Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

The challenging coexistence of forest elephants *Loxodonta cyclotis* and timber concessions in central Africa

Morgane SCALBERT* *Université de Liège – Gembloux Agro-Bio Tech, Forest is Life, Terra Teaching and Research Centre, Passage des Déportés 2, B-5030, Gembloux, Belgium. Email: morgane.scalbert@gmail.com*
Cédric VERMEULEN *Université de Liège – Gembloux Agro-Bio Tech, Forest is Life, Terra Teaching and Research Centre, Passage des Déportés 2, B-5030 Gembloux, Belgium. Email: cvermeulen@uliege.be*
Thomas BREUER *World Wide Fund for Nature Germany, Reinhardstr. 18, 10117, Berlin, Germany. Email: thomas.breuer@wwf.de*
Jean-Louis DOUCET *Université de Liège – Gembloux Agro-Bio Tech, Forest is Life, Terra Teaching and Research Centre, Passage des Déportés 2, B-5030, Gembloux, Belgium. Email: jldoucet@uliege.be*

Keywords
bark stripping, central Africa, forest elephant *Loxodonta cyclotis*, habitat use, seed dispersal, selective logging, timber species

*Correspondence

Received: 21 October 2021
Accepted: 18 July 2022
Editor: DR

doi: 10.1111/mam.12305

ABSTRACT

1. With a drastic decrease in their populations over the last decades, forest elephants *Loxodonta cyclotis* are facing increasing human pressure. Their decline will have serious ecological consequences, as they are key actors in shaping ecosystems. Whilst timber concessions host many mammal species, the interactions between selective logging and forest elephants remain unclear.
2. Through an extensive literature review, we discussed the following: 1) the ecological and human factors that drive the distribution of forest elephants on a large scale as well as in the specific context of logged forests; 2) the contribution of forest elephants to the regeneration of timber species; and 3) the damage caused by forest elephants to timber species.
3. Although human activities have the greatest impact on forest elephant distribution, it is the availability of food, water, and minerals that locally determines their use of the habitat. Under specific conditions, timber concessions may host large populations of forest elephants.
4. As effective seed dispersers, forest elephants contribute to the regeneration of at least 41 timber species, such as *Bobgunnia fistuloides* (pao rosa), one of the most expensive woods on the market.
5. Damage caused by forest elephants is diverse and affects a wide range of species. From branch breaking to bark stripping, at least 61 timber species are used by forest elephants, and little is known about the consequences for the tree's vitality and wood quality.
6. The interactions between forest elephants and logging are complex and involve many variables, requiring additional research. Nevertheless, this review suggests that timber concessions constitute key areas for forest elephant conservation, provided that low-impact logging and wildlife management are implemented.

Mots-clés
Afrique centrale, dispersion des graines, écorcement, éléphant de forêt *Loxodonta cyclotis*, essences de bois d'oeuvre, exploitation forestière sélective, utilisation de l'habitat

RÉSUMÉ EN FRANÇAIS

1. Avec une diminution drastique de leurs populations au cours des dernières décennies, les éléphants de forêt *Loxodonta cyclotis* font face à une pression humaine croissante. Jouant un rôle clé dans le façonnement des écosystèmes,

leur déclin aura d'importantes conséquences écologiques. Alors que les concessions forestières abritent de nombreuses espèces de mammifères, les interactions entre l'exploitation sélective du bois d'œuvre et les éléphants de forêt restent floues.

2. Par une revue approfondie de la littérature, nous avons examiné: 1) les facteurs écologiques et humains qui déterminent la distribution des éléphants de forêt à grande échelle ainsi que dans le contexte spécifique des forêts exploitées; 2) la contribution des éléphants de forêt à la régénération des espèces de bois de d'œuvre; et 3) les dommages causés par les éléphants de forêt aux espèces de bois d'œuvre.
3. Bien que les activités humaines soient le facteur le plus important dans la répartition géographique des éléphants de forêt, c'est la disponibilité en nourriture, en eau et en minéraux qui conditionne localement leur utilisation de l'habitat. Dans certaines conditions, les concessions forestières peuvent abriter de grandes populations d'éléphants de forêt.
4. En tant qu'important disperseur de graines, les éléphants de forêt contribuent à la régénération d'au moins 41 espèces de bois d'œuvre, telles que *Bobgunnia fistuloides* (pao rosa), l'un des bois les plus chers du marché.
5. Les dommages causés par les éléphants de forêt sont divers et touchent un large éventail d'espèces. Du cassage des branches à l'écorçage des arbres, au moins 61 espèces de bois d'œuvre sont concernées, et peu de choses sont connues quant aux conséquences sur la vitalité de l'arbre et la qualité du bois.
6. Les interactions entre les éléphants de forêt et l'exploitation forestière sont complexes et font intervenir de nombreuses variables, ce qui nécessite des recherches supplémentaires. Néanmoins, cette revue de la littérature suggère que les concessions forestières constituent des zones clés pour la conservation des éléphants de forêt, à condition qu'une exploitation à faible impact et une gestion de la faune soient mises en œuvre.

INTRODUCTION

Defaunation is at its highest level since the beginning of the Anthropocene (Dirzo et al. 2014, Young et al. 2016). Human impact has led to a significant loss of animals, especially large species in the Tropics (Dirzo et al. 2014). Iconic examples of dramatically declining species are the African savannah elephant *Loxodonta africana* and the African forest elephant *Loxodonta cyclotis* (Maisels et al. 2013, Chase et al. 2016). The forest elephant has been subject to the greatest loss (Maisels et al. 2013, Poulsen et al. 2017), with a decline of more than 80% of its population over the last four decades, leading to its International Union for Conservation of Nature Red List classification as Critically Endangered (Gobush et al. 2021). Coupled with fragmentation and habitat loss driven by the human population growth and infrastructure development, poaching for ivory is still the main threat to forest elephant persistence, even in areas where protection efforts are high (Gobush et al. 2021). These persistent threats make the future of forest elephants very uncertain.

Forest elephants interact closely with their environment, and the ecological implications are far reaching. Regularly referred to ecosystem engineers, forest elephants have the capacity to shape the composition and structure of Tropical ecosystems because of their enormous dietary requirements and the impact of their body size (e.g. via trampling damage; Terborgh et al. 2015, Rosin et al. 2017). Forest elephants induce a reduction in stem density, resulting in reduced competition amongst trees and the development of larger trees with higher wood density, positively impacting carbon sequestration (Berzaghi et al. 2019, Maicher et al. 2020). They also preserve the forest richness and diversity by dispersing the seeds of many species (Campos-Arceiz & Blake 2011). Forest elephants maintain nutrient cycles (Wolf et al. 2013), keep forest clearings open (Turkalo & Fay 1995), and their water-filled footprints provide habitat for aquatic macro-invertebrates (Remmers et al. 2017). Finally, their repeated movements create a vast network of trails that criss-cross the undergrowth. Through repeated passage of the forest elephants, these trails can be up to three metres wide (Vanleeuwe & Gautier-Hion 1998), particularly when they converge towards focal spots such as fruit trees and bais (natural forest clearings rich in minerals; Blake & Inkamba-Nkulu 2004).

As was previously observed with the reduction and subsequent extinction of other megaherbivores (Corlett 2013), a continuing decline of populations of forest elephants may have important negative ecological consequences (Poulsen et al. 2018). The associated reduced herbivory pressure greatly impacts vegetation (Corlett 2013). It also affects nutrient cycling, the behaviour of cohabiting species (Young et al. 2016), and other ecological processes (e.g. reduced seed dispersal of species with large fruits, resulting in higher density-dependant mortality and decreased genetic variability; Corlett 2013).

Whilst large forest elephant populations have been observed in protected areas (Turkalo et al. 2013, Breuer et al. 2021), recent studies also highlight the persistence of some important populations outside these areas (Laguardia et al. 2021, Wall et al. 2021), notably in logged forests (Clark et al. 2009, Stokes et al. 2010, Maisels et al. 2013, Fonteyn et al. 2020). Logged forests constitute 54 million hectares, corresponding to 27% of the central African rainforest area (Eba'a Atyi et al. 2022). This is twice the size of the protected areas, which cover 27 million hectares (Eba'a Atyi et al. 2022). According to several authors, timber concessions have a high conservation potential, playing a buffer role around the existing network of protected areas, if illegal activities are strictly controlled and sustainable management plans are properly implemented (Clark et al. 2009, Stokes et al. 2010, Putz et al. 2012).

Timber exploitation is a major economic sector in central Africa, requiring large areas. This industry is still expanding. For example, in Gabon, more than two-thirds of the forest area falls within commercial logging concessions, corresponding to nearly 60% of the country's area (Conseil National Climat Gabonais 2020). Many studies have highlighted the impacts of logging on birds, mammals, and other vertebrates (Dranzoa 1998, Haurez et al. 2016, Omeja et al. 2016). Whilst some species are negatively affected by logging operations, others can actually benefit (Poulsen et al. 2011, Haurez et al. 2016). However, the impacts of logging on forest elephants are not yet clearly established. Given their extent, timber concessions could be a major actor in forest elephant conservation, but it is still necessary to understand more clearly the impacts of logging on forest elephants, and, conversely, the impacts of forest elephants on timber resources, as elephants affect vegetation structure and composition strongly (Terborgh et al. 2015).

In this paper, we aim to synthesise the existing knowledge on the interactions between selective logging and forest elephants, by: 1) describing the ecological and human factors that drive the distribution of forest elephants on a large scale, as well as in the specific context of logged forests; 2) outlining the role of forest elephants in the regeneration of timber species; and 3) characterising the damage caused by forest elephants to timber species. Finally, the contribution of timber concessions to the conservation of forest elephants and further research prospects are discussed.

METHODS

We conducted a literature search on the search engines Scopus and Google Scholar using the following keywords and their combinations, in both English and French: 'elephant', '*Loxodonta cyclotis*', 'forest', 'habitat', 'abundance', 'distribution', 'movement', 'logging', 'timber', 'seed dispersal', 'seed predation', 'herbivory', 'damage' and 'bark stripping'. Peer-reviewed publications were preferred, but MSc and PhD theses, as well as reports from the 'grey literature', were also included. No date limit was imposed. The selection of articles was first based on their title and then on their abstract. A paper was considered relevant if it addressed one of the objectives of our review, either by being directly related to the forest elephant or by being about an ecological process covered in this paper (seed dispersal or predation, herbivory damage etc.). Once we finished scanning Scopus and Google Scholar in December 2019, we created email alerts on these search engines using the same keywords to be notified of newly published articles. We also obtained information from the literature cited in the selected papers and from the articles referencing these papers. Given the limited documentation on forest elephants, some additional useful references on savannah elephants were added.

RESULTS AND DISCUSSION

Drivers of forest elephant distribution and abundance

Anthropogenic impact is the main driver of the current distribution of forest elephants (Wall et al. 2021). Since humans have been shaping the African rainforest for thousands of years (Oslisly et al. 2013), they have also been impacting forest elephant distribution and abundance. Since the onset of the ivory trade during colonial times, millions of forest elephants have been hunted for their tusks (Poulsen et al. 2018), leading to extremely low densities and occasionally even to local extinction, particularly in the Democratic Republic of Congo. In the former French colonies, people living in the rainforest have been resettled (Morin-rivat et al. 2017), leaving large tracts of rainforest free from human impact, such as seen in northern Congo, Gabon, and south-eastern Cameroon, where many protected areas have been established. Thus, it is not surprising that these landscapes sustain the highest forest elephant densities (Blake et al. 2007), or that this is where most of our current knowledge of ecological factors shaping forest elephant abundance has been revealed.

ECOLOGICAL FACTORS

Forest elephants generally live and travel in small family units or range on their own (Morgan & Lee 2007, Fishlock et al. 2008, Fishlock & Lee 2013, Turkalo et al. 2013), but Beirne et al. (2021) noted that the individual behaviours of forest elephants are very diverse and therefore difficult to predict, highlighting the need for further research.

The few studies that have investigated habitat use and movements of forest elephants showed an increase in range and travel distances with changes in water availability (Beirne et al. 2021, Wall et al. 2021), and a strong habitat selectivity with seasonal and daily variations (Morgan & Lee 2007, Mills et al. 2018, Beirne et al. 2021) particularly related to fruit availability (Short 1983, White 1994, Morgan 2009).

More abundant and wider tracks, indicating repeated passage, around areas with high concentrations of mineral deposits suggest that forest elephants are attracted to them (Blake & Inkamba-Nkulu 2004). Indeed, forest elephants are often found in abundance around bais (Clark et al. 2009, Stokes et al. 2010, Breuer et al. 2021). In certified logging concessions, such areas are therefore generally included in the conservation series (Daïnou et al. 2016, Haurez et al. 2020).

Topography also influences the behaviour of forest elephants: although they access almost all areas, they tend to avoid very steep slopes (Terborgh et al. 2015, Ngama et al. 2019, Wall et al. 2021).

ANTHROPOGENIC FACTORS

Poaching, habitat loss, and fragmentation are the greatest threats to the forest elephant (Gobush et al. 2021). Human population growth coupled with industrial development has led to the expansion of the road network, which is one of the most significant human impacts on landscapes and wildlife behaviour (Blake et al. 2008, Schuttler et al. 2012, Vanthomme et al. 2013, Kleinschroth et al. 2019). Although roads facilitate the movement of elephants, they also ease access to areas that were previously unreachable for poachers. Associated with greater hunting pressure in their surroundings (Laurance et al. 2006, Blake et al. 2007, Van Vliet & Nasi 2008), active roads are generally avoided by forest elephants (Barnes et al. 1991, Blom et al. 2005, Blake et al. 2008, Maisels et al. 2013). However, roads with restricted and controlled access are less detrimental to wildlife because the threat is lower and hunting is limited (Laurance et al. 2006, Vanthomme et al. 2013, Mills et al. 2018). Furthermore, secondary forests, prized by forest elephants for the abundance of forage they provide, grow along the roads (Barnes et al. 1997).

Generally, forest elephants do not approach human settlements, in order to avoid risky confrontations (Barnes et al. 1991, Blom et al. 2005), but they may do so when they feel safe, potentially increasing human–elephant conflict (e.g. by crop raiding, consumption of fruit trees planted by humans; Nsonsi et al. 2017, Mills et al. 2018, Beirne et al. 2019, Ngama et al. 2019).

IMPACT OF TIMBER EXTRACTION

Logging in central Africa is very selective. Only trees of high economic value are harvested, with 0.7–2 stems cut per hectare (Ruiz Pérez et al. 2005). Logging is organised in felling cycles, meaning that the same part of the forest can only be logged every 25–30 years, depending on the country (Fargeot et al. 2004). Certified timber companies are subject to numerous regulations, in terms of legality, environmental protection, and socio-economic development (Lescuyer et al. 2021). For instance, timber companies must produce a management plan, respect minimum cutting diameters that are site- and species-specific, define conservation areas where no logging is allowed, and implement reduced-impact logging techniques (Bayol & Borie 2004, Ruiz Pérez et al. 2005).

Although standards exist to limit the environmental impact of logging, it is self-evident that this industry introduces in its surroundings landscape fragmentation, human settlements, and poaching, factors that are known to impact the presence of forest elephants. Indeed, logging requires the development of numerous infrastructures and the opening of hundreds of kilometres of roads within the forest. It also induces an increase in the human population in the vicinity. Moreover, the removal of fruit trees could have long-term impact on forest elephants (Blake 2002, Bush et al. 2020). We might therefore assume that they would move away from logged areas, but this has not been verified by the few studies that addressed the question

(Merz 1981, Struhsaker et al. 1996, Clark et al. 2009, Stokes et al. 2010, Poulsen et al. 2011, Omeja et al. 2014).

In the northern Republic of Congo, Poulsen et al. (2011) and Clark et al. (2009) found higher forest elephant abundance in logged than in unlogged areas. The number of individuals increased during 15 years after logging and then returned to a lower abundance, similar to that straight after logging and still higher than in the nearby unlogged forests (Clark et al. 2009). The results of Stokes et al. (2010) are not as conclusive, with some logged forests hosting higher and some lower forest elephant densities than the surrounding protected area. In Kibale National Park in western Uganda, where logging ended in 1969, elephant dung and trail surveys conducted in 1996, 2005, 2008, and 2014 consistently recorded higher elephant abundance in the heavily logged area of the park than in the lightly logged and unlogged areas (Struhsaker et al. 1996, Omeja et al. 2016). Finally, in Tai National Park (Ivory Coast), a study conducted two years after the cessation of timber extraction showed that forest elephants used secondary forest resources more intensively than primary forest, but the combination of the two habitats was essential (Merz 1981).

Three complementary hypotheses are put forward by the authors to explain the high abundance of forest elephants in logged areas. First, light conditions and the micro-climate resulting from gaps in the canopy favour the development of light-demanding herbaceous and shrub species particularly appreciated by forest elephants (Merz 1981, Struhsaker et al. 1996, Stokes et al. 2010, Poulsen et al. 2011, Omeja et al. 2014). Moreover, there are more young trees in secondary forests than in undisturbed forests, so forest elephants can easily access the leaves by breaking branches or knocking down the tree (Merz 1981). Second, the presence of villages close to logged areas could attract forest elephants that raid crops (Clark et al. 2009, Poulsen et al. 2011). Finally, law enforcement efforts to protect wildlife in some concessions directly benefit forest elephants in the areas under surveillance (Poulsen et al. 2011).

Other studies conducted in timber concessions have explored the influence of logging roads and noise disturbance on forest elephants. However, these studies are too sparse to draw general conclusions. Old logging roads facilitate wildlife movement and provide abundant forage due to vegetation that recovers about four years after logging (Kleinschroth & Healey 2017). Van Vliet and Nasi (2008) found that logging roads have no effect on the distribution of forest elephants, whilst other researchers showed negative impact (Clark et al. 2009, Stokes et al. 2010, Maisels et al. 2013), suggesting potentially confounding effects of other variables such as poaching pressure (Blake et al. 2007) and distance to settlements (Lhoest et al. 2020). Furthermore, the road network within a forest concession consists of different types of roads, and additional research is still needed to clarify their potential impacts, especially impacts associated with old roads and skid trails (i.e. temporary paths used to extract the logs from the place where the trees were cut) that are less studied.

Very limited information is available on the response of forest elephants to noise disturbance. A study in Gabon showed that the frequencies of sounds from logging overlap with the frequencies of forest elephant rumbles, potentially compromising communication between individuals (Wrege et al. 2017). Acoustic surveys suggest that forest elephants are more active at night than during the day, in places where they are exposed to human disturbance (Wrege et al. 2010, 2012). Research on changes in forest elephant behaviour caused by logging is rare but would provide essential insights into the short-term impact of logging on the ecology of this iconic species.

Forest elephant-mediated seed dispersal

BENEFITS OF FOREST ELEPHANT-MEDIATED SEED DISPERSAL

Numerous studies have demonstrated the dispersal potential of forest elephants for many Tropical plant species (Blake 2002, Nchanji & Plumptre 2003, Beirne et al. 2020). Through the large amount of fruits they consume and the long distances forest elephants are able to travel, they contribute strongly to the dissemination of endozoochorous species (Poulsen et al. 2018). Campos-Arceiz and Blake (2011) compiled the results of existing studies and identified 335 plant species occurring in the faeces of African savannah and forest elephants. For plants, multiple benefits result from forest elephant-mediated seed dispersal, including less competition between seeds, reduced germination time, faster growth, and better development conditions (Poulsen et al. 2018). Nonetheless, the ingestion of a fruit by the forest elephant does not systematically lead to the dispersal of its seed. It may have been crushed or destroyed during the digestion process, in which case, the forest elephant is actually acting as a predator (Morgan & Lee 2007).

Although forest elephants are very effective dispersers, the fate of a seed does not exclusively depend on the quality of the primary dispersion. The local conditions of the environment where the seed is dropped and the subsequent secondary processes are fundamental to the survival of the disseminated seeds and the establishment of seedlings (Balcomb & Chapman 2003). A seed can be predated in a faeces by granivores such as bushpigs *Potamochoerus porcus* and sitatungas *Tragelaphus spekii* as observed by Magliocca et al. (2003), or be dispersed elsewhere by a secondary agent (Vander Wall et al. 2005, Theuerkauf et al. 2009, Midgley et al. 2012). Studies regarding secondary processes are less common than those on primary dispersion. However, it is essential to quantify these processes to establish the most reliable predictions of the evolution of Tropical tree communities (Granados et al. 2017).

DISPERSAL OF VALUABLE TIMBER SPECIES

From 27 studies on seeds found in elephant dung in African forests, we listed the African rainforest timber species dispersed by the forest elephant: 18 main timber species were identified (Table 1; ATIBT 2016). Twenty-three additional lesser-known timber species, which are not very widely marketed but whose wood has interesting properties (Gérard et al. 2016), are listed in Appendix S1. Considering Table 1 and Appendix S1, the genera most frequently found in forest elephant dung are *Parinari*, *Klainedoxa*, *Antrocaryon*, *Tieghemella*, *Detarium*, *Bobgunnia*, and *Chrysophyllum*. They do not represent high volumes exploited (FRMi 2018), but *Bobgunnia fistuloides* is one of the most expensive species on the market (ITTO 2019).

The forest elephant's ability to swallow very large seeds makes it an unequalled disperser (Feer 1995a). Indeed, the large size of some seeds prevents them from being swallowed by other animals such as duikers (Cephalophinae) or great apes (Hominidae; Tutin et al. 1991, Feer 1995b). Of the species that are thought to depend exclusively on forest elephants for their dispersal, four are commercial: *Autranella congolensis*, *Detarium macrocarpum*, *Klainedoxa gabonensis*, and *Mammea africana* (Campos-Arceiz & Blake 2011). The decline of forest elephant populations could jeopardise the regeneration of these species, as most of them would not be able to recruit sufficiently, as demonstrated by Beaune et al. (2013) in a Congolese forest, without forest elephants.

IMPACT OF LOGGING ON SEED DISPERSAL

Logging can disrupt seed dispersal processes by affecting disperser populations or by modifying their habitat use. A meta-analysis conducted by Markl et al. (2012) clarified the effects of fragmentation and logging coupled with hunting on the different components of the dispersal process. On average, logging and hunting have a negative impact on visitation rates, seed removal, and dispersal distance (Markl et al. 2012). These results are based on the hypothesis that frugivorous communities are strongly reduced in forests where logging decreases the number of fruit trees (Blake 2002), although this is not systematic, and where hunting is not regulated. It is very complex to distinguish the impacts of logging and hunting because these processes often act synergistically (Poulsen et al. 2011). Poulsen et al. (2013) and Nuñez et al. (2018) have also shown that dispersal distances are impacted by logging activities but not in a single direction: they increase or decrease, depending on the tree species and its mode of dispersal. Despite the existence of numerous studies, the general impact of logging on dispersal processes remains uncertain. It seems to vary according to the tree species and the dispersers on which they depend, as well as the intensity of hunting and logging.

The directed-dispersal hypothesis formulated by Howe and Smallwood (1982) suggests that some seeds dispersed by animals are deposited in locations propitious to their development. This has been verified for interactions with several dispersal agents, including the western lowland gorilla *Gorilla gorilla gorilla*, which prefers nesting in open areas and is known to play an important role in the dispersal of many tree species (Haurez et al. 2016). Selective logging does not seem to impact the efficiency of seed dispersal by this primate, which continues to nest in open areas, including forest zones opened by logging activities such as logging roads, skid trails, and felling gaps (Haurez et al. 2016). To our knowledge, no study has specifically looked at the use by forest elephants of these areas modified by logging, or at the impact of logging on forest elephant-mediated seed dispersal. However, it is evident that forest elephants travel a lot on the skid trails (Stiernon 2022), which may result in directed-dispersal processes. This could have long-term effects that are presently unknown, including on the distribution of megafaunal fruit species. As the forest elephant is reported to be one of the most effective seed dispersers in Tropical forests, further research is needed to assess the impact of logging on its dispersal activities.

As with seed dispersal, logging can impact secondary processes. In Malaysia, Granados et al. (2017) demonstrated that seed predation is higher in logged than in unlogged forests. In Mexico, logging activities affect the scatter-hoarder animal communities, resulting in declines in the quality and quantity of dispersion by those agents (Gutiérrez-Granados 2011). These findings underline the need to study seed predation and secondary seed dispersal in central Africa, especially in timber concessions where logging seems to positively affect rodents and negatively affect dung beetle communities (Laurance et al. 2006, Lhoest et al. 2020).

Table 1. Timber species found as seeds in the droppings of forest elephants *Loxodonta cyclotis*. Frequency is the percentage (mean calculated from the references in bold, with range in parentheses) of droppings containing seeds of the species. Harvested volume is the volume harvested in the Congo Basin, excluding Equatorial Guinea (source: FRMi 2018). Price is the commercial value (free on board) of exported logs (source: ITTO 2019, 2022). Species sold under the same commercial name are assigned the same volume and price

Botanical name of timber species	Commercial name	Frequency mean % (range)	Harvested volume, m^3 $year^{-1}$	Price, € m^{-3}	References
Anacardiaceae					
Antrocaryon klaineanum	Onzabili	3.6 (1.1–5.6)	15	No data	Gautier-Hion et al. (1985), White et al. (1993), **Feer (1995a), Blake (2002), Beirne et al. (2020)**
Antrocaryon micraster	Onzabili	15.1 (2–37)	15	No data	Alexandre (1978), **Short (1981), Nchanji and Plumptre (2003)**
Antrocaryon nannanii	Onzabili	3.6 (2.8–4.3)	15	No data	**Feer (1995a), Yumoto et al. (1995)**
Burseraceae					
Dacryodes buettneri	Ozigo	0.1	0	No data	**Beirne et al. (2020)**
Dacryodes normandii	Ossabel	0.5 (0.2–0.9)	No data	No data	Gautier-Hion et al. (1985), White et al. (1993), **Feer (1995a), Beirne et al. (2020)**
Fabaceae					
Afzelia bipindensis	Doussié	9	17853	No data	**Tchamba and Seme (1993)**
Bobgunnia fistuloides	Pao rosa	10.7 (1–18)	3795	400–430	Alexandre (1978), **Short (1981), White et al. (1993), Feer (1995a), Blake (2002)**, Mbété et al. (2010), **Beirne et al. (2020)**
Moraceae					
Milicia excelsa	Iroko	Frequent	160026	300	Short (1981), **Theuerkauf et al. (2000)**
Milicia regia	Iroko	Frequent	160026	300	**Theuerkauf et al. (2000)**
Myristicaceae					
Staudtia kamerunensis	Niové	0.8	4396	160	**Nchanji and Plumptre (2003)**
Rubiaceae					
Nauclea diderrichii	Bilinga	No data	18633	275	White et al. (1993)
Nauclea sp.	Bilinga	No data	18633	275	Morgan and Lee (2007)
Sapotaceae					
Autranella congolensis	Mukulungu	3 (0.1–7)	81161	No data	**Yumoto et al. (1995), Blake (2002)**, Inogwabini et al. (2011), **Beirne et al. (2020)**
Baillonella toxisperma	Moabi	1.5 (0.3–2.8)	9887	280	White et al. (1993), **Feer (1995a)**, Debroux (1998), **Nchanji and Plumptre (2003)**, Morgan and Lee (2007)
Chrysophyllum africanum	Longhi blanc	2.3 (2.1–2.5)	393	No data	White et al. (1993), **Yumoto et al. (1995), Nchanji and Plumptre (2003)**
Chrysophyllum lacourtianum	Longhi rouge	10.8 (0.7–21.1)	916	No data	Gautier-Hion et al. (1985), **Feer (1995a), Yumoto et al. (1995)**, Debroux (1998), **Blake (2002)**, Inogwabini et al. (2011)
Tieghemella africana	Douka	No data	4747	No data	White et al. (1993), Morgan and Lee (2007)
Tieghemella heckelii	Makoré	11 (10–12)	0	560 (sawnwood)	Alexandre (1978), Merz (1981), **Short (1981), Tchamba and Seme (1993)**, Theuerkauf et al. (2000)

Table 2. Timber species damaged by forest elephants *Loxodonta cyclotis*. All species listed are used by forest elephants. When the type of damage is mentioned in a reference, it is indicated by a cross in the corresponding column; uprooting was not reported for these species, but see Appendix S2. Harvested volume is the volume harvested in the Congo Basin, excluding Equatorial Guinea (source: FRMi 2018, Ngoya-Kessy 2020). Price is the commercial value (free on board) of exported logs (source: ITTO 2022). Species sold under the same commercial name are assigned the same volume and price

Botanical name of timber species	Commercial name	Branch breaking	Bark stripping	Harvested volume, m^3 $year^{-1}$	Price, € m^{-3}	References
Anacardiaceae						
Antrocaryon klaineanum	Onzabili		×	15	No data	White et al. (1993)
Antrocaryon micraster	Onzabili		×	15	No data	Blake (2002)
Combretaceae						
Terminalia ivorensis	Framiré		×	No data	No data	Short (1981), Theuerkauf et al. (2000)
Terminalia superba	Limba		×	122537	No data	Tchamba and Seme (1993), Theuerkauf et al. (2000)
Fabaceae						
Afzelia bipindensis	Doussié		×	17853	No data	Tchamba and Seme (1993)
Afzlia sp.	Doussié		×	17853	No data	White et al. (1993)
Cylicodiscus gabunensis	Okan		×	261929	230	Short (1981), White et al. (1993)
Guibourtia ehie	Ovengkol		×	2018[1]	No data	Short (1981), Theuerkauf et al. (2000)
Piptadeniastrum africanum	Dabéma	×	×	85103	No data	Wing and Buss (1970), White et al. (1993), Theuerkauf et al. (2000)
Prioria oxyphylla	Tchitola		×	5684	No data	Blake (2002)
Sindoropsis letestui	Ghéombi		×	0	No data	White et al. (1993)
Malvaceae						
Nesogordonia papaverifera	Kotibé		×	45	No data	Short (1981)
Nesogordonia sp.	Kotibé		×	45	No data	Blake (2002)
Triplochiton scleroxylon	Ayous		×	803548	250	Blake (2002)
Meliaceae						
Entandrophragma angolense	Tiama	×	×	21852	No data	Wing and Buss (1970), Short (1981), Tchamba and Seme (1993), Theuerkauf et al. (2000), Blake (2002)
Entandrophragma cylindricum	Sapelli	×		1148634	260	Wing and Buss (1970)
Entandrophragma sp.		×		NA	NA	Wing and Buss (1970)
Entandrophragma utile	Sipo		×	83948	260	Short (1981), Tchamba and Seme (1993), Blake (2002)
Khaya anthotheca	Acajou d'Afrique (African mahogany)		×	16815	265	Theuerkauf et al. (2000)
Khaya grandifoliola	Acajou d'Afrique (African mahogany)		×	0	265	Theuerkauf et al. (2000)
Khaya ivorensis	Acajou d'Afrique (African mahogany)		×	21646	265	Theuerkauf et al. (2000)
Moraceae						
Milicia excelsa	Iroko		×	160026	300	Sheil and Salim (2004)
Ochnaceae						
Lophira alata	Azobé			286084	275	Cardoso et al. (2019)
Sapotaceae						
Aningeria altissima	Aniégré	×	×	3364	No data	Wing and Buss (1970), Struhsaker et al. (1996)
Autranella congolensis	Mukulungu		×	81161	No data	Blake (2002)
Baillonella toxisperma	Moabi		×	9887	280	White et al. (1993)
Chrysophyllum lacourtianum	Longhi rouge		×	916	No data	Blake (2002)
Tieghemella heckelii	Makoré		×	0	560 (sawnwood)	Short (1981), Theuerkauf et al. (2000)

[1]Exported log volumes in 2018 from the Republic of Congo only.

Damage to trees and tree regeneration by forest elephants

DIFFERENT TYPES OF DAMAGE BY FOREST ELEPHANTS

Although forest elephants help the regeneration of many tree species, their feeding behaviour and large size also cause serious damage to the vegetation. They trample seedlings (Short 1981, Piiroinen et al. 2017, Rosin et al. 2020), snap saplings (Omeja et al. 2014, Terborgh et al. 2015), break branches (Wing & Buss 1970), uproot trees, and strip their bark (Wing & Buss 1970, Blake 2002). Besides fruits and grass, terminal twigs, leaves, and bark are dominant in the forest elephant's diet. Although forest elephants feed on hundreds of tree and liana species, a relatively low number of them constitute the majority of their diet (Merz 1981, Blake 2002). By browsing on small trees and debarking larger ones, forest elephants shape landscapes (Rosin et al. 2020), both in the interior and at the edge of forests (Cardoso et al. 2019). For instance, a study conducted in Mount Cameroon showed reduced tree diversity and shorter trees, but with larger diameter at breast height, in areas disturbed by forest elephants (Maicher et al. 2020).

In the central African forests, the damage caused by forest elephants to the vegetation is poorly documented compared with their role as seed dispersers (Poulsen et al. 2018). Yet, depending on the forest elephant density, the impact of megaherbivory damage on the structure and composition of vegetation can be greater than that of seed dispersal (Omeja et al. 2016). According to Clark et al. (2012), it could even be stronger than the effect of well-known ecological mechanisms such as density-dependent mortality or niche partitioning.

We found 13 studies that have listed tree species damaged by forest elephants in African rainforests. Based on them, we listed 28 important timber species (Table 2) and 33 lesser-known timber species (Appendix S2) used by forest elephants. Most studies were focussed on bark-stripping damage.

BARK STRIPPING

Bark stripping by African elephants has been widely studied in savannahs (Guldemond et al. 2017) where the mortality rate of debarked trees is particularly high (Löyttyniemi & Mikkola 1980, O'Connor 2017). Numerous studies have investigated the factors influencing debarking rates in arid environments (Gadd 2002, Fullman & Child 2013, Seloana et al. 2018).

Such research is less common in rainforests, where, however, debarking is also observed (Poulsen et al. 2018). In some forests, barks are even more important than fruits in the forest elephant's diet (White et al. 1993). Forest elephants have a preference for soft and fibrous bark (Blake 2002). They tend to debark large trees (Blake 2002, Cardoso et al. 2019) and sometimes spit out bark fragments (Short 1981). Table 3 and Appendix S3 list the frequency and severity of debarking on 24 timber tree species and 31 lesser-known timber species, respectively. For the same species, the impacts are very variable from one site to another. Depending on the area, forest elephants appear to be more or less selective about the species they debark. In Bia National Park (Ghana), 20 tree species, and in the Santchou Reserve (Cameroon), eight tree species are debarked (Short 1981, Tchamba & Seme 1993). By contrast, White et al. (1993) and Blake (2002) identified 85 and 121 debarked tree species at Lopé National Park (Gabon) and in the Ndoki Forest (Congo), respectively. Differences in available tree species and forest elephant needs may partially explain this difference (Short 1981). There are also intraspecific differences, with identical species debarked in some places and not damaged or less so in others (Morgan 2007), as observed in Table 3 and Appendix S3. The variation is probably due to environmental variations that affect the composition of the bark, making it more or less palatable to forest elephants (Short 1981, White et al. 1993), or to the presence and abundance of alternative food sources.

Some tree species are more affected by debarking than others, probably because of the structure of the bark and the compounds it contains, as it has been shown in savannahs (Ihwagi et al. 2012). Ngama (2018) has demonstrated that parasitised forest elephants feed preferentially on the leaves of banana *Musa* spp. and papaya *Carica papaya* trees, whose medicinal properties are known and used by local human communities. This suggests that the forest elephant selects its food not only for its nutritional value, but also for its medicinal properties (Ngama 2018). To our knowledge, no studies to date have investigated the bark composition of trees damaged by forest elephants. Such studies could, however, have important implications in the medical field, as shown by Ogboru et al. (2015) by identifying the phytochemical components of the bark of *Dacryodes edulis*.

DAMAGE BY FOREST ELEPHANTS IN LOGGING CONCESSIONS

Studies that have investigated damage caused by forest elephants in logged forests focus mainly on damage to seedlings, the impact on regeneration, and how elephants affect the structure and composition of the vegetation (Struhsaker et al. 1996, Chapman & Chapman 1997, Paul et al. 2004, Lawes & Chapman 2006, Omeja et al. 2014, Terborgh et al. 2015, Omeja et al. 2016, Piiroinen et al. 2017). In Kibale, elephants visit extensively the

Table 3. Frequency and severity of damage to debarked timber species, caused by forest elephants *Loxodonta cyclotis*. '% indiv.' = percentage of debarked trees and '% circ.' = percentage of circumference affected. Harvested volume is the volume harvested in the Congo Basin, excluding Equatorial Guinea (source: FRMi 2018, Ngoya-Kessy 2020). Price is the commercial value (free on board) of exported logs (source: ITTO 2022). Species sold under the same commercial name are assigned the same volume and price

Botanical name of timber species	Commercial name	Harvested volume, $m^3\,year^{-1}$	Price, € m^{-3}	% indiv	% circ.	Country	References
Anacardiaceae							
Antrocaryon klaineanum	Onzabili	15	No data	100[1]	No data	Gabon	White et al. (1993)
Antrocaryon micraster	Onzabili	15	No data	100[1]	Heavy	Rep. of Congo	Blake (2002)
Combretaceae							
Terminalia ivorensis	Framiré	No data	No data	100	39	Ghana	Short (1981)
				Frequent	No data	Ivory Coast	Theuerkauf et al. (2000)
Terminalia superba	Limba	122537	No data	60	17	Cameroon	Tchamba and Seme (1993)
				Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
Fabaceae							
Afzelia bipindensis	Doussié	17853	No data	87	34	Cameroon	Tchamba and Seme (1993)
Afzelia sp.	Doussié	17853	No data	100[1]	No data	Gabon	White et al. (1993)
Cylicodiscus gabunensis	Okan	261929	230	No data	No data	Ghana	Short (1981)
				100[1]	No data	Gabon	White et al. (1993)
Guibourtia ehie	Ovengkol	2018[2]	No data	65	34	Ghana	Short (1981)
				Frequent	No data	Ivory Coast	Theuerkauf et al. (2000)
Piptadeniastrum africanum	Dabéma	85103	No data	Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
				88	No data	Gabon	White et al. (1993)
				60	No data	Uganda	Wing and Buss (1970)
Prioria oxyphylla	Tchitola	5684	No data	31	Heavy	Rep. of Congo	Blake (2002)
Sindoropsis letestui	Ghéombi	0	No data	3	No data	Gabon	White et al. (1993)
Malvaceae							
Nesogordonia sp.	Kotibé	45	No data	2.7	Moderate	Rep. of Congo	Blake (2002)
Triplochiton scleroxylon	Ayous	803548	250	21.1	Heavy	Rep. of Congo	Blake (2002)

(Continues)

Table 3. (Continued)

Botanical name of timber species	Commercial name	Harvested volume, $m^3 year^{-1}$	Price, € m^{-3}	% indiv	% circ.	Country	References
Meliaceae							
Entandrophragma angolense	Tiama	21852	No data	13.6	Low	Rep. of Congo	Blake (2002)
				44	26	Ghana	Short (1981)
				35	23	Cameroon	Tchamba and Seme (1993)
				Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
				12.5	No data	Uganda	Wing and Buss (1970)
Entandrophragma utile	Sipo	83948	260	25	Moderate	Rep. of Congo	Blake (2002)
				79	26	Ghana	Short (1981)
				38	21	Cameroon	Tchamba and Seme (1993)
Khaya anthotheca	Acajou d'Afrique (African mahogany)	16815	265	Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
Khaya grandifoliola	Acajou d'Afrique (African mahogany)	0	265	Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
Khaya ivorensis	Acajou d'Afrique (African mahogany)	21646	265	Rare	No data	Ivory Coast	Theuerkauf et al. (2000)
Moraceae							
Milicia excelsa	Iroko	160026	300	14.3	No data	Uganda	Sheil and Salim (2004)
Sapotaceae							
Aningeria altissima	Aniégré	3364	No data	11.8	No data	Uganda	Wing and Buss (1970)
Autranella congolensis	Mukulungu	81161	No data	64.7	Heavy	Rep. of Congo	Blake (2002)
Baillonella toxisperma	Moabi	9887	280	100[1]	No data	Gabon	White et al. (1993)
Chrysophyllum lacourtianum	Longhi rouge	916	No data	16.7	Low	Rep. of Congo	Blake (2002)
Tieghemella heckelii	Makoré	0	560 (sawn-wood)	No data	No data	Ghana	Short (1981)
				Rare	No data	Ivory Coast	Theuerkauf et al. (2000)

[1]Fewer than five trees sampled.
[2]Exported log volumes in 2018 from the Republic of Congo only.

gaps in the logged areas, leading to more tree damage and slower regeneration than in unlogged areas (Chapman & Chapman 1997, Omeja et al. 2016). The development of herbaceous plants in the logging gaps can act in synergy with damage caused by elephants to slow down ecological succession, but the direct impact of elephants is greater than that of herbaceous plants (Lawes & Chapman 2006). Nonetheless, it is the proliferation of herbaceous plants that attracts these megaherbivores (Omeja et al. 2014). The intensity of logging is also a key factor: the larger the gap, the more herbaceous plants that develop rapidly and the more elephants are attracted to the area (Chapman & Chapman 1997). Although results are mostly consistent across studies, Piiroinen et al. (2017) showed that rodents, seeking shelter in dense vegetation of logging gaps, have a greater impact than elephants on seedling mortality.

Some timber concessions that are committed to sustainable forest management reforest in logging gaps, to help regenerate species that are being harvested or those that are of great importance to wildlife and local people (Doucet et al. 2009). Although much damage caused by mammals is observed in these reforested gaps (M. Scalbert, unpublished data), to date, there are no published studies that identify the mammals involved and tree species concerned, quantify the damage, and estimate the financial losses to the timber company.

Studies on tree damage are even scarcer. Most of the damage inflicted on trees is not fatal, but it can influence their growth and shape, directly impacting their commercial value (Struhsaker et al. 1996). Debarked trees, although exposed to external pathogens, can continue to live and reproduce for many years (Struhsaker et al. 1996). Therefore, debarking and other forms of damage may not directly impact forest composition and structure, but could strongly affect timber quality and lead to economic losses for forest managers, although this is not yet documented and should be investigated. In Tables 2 and 3, and Appendices S2 and S3, some of the most heavily exploited timber species are listed. *Entandrophragma cylindricum* and *Triplochiton scleroxylon* are the second and third most exploited species, after *Aucoumea klaineana*, with more than 1100000 and 800000 m^3 extracted per year, respectively (FRMi 2018). With almost 300000 m^3 exploited per year, *Cylicodiscus gabunensis* is also an important timber species prized by forest elephants.

CONCLUSION AND RESEARCH PERSPECTIVES

This literature synthesis highlights the existence of numerous interactions between forest elephants and logging. They can be favourable or detrimental to both. For example, logging can impact the abundance of food for forest elephants, by fostering the development of herbaceous species and seedlings in certain parts of the forest (Struhsaker et al. 1996), but also by reducing the number of fruit trees in other parts (Blake 2002). Timber concessions can host many forest elephants if poaching is controlled, but they can also facilitate poaching and harm forest elephant populations (Poulsen et al. 2011). Forest elephants can help the regeneration of some commercial tree species (Campos-Arceiz & Blake 2011), but they can also damage high-value individual trees (Short 1981).

The complexity of the interactions between logging and forest elephants, as well as the multiple variables involved, requires further research on this topic. We recommend that priority should be given to:

- The impact of logging on forest elephant abundance, behaviour and movements, and the consequences for forest regeneration patterns.
- The impact of logging on seed dispersal by forest elephants, including on post-seed-dispersal processes and on the fate of seedlings.
- The importance of bark in the forest elephant's diet, factors favouring the debarking of certain tree species, the volumes of timber lost due to damage by forest elephants, and the mortality rate of trees debarked by forest elephants.

In the current state of knowledge, it would be too ambitious to attempt to rule on the general impact of selective logging on forest elephants and, conversely, on the overall influence of forest elephants on the forest resource available in a timber concession. Nevertheless, this review suggests that timber concessions have an interesting potential as key habitat for forest elephants, especially if the actions required to preserve the forest and its wildlife are implemented, such as antipoaching patrols and the development of effective wildlife management plans (Haurez et al. 2020). Timber concessions could therefore become a key component of the forest elephant conservation strategy in central Africa, where logged forest makes up 27% of the forest area (Eba'a Atyi et al. 2022). However, wildlife management is not the main purpose of timber concessions, and incentives such as wildlife credits (https://wildlifecredits.com/) should be considered to encourage the preservation of forest elephants in these places.

ACKNOWLEDGEMENTS

Many thanks to Simon Lhoest and Davy Fonteyn for their suggestions on previous versions of the manuscript. We are grateful to Olivier Scalbert for his technical help in managing the many publications used in this work.

FUNDING

This work was supported by the Programme de Promotion de l'Exploitation Certifiée des Forêts (PPECF, grant C162) and the Precious Forests Foundation (PFF).

REFERENCES

Alexandre D-Y (1978) Le rôle disséminateur des éléphants en forêt de Tai, Côte d'Ivoire. *La Terre et la Vie* 32: 47–72.

ATIBT (2016) *Nomenclature Générale des Bois Tropicaux*. Association Technique Internationale des Bois Tropicaux (ATIBT), Paris, France.

Balcomb SR, Chapman CA (2003) Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecological Monographs* 73: 625–642.

Barnes RFW, Barnes KL, Alers MPT, Blom A (1991) Man determines the distribution of elephants in the rain forests of northeastern Gabon. *African Journal of Ecology* 29: 54–63.

Barnes RFW, Beardsley K, Michelmore F, Barnes KL, Alers MPT, Blom A (1997) Estimating forest elephant numbers with dung counts and a Geographic Information System. *Journal of Wildlife Management* 61: 1384–1393.

Bayol N, Borie J (2004) Itinéraires techniques d'aménagement des forêts de production en Afrique centrale. *Bois et Forets des Tropiques* 281: 35–49.

Beaune D, Fruth B, Bollache L, Hohmann G, Bretagnolle F (2013) Doom of the elephant-dependent trees in a Congo Tropical forest. *Forest Ecology and Management* 295: 109–117.

Beirne C, Meier AC, Mbele AE, Menie Menie G, Froese G, Okouyi J, Poulsen JR (2019) Participatory monitoring reveals village-centered gradients of mammalian defaunation in central Africa. *Biological Conservation* 233: 228–238.

Beirne C, Meier AC, Brumagin G, Jasperse-sjolander L, Lewis M, Masseloux J et al. (2020) Climatic and resource determinants of forest elephant movements. *Frontiers in Ecology and Evolution* 8: 1–14.

Beirne C, Houslay TM, Morkel P, Clark CJ, Fay M, Okouyi J, White LJT, Poulsen JR (2021) African forest elephant movements depend on time scale and individual behavior. *Scientific Reports* 11: 1–11.

Berzaghi F, Longo M, Ciais P, Blake S, Bretagnolle F, Vieira S, Scaranello M, Scarascia-Mugnozza G, Doughty CE (2019) Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience* 12: 725–729.

Blake S (2002) *The Ecology of Forest Elephant Distribution and Its Implications for Conservation*. PhD thesis, University of Edinburgh, Edinburgh, UK.

Blake S, Inkamba-Nkulu C (2004) Fruit, minerals, and forest elephant trails: do all roads lead to Rome? *Biotropica* 36: 392–401.

Blake S, Strindberg S, Boudjan P, Makombo C, Bila-Isia I, Ilambu O et al. (2007) Forest elephant crisis in the Congo Basin. *PLoS Biology* 5: e111.

Blake S, Deem SL, Strindberg S, Maisels F, Momont L, Isia IB, Douglas-Hamilton I, Karesh WB, Kock MD (2008) Roadless wilderness area determines forest elephant movements in the Congo Basin. *PLoS ONE* 3: e3546.

Blom A, Van Zalinge R, Heitkönig IMA, Prins HHT (2005) Factors influencing the distribution of large mammals within a protected central African forest. *Oryx* 39: 381–388.

Breuer T, Breuer-Ndoundou Hockemba M, Strindberg S (2021) Small-scale dung survey reveals high forest elephant density and preference for mixed species forest in an intact protected area. *Biodiversity and Conservation* 30: 2671–2688.

Bush ER, Whytock RC, Bahaa-el-din L, Bourgeois S, Bunnefeld N, Cardoso AW et al. (2020) Long-term collapse in fruit availability threatens central African forest megafauna. *Science* 370: 1–8.

Campos-Arceiz A, Blake S (2011) Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica* 37: 542–553.

Cardoso AW, Malhi Y, Oliveras I, Lehmann D, Ndong JE, Dimoto E et al. (2019) The role of forest elephants in shaping Tropical forest–savanna coexistence. *Ecosystems* 23: 602–616.

Chapman CA, Chapman LJ (1997) Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29: 396–412.

Chase MJ, Schlossberg S, Griffin CR, Bouché PJC, Djene SW, Elkan PW et al. (2016) Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* 2016: 1–24.

Clark CJ, Poulsen JR, Malonga R, Elkan PW (2009) Logging concessions can extend the conservation estate for central African Tropical forests. *Conservation Biology* 23: 1281–1293.

Clark CJ, Poulsen JR, Levey DJ (2012) Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. *Ecology* 93: 554–564.

Conseil National Climat Gabonais (2020) *Gabon National Results Report Results-Based Payments under the Central African Forest*. https://www.cafi.org/sites/default/files/2021-06/Gabon%20National%20Results%20Report_submitted_18Dec2020.pdf

Corlett RT (2013) The shifted baseline: prehistoric defaunation in the Tropics and its consequences for biodiversity conservation. *Biological Conservation* 163: 13–21.

Daïnou K, Bracke C, Vermeulen C, Haurez B, De Vleeschouwer J-Y, Fayolle A, Doucet J-L (2016) *Hautes Valeurs de Conservation (HVC) dans les Unités Forestières d'Aménagement du Cameroun: Concepts, Choix et Pratiques*. Presses Agronomiques de Gembloux, Gembloux, Belgium.

Debroux L (1998) *L'Aménagement des Forêts Tropicales Fondé sur la Gestion des Populations d'Arbres: l'Exemple du Moabi (Baillonella toxisperma Pierre) dans la Forêt du Dja, Cameroun*. PhD thesis, Faculté Universitaire des Sciences Agronomiques, Gembloux, Belgium.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science* 345: 401–406.

Doucet JL, Kouadio YL, Monticelli D, Lejeune P (2009) Enrichment of logging gaps with moabi (*Baillonella toxisperma* Pierre) in a central African rain forest. *Forest Ecology and Management* 258: 2407–2415.

Dranzoa C (1998) The avifauna 23 years after logging in Kibale National Park, Uganda. *Biodiversity and Conservation* 7: 777–797.

Eba'a Atyi R, Hiol Hiol F, Lescuyer G, Mayaux P, Defourny P, Bayol N et al. (2022) *Les Forêts du Bassin du Congo: État des Forêts 2021*. CIFOR, Bogor, Indonesia.

Fargeot C, Forni É, Nasi R (2004) Réflexions sur l'aménagement des forêts de production dans le bassin du Congo. *Bois et Forets des Tropiques* 281: 19–34.

Feer F (1995a) Morphology of fruits dispersed by African forest elephants. *African Journal of Ecology* 33: 279–284.

Feer F (1995b) Seed dispersal in African forest ruminants. *Journal of Tropical Ecology* 11: 683–689.

Fishlock V, Lee PC (2013) Forest elephants: fission-fusion and social arenas. *Animal Behaviour* 85: 357–363.

Fishlock V, Lee PC, Breuer T (2008) Quantifying forest elephant social structure in central African bai environments. *Pachyderm* 44: 19–28.

Fonteyn D, Vermeulen C, Deflandre N, Cornelis D, Lhoest S, Houngbégnon F, Doucet J-L, Fayolle A (2020) Wildlife trail or systematic? Camera trap placement has little effect on estimates of mammal diversity in a Tropical forest in Gabon. *Remote Sensing in Ecology and Conservation* 7: 321–336.

FRMi (2018) *Vision Stratégique et Industrialisation de la Filière Bois dans les 6 Pays du Bassin du Congo – Horizon 2030 – Rapport Stratégique Régional (Résumé)*. FRM, Montpellier, France.

Fullman TJ, Child B (2013) Water distribution at local and landscape scales affects tree utilization by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 51: 235–243.

Gadd ME (2002) The impact of elephants on the marula tree *Sclerocarya birrea*. *African Journal of Ecology* 40: 328–336.

Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP et al. (1985) Fruit characters as a basis of fruit choice and seed dispersal in a Tropical forest vertebrate community. *Oecologia* 65: 324–337.

Gérard J, Guibal D, Cerre JC, Paradis S (2016) *Atlas des Bois Tropicaux: Caractéristiques Technologiques et Utilisations*. Editions Quae, Versailles, France.

Gobush KS, Edwards CT, Maisels F, Wittemyer G, Balfour D, Taylor RD (2021) *Loxodonta cyclotis*. IUCN Red List of Threatened Species 2021: e.T181007989A181019888.

Granados A, Brodie JF, Bernard H, O'Brien MJ (2017) Defaunation and habitat disturbance interact synergistically to alter seedling recruitment. *Ecological Applications* 27: 2092–2101.

Guldemond RAR, Purdon A, Van Aarde RJ (2017) A systematic review of elephant impact across Africa. *PLoS ONE* 12: 1–12.

Gutiérrez-Granados G (2011) Effect of logging on rodent scatter-hoarding dynamics in Tropical forests: implications for plant recruitment. *Integrative Zoology* 6: 74–80.

Haurez B, Tagg N, Petre C, Vermeulen C, Doucet J-L (2016) Short term impact of selective logging on a western lowland gorilla population. *Forest Ecology and Management* 364: 46–51.

Haurez B, Fonteyn D, Toint S, Bracke C, Doucet J-L, Daïnou K, Kéhou S, Vermeulen C (2020) *Élaboration et Mise en Œuvre d'Un Plan de Gestion de la Faune – Guide Technique à Destination des Gestionnaires des Forêts de Production d'Afrique Centrale*. Presses Agronomiques de Gembloux, Gembloux, Belgium.

Howe F, Smallwood J (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Ihwagi FW, Chira RM, Kironchi G, Vollrath F, Douglas-Hamilton I (2012) Rainfall pattern and nutrient content influences on African elephants' debarking behaviour in Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology* 50: 152–159.

Inogwabini BI, Mbende L, Mbenzo A (2011) The relic population of forest elephants near Lake Tumba, Democratic Republic of Congo: abundance, dung lifespan, food items and movements. *Pachyderm* 49: 40–47.

ITTO (2019) Tropical Timber Market Report. https://www.itto.int/direct/topics/topics_pdf_download/topics_id=6116&no=1

ITTO (2022) Tropical Timber Market Report. https://www.itto.int/files/user/mis/MIS_1-15_Apr2022.pdf

Kleinschroth F, Healey JR (2017) Impacts of logging roads on Tropical forests. *Biotropica* 49: 620–635.

Kleinschroth F, Laporte N, Laurance WF, Goetz SJ, Ghazoul J (2019) Road expansion and persistence in forests of the Congo Basin. *Nature Sustainability* 2: 628–634.

Laguardia A, Bourgeois S, Strindberg S, Gobush KS, Abitsi G, Banga LFS, White LJT, Stokes EJ (2021) Nationwide abundance and distribution of African forest elephants across Gabon using non-invasive SNP genotyping. *Global Ecology and Conservation* 32: e01894.

Laurance WF, Croes BM, Tchignoumba L, Lahm SA, Alonso A, Lee ME, Campbell P, Ondzeano C (2006) Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology* 20: 1251–1261.

Lawes MJ, Chapman CA (2006) Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest Ecology and Management* 221: 278–284.

Lescuyer G, Tsanga R, Nziengui S, Forni E, Romero C (2021) Influence of FSC certification on the governance of the logging sector in the Congo basin. *Natural Resources Forum* 45: 289–304.

Lhoest S, Fonteyn D, Daïnou K, Delbeke L, Doucet JL, Dufrêne M et al. (2020) Conservation value of Tropical forests: distance to human settlements matters more than management in central Africa. *Biological Conservation* 241: 1–11.

Löyttyniemi K, Mikkola L (1980) Elephant as a pest of pines in Zambia. *Tropical Pest Management* 26: 167–169.

Magliocca F, Quérouil S, Gautier-Hion A (2003) Seed eating in elephant dung by two large mammals in the Congo Republic. *Revue d'Ecologie (Terre et Vie)* 58: 143–149.

Maicher V, Delabye S, Murkwe M, Doležal J, Altman J, Kobe I et al. (2020) Effects of disturbances by forest elephants on diversity of trees and insects in Tropical rainforests on Mount Cameroon. *Scientific Reports* 10: 1–11.

Maisels F, Strindberg S, Blake S, Wittemyer G, Hart J, Williamson EA et al. (2013) Devastating decline of forest elephants in central Africa. *PLoS ONE* 8: e59469.

Markl JS, Schleuning M, Forget PM, Jordano P, Lambert JE, Traveset A, Wright SJ, Böhning-Gaese K (2012) Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology* 26: 1072–1081.

Mbété P, Ngokaka C, Akouango F, Inkamba-Nkulu C, Pandi Kala F (2010) Contribution to the survey of the food regime of the forest elephant in the peripheral sone in the National Park Ogooue Leketi. *Pakistan Journal of Nutrition* 9: 1141–1148.

Merz G (1981) Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt, *Loxodonta africana cyclotis* Matschie, 1900. *Mammalia* 45: 299–312.

Midgley JJ, Gallaher K, Kruger LM (2012) The role of the elephant (*Loxodonta africana*) and the tree squirrel (*Paraxerus cepapi*) in marula (*Sclerocarya birrea*) seed predation, dispersal and germination. *Journal of Tropical Ecology* 28: 227–231.

Mills EC, Poulsen JR, Michael Fay J, Morkel P, Clark CJ, Meier A, Beirne C, White LJT (2018) Forest elephant movement and habitat use in a Tropical forest-grassland mosaic in Gabon. *PLoS ONE* 13: 1–17.

Morgan BJ (2007) Unusually low incidence of debarking by forest elephants in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology* 45: 664–666.

Morgan BJ (2009) *Sacoglottis gabonensis* – a keystone fruit for forest elephants in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology* 47: 154–163.

Morgan BJ, Lee PC (2007) Forest elephant group composition, frugivory and coastal use in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology* 45: 519–526.

Morin-rivat J, Fayolle A, Favier C, Bremond L, Gourlet-fleury S, Bayol N, Lejeune P, Beeckman H (2017) Present-day central African forest is a legacy of the 19th Century human history. *eLife* 6: 1–18.

Nchanji AC, Plumptre AJ (2003) Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. *Journal of Tropical Ecology* 19: 229–237.

Ngama S (2018) *Introduction to Elephant Ecophysiology: Principles, Methods and Case Studies on Forest Elephant* (Loxodonta africana cyclotis) *Crop Raiders in Gabon*. PhD thesis, Gembloux Agro-Bio Tech (University of Liège), Gembloux, Belgium.

Ngama S, Bindelle J, Poulsen JR, Hornick JL, Linden A, Korte L, Doucet JL, Vermeulen C (2019) Do topography and fruit presence influence occurrence and intensity of crop-raiding by forest elephants (*Loxodonta africana cyclotis*)? *PLoS ONE* 14: 1–15.

Ngoya-Kessy AM (2020) *Etat des Lieux des Acteurs du Secteur Privé de la Filière Forêt-Bois au Congo*. ATIBT, Brazzaville, Republic of Congo.

Nsonsi F, Heymans JC, Diamouangana J, Mavinga FB, Breuer T (2017) Perceived human–elephant conflict and its impact for elephant conservation in northern Congo. *African Journal of Ecology* 56: 208–215.

Nuñez CL, Clark JS, Clark CJ, Poulsen JR (2018) Low-intensity logging and hunting have long-term effects on seed dispersal but not fecundity in Afrotropical forests. *AoB PLANTS* 11: 1–17.

O'Connor TG (2017) Demography of woody species in a semi-arid African savanna reserve following the re-introduction of elephants. *Acta Oecologica* 78: 61–70.

Ogboru R, Okolie P, Agboje I (2015) Phytochemical screening and medicinal potentials of the bark of *Dacryodes edulis* (G. Don) HJ Lam. *Journal of Environmental Analytical Chemistry* 2: 2380–2391.

Omeja PA, Jacob AL, Lawes MJ, Lwanga JS, Rothman JM, Tumwesigye C, Chapman CA (2014) Changes in elephant abundance affect forest composition or regeneration? *Biotropica* 46: 704–711.

Omeja PA, Lawes MJ, Corriveau A, Valenta K, Sarkar D, Paim FP, Chapman CA (2016) Recovery of tree and mammal communities during large-scale forest regeneration in Kibale National Park, Uganda. *Biotropica* 48: 770–779.

Oslisly R, White L, Bentaleb I, Favier C, Fontugne M, Sebag D (2013) Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 1–10.

Paul JR, Randle AM, Chapman CA, Chapman LJ (2004) Arrested succession in logging gaps: is tree seedling growth and survival limiting? *African Journal of Ecology* 42: 245–251.

Piiroinen T, Valtonen A, Roininen H (2017) Vertebrate herbivores are the main cause of seedling mortality in a logged African rainforest—implications for forest restoration. *Restoration Ecology* 25: 442–452.

Poulsen JR, Clark CJ, Bolker BM (2011) Decoupling the effects of logging and hunting on an Afrotropical animal community. *Ecological Applications* 21: 1819–1836.

Poulsen JR, Clark CJ, Palmer TM (2013) Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biological Conservation* 163: 122–130.

Poulsen JR, Koerner SE, Moore S, Medjibe VP, Blake S, Clark CJ et al. (2017) Poaching empties critical central African wilderness of forest elephants. *Current Biology* 27: 134–135.

Poulsen JR, Rosin C, Meier A, Mills E, Nuñez CL, Koerner SE et al. (2018) Ecological consequences of forest elephant declines for Afrotropical forests. *Conservation Biology* 32: 559–567.

Putz FE, Zuidema PA, Synnott T, Peña-Claros M, Pinard MA, Sheil D et al. (2012) Sustaining conservation values in selectively logged Tropical forests: the attained and the attainable. *Conservation Letters* 5: 296–303.

Remmers W, Gameiro J, Schaberl I, Clausnitzer V (2017) Elephant (*Loxodonta africana*) footprints as habitat for aquatic macroinvertebrate communities in Kibale National Park, south-west Uganda. *African Journal of Ecology* 55: 342–351.

Rosin C, Poulsen JR, Swamy V, Granados A (2017) A pantropical assessment of vertebrate physical damage to forest seedlings and the effects of defaunation. *Global Ecology and Conservation* 11: 188–195.

Rosin C, Beals KK, Belovitch MW, Harrison RE, Pendred M, Sullivan MK, Yao N, Poulsen JR (2020) Assessing the effects of elephant foraging on the structure and diversity of an Afrotropical forest. *Biotropica* 52: 1–7.

Ruiz Pérez M, De Blas DE, Nasi R, Sayer JA, Sassen M, Angoué C et al. (2005) Logging in the Congo Basin: a multi-country characterization of timber companies. *Forest Ecology and Management* 214: 221–236.

Schuttler SG, Blake S, Eggert LS (2012) Movement patterns and spatial relationships among African forest elephants. *Biotropica* 44: 445–448.

Seloana MQ, Jordaan JJ, Potgieter MJ, Kruger JW (2018) Feeding patterns of elephants at the Atherstone Collaborative Nature Reserve. *African Journal of Ecology* 56: 445–454.

Sheil D, Salim A (2004) Forest tree persistence, elephants, and stem scars. *Biotropica* 36: 505–521.

Short J (1981) Diet and feeding behaviour of the forest elephant. *Mammalia* 45: 177–186.

Short JC (1983) Density and seasonal movements of forest elephant (*Loxodonta africana cyclotis*, Matschie) in Bia National Park, Ghana. *African Journal of Ecology* 21: 175–184.

Stiernon Q (2022) *Use of Logging Roads by Large Mammals in a Timber Concession of Southeast Cameroon*. Masters thesis, Gembloux Agro-Bio Tech (University of Liège), Gembloux, Belgium.

Stokes EJ, Strindberg S, Bakabana PC, Elkan PW, Iyenguet FC, Madzoké B et al. (2010) Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. *PLoS ONE* 5: e10294.

Struhsaker TT, Lwanga JS, Kasenene JM (1996) Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *Journal of Tropical Ecology* 12: 45–64.

Tchamba MN, Seme PM (1993) Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *African Journal of Ecology* 31: 165–171.

Terborgh J, Davenport LC, Niangadouma R, Dimoto E, Mouandza JC, Scholtz O, Jaen MR (2015) Megafaunal influences on tree recruitment in African equatorial forests. *Ecography* 39: 180–186.

Theuerkauf J, Waitkuwait WE, Guiro Y, Ellenberg H, Porembski S (2000) Diet of forest elephants and their role in seed dispersal in the Bossematié Forest Reserve, Ivory Coast. *Mammalia* 64: 447–460.

Theuerkauf J, Rouys S, Henegouwen ALVB, Krell F, Mazur S, Mühlenberg M (2009) Colonization of forest elephant dung by invertebrates in the Bossematié Forest Reserve, Ivory Coast. *Zoological Studies* 48: 343–350.

Turkalo A, Fay MJ (1995) Studying forest elephants by direct observation: preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm* 20: 45–54.

Turkalo AK, Wrege PH, Wittemyer G (2013) Long-term monitoring of Dzanga Bai forest elephants: forest clearing use patterns. *PLoS ONE* 8: 1–12.

Tutin CEG, Williamson EA, Rogers ME, Fernandez M (1991) A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon. *Journal of Tropical Ecology* 7: 181–199.

Van Vliet N, Nasi R (2008) Mammal distribution in a central African logging concession area. *Biodiversity and Conservation* 17: 1241–1249.

Vander Wall SB, Kuhn KM, Beck MJ (2005) Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801–806.

Vanleeuwe H, Gautier-Hion A (1998) Forest elephant paths and movements at the Odzala National Park, Congo: the

role of clearings and marantaceae forests. *African Journal of Ecology* 36: 174–182.
Vanthomme H, Kolowski J, Korte L, Alonso A (2013) Distribution of a community of mammals in relation to roads and other human disturbances in Gabon, central Africa. *Conservation Biology* 27: 281–291.
Wall J, Wittemyer G, Klinkenberg B, LeMay V, Blake S, Strindberg S et al. (2021) Human footprint and protected areas shape elephant range across Africa. *Current Biology* 31: 1–9.
White LJT (1994) *Sacoglottis gabonensis* fruiting and the seasonal movements of elephants in the Lope Reserve, Gabon. *Journal of Tropical Ecology* 10: 121–125.
White LJT, Tutin CE, Fernandez M (1993) Group composition and diet of forest elephants *Loxodonta africana cyclotis*. *African Journal of Ecology* 31: 181–189.
Wing LD, Buss IO (1970) Elephants and forests. *Wildlife Monographs* 19: 3–92.
Wolf A, Doughty CE, Malhi Y (2013) Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS ONE* 8: 1–10.
Wrege PH, Rowland ED, Thompson BG, Batruch N (2010) Use of acoustic tools to reveal otherwise cryptic responses of forest elephants to oil exploration. *Conservation Biology* 24: 1578–1585.
Wrege PH, Rowland ED, Bout N, Doukaga M (2012) Opening a larger window onto forest elephant ecology. *African Journal of Ecology* 50: 176–183.
Wrege PH, Rowland ED, Keen S, Shiu Y (2017) Acoustic monitoring for conservation in Tropical forests: examples from forest elephants. *Methods in Ecology and Evolution* 8: 1292–1301.
Young HS, McCauley DJ, Galetti M, Dirzo R (2016) Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47: 333–358.
Yumoto T, Maruhashi T, Yamagiwa J, Mwanza N (1995) Seed-dispersal by elephants in a Tropical rain forest in Kahuzi-Biega National Park, Zaire. *Biotropica* 27: 526–530.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Lesser-known timber species found as seeds in the droppings of forest elephants.
Appendix S2. Lesser-known timber species damaged by forest elephants.
Appendix S3. Frequency and severity of damage to debarked lesser-known timber species, caused by forest elephants.