TYPE Review
PUBLISHED 09 November 2023
DOI 10.3389/fcosc.2023.1225911

OPEN ACCESS

EDITED BY
Maria Cristina Duarte,
University of Lisbon, Portugal

REVIEWED BY
Andreia Garces,
University of Trás-os-Montes and Alto Douro, Portugal
Maria Joana Ferreira Da Silva,
Centro de Investigacao em Biodiversidade e Recursos Geneticos (CIBIO-InBIO), Portugal

*CORRESPONDENCE
Erik Meijaard
emeijaard@borneofutures.org

†These authors have contributed equally to this work

RECEIVED 20 May 2023
ACCEPTED 09 October 2023
PUBLISHED 09 November 2023

CITATION
Meijaard E, Unus N, Ariffin T, Dennis R, Ancrenaz M, Wich S, Wunder S, Goh CS, Sherman J, Ogwu MC, Refisch J, Ledgard J, Sheil D and Hockings K (2023) Apes and agriculture.
Front. Conserv. Sci. 4:1225911.
doi: 10.3389/fcosc.2023.1225911

Apes and agriculture

Erik Meijaard[1,2*], Nabillah Unus[1], Thina Ariffin[1], Rona Dennis[1], Marc Ancrenaz[1,3], Serge Wich[4], Sven Wunder[5,6], Chun Sheng Goh[7,8], Julie Sherman[9], Matthew C. Ogwu[10], Johannes Refisch[11], Jonathan Ledgard[12], Douglas Sheil[13†] and Kimberley Hockings[14†]

[1]Borneo Futures, Bandar Seri Begawan, Brunei, [2]Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom, [3]HUTAN-Kinabatangan Orangutan Conservation Programme (HUTAN – KOCP), Sandakan, Malaysia, [4]School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, United Kingdom, [5]European Forest Institute, Barcelona, Spain, [6]Center for International Forestry Research, Lima, Peru, [7]Jeffrey Sachs Center on Sustainable Development, Sunway University, Kuala Lumpur, Malaysia, [8]Harvard University Asia Center, Cambridge, MA, United States, [9]Wildlife Impact, Portland, OR, United States, [10]Goodnight Family Sustainable Development Department, Appalachian State University, Boone, NC, United States, [11]Great Apes Survival Partnership, United Nations Environment Program, Nairobi, Kenya, [12]Artificial Intelligence Center, Czech Technical University, Prague, Czechia, [13]Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, Netherlands, [14]Center for Ecology and Conservation, University of Exeter, Penryn, United Kingdom

Non-human great apes – chimpanzees, gorillas, bonobos, and orangutans – are threatened by agricultural expansion, particularly from rice, cacao, cassava, maize, and oil palm cultivation. Agriculture replaces and fragments great ape habitats, bringing them closer to humans and often resulting in conflict. Though the impact of agriculture on great apes is well-recognized, there is still a need for a more nuanced understanding of specific contexts and associated negative impacts on habitats and populations. Here we review these contexts and their implications for great apes. We estimate that within their African and South-East Asian ranges, there are about 100 people for each great ape. Given that most apes live outside strictly protected areas and the growing human population and increasing demand for resources in these landscapes, it will be challenging to balance the needs of both humans and great apes. Further habitat loss is expected, particularly in Africa, where compromises must be sought to re-direct agricultural expansion driven by subsistence farmers with small fields (generally <0.64 ha) away from remaining great ape habitats. To promote coexistence between humans and great apes, new approaches and financial models need to be implemented at local scales. Overall, optimized land use planning and effective implementation, along with strategic investments in agriculture and wildlife conservation, can improve the synergies between conservation and food production. Effective governance and conservation financing are crucial for optimal outcomes in both conservation and food security. Enforcing forest conservation laws, engaging in trade policy discussions, and integrating policies on trade, food security, improved agricultural techniques, and sustainable food systems are vital to prevent further decline in great ape populations. Saving great apes requires a thorough consideration of specific agricultural contexts.

KEYWORDS

conservation, conservation finance, crop foraging, food security, food systems, great apes, poverty, rural development

1 Introduction

Agricultural expansion is the leading cause of biodiversity loss, with global cropland estimated at 1,244 Mha in 2019 (Potapov et al., 2022) and predicted to expand further by 193–317 Mha by 2050, mainly in Africa (Schmitz et al., 2014). This expansion will reduce available habitat for 87.7% of the 19,859 terrestrial vertebrate species recently reviewed by Williams et al. (2021), with 1,280 species losing >25% of their remaining range. Balancing the demands for crops and conservation is one of the biggest challenges of the 21st century (Dudley and Alexander, 2017), especially in the tropics, where species diversity is high, and large natural ecosystems are declining due to human impacts (Cincotta et al., 2000; Pendrill et al., 2022). The impact of agriculture on non-human great apes (further referred to as "great apes") in the Asian and African tropics is of particular concern, with chimpanzees, bonobos, Western and Eastern gorillas, and three species of orangutans all in decline and threatened with extinction within the coming decades (Figure 1, for scientific names see Table 1). The distribution and density of these species are primarily determined by habitat availability, disease, killing for meat and other purposes, and people's attitudes to sharing landscapes with great apes. Despite national legislation legally protecting these species in all 23 countries they occur in, the threat to their survival remains high (Caldecott and Miles, 2006; Bettinger et al., 2021).

The remaining great apes (750,000-1,250,000, see Figure 1) share their distribution ranges with around 97 million people (1 great ape per 77-129 people, see Supplementary Materials and Table 1). In simple terms, one great ape shares resources with 100 humans, mainly in countries with high human population growth and poverty (i.e., income of less than US$2 per day), and low food security. For instance, according to World Bank data, the

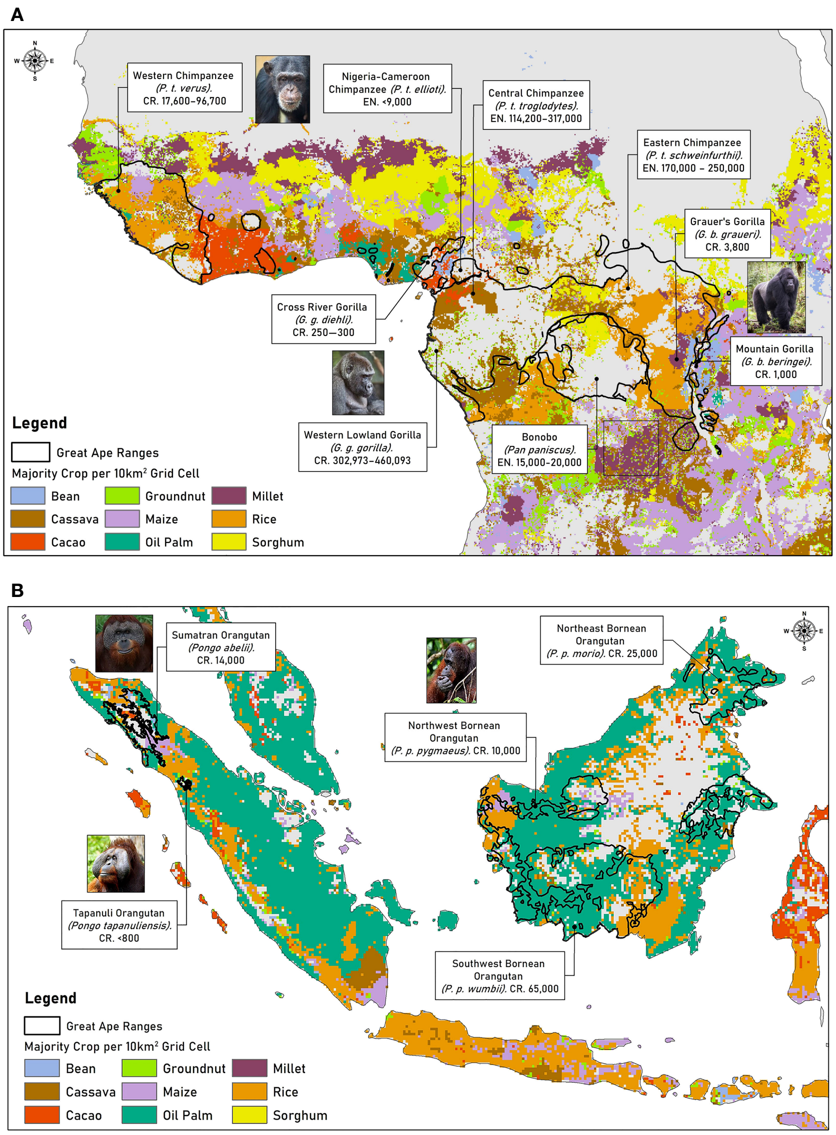

FIGURE 1
(A) African great ape subspecies ranges in relation to the distribution of crops expressed as majority crop per 10*10 km grid cell (You et al., 2017). **(B)** Asian great ape subspecies. Population estimates from Rainer et al. (2020) and ranges based on IUCN Red List data for individual species.

TABLE 1 Great ape taxa, the number of people within the great ape ranges (Schiavina et al., 2022), the primary drivers of forest cover loss (Laso Bayas et al., 2022), and main crops in great ape ranges (Meijaard et al., 2021).

Great ape species or subspecies	Scientific name	Estimated number of people within great ape range in 2020 (predicted annual growth rate in % 2020-2030)	Two main primary driver(s) of forest cover loss for the period 2008 to 2019 within great ape ranges	Two main crops based on largest area within (sub) species range
Nigeria-Cameroon chimpanzee	*Pan t. ellioti*	2,411,401 (2.8)	Subsistence agriculture and other natural disturbances	Oil palm, cacao
Western chimpanzee	*P. t. verus*	28,170,665 (2.6)	Subsistence agriculture and pasture	Rice, cacao
Eastern chimpanzee	*P. t. schweinfurthii*	32,135,959 (2.4)	Subsistence agriculture and other natural disturbances	Cassava, maize
Central chimpanzee	*P. t. troglodytes*	14,222,850 (3.2)	Subsistence agriculture and other natural disturbances	Cassava, cacao
Bonobo	*Pan paniscus*	3,758,691 (1.5)	Subsistence agriculture and other natural disturbances	Cassava, maize
Western lowland gorilla	*Gorilla. g. gorilla*	12,020,627 (3.3)	Subsistence agriculture and other natural disturbances	Cassava, cacao
Cross-River gorilla	*G. g. diehli*	57,798 (2.7)	Subsistence agriculture and other natural disturbances	Cassava, vegetables
Grauer's gorilla	*G. b. graueri*	938,866 (2.4)	Subsistence agriculture and other natural disturbances	Beans, maize
Mountain gorilla	*G. b. beringei*	826 (26.9)	No data	Beans, potatoes
Northwest Bornean orangutan	*Pongo p. pygmaeus*	501,084 (1.5)	Subsistence agriculture and commercial oil palm/other plantations	Oil palm, tree crops
Southwest Bornean orangutan	*Pongo p. wurmbi*	1,441,523 (0.9)	Subsistence agriculture and commercial oil palm/other plantations	Oil palm, tree crops
Northeast Bornean orangutan	*Pongo p. morio*	1,080,217 (3.0)	Subsistence agriculture and commercial oil palm/other plantations	Oil palm, tree crops
Sumatran orangutan	*P. abelii*	16,526 (1.7)	Subsistence agriculture and commercial oil palm/other plantations	Oil palm, tree crops
Tapanuli orangutan	*P. tapanuliensis*	674 (0.6)	Subsistence agriculture, pasture and commercial oil palm/other plantations	Oil palm, tree crops

Democratic Republic of the Congo (DRC) has a 2.9% annual population growth rate, which could double the number of people living alongside great apes in 25 years. Some of the great ape range countries are also those with the highest levels of undernourishment: 21% of the Sub-Saharan people were undernourished in 2020 (The World Bank, 2022a). Thus, there is an urgent need for increased local food production and more equal distribution of food to improve food availability, affordability, and security. Growing human populations and a drive for economic development, alongside growing international demand, remain key drivers of deforestation (Busch and Ferretti-Gallon, 2017) and therefore great ape habitat loss.

The threats to great apes related to agriculture include habitat loss and fragmentation due to agricultural expansion, the resulting genetic factors related to small and isolated populations, agriculture-related diseases, as well as the human-great ape conflict, and ape killing, capture, and trade (Figure 2). In terms of agricultural expansion, we focus on crops rather than livestock, because in the orangutan ranges livestock-related forest loss is rare, while, in Africa, such losses are concentrated in the drier parts where great apes generally do not occur (although chimpanzee habitat in Tanzania, Senegal, and Mali is a local exception). Maize (*Zea mays* L.), rice (*Oryza* spp.), millet (various species), and cassava (*Manihot esculenta* Crantz) are the main crops of concern (for details see Tables S1–S3). These are mostly grown in smallholder, subsistence agriculture contexts (Table 1), with fields typically <0.64 ha in size (Lesiv et al., 2019), and further field size reduction ongoing (Abraham and Pingali, 2020). Rice, maize, and cassava show the most rapid expansion, while other crops such as sesame (*Sesamum indicum* L.), sunflower (*Helianthus annuus* L.), cotton (*Gossypium* L.) and okra (*Abelmoschus esculentus* (L.) Moench) have expanded but use up less land (FAOSTAT, 2023).

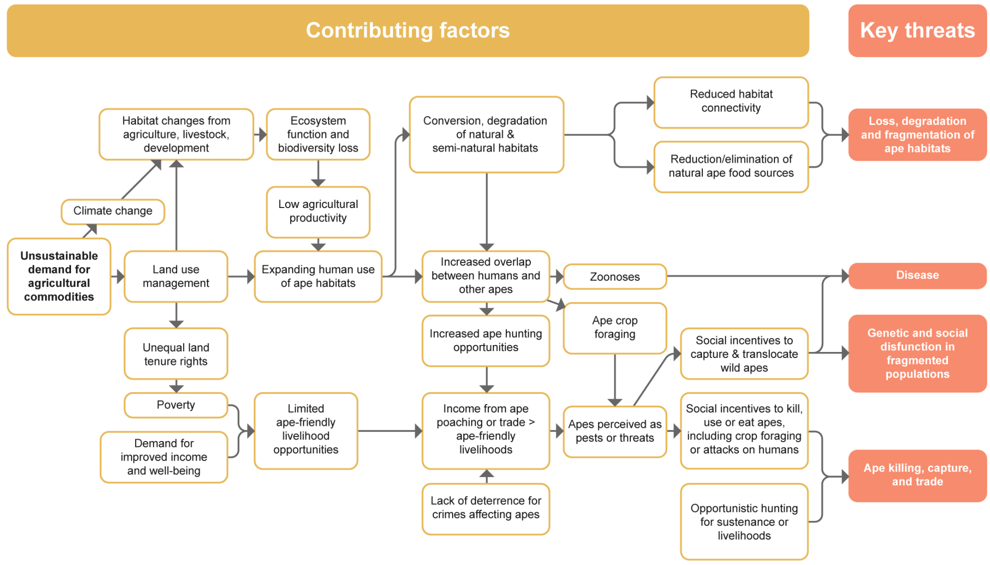

FIGURE 2
Causal transmission chain of (negative) change between human expansion in land use and the fate of the great apes (referred to as "apes").

African oil palm (*Elaeis guineensis* Jacq.) is another crop that has been a driver of deforestation, especially in Southeast Asia's orangutan ranges (Table S4), with concerns about its expansion in Africa and potential impact on great apes (Linder, 2013; Wich et al., 2014). While the media has extensively covered the effects of industrial oil palm expansion on great apes, there has been relatively little scrutiny on the impacts of other crops (Jayathilake et al., 2021).

There is considerable variation in the type of crops grown across the great ape range (Supplementary Materials). Most African great apes reside in tropical evergreen forests, but some populations are also found in deciduous woodland and drier savannah-dominated habitats interspersed with gallery forests. The crops grown in these areas are adapted to equatorial fully humid, monsoonal, summer dry, and winter dry conditions (Kottek et al., 2006). The regions primarily cultivate annual crops, although there are also perennial crops such as oil palm, tree crops, and cacao (Table 2). The use of crop areas by great apes for feeding or dispersal, and the level of persecution they face for consuming different crops, vary depending

TABLE 2 Typology of main crops that occur in great ape ranges and are likely to cause most great ape habitat loss.

Crop	Total area W, C, and E Africa and SE Asia 2021 (ha)	Regional rate of expansion (% increase 2010-2021)	Main great ape species using these crops	Type of crop	Primary local crop use (subsistence or cash)	Primary global crop use	References
Paddy (rice)	60,423,297	2.9%	Among others, chimpanzees forage on paddy	Annual (up to 2-3 crop cycles per year).	In Africa (especially West) increasingly used in urban communities. Staple in Asia. Important cash crop.	Food	(McLennan and Hockings, 2014; Muthayya et al., 2014; Zenna et al., 2017)
Maize (corn)	47,035,255	21.3%	Chimpanzees, Western and Eastern Gorilla forage on maize	Annual (5–6-month crop cycle). Rotated with other crops	80% used for food (especially in East Africa).	56% used for livestock feed, remainder for food, ethanol, starch, oil, beverages, glue	(Naughton-Treves et al., 1998; Ranum et al., 2014; Hill, 2017; Ekpa et al., 2019; Erenstein et al., 2022)
Cassava. fresh	27,107,655	47.5%	Chimpanzees forage on cassava	Annual. Long growth cycle (10-12 months or more)	80% of global production from Africa and Asia. Food crop and income. Export crop in Asia	Livestock feed and food	(Caccamisi, 2010; Hockings et al., 2015; Garriga et al., 2018)

(Continued)

TABLE 2 Continued

Crop	Total area W, C, and E Africa and SE Asia 2021 (ha)	Regional rate of expansion (% increase 2010-2021)	Main great ape species using these crops	Type of crop	Primary local crop use (subsistence or cash)	Primary global crop use	References
Oil palm fruit	26,898,747	45.7%	Orangutans and chimpanzees feed on fruits and use crop for dispersal	Perennial (25-year cycle)	Cash crop and local use. Export commodity in Asia	Food, biofuel, cosmetics	(Ancrenaz et al., 2015; Garriga et al., 2018; Meijaard et al., 2020)
Sorghum	21,172,564	3.4%	No major crop foraging by great apes reported	Perennial plant but grown in annual cycles (perennial tropical grass with a growing season of 4-5 months)	Mostly local food subsistence use in Africa. Not much used in SE Asia. Various stover uses	Livestock feed, biofuel and food	(Mundia et al., 2019)
Groundnuts, excluding shelled	16,161,007	22.6%	No major crop foraging by great apes reported	Annual (4–5-month crop cycle). Rotated with other crops	Local use for food, oil and feed. Nigeria and Indonesia major producers. Cash crop.	Important source of oil and protein	(Fletcher and Shi, 2016)
Millet	15,697,663	-19.5%	No major crop foraging by great apes reported	Depends on species. Grown in annual cycles (4-5 months). Low fertilizer and pesticide needs	Mostly local food subsistence use in Africa, also livestock feed. Not much used in SE Asia.	Increasing global demand for food. Drought-resistant and considered a “healthy” grain	(Kumar et al., 2018; Antony Ceasar and Maharajan, 2022)
Cow peas, dry	14,556,604	28.2%	No major crop foraging by great apes reported	Annual crop of semi-arid areas. Intercropped because of nitrogen-fixation	Mostly grown in Nigeria and Niger. Subsistence and cash crop used for food and feed.	Increasing demand from food & beverages industry	(Siddiq et al., 2022)
Beans (dry). Different species, e.g., lentils, chickpeas	11,777,348	15.2%	Western and Eastern gorilla forage on beans	Annuals. Crop cycle depends on species. Primarily grown at higher elevations	Subsistence and cash crop	Growing demand because of health benefits	(Siddiq et al., 2022)
Rubber	11,111,673	39.6%	Some bark stripping and nesting reported by orangutans	Perennial	Cash crop. Indonesia and Malaysia major producers	Various industrial uses	(Umar et al., 2011; Campbell-Smith et al., 2012)
Cacao	9,444,854	20.0%	Chimpanzees and Western gorilla feed on cacao	Perennial	Cash crop, mostly for export	Chocolate products	(McLennan, 2013)

All crop data (FAOSTAT, 2023).

on the type of crop cultivated and species ecology (Supplementary Materials). Soil fertility may also influence great ape presence, with areas in Borneo that have low soil fertility and are poorly suited to agriculture, traditionally being used by nomadic hunter-gatherer people who likely hunted out orangutans in the past (Meijaard, 2017). It remains unclear whether this also applies to Africa, although the more fertile parts, such as volcanic mountain slopes (see, e.g., Hengl et al., 2021) seem to retain species such as mountain gorillas.

Only some areas of the remaining great ape habitat are formally protected. For example, 83% of chimpanzees in West Africa (Heinicke et al., 2019) and about 80% of central chimpanzees and western gorillas in Central Africa reside outside protected areas (Kormos et al., 2003; Brncic et al., 2015; Tweh et al., 2015; Strindberg et al., 2018). Additionally, about 50% of orangutans in Indonesian Borneo reside outside protected areas (Meijaard et al., 2022b). These unprotected habitats are under particular threat from agricultural expansion, though even protected areas can be vulnerable – depending on management, and the extent to which community needs are integrated into protected area management. Overall, understanding the distribution and ecology of great apes is crucial in understanding the threat posed by agriculture.

The different characteristics of the fourteen great ape species and subspecies (Table 1, Supplementary Materials), the different regions of the world in which they occur, and the different agricultural crops that may threaten their habitats or provide some ecological opportunities to them (Table 2), result in a complex picture regarding the relationship between agriculture and great apes. This is further confounded by the scales at which crops are produced (e.g., smallholder or industrial scale), growth types (annual or perennial, monoculture or inter-cropped) or whether crops are produced for subsistence or cash-income purposes. Here we review the literature on great apes and agriculture. Because of the complex nature of the topic and the often qualitative evidence presented in published sources, we use literature review with narrative synthesis to generate insights about the apes and agriculture interface (Grant and Booth, 2009). We searched the scientific literature for papers on great apes in agricultural contexts using species names as search terms, combined with agriculture-related search terms, but did not conduct a formal quality assessment. Trends in land use associated with various crops were determined using data provided by the United Nations Food and Agriculture Organization. Our objectives are to 1) assess the dominant crops and food systems in the ranges of the 14 great ape species and subspecies; 2) identify antagonistic and synergistic co-occurrences; 3) understand economic and political factors that might influence future agricultural developments; and 4) provide recommendations towards improved co-existence between apes and agriculture. We hope to clarify how future agricultural developments are likely to affect different great ape taxa, and what can be done to minimize negative impacts.

2 Key agricultural trends where apes and crops converge

In Africa, agricultural production mainly serves domestic consumption with few crops generating export revenues (Rakotoarisoa et al., 2012). Smallholder farming dominates, although a transition to business-oriented processes is underway (Mukasa et al., 2017; Giller, 2020). Farms still struggle to provide food security or living incomes. Production is expected to increase (Sanchez, 2002; Pendrill et al., 2022; Potapov et al., 2022), putting further pressure on land, especially in Ghana, Ivory Coast, Benin, Nigeria, and Cameroon (Halpern et al., 2022). Infrastructural development related to extractive industries (Weng et al., 2013) is linked to agricultural growth corridors (Independent Science and Partnership Council, 2016), impacting areas of high biodiversity (Laurance et al., 2015).

Agricultural expansion on Borneo and Sumatra has led to major forest loss since the 1970s (Wilcove et al., 2013). These tropical islands are highly suitable for the cultivation of crops such as oil palm, with rice, rubber (*Hevea brasiliensis* Müll. Arg.), maize, coconut (*Cocos nucifera* L.), and coffee (*Coffea arabica* L.) also grown (Table S4). Oil palm agriculture is dominated by large-holders, but while there is more industrial-scale agriculture compared to African great ape ranges (Table 1), forest loss has declined recently due to improved governance of this sector (Gaveau et al., 2019; Gaveau et al., 2022). Nevertheless, soil impoverishment and economic factors drive smallholder farmers to clear forests (Duffy et al., 2021), especially low nutrient peat swamp forests that are important for orangutans (Meijaard et al., 2010).

Across Sub-Saharan Africa and South-East Asia, agricultural expansion is leading to significant changes in land use patterns, with certain crops showing particularly rapid rates of growth. Cassava, oil palm, and rubber have been the crops with the greatest regional expansion rates (Table 2). Meanwhile, land under maize is also expanding, and if current regional trends continue, it may approach equivalence with the area under rice within the next decade. Two other crops, yams (*Dioscorea* spp.) and plantain (*Musa* spp.) have also seen significant increases in area between 2010 and 2021, with respective growth rates of 87.0% and 55.2% (FAOSTAT, 2023).

There is considerable variation in crop distribution across different regions. In Central Africa, for instance, which is home to bonobos, chimpanzees, and Western gorillas, the largest areas are allocated to cassava, maize, groundnuts (*Arachis hypogaea* L.), sorghum (*Sorghum bicolor* L. Moench), and rice (Table S1). Meanwhile, in West Africa, which is home to chimpanzees and Cross-River gorillas, sorghum, maize, and cow peas dominate (Table S2). While the effects of climate change on crop distribution are unclear, it is likely that areas with rain-fed agriculture and limited economic and institutional capacity to respond to climate variability and change, such as some parts of West Africa, will be negatively impacted through yield losses (Sultan and Gaetani, 2016). Such losses could increase pressure on the remaining forested areas where great apes live. In Borneo, predicted reductions in rainfall and increases in temperature (McAlpine et al., 2018) are likely to limit areas suitable for crops such as oil palm, which is vulnerable to prolonged drought, and reduce available orangutan habitat (Struebig et al., 2015).

Great apes react differently to reduction in forest habitats and changing foraging opportunities and threats (see Supplementary Materials for short species ecology reviews). The species are primarily adapted to a plant diet – with meat consumption by chimpanzees being an exception (Fahy et al., 2013) – and may target crops in fields or fruit and trees in orchards and plantations, especially when wild foods are scarce, but also because these may be preferred, since they are highly nutritious and easy to access (Hockings and Humle, 2009; Hockings et al., 2009; Campbell-Smith et al., 2011; Hockings and McLennan, 2012; Seiler and Robbins, 2016). Great apes and humans also share the need for water (Box 1).

Preliminary studies indicate that individuals in some great ape species change their behavior over time to human-dominated landscapes (Hockings et al., 2015), changing food items as they learn what is edible and learning to navigate agricultural lands (McLennan and Hockings, 2014; Ancrenaz et al., 2015; McLennan et al., 2021). These behaviors are often maladaptive, as the nutritional benefits can be outweighed by the costs of increased

BOX 1 The crucial role of access to water for great apesn.

Apes obtain water from their food and by drinking surface water or water collected in tree holes, sometimes with the use of leaf tools, with some communities of chimpanzees digging wells (Figure 3). However, agriculture and climate change have reduced the availability of water (Akpabio, 2007), affecting great apes' health, behavior, and social interactions. For instance, apes in sub-Saharan Africa are facing water scarcity due to increased competition and climate change effects (Vise-Thakor, 2022). Reduced water sources force great apes to drink from fewer shared drinking spots, which increases disease risk (Wright et al., 2022) and the likelihood of aggressive interactions with people, especially children. The proximity of water sources for agricultural areas can also lead to contamination of water sources with pesticides (Masi et al., 2012; Shively and Day, 2015; Sharma et al., 2016). Great apes might be able to adapt to these challenges by developing new behaviours or adapting existing ones, such as well digging (Kalan et al., 2020; Péter et al., 2022), but conservation planning must focus on ensuring safe access to water for great apes as part of forest protection.

FIGURE 3
Adult male chimpanzee at a drinking hole at Cantanhez National Park. Reprinted with permission from Joanna Bessa (Cantanhez Chimpanzee Project).

mortality through accidental snaring, retaliatory killings, and disease. As species with low reproductive outputs, retaliatory killings of apes by humans in response to crop consumption are unlikely to be sustainable. Disagreements between different human groups over how to manage problematic great ape behavior can follow (Campbell-Smith et al., 2011; Hockings and McLennan, 2012).

3 Reducing antagonistic co-occurrences between great ape conservation and agriculture

Great apes can coexist with humans in shared landscapes, but local attitudes towards them determine whether this is beneficial or harmful. Coexistence requires humans and wildlife to co-occur (Harihar et al., 2013), with tolerable risks to both, and should be sustainable (Carter and Linnell, 2016). Some sites have shown co-adaptation between chimpanzees and smallholder agriculture (Halloran, 2016; Bersacola et al., 2021; McLennan et al., 2021), while orangutans survive in forest fragments in Malaysian oil palm landscapes because people accept their presence (Ancrenaz et al., 2021). People in the latter landscape are generally not concerned about orangutans or crop losses, and orangutans are generally safe, although it is unclear if these fragmented populations will remain viable in the long-term (Oram et al., 2022). Conservation planning for great apes needs to consider whether agricultural expansion is driven by poverty and if killing of great apes may continue, or if more stable conditions can be achieved.

Preventing agricultural expansion is the best way to minimize negative impacts on great apes, but this can be difficult in regions with undernourishment and poverty (Meijaard et al., 2022a). Areas of poverty often coincide with relatively good forest protection (Busch and Ferretti-Gallon, 2017), but transitioning to middle-income levels may accelerate agricultural development and pose a threat. Reducing poverty without deforestation requires greater stakeholder engagement (Garcia et al., 2020), such as involving communities in forest enterprise (Santika et al., 2019), although the broader applicability of such models across great ape ranges remains unclear. Also, even when deforestation rates can be reduced, reducing poaching rates is challenging and requires long-term financing (Sandker et al., 2009).

Efforts to reduce forest loss and poaching rates whilst alleviating poverty could help reduce pressures on great ape populations and habitats as economies develop, i.e., the forest transition (Mather and Needle, 1998). In Africa, deforestation is thought to be positively related to real Gross Domestic Product (GDP) per capita until a turning point around USD 3,000 per capita income, beyond which deforestation is expected to decline (Ajanaku and Collins, 2021). African apes are most threatened in areas with low to medium poverty, growing GDP, expanding agriculture, and growing rural populations (Tranquilli et al., 2012). Local economic development that spares forest or development away from forest areas could reduce population pressure and forest losses. The Sub-Saharan region is already undergoing rapid urbanization with forecasts indicating that ca. 58% of its population is going to live in cities by 2050 compared to ca. 40% now (UNDESA, 2019). Nevertheless, although overall annual growth rates have declined from 2.4% in

1980 to 1.7% in 2021 (The World Bank, 2022b), rural population growth is likely to continue. Resulting migration patterns in Sub-Saharan Africa are complex, even more so when driven by armed conflict (Mercandalli et al., 2019). While poverty levels may locally prevent deforestation, these may not be a good predictor of great ape survival itself. Ordaz-Németh et al. (2021) found a negative quadratic relationship between African great ape densities and GDP, with decreasing great ape densities, partially poaching-related, above a nationwide GDP of $5 billion annually, which translates into a per capita GDP for these countries between USD 500 and 2,500. The effects of GDP maybe therefore play out differently on deforestation and poaching, and poverty and income levels as such may be poor predictors of great ape survival.

The debate on land sharing versus land sparing is relevant to reducing negative interactions between people and great apes (Phalan et al., 2011; Law and Wilson, 2015). Land sparing aims to set aside large tracts of land for exclusive wildlife use while intensifying agriculture on existing farmland to keep people and great apes apart. Land sharing seeks coexistence between people and great apes through small-scale farming and sustainable forest management in patchworks of low-intensity agriculture. Empirical evaluations suggest that land sparing results in better outcomes for wildlife diversity and abundance in the short term (Phalan et al., 2011; Hulme et al., 2013; Williams et al., 2017), but others note that isolated protected areas within an agricultural matrix can increase inbreeding and vulnerability to extinction (Kremen and Merenlender, 2018). This has been demonstrated in orangutans (Bruford et al., 2010) and Cross-River gorillas (Bergl et al., 2008), although such effects will depend on the extent to which apes use the matrix. The impacts of intensive agriculture, such as the use of fertilizers, herbicides, fungicides, and pesticides (Matson and Vitousek, 2006; Dudley and Alexander, 2017), can also be harmful to great apes (Krief et al., 2017). Research suggests that intensification does not necessarily reduce the area under agriculture because high yields drive further agricultural expansion (Byerlee et al., 2014; Balmford, 2021). The reality for great apes is likely to remain a mixed sharing and sparing model, where parts of their remaining range will need to be included in protected areas while others will need to be shared with farmers (Meijaard et al., 2022b). Protected land is still necessary in these shared landscapes due to the low reproductive rates of great apes, their area requirements, and crop foraging. Therefore, land sparing-type solutions that safely protect habitat fragments and keep them connected are required for the synergistic coexistence of people and great apes (Ancrenaz et al., 2021).

4 Solutions for saving great apes in secure food systems

The coexistence of great apes and agriculture is challenging and a win-win situation for both is difficult to achieve. Agricultural expansion, often associated with people without prior experience of great ape coexistence moving into great ape areas, is likely to cause further declines in ape populations. This makes sustainable and resilient interactions between people and nature difficult to achieve. If we truly want to save great apes from extinction, then we must prioritize implementing strict spatial planning and rigorous enforcement measures, that are ideally co-developed with local communities. This includes designating no-farming areas, improving crop productivity and diversification, resolving human-wildlife conflicts, securing adequate conservation financing, and clearly defining the roles and responsibilities of different stakeholders (Table 3). Without a committed and sustained effort in these areas, the survival of great apes will remain uncertain, and the consequences of their extinction will be irreversible. Finding solutions that work for great apes would have implications for many other threatened species in similar socio-ecological contexts across the tropics.

Great apes face competition for land and resources with humans, particularly where crops such as rice, cassava, maize, cacao, and oil palm are grown within their ranges (Table 3). This creates trade-offs between reducing poverty, feeding people, and

TABLE 3 Primary food system archetypes for each great ape taxon based on country profiles by Marshall et al. (2021).

Great ape species or subspecies	Primary food system	Main crops concern for expansion or foraging	Key strategies to facilitate coexistence
Nigeria-Cameroon Chimpanzee	Emerging and Diversifying	Oil palm, rice, cassava	Produce and protect, threat management and finance, yield increases
Western Chimpanzee	Mostly Rural and Traditional; Some Informal and Expanding	Rice, cacao, cassava, groundnut	Produce and protect, threat management and finance, yield increases
Eastern Chimpanzee	Mostly Rural and Traditional	Cassava, plantain, maize	Produce and protect, threat management and finance, payment for biodiversity
Central Chimpanzee	Informal and Expanding; Emerging and Diversifying	Cassava, plantain, rice	Produce and protect, threat management and finance, payment for biodiversity
Bonobo	Rural and Traditional	Cassava, groundnut, maize	Produce and protect, threat management and finance, payment for biodiversity
Western Lowland Gorilla	Informal and Expanding; Emerging and Diversifying	Plantain	Produce and protect, threat management and finance, payment for biodiversity
Cross River Gorilla	Informal and Expanding	Vegetables	Produce and protect, threat management and

(Continued)

TABLE 3 Continued

Great ape species or subspecies	Primary food system	Main crops concern for expansion or foraging	Key strategies to facilitate coexistence
			finance, yield increases
Grauer's Gorilla	Rural and Traditional	Beans	Yield increases, produce and protect, threat management and finance
Mountain Gorilla	Rural and Traditional	Beans, vegetables, fruit	Eco-tourism, payment for biodiversity, community engagement
Northwest Bornean orangutan	Informal and Expanding	Oil palm, tree crops, rice	Produce and protect, threat management and finance
Southwest Bornean orangutan	Informal and Expanding	Oil palm, tree crops, rice	Produce and protect, threat management and finance
Northeast Bornean orangutan	Modernizing and Formalizing	Oil palm	Key stakeholders and jurisdictional approach, produce and protect
Sumatran Orangutan	Informal and Expanding	Oil palm, rice	Produce and protect, threat management and finance
Tapanuli Orangutan	Informal and Expanding	Fruit, rice	Produce and protect, threat management and finance

Food systems in Democratic Republic Congo and Central African Republic are assumed to be Rural and Traditional. For food system description see Table S8.

conserving the environment. To address this, strategies must tackle the root causes of the problem, including land use competition. We suggest a framework for discussion, presented in Figure 5, focused on three directions. The first is to increase food production sustainably through agricultural innovations and smarter land use practices. The second is to modify food consumption patterns and distribution systems to reduce pressure on land and resources. Alternative food sources with minimal impact on great apes, including imported foods, might be effective under specific conditions. Though such lifestyle changes could raise complex issues related to food security and trade considerations. The third direction focuses on generating alternative income.

We emphasize the importance of adopting a landscape and jurisdictional approach in managing the competition between humans and great apes (Sayer et al., 2013). Within this framework, we propose several solutions, including strategies to increase yield, produce-and-protect practices, and threat management techniques. Next, we explore potential strategies to improve alternative income sources for communities, thereby reducing the need for land exploitation that can trigger competition with great apes (Figure 4). Finally, we consider the need to rethink our food systems in the context of the competition with great apes. We analyze potential solutions on both the consumption side and the production side, including modifying local food systems (e.g., by promoting dietary changes among local communities, such as switching from rice or maize to other crops) and global food systems (e.g., by reducing waste and rethinking food versus materials use) (Figure 5).

4.1 Land use planning and landscape management

To resolve the great ape habitat-agricultural conflict, land use planning and implementation must consider crop impact on trade,

FIGURE 4
An adult male chimpanzee at Bossou in Guinea crossing a village homestead having foraged on a papaya fruit. Reprinted with permission from Kimberley Hockings (Cantanhez Chimpanzee Project).

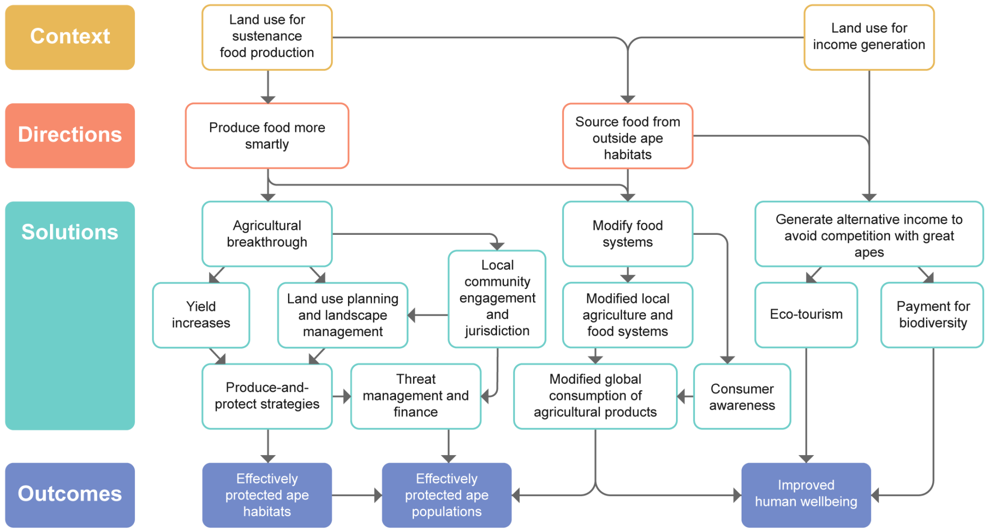

FIGURE 5
Theory of Change and structure of Discussion.

consumption, and the environment. Plans should respect human rights and balance agricultural development with conservation in each priority area. They should assess crops and ecosystems, production scale and methods (Jansen et al., 2020). Smallholder agriculture, which dominates much of great ape habitat, can be challenging to regulate, and new financial models are needed to facilitate change among smallholders. An effective approach could focus on food systems rather than crops themselves (Marshall et al., 2021) (Figure 6) and the transformations these systems are undergoing (Dornelles et al., 2022). To diversify food systems, nutrient-rich legumes, pulses, horticulture crops, and livestock may be introduced. Investing in rural market infrastructure enables smallholders to commercialize and improve the availability of perishable products (Abraham and Pingali, 2020). Different food systems offer different transformation pathways, either in an agroecological direction based on the redesign and

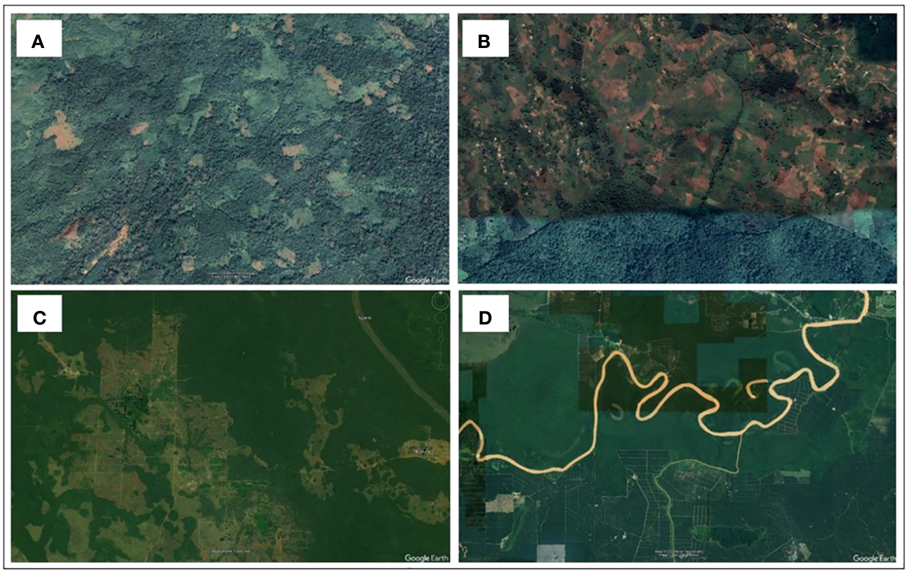

FIGURE 6
Example of different primary food systems with great apes. **(A)** Rural and traditional; smallholder farm area in Sierra Leone near Gola Rainforest National Park. Google Earth image © 2023 Maxar Technologies and © 2023 CNES/Airbus; **(B)** Informal and expanding: farm area to the north of Bwindi Impenetrable Forest, Uganda Google Earth image © 2023 CNES/Airbus and © 2023 Maxar Technologies; **(C)** Emerging and diversifying; new oil palm development in Gabon in areas with chimpanzee and western gorilla populations. Google Earth image © Landsat/Copernicus; **(D)** Modernizing and formalizing: Lower Kinabatangan area in Sabah, Malaysia where 800 orangutans live in forest fragments surrounded by industrial-scale oil palm. Google Earth image © 2023 Maxar Technologies and © 2023 CNES/Airbus.

diversification of agroecosystems or following Fourth Industrial Revolution pathways characterized by new technologies (Pimbert, 2022).

Government, farmers, industry, financial institutions, scientists, and civil society must collaborate for food system transformation. They should identify areas where the costs of agricultural conversion outweigh the benefits, considering environmental, social, and economic factors. Evaluating ecosystems' economic, environmental, and social value before development is crucial. This includes assessing potential agricultural revenues and socio-political dynamics. Trade agreements and international finance are vital policy tools. Great apes play a key role in Performance Standard 6 of the International Finance Corporation, linking finance to conservation outcomes and avoiding negative impacts on apes. Priority great ape areas must be protected, and conservation organizations should engage stakeholders to establish "no-go" development zones based on factors such as food security and the importance of these areas for great ape populations (Ancrenaz et al., 2016). The World Bank and other financing entities adhere to these standards, allowing projects in great ape habitats only in exceptional circumstances.

Planning and implementation at the landscape scale is vital for great ape survival in human-dominated habitats. Orangutan populations are maintained in some oil palm concessions in Indonesia and Malaysia with selected areas of protected forest from a few hundred to several thousand hectares connected by forest corridors and riparian areas (Ancrenaz et al., 2015). Similarly, in Gabon, populations of chimpanzees and Western gorillas are maintained in areas of forest within an oil palm concession (Ancrenaz et al., 2016). Preliminary studies indicate that both orangutans and chimpanzees retain dispersal dynamics in fragmented landscapes that mirror those in large forests (i.e., female dispersal in chimpanzees and male dispersal in orangutans), as long as they are not hunted (McCarthy et al., 2018; Ancrenaz et al., 2021), and that the presence of corridors and small patches in the agricultural matrix likely increases population viability in orangutans (Seaman et al., 2021; Seaman et al., 2023).

4.1.1 Yield increases

Increasing productivity on existing agricultural lands can reduce the need for expansion (Zhang et al., 2021), but closing yield gaps for food security is challenging, potentially leading to more land expansion unless local demand is met by imports (van Ittersum et al., 2016). Boosting productivity through reduced fallow duration, multiple cropping, early-maturing varieties, intercropping, catch crops, and enhanced irrigation offers the largest potential for production increases (Poore and Nemecek, 2018). Furthermore, as productivity increases so do agricultural land rents, which could create new incentives for agricultural expansion and deforestation (Phelps et al., 2013). However, rising productivity in pre-established agricultural areas can attract local immigration away from vulnerable frontiers, promoting land sparing and nature conservation (Laurance et al., 2009; Laurance et al., 2015). Technological advances in established agricultural lands can help reduce deforestation if increased supply lowers market prices (Angelsen and Kaimowitz, 2001). This aligns with the Borlaug hypothesis – i.e., improvements in agricultural technology will enable farmers to produce more food from a given piece of land, thereby enabling growth in food supply without leading to increased deforestation – and the experience of the Green Revolution (Stevenson et al., 2013). Non-expansion and abandonment of marginal agricultural lands on the forest frontier are crucial for 'forest transition' processes, i.e., the stabilization or even increase of forest cover at high levels per-capita income (Mather and Needle, 1998; Meyfroidt and Lambin, 2011).

4.1.2 Produce-and-protect strategies

Another strategy could be to combine both policy tools – i.e., on the one hand land-use planning of 'no-go' conservation reserves on forest land with poor agricultural potential, and on the other improving agricultural yields on already cultivated land (Zhang et al., 2021). Such 'produce-and-protect' type of strategies of combining land-sparing agriculture with protected areas and private reserves for the provision of biodiversity services, indigenous lands and other actively enforced protection strategies may also be the most promising pathways for meeting the goals of great ape conservation and food production (Hanson and Ranganathan, 2022). Their attractive element is above all in their mutually reinforcing effects. On the one hand, effectively closing the agricultural frontier hampers land extensification and is inducive to the adoption of land-saving technologies that can increase producer incomes. Conversely, protecting land areas from crop expansion is easier when supply of the same crop is increasing and prices are not, thus counteracting any 'leakage' of forest pressures from the newly protected area to elsewhere (Meyfroidt et al., 2020).

Robust governance and increasing conservation incentives can help ensure land sparing, but implementation of these strategies may require tracking future agricultural land rents (Phelps et al., 2013) and targeting development planning away from core great ape areas (e.g., avoiding road building into or through priority habitats). This can stimulate economic growth and draw people away from frontier areas while increasing the value of natural ecosystems. Targeting development far from priority great ape areas makes sense as impacts on biodiversity are most severe in the earliest stages of agricultural expansion, especially when conversion occurs in forest interiors (Chaplin-Kramer et al., 2015). Conservation organizations should collaborate with governments and industry partners to build consensus about "no-go" areas for development based on the presence of priority great ape populations and other high-risk factors.

4.1.3 Food forests, regenerative agriculture and agroforestry

Improved agricultural methods are needed that reduce soil degradation and other negative environmental impacts and provide potential for climate solution (Terasaki Hart et al., 2023). This includes the increased use of agroforestry systems, which are thought to be more resilient than monocultures of annual crops (Mbow et al., 2014) and nitrogen-fixing legumes which increase soil fertility and reduce fertilizer needs and run-off (Roupsard et al., 2020). Agroforestry systems and perennial crops may also increase great ape dispersal between forest fragments as recorded in orangutans and chimpanzees. Mixing crops and forest patches does not necessarily reduce yields, because forests provide ecological benefits to surrounding agriculture that improves nearby yields, as demonstrated in Indonesian oil palm (Zemp et al., 2023). Many food forests are not yet economically viable but could be if other income could be generated from ecosystem services (Albrecht and Wiek, 2021).

4.1.4 Threat management and finance

Threat prevention strategies for great ape conservation require sustained external funding, which can come from various sources such as nature-based tourism (Maekawa et al., 2013) or funding from industry (Larson et al., 2021). Increased investment in patrolling and law enforcement, as well as the presence of civil society organizations, can help reduce pressure on great ape populations and habitats. To achieve this, there need to be new species action plans that call for a significant increase in and reallocation of conservation funding. Increasing the market value of biodiversity and allowing this to finance conservation services from nearby rural communities is one way to close the funding gap, while ensuring that funds end up where decisions about great apes are made (Ledgard and Meijaard, 2021; Fergus et al., 2023). The engagement of the private sector in conservation is another way to increase investment into biodiversity conservation, such as through offsetting biodiversity impacts or managing and maintaining species habitats (Bull and Strange, 2018). For example, palm oil certified through the Roundtable on Sustainable Palm Oil requires that areas of high conservation value are protected and values retained (RSPO, 2018). Effective management of great ape populations requires funding, manpower, and infrastructure which many companies have access to, but do not necessarily possess the knowledge to implement evidence-based conservation strategy. Furthermore, facilitating collaboration between industrial-scale operators and smallholders, such as has been attempted in the palm oil industry, can speed up knowledge transfer and increase yields for smallholders.

Increased funding is not enough. Efficient allocation of funds to more effective interventions is crucial. One billion USD allocated over 20 years to orangutan conservation was insufficient to stop their decline, probably due to inefficient allocation of funds (Santika et al., 2022). In summary, great ape conservation efforts require sustained external funding input and efficient allocation of funds to effective interventions. Increased investment in patrolling and law enforcement, preferably with the involvement of local communities, as well as the engagement of the private sector in conservation, can help achieve conservation goals. However, it is important to ensure that funds end up where ultimate decisions are made about great ape survival and that conservation efforts address not only habitat protection but also the safety of great apes from hunting, poaching, and disease. Evidence-based conservation is needed to investigate and determine what solutions will be most effective in different contexts local situations (Junker et al., 2020).

4.1.5 Key stakeholders and jurisdictional approach

Respecting human rights and effective engagement and motivation of communities living in proximity to great apes, in addition to earlier mentioned financial benefits, is essential for successful conservation (Chua et al., 2020; Bettinger et al., 2021). This needs to address the key question of what communities can gain from participating in conservation programs, and if they can help guide goals, planning and execution, i.e. "Whose Conservation" (see, e.g., Kaimowitz and Sheil, 2007; Mace, 2014). Engaging communities in conservation planning alongside broader village development planning could ensure that conservation objectives become integral to these broader plans (Vermeulen and Sheil, 2007; Meijaard et al., 2022b). Considerable experience exists in exploring, developing and implementing such initiatives (Lynam et al., 2007; Margules et al., 2020). The opportunities are generally greater than is assumed (Padmanaba and Sheil, 2007; Vermeulen and Sheil, 2007) as local people will often have goals and interests of their own that overlap with those of conservationists (Sheil et al., 2006; Chua et al., 2020). Working together to identify and achieve locally defined goals can be a useful means to build trust, reduce conflict and build a consensus towards addressing wider conservation goals (Sayer et al., 2013; Sheil et al., 2017). This could overcome the current problem that provisions for great ape conservation are often written by people who have little connection to or understanding of the livelihood strategies and patterns of indigenous communities (Chua et al., 2020).

4.2 Alternative income to avoid land competition with great apes

Achieving direct and immediate benefits for people who are asked to live side-by-side with great apes, for example through ecotourism (Robbins, 2021) or payments for conservation services (Ledgard and Meijaard, 2021; Fergus et al., 2023), could encourage more positive perceptions regarding apes that are becoming accustomed to human-dominated landscapes (Chua et al., 2020).

4.2.1 Eco-tourism

Eco-tourism provides a potential solution for achieving poverty eradication and conservation goals for communities facing imminent threats of agricultural expansion. The successful conservation of mountain gorillas has been largely funded by nature-based tourism (Maekawa et al., 2013), but this has also resulted in increased negative interactions between habituated gorillas and local communities (Hill, 2005; Seiler and Robbins, 2015; Robbins, 2021), highlighting the complexity of eco-tourism contexts. Nevertheless, the value of nature-based tourism to countries such as Rwanda is high with tourism accounting for 23%of export earnings in 2020 (World Bank and Government of Rwanda, 2020) and mountain gorillas alone accounting for 2% of GDP in 2023. In Borneo, eco-tourism businesses also contribute significantly to regional income (Goh and Potter, 2023), but scaling up tourism to cover the entire range of Bornean orangutan is challenging and may result in lower prices due to increased competition. While nature-based tourism can benefit great apes and local communities, it is unlikely to positively influence significant parts of the great apes' range soon. The pandemic and the associated travel restrictions and periodic suspension of great ape visits have revealed the over-dependency on tourism (Ezra et al., 2021). Alternative financial mechanisms are needed to provide a safety net for communities when tourism does not bring in the much-needed resources.

4.2.2 Payment for biodiversity

Often the people who live with great apes see few economic benefits. As an example, around Bwindi Impenetrable Forest National Park, communities living within 0.5km of the boundaries are significantly poorer and are more affected by wild crop foraging animals than those living further away (Twinamatsiko et al., 2014). Conservation efforts, particularly the management of national parks, have historically exacerbated rural poverty by restricting access to forest resources, fining for minor acts and the loss of crops and livestock to protected wildlife (Blomley et al., 2010). Improved compensation schemes for conservation are therefore needed to finance the conservation of great apes and provide financial benefits to those living alongside them.

Developing payment for ecosystem services (PES) programs that financially incentivize local communities to conserve critical forested areas for great ape survival could be a potential approach (Wunder, 2005). To jumpstart financing for great ape conservation, compensation schemes for conservation could be combined with carbon credit schemes. To tackle this issue, a nested approach can be employed, incorporating carbon credits into a larger conservation project that encompasses biodiversity preservation and additional ecosystem services. (Law et al., 2012). The conservation project can generate carbon credits that can finance the broader conservation activities (but see West et al., 2023). The revenue generated can be used to compensate communities living with great apes or to restore degraded great ape habitat (Darusman et al., 2021). This approach can ensure that both biodiversity and carbon sequestration goals are achieved, and local communities benefit from conservation efforts.

One potential strategy is to establish fair and transparent compensation mechanisms to offset the costs that communities incur from living alongside great apes, such as damage to crops and livestock. Compensation programs can provide financial or material support to alleviate the economic losses inflicted by great apes, thus reducing conflicts between humans and wildlife and increasing the likelihood of coexisting with great apes in the long term. These programs can be supported by various sources, including conservation groups, government entities, and concerned private sector entities. Once such compensation schemes are established, they may need to remain in place indefinitely, and we acknowledge that running fair and transparent compensation schemes in many ape range countries would be a huge challenge.

Biocredits have emerged as an economic instrument to incentivize conservation in remote areas with great apes (Porras and Steele, 2020). Similar to carbon credits, they generate revenue by selling units of biodiversity resulting from improved conservation actions; how these units will be defined, measured and verified is yet unclear. Once this is resolved, biocredits can be purchased by government bodies, philanthropic organizations, and private companies. German companies have already expressed interest in purchasing biocredits for conservation through an online marketplace (Krause and Matzdorf, 2019). These mechanisms provide direct financial contributions to conservation organizations and communities, supporting initiatives like citizen science monitoring and tree planting. The use of biocredits for direct payments to individuals, communities, and local conservation managers is still limited but shows promise for the future (Community Conservation Namibia, 2023).

Interspecies Money is a proposed system designed to collect data on various species, provide them with a unique digital identity and digital wallets, and allocate based on the importance to conservation (Ledgard, 2022). Recent technological advancements, including low-cost sensors, drones, camera traps, bioacoustics, eDNA sampling, and artificial intelligence, enable data collection and analysis of population trends in their habitats (Ledgard and Kharas, 2022). This data-driven approach allows for the distribution of Interspecies Money based on conservation outcomes (increased abundance based on human behavior, e.g., a local farmer not cutting down a tree or not harming a great ape). This approach aims to simplify conservation finance, allowing easier upscaling and reducing the reliance on conservation organizations or governments. However, successful implementation requires redefining economic rules and piloting projects in natural settings to assess feasibility and effectiveness (Ledgard, 2022). The approach is being piloted in Rwanda.

4.3 Rethinking agriculture and food systems

4.3.1 Modifying global consumption and local agriculture

To address deforestation and protect great apes, requires understanding the consumption dynamics and underlying causes of agricultural expansion. Palm oil, for example, satisfies a significant portion of global vegetable oil demand (FAOSTAT, 2022), but reducing its use requires a shift in global consumption patterns (Goh, 2016; Meijaard and Sheil, 2019). Efforts to reduce reliance on palm oil must also consider potential adverse impacts on other regions and conservation efforts (Meijaard et al., 2020). Protecting great apes within the context of modern agriculture necessitates a comprehensive approach that considers the complex factors driving agricultural expansion, including internationally traded cash crops like cocoa, coffee, and oil palm. While a radical change in global consumption patterns solely for great ape protection is unlikely, efforts should be tied to larger issues such as climate change.

Promoting dietary changes within local communities can help reduce the demand for food production that destroys great ape habitats (Abraham and Pingali, 2020), as do reductions in food losses through improved storage and transportation. However, balancing conservation efforts with the food security of these communities presents a major challenge. Subsistence agriculture is vital for many people living in great ape regions, and altering their dietary choices and agricultural practices can have significant economic implications. Cultural and social barriers further complicate the process, requiring time and effort to implement changes. Education and capacity building programs can help transition local food systems to more sustainable practices. Such interventions must be approached with caution as they involve changing traditional ways of life.

4.3.2 Consumers' awareness

There is an important role of consumers in putting pressure on retailers, producers and governments to ensure that the products they use are not associated with the loss of great apes and their habitats, or more generally, with the loss of biodiversity in tropical habitats. Currently, there is some consumer awareness about the environmental impacts of palm oil production on orangutans (e.g., Ostfeld et al., 2019), but much less so about, for example, chocolate consumption and chimpanzees. Providing consumers with fact-based and transparent information, e.g., through labelling processes, about the impact of the production rice, cassava, peanut, cacao and other crops in great apes' ranges would give them a more informed choice and an ability to influence markets and land-use decision-making (Meijaard and Sheil, 2019). The European Union's New Deforestation Regulation, although criticized by tropical producing countries such as Indonesia and Malaysia, provides a tool for consumers to differentiate products not on what they contain (e.g., a no-palm oil label) but rather as to how ingredients were produced ("great ape safe" or "deforestation free"). Also verified sustainable production practices such as those certified under the Roundtable on Sustainable Palm Oil can give consumers a more informed choice.

5 Conclusion

Great apes face significant threats from agriculture driven by poverty and demand for agricultural resources. Ensuring coexistence between great apes and people is of paramount importance, particularly considering that most great apes live outside protected areas. However, the challenge lies in the fact that on average each great ape shares its distribution range with approximately 100 people. Achieving successful coexistence requires significant incentives and efforts to protect and preserve these conservation flagships. New financial models are needed that can more easily be scaled up and attract =more investment. Optimized land use planning, guided by strategic investments in agricultural development and wildlife conservation, can maximize synergies between conservation and food production goals. It is vital to support effective economic development policies, enforce forest conservation and environmental laws, engage in trade policy discussions, and link policies on trade, food security, improved agricultural techniques, and sustainable food systems with forest and great ape impact monitoring. The global agenda should focus on closing crop yield gaps, promoting healthier diets, reducing food loss and waste, and allocating more research funding to address the challenges of great ape and human coexistence.

Author contributions

EM, RD, MA, SWi and DS contributed to conception and design of the study. NU, TA and RD organized the database and spatial analysis of crop and other data. JS developed the causal change diagrams. EM wrote the first draft of the manuscript. KH, SWu, CG, MO, JL, JR, and DS wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

Funding

Work was supported via a grant from UNEP GRASP (SSFA/2021/4079) and a grant from UNEP under the GEF funded Congo Basin Impact Program (PCA/2022/5067) and the Darwin Initiative (grant number, 26-018) to KH.

Conflict of interest

EM, NU, TA, RD and MA were employed by Borneo Futures.

EM declares that he co-chairs the IUCN Oil Crops Task Force that studies oil crops. He has received funding from palm oil producing companies and the Roundtable on Sustainable Palm Oil, which could be construed as a potential conflict of interest.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2023.1225911/full#supplementary-material

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