Apes and Agriculture

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Abstract

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 more nuanced understanding of specific contexts and associated effects on habitats and populations. Here we review these contexts and highlight synergistic and antagonistic co-occurrences between agriculture, both subsistence and commercial, and great apes. We estimate that one individual great ape shares its habitat with about 100 people, mostly outside protected areas. This makes it challenging to balance the needs of both humans and great apes given the growing human population and increasing demand for resources. 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. More broadly, optimized land use planning, along with strategic investments in agriculture and wildlife conservation, can maximize the synergy 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, circular agriculture, and sustainable food systems are vital to prevent further decline in great ape populations. Saving great apes requires consideration of the specific agricultural contexts, not just focusing on the apes themselves.

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 by 193–317 Mha by 2050, mainly in Africa (Schmitz et al., 2014). This expansion will result in the loss of habitat for 87.7% of the 19,859 terrestrial vertebrate species recently reviewed, with 1,280 species losing over 25% of their remaining range (Williams et al., 2021). Balancing the demands for crops and conservation is one of the biggest challenges of the twenty-first century (Dudley and Alexander, 2017), especially in the tropics, where species diversity is high, and large natural ecosystems are declining due to human population growth (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). 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 habitat 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, poverty (i.e., income of less than US$2 per day), and low food security. For instance, according to World Bank data, the 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, for example 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 to improve food availability and security. Growing human populations and a drive for economic development through agriculture, alongside growing international demand, are, however, key drivers of deforestation (Busch and Ferretti-Gallon, 2017) and therefore great ape habitat loss.

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.

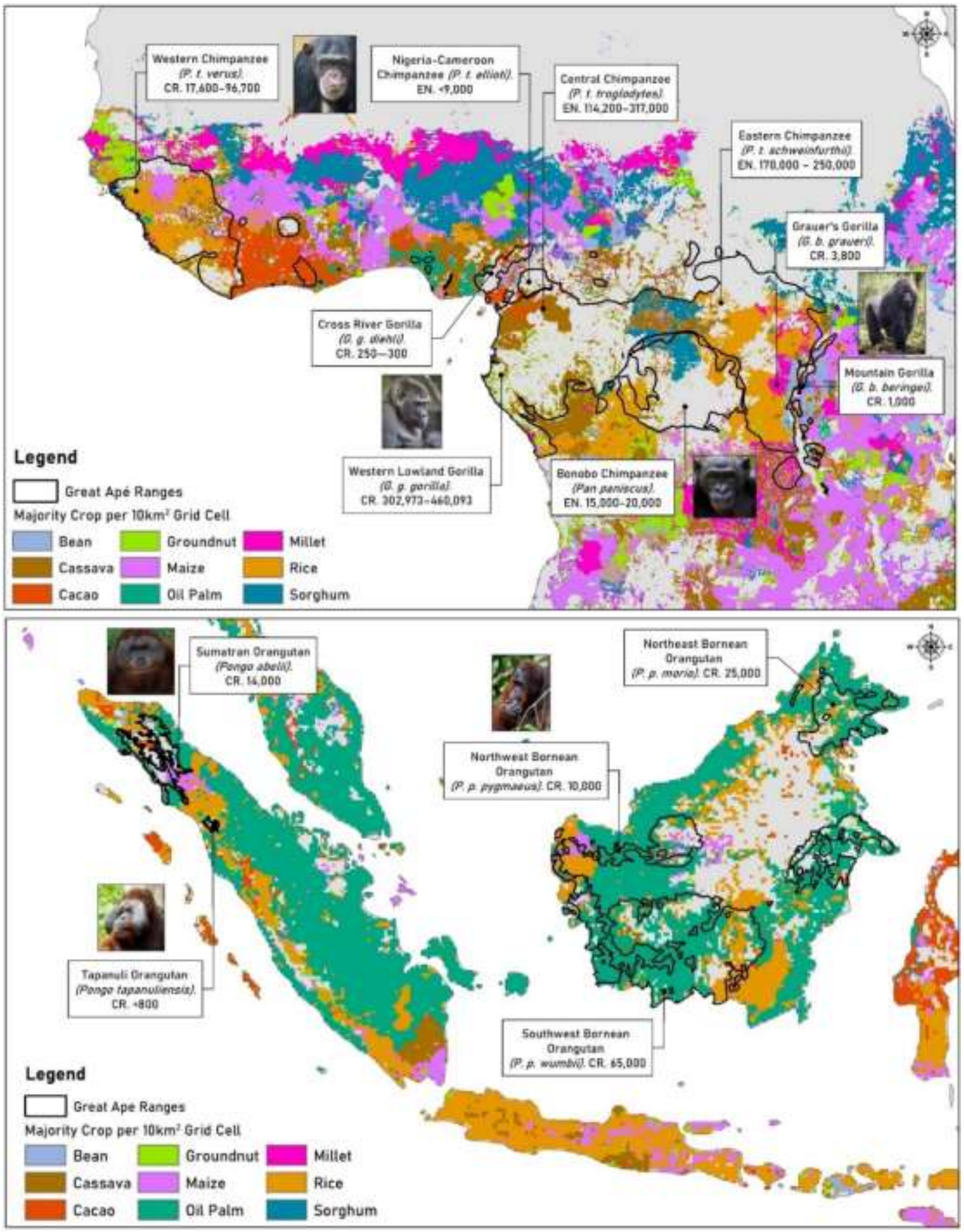

Table 1. Great ape taxa, the number of people within the great ape ranges (Schiavina et al., 2022), the primary drivers of forest cover loss (Laso Bayas et al., 2022), and main crops in great ape ranges (Meijaard et al., 2021).

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

Agriculture poses a threat to great apes, with factors such as unsustainable use of natural resources, agricultural expansion, disease, genetic and social factors, and ape killing, capture, and trade negatively affecting their habitats (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 chimpanzees in Tanzania and very dry areas in Senegal and Mali are an exception). Crop expansion is a major contributor to this threat, with crops such as maize (*Zea mays* L.), rice (*Oryza* spp.), millet (various species) and cassava (*Manihot esculenta* Crantz) predominating (for details see Table S1, Table S2, Table S3). These crops are mostly grown in smallholder, subsistence agriculture contexts (Table 1), with fields typically being less than 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). African oil palm (*Elaeis guineensis* Jacq.) is another crop that has been a driver of deforestation, especially in Southeast Asia's orangutan range and is rapidly expanding in that region (Table S4), with concerns about its expansion in Africa and potential impact on great apes (Linder, 2013; Wich et al., 2014). While there has been much media attention on the impact of oil palm expansion on great apes, other crops such as rice and cassava have largely escaped scrutiny (Jayathilake et al., 2021). We did not conduct a systematic review of crop foraging by each great ape species but highlighted some crops of specific concern for both expansion and foraging.

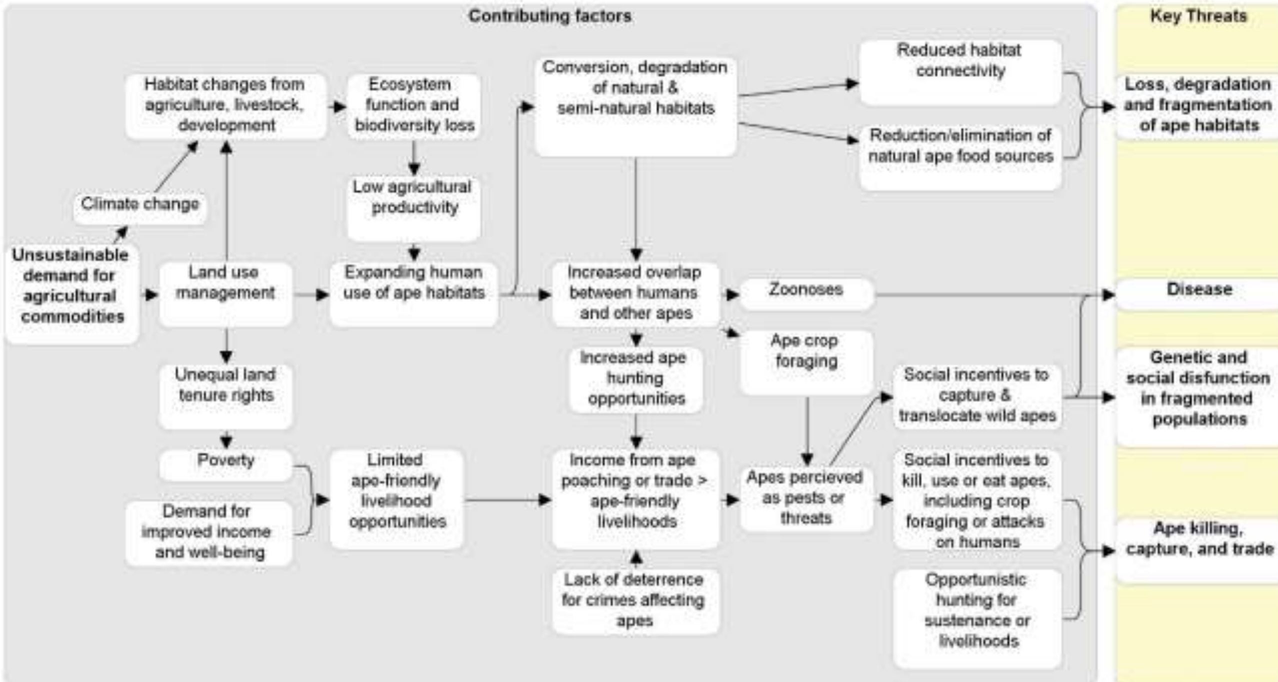

Figure 2. Causal transmission chain of (negative) change between human expansion in land use and the fate of the great apes (referred to as "apes")

Great apes are mainly found in tropical and subtropical regions that are favorable for specific crops. There is, however, considerable variation in the type of crops grown across the great ape range. 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, including warm temperate areas in East Africa and more arid lands (Kottek et al., 2006). The crops grown in these regions are mostly annuals, with some crops like oil palm, tree crops, and cacao being perennial (Table 2). The usage of crop areas by great apes for feeding or dispersal, and the level of persecution they face for consuming different crops, vary depending on the type of crop cultivated. Furthermore, 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.

It is worth noting that not all remaining great ape habitats are formally protected, and much land outside protected areas is used for agriculture. 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 threat from agricultural expansion, but this is also taking place within protected areas, depending on the type of protective management, the degree and effectiveness of enforcement of the protective management regime, and the extent to which community needs are integrated. Overall, understanding the distribution and ecology of great apes is crucial in understanding the impact of agricultural crops on them.

Table 2. Typology of main crops that occur in great ape ranges and are likely to cause most great ape habitat losses. All crop data (FAOSTAT, 2023)

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
Rice	60,423,297	2.9%	Among others, chimpanzees forage on rice	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)
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., 2020b)
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	Mostly local food subsistence use in Africa, also livestock feed.	Increasing global demand for food. Drought-resistant and considered a “healthy” grain	(Kumar et al., 2018; Antony Ceasar and Maharajan, 2022)

				fertilizer and pesticide needs	Not much used in SE Asia.		
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)
Natural rubber in primary forms	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)

The different characteristics of the fourteen great ape species and subspecies (Table 1), 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 conpounded 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 with the objective to 1) assess the dominant crops and food systems in the ranges of the 14 great ape species; 2) identify antagonistic and synergistic co-occurrences; 3) understand economic and political factors that 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 species, and what can be done to minimize negative impacts and facilitate synergies between conservation and agriculture.

2 Key agricultural trends where apes and crops converge

We analyze agricultural dynamics in areas with great apes. Agricultural production in Africa mainly serves domestic consumption with a few crops generating export revenues (Rakotoarisoa et al., 2012). Smallholder farming dominates, but the transition to business-oriented processes is underway (Mukasa et al., 2017; Giller, 2020). However, farms still struggle to provide food security or living income. 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 Parnership Council, 2016), impacting areas of high biodiversity like protected areas (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 those with low nutrient peat swamp forests that are important for orangutans (Meijaard et al., 2010b).

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. According to data from FAOSTAT, cassava, oil palm, and rubber have been the crops with the greatest regional expansion rates (Table 2). Meanwhile, land under maize is also growing, 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 remaining forest areas, where great apes live. In Borneo, reductions in rainfall and increases in temperature (McAlpine et al., 2018) are likely to limit areas suitable for crops such as oil palm, which are vulnerable to prolonged drought, and thus reduce available orangutan habitat (Struebig et al., 2015).

3 Great ape ecology and agriculture

Great apes are primarily adapted to a plant diet, with meat consumption by chimpanzees being an exception (Fahy et al., 2013). Great apes 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; 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 behaviour over time to human-dominated landscapes, 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). As species with low reproductive outputs, retaliatory killings of apes by humans in response to crop consumption is unlikely to be sustainable. Disagreements between different human groups over how to manage problematic great ape behaviour can follow (Campbell-Smith et al., 2011; Hockings and McLennan, 2012).

While some 310,000-672,000 chimpanzees remain (Figure 1), primarily in the central part of their range, populations in the western part of their range are much smaller and highly fragmented due to agricultural expansion. Rice, cacao, and cassava are major concerns in the chimpanzee range (Figure 1a and Table S1, Table S2, Table S3), with high-value cacao being particularly problematic. In Southwest Cameroon, Nigeria-Cameroon chimpanzees overlap with an important and expanding cacao production area, where forest areas, including protected forest reserves that contained chimpanzees have been converted to cacao production (Klarer, 2014). Also, in Côte d'Ivoire, cacao was the main crop grown inside the national parks and forest reserves surveyed in one study, being present in 20 of 23 protected areas (Bitty et al., 2015; Kouassi et al., 2021), threatening "protected" Western chimpanzee populations (Barima et al., 2020; Abu et al., 2021). As cacao is a perennial crop, it may have some value for chimpanzees as a dispersal habitat, though the animals sometimes forage on cacao crops at times of low fruit availability (Humle, 2003; Tehoda et al., 2017; Payne, 2019; Wade, 2020). Rice and cassava are also targeted by chimpanzees in, for example Sierra Leone (Garriga et al., 2018) and Guinea (Hockings et al., 2009), although other species such as cane rats (*Thryonomys swinderianus*), can cause more damage (Garriga et al., 2018). Not all crop feeding is problematic, however. Chimpanzees in Cantanhez National Park in Guinea-Bissau are not considered to cause significant damage to the main cash crop, cashew (*Anacardium occidentale* L.), as chimpanzees feed only on the cashew pseudofruit, leaving the economically valuable cashew nut undamaged (Hockings and Sousa, 2013).

Bonobos are mostly found in primary forests and seasonally-inundated swamp forests (Fruth et al., 2016), and they are affected by forest loss caused by swidden subsistence agriculture (Fruth et al., 2016; Molinario et al., 2020). Table S1 suggests that most of this subsistence agriculture involves cultivation of cassava, maize, rice, plantain, and groundnut, while in the northern parts of the range, sorghum production dominates (Figure 1a). Especially cassava cultivation seems problematic for bonobos. A recent study predicted that 75% of the deforestation in the western Democratic Republic of the Congo (DRC) province of Bandundu will be driven by expansion of cassava (Mosnier et al., 2016), and that similarly, cassava will likely be the biggest driver of forest loss related to the development of road infrastructure in the DRC (Li et al., 2015). Bonobos are not normally associated with crop foraging (Fruth et al., 2006), although one study found the presence of sugar cane, banana, maize, papaya, pineapple, sweet potatoes and cocoa in the bonobo's diet (Inogwabini and Matungila, 2009), and crop foraging could be understudied. According to Terada et al. (2015), habitats that are often considered minor-use, such as human-modified and inundated areas, may be more significant for bonobos than currently acknowledged. These areas have likely been overlooked in the past because the species does not create nests in these habitats.

Compared to chimpanzees, gorillas require larger forest areas and are less adaptable to diverse ecological conditions. They usually inhabit open Marantaceae forests with dense ground vegetation and have less preference for open agricultural areas than chimpanzees. The critically endangered Cross-River gorilla faces a significant threat from agricultural expansion, restricting its habitat to hilly areas due to human activities, particularly hunting, rather than the availability of preferred food sources (Bergl et al., 2016). The Cross-River gorilla's natural habitat has been destroyed for the cultivation of crops like potato, beans, maize, rice, groundnuts, oil palm, and cassava (Tume et al., 2020). This trend continues in areas with high human populations (Dunn et al., 2014). In the case of the Western lowland gorilla, the dominant crops grown in their habitat include cassava, cacao, plantain, vegetables, and oil palm (Table S6). These crops are often cultivated in agro-forestry systems that overlap with gorilla habitat, and gorillas can cause significant damage to plantain crops (Naughton-Treves and Treves, 2005). Cacao farms, which are a source of income for local communities, may also be damaged by gorillas in areas where they overlap (Naughton-Treves and Treves, 2005).

Like Cross-River gorillas, mountain gorillas are also limited by cultivated areas that surround their forest habitats, including bamboo, mixed, and subalpine forests. Common crops in the range of Grauer's gorillas include beans (Meijaard et al., 2021) (not shown in Table S6, but taking up 62,427 ha), maize, plantain, and rice (Table S6), while mountain gorillas' range is dominated by beans and potatoes (Meijaard et al., 2021). Deforestation in Bwindi has primarily been driven by small-scale farming and tea plantations (Twongyirwe et al., 2011). Some mountain gorillas in Bwindi have become habituated to human presence and often spend time feeding outside the protected forest with negative impacts on banana, sweet potato, maize, passion fruit, beans and coffee (Akampulira et al., 2015; McLennan and Hockings, 2016; Seiler and Robbins, 2016).

Box 1. The crucial role of access to water for great apes

Apes obtain water from their food and by drinking surface water or water collected in tree holes (Figure 3). However, agriculture and climate change have reduced the availability of water (Akpabio, 2007), affecting great apes' health, behaviour, 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. It can also lead to contamination of water sources with pesticides and increased sharing of water sources between great apes and humans, which can increase pathogen sharing load (Masi et al., 2012; Shively and Day, 2015; Sharma et al., 2016). Great apes are adapting to these challenges by developing new traits (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. Photo by Joana Bessa, Cantanhez Chimpanzee Project

Orangutans can adapt to habitat changes, as seen in their presence and feeding in different environments such as *Acacia mangium* Willd. plantations in East Kalimantan (Meijaard et al., 2010a), mixed agriculture mosaics in Sumatra (Campbell-Smith et al., 2011), and oil palm plantations in Borneo (Ancrenaz et al., 2015) and in forests used for timber (Ancrenaz et al., 2010;

Wich et al., 2016) (Figure 1b and Table S7). They prefer lowland forests which are also suitable for agriculture (Santika et al., 2017). However, historically, lowland peat swamp forests were not utilized for agriculture until the advent of modern farming practices and drainage. These peat swamp forests likely served as a refuge from hunting for the great apes (Meijaard, 2017). Oil palm has the greatest range overlap with all three orangutan species (Table S7), and has contributed to their habitat decline (Wich et al., 2012; Wich et al., 2016; Santika et al., 2017; Voigt et al., 2018), although remaining orangutan habitat may be stabilizing in some areas (Meijaard et al., 2022b). Orangutans feed on young oil palm shoots and fruits, but they are not a major crop pest (Ancrenaz et al., 2015). Rice cultivation has impacted orangutan habitat in some areas, such as the Central Kalimantan peat swamp forests (Boehm and Siegert, 2001) and Sumatra (Jayathilake et al., 2021).

Figure 4. An adult male chimpanzee at Bossou in Guinea crossing a village homestead having foraged on a papaya fruit. Photo by Kimberley Hockings

4 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). Wealthy people in the latter landscape are generally not concerned about orangutans or crop losses, and orangutans are generally safe, although it is unclear if they will remain viable in the long-term.

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 anticipated.

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 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). Deforestation is positively related to real 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). However, in areas with low to medium poverty, growing GDP, expanding agriculture, and growing rural populations, African apes are most threatened (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 urbanisation 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). We also note that 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 thus 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. On the other hand, land sharing seeks coexistence between people and great apes through small-scale eco-friendly 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). The offsite 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 significant and 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., 2022c). 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).

5 Discussion

The coexistence of great apes and agriculture is challenging, and our study finds that synergies between the two are mostly absent, making it difficult to achieve win-wins for both. Positive examples of coexistence occur in areas with high local welfare, stable forest cover, and long-term conservation programs or revenue from tourism. However, crop consumption by apes can result in negative interactions with people, leading to retaliatory killings to protect crops or for personal safety. Agricultural expansion is likely to cause further declines in ape populations, making 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. This includes designating no-go areas, improving crop productivity, resolving human-wildlife conflicts, securing adequate conservation finance, 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.

Table 3. Primary food system archetypes for each great ape taxon based on country profiles by Marshall et al. (2021). Food systems in Democratic Republic Congo and Central African Republic are assumed to be Rural and Traditional. For food system description see Table S8.

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 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

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 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, could be explored. However, this may require significant lifestyle changes and could raise complex issues related to food security and trade considerations. The third direction focuses on generating alternative income.

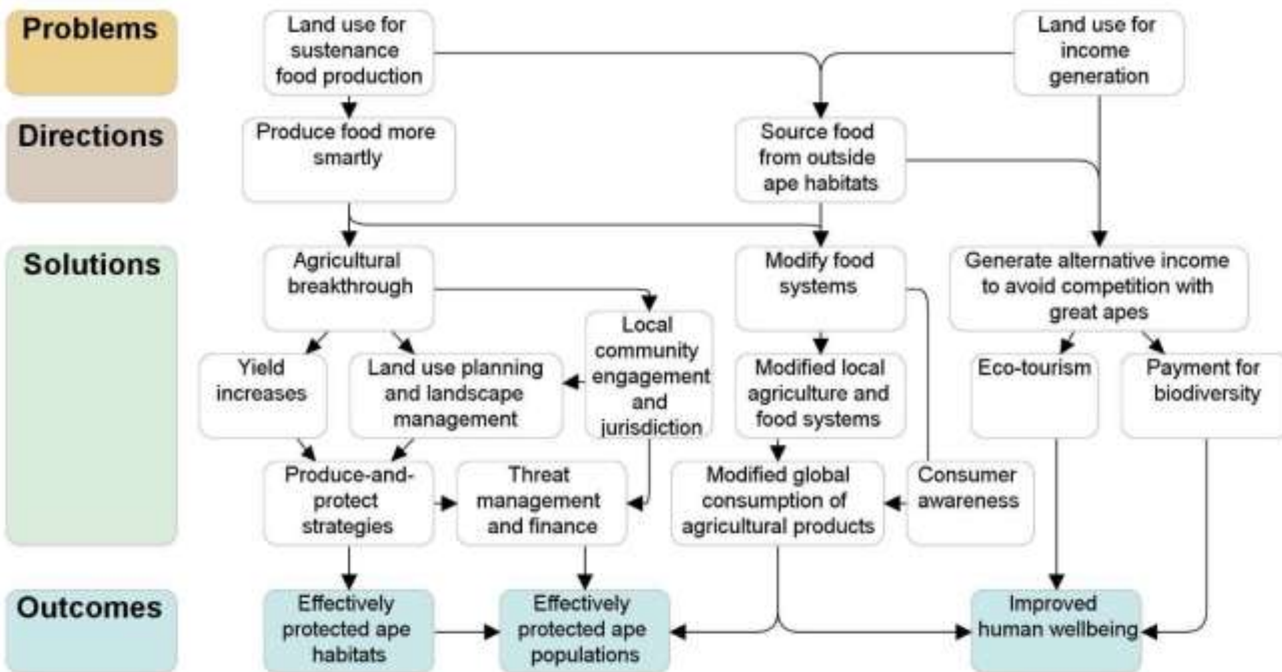

Figure 5. Theory of Change and structure of Discussion

We emphasize the importance of adopting a landscape approach in managing the competition between humans and great apes. 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. Finally, we consider the need to rethink our food systems in the context of the competition with great apes. We analyse 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 to other crops) and global food systems (e.g., by reducing waste and rethinking food versus materials use) (Figure 5).

5.1 Land use planning and landscape management

To effectively address the conflict between great ape habitats and agricultural development, land use planning should consider the impact of different crops on local and international trade and consumption, as well as the scale of agricultural development and environmental impact. For each great ape priority area, a locally supported plan that balances agriculturally driven development and conservation is necessary. These plans should consider the location of agriculture and natural ecosystems, the scale and mode of production, and crop choice (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). Encouraging diversification of food systems is needed, for example, through introduction of nutrition-rich legumes, pulses, horticulture crops and livestock, while investment in rural market infrastructure allows smallholders to commercialize and enhance the supply of perishable products (Abraham and Pingali, 2020). Different food systems offer different transformation pathways, either in an agroecological direction based on the redesign and diversification of agroecosystems or following Fourth Industrial Revolution pathways characterized by new technologies (Pimbert, 2022). Therefore, it is crucial to understand the socio-ecological context in which crops are grown, which is often more critical for land use and conservation planning than the crop itself, except when great apes forage on specific crops.

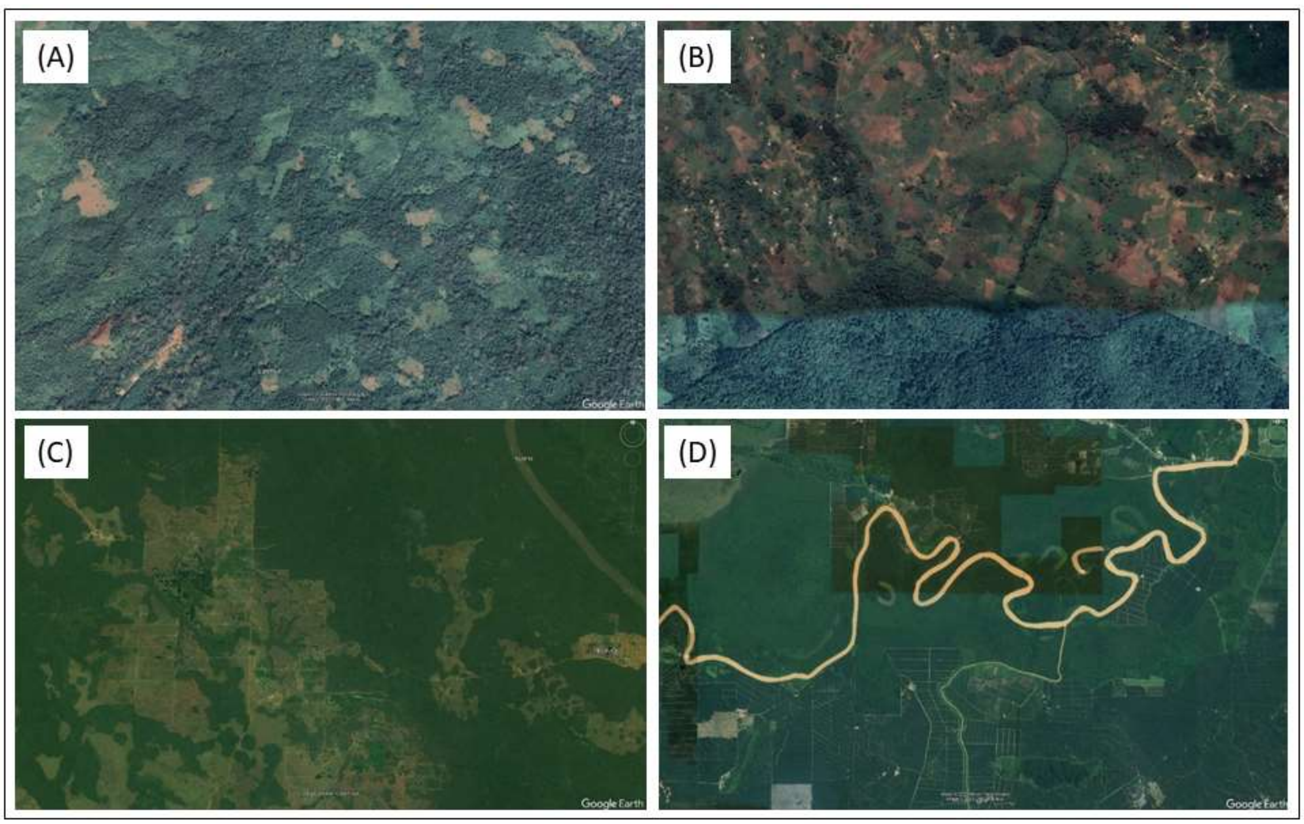

Figure 6. Example of different primary food systems with great apes. A. Rural and traditional; smallholder farm area in Sierra Leone near Gola Rainforest National Park. Google Earth image © 2023 Maxar Technologies and © 2023 CNES/Airbus; B. Informal and expanding: farm area to the north of Bwindi Impenetrable 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.

Governments, industry, financial institutions, scientists, and civil society stakeholders should work together to achieve food system transformation by identifying areas where environmental, social, and economic costs of conversion to agriculture outweigh the benefits (net-positive benefits). The economic, environmental, and social value of ecosystems should be evaluated before development, including understanding the potential net revenues from agriculture and the socio-political dynamics (Goh, 2020). Trade agreements, as the key policy tools that are enforceable, play an important role, as does international finance. Great apes play a crucial role in Performance Standard 6 of the International Finance Corporation, which seeks to avoid negative impacts on apes and link finance to conservation outcomes. Any area recognized as having priority great ape populations cannot be developed, and conservation organizations should collaborate with other stakeholders to build a consensus on "no-go" areas for development based on factors such as food security and the importance of areas for great ape populations (Ancrenaz et al., 2016). The World Bank and other financing entities also follow such standards, and projects in areas with great apes are acceptable only in exceptional circumstances and require involvement of the International Union for the Conservation of Nature (IUCN) experts.

Planning 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, populations of chimpanzee and Western gorilla are maintained in areas of forest within an oil palm concession in Gabon (Ancrenaz et al., 2016). How such management contexts affect longer term population viability remains poorly understood. 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) (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., 2022).

5.1.1 Yield increases

Increasing the productivity on existing agricultural lands can reduce the need for agricultural expansion (Zhang et al., 2021), but closing yield gaps to achieve food security seems challenging and more land expansion is likely, unless additional local demand is met by imports (van Ittersum et al., 2016). The largest potential production increases relate to fallow duration and multiple cropping rather than single crop yields, and key components of boosting productivity and reducing impacts include the use of early-maturing varieties, intercropping, catch crops, and enhanced irrigation (Poore and Nemecek, 2018). Land expansion rates will especially be high in countries such as Nigeria and Ghana with rapid human population growth, export-driven agricultural production growth, emerging and diversifying food systems, and limited available agricultural land, thus affecting species such as chimpanzee and Western gorilla. Furthermore, as productivity increases so do agricultural land rents, which could create new incentives for agricultural expansion and deforestation (Phelps et al., 2013).

On the other hand, rising agricultural productivity and profits in pre-established agricultural areas could act as magnets for local immigration, drawing them away from vulnerable frontier areas and helping to promote land sparing for nature conservation (Laurance et al., 2009; Laurance et al., 2015). Widespread technology adoption processes that substantially increase agricultural productivity in pre-established agricultural lands could, depending on their effect on the demand for production factors (labour, capital, land), still reduce deforestation, to the extent that increased product supply reduces agricultural market prices (Angelsen and Kaimowitz, 2001). Improved agricultural technologies on pre-cultivated prime agricultural lands could thus help slowing forest conversion, or even abandonment of marginal agricultural lands – including the ones where great apes traditionally compete with agricultural expansion. Globally, this argument has been referred to as the Borlaug hypothesis, related e.g., to the impact of the 20th century Green Revolution on reduced pressures for expanding upland, low-productive agriculture – and has some empirical support (Stevenson et al., 2013). On sub-global scales, the non-expansion and abandonment of marginal agricultural lands is also key to the aforementioned 'forest transition' processes, i.e., of forest cover stabilizing or even increasing at high levels per-capita income (Mather and Needle, 1998; Meyfroidt and Lambin, 2011).

5.1.2 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 forestland 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 increasing, 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). Therefore, new financing models are needed to protect natural ecosystems, and conservation organizations should collaborate with governments and industry partners to build a consensus about "no-go" areas for development based on the presence of priority great ape populations and other high-risk factors.

5.1.3 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). However, the success of conservation efforts is not only about protecting habitats but also ensuring the safety of great apes from hunting, poaching, and diseases such as Ebola (Rizkalla et al., 2007; Strindberg et al., 2018; Sherman et al., 2022). 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 needs to be 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 surviving 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. 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.

It is important to note that simply increasing 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, 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 diseases.

5.1.4 Key stakeholders and jurisdictional approach

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 programmes, 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). 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, 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).

Despite the challenges there is some optimism with ongoing development and improving forest governance reducing forest loss at least in some great ape range areas. More funding needs to be made available for spatial planning and implementation that considers both agricultural development and environmental conservation objectives and steers agricultural expansion away from great ape priority areas. In areas where great apes and people co-exist, higher values of biodiversity and other ecosystem services are needed that can make conservation competitive when compared to agricultural expansion. The fate of great apes is highly symbolic for the global environmental crisis, which calls for the highest government support to make sure the world can both feed its people and maintain our hominid cousins.

5.2 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 avoid negative perceptions regarding apes that are becoming accustomed to human-dominated landscapes (Chua et al., 2020).

5.2.1 Eco-tourism

Eco-tourism has been recognized as 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 obvious. In Borneo, eco-tourism businesses also contribute significantly to the regional GDP (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 eco-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.

5.2.2 Payment for biodiversity

Often the people who live with great apes do not see any economic benefits. As an example, around Bwindi Impenetrable Forest National Park, communities living within 0.5km of the boundaries are significantly poorer than those living further away and are affected by wild crop raiding animals (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; however, it's crucial to ensure that biodiversity conservation isn't overshadowed. To address this concern, a nested approach can be used, where carbon credits are nested within a broader conservation project that includes biodiversity conservation and other ecosystem services (Law et al., 2012). The conservation project can generate carbon credits that can be sold on the carbon market to finance the broader conservation project. 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 offer communities 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 private sector entities with an interest in preserving great apes and their habitats. However, it is crucial to acknowledge that once these compensation schemes are established, they will likely need to remain in place indefinitely.

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. 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).

Finally, interspecies money proposes a system to acquire data on other species and direct significant funds based on their continued existence (Ledgard, 2022). Technological advancements, such as low-cost sensors, drones, eDNA sampling, and artificial intelligence, enable the gathering and interpretation of data in the wild (Ledgard and Kharas, 2022). This allows for the allocation of interspecies money, determined by actual conservation results and verified presence of individual great apes through face recognition. Implementing this novel concept requires rewriting economic rules transparently and accurately, as well as financing and executing pilot projects in the wild to test its validity (Ledgard, 2022).

5.3 Rethinking agriculture and food systems

5.3.1 Modifying global consumption and local agriculture

To address deforestation and protect great apes, it is crucial to understand 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., 2020b). 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). 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. However, such interventions must be approached with caution as they involve changing traditional ways of life.

5.3.2 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. 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. Although a complex undertaking, 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 more sustainable production practices such as those certified under the Roundtable on Sustainable Palm Oil can give consumers a more information choice.

6 Conclusion

Great apes face significant threats from unsustainable agriculture driven by high 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 each individual ape shares its habitat with approximately 100 people. Achieving successful coexistence requires significant incentives and efforts from people to protect and preserve these conservation icons. New financial models are needed to facilitate this coexistence. 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, circular agriculture, 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.

7 Conflict of Interest

The 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.

8 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, CSG, MO, and DS wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version."

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11 Data Availability Statement

The datasets analysed for this study can be found in the [NAME OF REPOSITORY, TBD] [LINK].

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13 Supplementary Material

We estimated the number of people living within great ape range areas by overlaying the GHS population grid multitemporal (1975-2030) data (Schiavina et al., 2022) with the IUCN Red List distribution ranges for the great ape taxa (2022).

To map the dominant crops per grid cells we used the SPAM 2017 v2.1 Sub-Saharan Africa for the Great Ape ranges in Africa and the SPAM 2010 v2.0 Global Data for ranges in Borneo and Sumatra (You et al., 2017). We decided to use the Physical Area values from the SPAM dataset, although other values such as Harvested Area, Production, and Yield are also available. The Physical area is measured in hectares and represents the actual area where a crop is grown, not counting how often production was harvested from it. Physical area is calculated for each production system (e.g., irrigated, rainfed) and crop, and the sum of all physical areas of the four production systems constitute the total physical area for that crop. The sum of the physical areas of all crops in a pixel may not be larger than the pixel size. We used a script developed by Meijaard et al. (2020a) to extract the dominant crop for each grid cells. All spatial analyses were conducted in the Environmental Systems Research Institute (ESRI) ArcGIS 10.8 software environment.

Supplementary Tables

Table S1. Harvested areas of agricultural crops in Central Africa in 2019, and their percentage change between 2010 and 2019 (FAOSTAT, 2021).

Crop	Area harvested in 2021 (ha)	Change between 2010 and 2021
Cassava, fresh	7,535,577	36.7%
Maize (corn)	7,322,685	47.6%
Groundnuts, excluding shelled	2,254,953	-4.0%
Sorghum	2,045,456	-14.7%
Rice	1,942,118	47.2%
Beans, dry	1,704,971	25.0%
Plantains and cooking bananas	1,526,485	54.2%
Millet	1,424,628	-15.7%
Cocoa beans	869,219	18.7%
Seed cotton, unginned	680,492	79.8%
Oil palm fruit	553,457	65.2%
Bananas	513,053	63.6%

Table S2. Harvested areas of agricultural crops in West Africa in 2019, and their percentage change between 2010 and 2019 (FAOSTAT, 2021).

Crop	Area harvested in 2021 (ha)	Change between 2010 and 2021
Sorghum	13,737,918	8.1%
Maize (corn)	13,520,502	52.6%
Cow peas, dry	13,106,130	29.0%
Millet	12,691,978	-20.9%
Cassava, fresh	12,546,809	117.7%
Rice	10,104,389	55.2%
Groundnuts, excluding shelled	9,040,324	34.5%
Yams	8,201,417	87.0%
Cocoa beans	6,922,895	28.4%
Oil palm fruit	5,173,715	21.3%
Cashew nuts, in shell	3,204,429	57.4%
Seed cotton, unginned	3,124,338	98.0%

Okra	1,791,114	247.3%

Table S3. Harvested areas of agricultural crops in Eastern Africa in 2019, and their percentage change between 2010 and 2019 (FAOSTAT, 2021).

Crop	Area harvested in 2021 (ha)	Change between 2010 and 2021
Maize (corn)	17,025,842	12.4%
Beans, dry	6,054,096	24.8%
Sorghum	5,122,364	0.2%
Cassava, fresh	3,739,221	-0.1%
Cereals n.e.c.	3,298,590	16.1%
Rice	3,289,855	11.1%
Groundnuts, excluding shelled	3,103,205	36.1%
Sesame seed	2,348,819	135.7%
Wheat	2,334,855	24.1%
Sweet potatoes	1,983,550	15.6%
Coffee, green	1,886,433	32.0%
Sunflower seed	1,574,202	103.1%

Table S4. Harvested areas of agricultural crops in Southeast Asia in 2019, and their percentage change between 2010 and 2019 (FAOSTAT, 2021).

Crop	Area harvested in 2021 (ha)	Change between 2010 and 2021
Rice	45,086,935	-5.9%
Oil palm fruit	21,155,398	52.9%
Natural rubber in primary forms	9,976,282	38.5%
Maize (corn)	9,166,226	-6.6%
Coconuts, in shell	6,913,482	-2.7%
Cassava, fresh	3,286,048	-2.2%
Beans, dry	3,216,386	-5.8%
Sugar cane	2,868,954	27.1%
Other vegetables, fresh n.e.c.	2,253,388	34.7%
Coffee, green	2,183,649	5.0%

Table S5. Ten largest crops in terms of physical crop area within the ranges of each of the four Chimpanzee subspecies based on SPAM 2017 data (International Food Policy Research Institute, 2020) and the IUCN Red List species ranges (IUCN, 2022). PA = Crop Physical Area

(in hectares); % = Percentage of crop relative to total subspecies range. Sorted by Total % of ranges for each crop. Data from Meijaard et al. (2021).

	Nigeria-Cameroon *P. t. ellioti*		**Western** *P. t. verus*		**Eastern** *P. t. schweinfurthii*		**Central** *P. t. troglodytes*		***All subspecies***
Crops	PA	%	PA	%	PA	%	PA	%	Total crop area
Rice	66,731	0.7	2,957,486	5.4	638,031	0.6	12,037		3,674,285
Cacao	240,845	2.5	1,824,436	3.4	17,043	0.0	288,618	0.4	2,370,942
Cassava	233,129	2.4	448,959	0.8	1,248,391	1.3	346,736	0.5	2,277,215
Maize	109,017	1.1	743,662	1.4	884,190	0.9	52,986	0.1	1,789,855
Plantain	118,544	1.2	253,137	0.5	827,407	0.8	214,711	0.3	1,413,799
Groundnut	22,578	0.2	822,439	1.5	149,315	0.2	54,233	0.1	1,048,565
Oil palm	294,777	3.0	435,654	0.8	148,262	0.2	63,908	0.1	942,601
Vegetables	204,826	2.1	299,785	0.6	133,096	0.1	119,349	0.2	757,056
Other cereals	0	0.0	636,381	1.2	10,427		3,080	0.0	649,888
Beans	58,378	0.5	8,125	0.0	473,522	0.5	14,513	0.0	554,538
total	1,348,825	13.7	8,430,064	15.6	4,529,684	4.6	1,170,171	1.7	

Table S6. Ten largest crops in terms of physical crop area within the ranges of Bonobo, Western and Eastern Gorilla based on SPAM 2017 data (International Food Policy Research Institute 2020) and the IUCN Red List species ranges (IUCN 2022). PA = Crop Physical Area (in hectares); % = Percentage of crop relative to total subspecies range. Sorted by Total % of ranges for each crop. Data from Meijaard et al. (2021).

	Bonobo *Pan paniscus*		**Western Lowland Gorilla** ***G. g. gorilla***		**Cross River Gorilla** **G. g.** ***diehli***		**Grauer's Gorilla** ***G. b. graueri***		**Mountain Gorilla** ***G.b. beringei***	
Crops	PA	%	PA	%	PA	%	PA	%	Total crop area	Total %
Rice	63,692	0.2	3,925	0.0	1,243	0.3	13,532	0.3	2,545	3.2
Cacao	900	0.0	245,282	0.4	3,771	1.0	16	0.0	14	0.0
Cassava	270,995	0.7	284,152	0.4	15,271	4.2	11,481	0.2	3,171	4.0
Oil palm	13,620	0.0	51,516	0.1	6,881	1.9	45	0.0	0	0.0
Maize	131,983	0.3	35,983	0.1	3,011	0.8	25,568	0.5	10,251	13.0
Vegetables	4,505	0.0	111,432	0.2	13,549	3.7	2,985	0.1	1,914	2.4
Plantain	39,594	0.1	209,240	0.3	2,922	0.8	17,956	0.4	7,414	9.4
Yams	2,551	0.0	38,001	0.1	10,470	2.8	204	0.0	80	0.0
Groundnut	22,707	0.1	35,108	0.1	1,590	0.4	675	0.0	556	0.8

Table S7. Eleven largest crops in terms of physical crop area within the ranges of Bornean, Sumatran and Tapanuli Orangutan based on SPAM 2010 data (International Food Policy

Research Institute 2020) and the IUCN Red List species ranges (IUCN 2022). PA = Crop Physical Area (in hectares); % = Percentage of crop relative to total subspecies range. Sorted by Total % of ranges for each crop. Data from Meijaard et al. (2021).

	Bornean Orangutan ***P. pygmaeus***		**Sumatran Orangutan** ***P. abelii***		**Tapanuli Orangutan** ***P. tapanuliensis***		
Crops	**PA**	**%**	**PA**	**%**	**PA**	**%**	**Total crop area**
Oil palm	1,240,878	5.5	100,982	5.6	7,687	7.5	1,349,547
Tree crops	392,588	1.7	83,422	4.6	5,748	5.6	481,758
Rice	231,035	1.0	59,861	3.3	3,647	3.6	294,543
Coconut	118,919	0.5	14,452	0.8	145	0.0	133,516
Vegetables	27,209	0.1	7,105	0.4	1,219	1.2	35,533
Maize	24,854	0.1	61,340	3.4	627	0.6	86,821
Cacao	21,351	0.1	31,072	1.7	686	0.7	53,109
Other oil crops	20,286	0.1					20,286
Tropical fruit	17,283	0.1					17,283
Coffee			59,792	3.3	1,779	1.7	61,571
Totals	2,094,403	9.2	418,026	23.1	21,538	20.9	2,533,967

Table S8. Food system archetypes and their typical characteristics (after van Berkum and Ruben, 2021)

Food system archetypes	**Description**
Rural and traditional	Farming mainly done by smallholders, with low agricultural yields and limited diversity. Scarce infrastructure results in seasonal variation and large food losses. Most food is sold locally in informal open market, small shops and street vendors.
Informal and expanding	Rising incomes, formal employment and urbanization, with demand for processed and packaged foods from locally-sourced and imported ingredients. Coexistence of informal markets (fresh food) and supermarkets (convenience foods) but limited quality standards and no regulation.
Emerging and diversifying	Increasing number of medium- and large-scale commercial farms linked to markets. Modern supply chains for fresh foods, and supermarkets expansion to smaller towns. Processed foods are common in urban and many rural areas, but fresh food continues to be acquired through informal markets.
Modernizing and formalizing	Higher agricultural productivity and larger farms that rely on mechanization and input-intensive practices. More sophisticated food infrastructures result in fewer food losses. Food imports enable year-round availability of diverse basket of foods. Public safety and quality regulation is common.
Industrialized and consolidated	Large-scale, input-intensive farms serve specialized markets. Supermarket density is high and formal food sector captures nearly all of the food intake, including fresh foods, fast food and home delivery. Food policies focus on banning trans fats and the reformulation of processed foods.