Lett.* 7, 723–726 (2011).
- Laurance, W. F. Does research help to safeguard protected areas? Trends Ecol. Evol. 28, 261–266 (2013).
- Blaustein, R. J. Protected areas and equity concerns. *BioScience* 57, 216–221 (2007).
- 17. Wich, S. A. et al. Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean orang-utan? *PLoS ONE* **7**, e49142 (2012).
- Strindberg, S. et al. Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. Sci. Adv. 4, eaar2964 (2018).
- Junker, J. et al. Recent decline in suitable environmental conditions for African great apes. *Divers. Distrib.* 18, 1077–1091 (2012).
- Voigt, M. et al. Deforestation projections imply range-wide population decline for critically endangered Bornean orangutan. *Perspect. Ecol. Conserv.* 20, 240–248 (2022).
- 21. Hockings, K. J. et al. Apes in the Anthropocene: flexibility and survival. *Trends Ecol. Evol.* **30**, 215–222 (2015).
- 22. McLennan, M. R. et al. Surviving at the extreme: chimpanzee ranging is not restricted in a deforested human-dominated landscape in Uganda. *Afr. J. Ecol.* **59**, 17–28 (2021).
- 23. McLennan, M. R. & Hockings, K. J. in *Problematic Wildlife* (ed. Angelici, F. M.) 373–394 (Springer, 2016).
- Etiendem, D., Tagg, N., Hens, L. & Pereboom, Z. Impact of human activities on Cross River gorilla *Gorilla gorilla diehli* habitats in the Mawambi Hills, southwest Cameroon. *Endanger. Species Res.* 20, 167–179 (2013).
- 25. Meijaard, E. et al. Declining orangutan encounter rates from Wallace to the present suggest the species was once more abundant. *PLoS ONE* **5**, e12042 (2010).
- 26. Plumptre, A. J. et al. Catastrophic decline of world's largest primate: 80% loss of Grauer's gorilla (*Gorilla beringei graueri*) population justifies critically endangered status. *PLoS ONE* **11**, e0162697 (2016).
- 27. Clough, C. & May, C. Illicit Financial Flows and the Illegal Trade in Great Apes (Global Financial Integrity, 2018).
- Blom, A., van Zalinge, R., Mbea, E., Heitkonig, I. M. A. & Prins, H. H. T. Human impact on wildlife populations within a protected Central African forest. *Afr. J. Ecol.* 42, 23–31 (2004).
- Fa, J. E. et al. Getting to grips with the magnitude of exploitation: bushmeat in the Cross–Sanaga rivers region, Nigeria and Cameroon. *Biol. Conserv.* 129, 497–510 (2006).
- Mbete, R. A. et al. Household bushmeat consumption in Brazzaville, the Republic of the Congo. *Trop. Conserv. Sci.* 4, 187–202 (2011).
- 31. Report to the CITES Standing Committee on the Status of Great Apes (GRASP, IUCN, 2018).
- Dunay, E., Apakupakul, K., Leard, S., Palmer, J. L. & Deem, S. L. Pathogen transmission from humans to great apes is a growing threat to primate conservation. *EcoHealth* 15, 148–162 (2018).
- Köndgen, S. et al. Pandemic human viruses cause decline of endangered great apes. *Curr. Biol.* 18, 260–264 (2008).

- Kaur, T. et al. Descriptive epidemiology of fatal respiratory outbreaks and detection of a human-related metapneumovirus in wild chimpanzees (*Pan troglodytes*) at Mahale Mountains National Park, Western Tanzania. *Am. J. Primatol.* **70**, 755–765 (2008).
- 35. Scully, E. J. et al. Lethal respiratory disease associated with human rhinovirus C in wild chimpanzees, Uganda, 2013. *Emerg. Infect. Dis.* **24**, 267–274 (2018).
- Negrey, J. D. et al. Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin. *Emerg. Microbes Infect.* 8, 139–149 (2019).
- Van Hamme, G., Svensson, M. S., Morcatty, T. Q., Nekaris, K. A. & Nijman, V. Keep your distance: using Instagram posts to evaluate the risk of anthroponotic disease transmission in gorilla ecotourism. *People Nat.* **3**, 325–334 (2021).
- Nuno, A. et al. Protecting great apes from disease: Compliance with measures to reduce anthroponotic disease transmission. *People Nat.* 4, 1387–1400 (2022).
- 39. Junker, J. et al. A severe lack of evidence limits effective conservation of the world's primates. *BioScience* **70**, 794–803 (2020).
- 40. Schoneveld-de Lange, N., Meijaard, E. & Löhr, A. South to south learning in great ape conservation. *Am. J. Primatol.* **78**, 669–678 (2016).
- Moore, J. F. et al. Are ranger patrols effective in reducing poachingrelated threats within protected areas? J. Appl. Ecol. 55, 99–107 (2018).
- 42. Blom, A., Yamindou, J. & Prins, H. H. T. Status of the protected areas of the Central African Republic. *Biol. Conserv.* **118**, 479–487 (2004).
- Struhsaker, T. T., Struhsaker, P. J. & Siex, K. S. Conserving Africa's rain forests: problems in protected areas and possible solutions. *Biol. Conserv.* 123, 45–54 (2005).
- Campbell, G., Kuehl, H., N'Goran Kouamé, P. & Boesch, C. Alarming decline of West African chimpanzees in Côte d'Ivoire. *Curr. Biol.* 18, R903–R904 (2008).
- 45. Greengrass, E. J. Chimpanzees are close to extinction in southwest Nigeria. *Primate Conserv.* **24**, 77–83 (2009).
- 46. Tranquilli, S. et al. Lack of conservation effort rapidly increases African great ape extinction risk: conservation efforts prevent ape extinction. *Conserv. Lett.* **5**, 48–55 (2012).
- 47. Tranquilli, S. et al. Protected areas in tropical Africa: assessing threats and conservation activities. *PLoS ONE* **9**, e114154 (2014).
- Sherman, J. et al. Orangutan killing and trade in Indonesia: wildlife crime, enforcement, and deterrence patterns. *Biol. Conserv.* 276, 109744 (2022).
- 49. Hilborn, R. et al. Effective enforcement in a conservation area. *Science* **314**, 1266 (2006).
- 50. Peh, K. S.-H. & Drori, O. Fighting corruption to save the environment: Cameroon's experience. *Ambio* **39**, 336–339 (2010).
- Oklander, L. I., Caputo, M., Solari, A. & Corach, D. Genetic assignment of illegally trafficked neotropical primates and implications for reintroduction programs. *Sci. Rep.* **10**, 3676 (2020).
- 52. Nijman, V. Orangutan trade, confiscations, and lack of prosecutions in Indonesia. *Am. J. Primatol.* **79**, 22652 (2017).
- 53. N'Goran, P. K. et al. Hunting, law enforcement, and African primate conservation. *Conserv. Biol.* **26**, 565–571 (2012).
- 54. Plumptre, A. J. in *Artificial Intelligence and Conservation* (eds. Fang, F. et al.) 17–28 (Cambridge Univ. Press, 2019).
- Gaveau, D. L. A., Linkie, M., Suyadi, Levang, P. & Leader-Williams, N. Three decades of deforestation in southwest Sumatra: effects of coffee prices, law enforcement and rural poverty. *Biol. Conserv.* 142, 597–605 (2009).
- 56. Challender, D. W. S. & MacMillan, D. C. Poaching is more than an enforcement problem. *Conserv. Lett.* **7**, 484–494 (2014).

- Williamson, E. A. & Fawcett, K. A. in Science and Conservation in African Forests (eds. Wrangham, R. & Ross, E.) 213–229 (Cambridge Univ. Press, 2008).
- Imong, I., Kühl, H. S., Robbins, M. M. & Mundry, R. Evaluating the potential effectiveness of alternative management scenarios in ape habitat. *Environ. Conserv.* 43, 161–171 (2016).
- 59. Weber, W. & Vedder, A. In the Kingdom of Gorillas: Fragile Species in a Dangerous Land (Simon & Schuster, 2001).
- Sabuhoro, E., Wright, B., Munanura, I. E., Nyakabwa, I. N. & Nibigira, C. The potential of ecotourism opportunities to generate support for mountain gorilla conservation among local communities neighboring Volcanoes National Park in Rwanda. *J. Ecotourism* 20, 1–17 (2017).
- Kalpers, J. et al. Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx* 37, 326–327 (2003).
- 62. Alluri, R. M. The Role of Tourism in Post-Conflict Peacebuilding in Rwanda (Swisspeace, 2009).
- Kiss, A. Is community-based ecotourism a good use of biodiversity conservation funds? *Trends Ecol. Evol.* 19, 232–237 (2004).
- 64. Breuer, T., Mavinga, F. B., Evans, R. & Lukas, K. E. Using video and theater to increase knowledge and change attitudes. Why are gorillas important to the world and to Congo? *Am. J. Primatol.* **79**, e22692 (2017).
- Akenji, L. et al. Community-based monitoring of Cross river gorillas in south west region, Cameroon. *Afr. Primates* 13, 29–38 (2019).
- Bettinger, T. & Leighty, K. The evolution of conservation education and its role in saving apes in Africa. *Am. J. Primatol.* 83, e23203 (2021).
- Narat, V., Pennec, F., Simmen, B., Ngawolo, J. C. B. & Krief, S. Bonobo habituation in a forest–savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context. *Primates* 56, 339–349 (2015).
- Hobaiter, C., Akankwasa, J. W., Muhumuza, G., Uwimbabazi, M. & Koné, I. The importance of local specialists in science: where are the local researchers in primatology? *Curr. Biol.* **31**, R1367–R1369 (2021).
- Meijaard, E., Wich, S., Ancrenaz, M. & Marshall, A. J. Not by science alone: why orangutan conservationists must think outside the box: orangutan conservation. *Ann. N. Y. Acad. Sci.* 1249, 29–44 (2012).
- Boedhihartono, A. K. et al. Conservation science and practice must engage with the realities of complex tropical landscapes. *Trop. Conserv. Sci.* 11, 194008291877957 (2018).
- Chua, L. et al. Conservation and the social sciences: beyond critique and co-optation. A case study from orangutan conservation. *People Nat.* 2, 42–60 (2020).
- Meijaard, E. in An Introduction to Primate Conservation (eds. Wich, S. A. & Marshall, A. J.) 205–218 (Oxford Univ. Press, 2016).
- 73. Spehar, S. N. et al. Orangutans venture out of the rainforest and into the Anthropocene. *Sci. Adv.* **4**, e1701422 (2018).
- 74. Marshall, A. J. in Primatology, Bio-cultural Diversity and Sustainable Development in Tropical Forests 50–71 (UNESCO, 2018).
- McLennan, M. R., Howell, C. P., Bardi, M. & Heistermann, M. Are human-dominated landscapes stressful for wild chimpanzees (*Pan troglodytes*)? *Biol. Conserv.* 233, 73–82 (2019).
- McLennan, M. R., Lorenti, G. A., Sabiiti, T. & Bardi, M. Forest fragments become farmland: dietary response of wild chimpanzees (*Pan troglodytes*) to fast-changing anthropogenic landscapes. *Am. J. Primatol.* 82, e23090 (2020).
- 77. Satsias, Z. M. et al. Sex-specific responses to anthropogenic risk shape wild chimpanzee social networks in a human-impacted landscape. *Anim. Behav.* **186**, 29–40 (2022).

- 78. Rands, M. R. W. et al. Biodiversity conservation: challenges beyond 2010. *Science* **329**, 1298–1303 (2010).
- 79. Ancrenaz, M., Dabek, L. & O'Neil, S. The costs of exclusion: recognizing a role for local communities in biodiversity conservation. *PLoS Biol.* **5**, e289 (2007).
- Jones, I. J. et al. Improving rural health care reduces illegal logging and conserves carbon in a tropical forest. *Proc. Natl Acad. Sci. USA* 117, 28515–28524 (2020).
- Garcia-Ulloa, J. & Koh, L. P. in An Introduction to Primate Conservation (eds. Wich, S. A. & Marshall, A. J.) 257–268 (Oxford Univ. Press, 2016).
- Hockings, K. J. & McLennan, M. R. From forest to farm: systematic review of cultivar feeding by chimpanzees – management implications for wildlife in anthropogenic landscapes. *PLoS ONE* 7, e33391 (2012).
- 83. Lenzen, M. et al. International trade drives biodiversity threats in developing nations. *Nature* **486**, 109–112 (2012).
- Geissdoerfer, M., Savaget, P., Bocken, N. M. P. & Hultink, E. J. The circular economy – A new sustainability paradigm? *J. Clean. Prod.* 143, 757–768 (2017).
- 85. Rothrock, P., Ellis, K. & Weatherer, L. Corporate Progress on No Deforestation and 'Nature Positive' Post 2020 (Forest Trends, 2022).
- Campbell, G. Primate Specialist Group ARRC Task Force. Oryx 55, 495–496 (2021).
- 87. Rainer, H., White, A. R. T. & Lanjouw, A. Industrial Agriculture and Ape Conservation (Cambridge Univ. Press, 2015).
- Marshall, A. J., Wich, S. & Ancrenaz, M. Fresh strategies to save orangutans. *Nature* 535, 493 (2016).
- Morgan, D. et al. Great Apes and FSC: Implementing 'Ape Friendly' Practices in Central Africa's Logging Concessions (IUCN/SSC Primate Specialist Group, 2013).
- Ancrenaz, M., Meijaard, E., Wich, S. A. & Simery, J. Palm Oil Paradox: Sustainable Solutions to Save the Great Apes (UNEP, GRASP, 2016).
- 91. Wilkie, D. S. et al. Eating and conserving bushmeat in Africa. *Afr. J. Ecol.* **54**, 402–414 (2016).
- 92. Nicholas, A. et al. Successes in community-based monitoring of Cross river gorillas (Gorilla gorilla diehli) in Cameroon. Afr. Primates **7**, 55–60 (2010).
- Abwe, E. E., Mfossa, D. M. & Morgan, B. A. Community-led conservation action in the Ebo forest, Cameroon. *Gorilla J.* 50, 14–17 (2015).
- 94. van Vliet, N. & Mbazza, P. Recognizing the multiple reasons for bushmeat consumption in urban areas: a necessary step toward the sustainable use of wildlife for food in Central Africa. *Hum. Dimens. Wildl.* **16**, 45–54 (2011).
- Randolph, S. G., Ingram, D. J., Curran, L. M., Holland Jones, J. & Durham, W. H. Urban wild meat markets in Cameroon: actors and motives. *World Dev.* 160, 106060 (2022).
- Chausson, A. M., Rowcliffe, J. M., Escouflaire, L., Wieland, M. & Wright, J. H. Understanding the sociocultural drivers of urban bushmeat consumption for behavior change interventions in Pointe Noire, Republic of Congo. *Hum. Ecol.* 47, 179–191 (2019).
- 97. van Vliet, N. 'Bushmeat crisis' and 'cultural imperialism' in wildlife management? Taking value orientations into account for a more sustainable and culturally acceptable wildmeat sector. *Front. Ecol. Evol.* **6**, 112 (2018).
- Sherman, J. & Greer, D. in State of the Apes: Infrastructure Development and Ape Conservation Vol. 3, 225–255 (Cambridge Univ. Press, 2018).
- 99. Narat, V. et al. Unexpected higher convergence of human-great ape enteric viromes in Central African forest than in a European zoo: a One Health analysis. *Nat. Commun.* **14**, 3674 (2023).
- 100. DeVore, I. Primate Behavior: Field Studies of Monkeys and Apes (Holt, Rinehart and Winston, 1965).

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- Altmann, J. Observational study of behavior: sampling methods. Behaviour 49, 227–266 (1974).
- 102. Zwerts, J. A. et al. Methods for wildlife monitoring in tropical forests: comparing human observations, camera traps, and passive acoustic sensors. *Conserv. Sci. Pract.* **3**, e568 (2021).
- 103. Kalan, A. K. et al. Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecol. Indic.* 54, 217–226 (2015).
- 104. Arandjelovic, M. & Vigilant, L. Non-invasive genetic censusing and monitoring of primate populations. *Am. J. Primatol.* 80, e22743 (2018).
- 105. Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. Terrestrial animal tracking as an eye on life and planet. Science **348**, aaa2478 (2015).
- 106. Piel, A. K. et al. Noninvasive technologies for primate conservation in the 21st century. *Int. J. Primatol.* **43**, 133–167 (2022).
- 107. Redford, K., Roe, D. & Sunderland, T. Linking Conservation and Poverty Alleviation: A Discussion Paper on Good and Best Practice in the Case of Great Ape Conservation (Poverty and Conservation Learning Group, 2013).
- 108. Kormos, R. et al. Great apes and biodiversity offset projects in Africa: the case for national offset strategies. *PLoS ONE* 9, e111671 (2014).
- 109. Büscher, B. & Fletcher, R. The Conservation Revolution: Radical Ideas for Saving Nature Beyond the Anthropocene (Verso, 2020).
- 110. Meijaard, E. et al. Restoring the orangutan in a Whole- or Half-Earth context. Oryx **57**, 566–577 (2022).
- 111. Venter, O. et al. Carbon payments as a safeguard for threatened tropical mammals. *Conserv. Lett.* **2**, 123–129 (2009).
- 112. Noonan, P. & Zagata, M. Wildlife in the market place: using the profit motive to maintain wildlife habitat. *Wildl. Soc. Bull.* **10**, 46–49 (1982).
- Dinerstein, E. et al. Enhancing conservation, ecosystem services, and local livelihoods through a wildlife premium mechanism: incentives for wildlife conservation. *Conserv. Biol.* 27, 14–23 (2013).
- 114. Katjingisiua, I. & Mauney, G. Wildlife Credits: Innovation in Conservation by and for Namibians (Conservation Namibia, 2020).
- Berzaghi, F., Chami, R., Cosimano, T. & Fullenkamp, C. Financing conservation by valuing carbon services produced by wild animals. *Proc. Natl Acad. Sci. USA* **119**, e2120426119 (2022).
- 116. Dasgupta, P. The Economics of Biodiversity: the Dasgupta Review: Full Report (HM Treasury, 2021).
- 117. The ARRC Task Force of the IUCN SSC Primate Specialist Group. Moyen Bafing National Park as an offset for chimpanzees. (IUCN, 2021).
- 118. Goodall, J. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* **201**, 1264–1266 (1964).
- Idani, G. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. *Afr. Study Monogr.* 11, 153–186 (1990).
- 120. van Schaik, C. P. et al. Orangutan cultures and the evolution of material culture. *Science* **299**, 102–105 (2003).
- 121. Langergraber, K. E. et al. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc. Natl Acad. Sci. USA* **109**, 15716–15721 (2012).
- 122. Nishida, T. The social group of wild chimpanzees in the Mahali Mountains. *Primates* **9**, 167–224 (1968).
- 123. Hansen, M. F., Kalan, A., Riley, E. & Waters, S. Evaluating the need to habituate: modern approaches to field primatology during the COVID-19 pandemic and beyond. *Primate Conserv.* **36**, 1–13 (2021).
- 124. Shutt, K. et al. Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biol. Conserv.* **172**, 72–79 (2014).
- 125. Gruen, L., Fultz, A. & Pruetz, J. Ethical issues in African great ape field studies. *ILAR J.* **54**, 24–32 (2013).

- 126. de Manuel, M. et al. Chimpanzee genomic diversity reveals ancient admixture with bonobos. *Science* **354**, 477–481 (2016).
- 127. Boesch, C. et al. Chimpanzee ethnography reveals unexpected cultural diversity. *Nat. Hum. Behav.* **4**, 910–916 (2020).
- 128. Knott, C. D. et al. The Gunung Palung Orangutan Project: twenty-five years at the intersection of research and conservation in a critical landscape in Indonesia. *Biol. Conserv.* 255, 108856 (2021).
- 129. Dwivedi, Y. K. et al. Metaverse beyond the hype: multidisciplinary perspectives on emerging challenges, opportunities, and agenda for research, practice and policy. *Int. J. Inf. Manag.* **66**, 102542 (2022).
- 130. Whiten, A. et al. Cultures in chimpanzees. *Nature* **399**, 682–685 (1999).
- McCarthy, M. S. et al. An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **80**, e22904 (2018).
- 132. Imanishi, K. Doubutsu no hakai (Animal Societies) (Shisaku-sha, 1972).
- 133. Goodall, J. & Hamburg, D. Chimpanzee behavior as a model for the behavior of early man: new evidence of possible origins of human behavior. *Am. Handb. Psychiatry* **6**, 14–43 (1975).
- 134. Meijaard, E. & Sheil, D. A modest proposal for wealthy countries to reforest their land for the common good. *Biotropica* 43, 524–528 (2011).
- 135. Carvalho, J. S. et al. Predicting range shifts of African apes under global change scenarios. *Divers. Distrib.* **27**, 1663–1679 (2021).
- 136. Game, E. T., Kareiva, P. & Possingham, H. P. Six common mistakes in conservation priority setting. *Conserv. Biol.* **27**, 480–485 (2013).
- 137. World population prospects: total population. *United Nations* https://population.un.org/wpp/Graphs/Probabilistic/POP/ TOT/900 (accessed 2 February 2024).
- 138. Gaveau, D. L. A. et al. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conserv. Lett.* **12**, e12622 (2019).
- 139. Parliament adopts new law to fight global deforestation. *European Parliament* https://www.europarl.europa. eu/news/en/press-room/20230414IPR80129/ parliament-adopts-new-law-to-fight-global-deforestation (19 April 2023).

Competing interests

G.C. leads an IUCN Task Force that advises businesses and banks regarding how to reduce the negative impacts of their activities on great apes and contribute to their conservation.

Additional information

Correspondence should be addressed to John C. Mitani.

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