Conservation Biology

Essay

Ecological consequences of forest elephant declines for Afrotropical forests

John R. Poulsen,[1,3]* Cooper Rosin,[1] Amelia Meier,[1] Emily Mills,[1] Chase L. Nuñez,[1,3] Sally E. Koerner,[1,2] Emily Blanchard,[1] Jennifer Callejas,[1] Sarah Moore,[1] and Mark Sowers[1]

[1]Nicholas School of the Environment, Duke University, P.O. Box 90328, Durham, NC 27708, U.S.A.
[2]Department of Biology, University of North Carolina Greensboro, Greensboro, NC 27412, U.S.A.
[3]University Program in Ecology, Duke University, Durham, NC 27708, U.S.A.

Abstract: *Poaching is rapidly extirpating African forest elephants* (Loxodonta cyclotis) *from most of their historical range, leaving vast areas of elephant-free tropical forest. Elephants are ecological engineers that create and maintain forest habitat; thus, their loss will have large consequences for the composition and structure of Afrotropical forests. Through a comprehensive literature review, we evaluated the roles of forest elephants in seed dispersal, nutrient recycling, and herbivory and physical damage to predict the cascading ecological effects of their population declines. Loss of seed dispersal by elephants will favor tree species dispersed abiotically and by smaller dispersal agents, and tree species composition will depend on the downstream effects of changes in elephant nutrient cycling and browsing. Loss of trampling and herbivory of seedlings and saplings will result in high tree density with release from browsing pressures. Diminished seed dispersal by elephants and high stem density are likely to reduce the recruitment of large trees and thus increase homogeneity of forest structure and decrease carbon stocks. The loss of ecological services by forest elephants likely means Central African forests will be more like Neotropical forests, from which megafauna were extirpated thousands of years ago. Without intervention, as much as 96% of Central African forests will have modified species composition and structure as elephants are compressed into remaining protected areas. Stopping elephant poaching is an urgent first step to mitigating these effects, but long-term conservation will require land-use planning that incorporates elephant habitat into forested landscapes that are being rapidly transformed by industrial agriculture and logging.*

Keywords: Central Africa, herbivory, *Loxodonta cyclotis*, nutrient recycling tropical forest, seed dispersal

Consecuencias Ecológicas de las Declinaciones de Elefantes del Bosque para los Bosques Afrotropicales

Resumen: *La caza furtiva está extirpando rápidamente a los elefantes africanos del bosque* (Loxodonta cyclotis) *de la mayor parte de su extensión histórica, lo que deja áreas extensas de bosque tropical libres de elefantes. Los elefantes son ingenieros ecológicos que crean y mantienen el hábitat del bosque; por esto, su pérdida tendrá consecuencias para la composición y la estructura de los bosques afrotropicales. Por medio de una revisión exhaustiva de la literatura, evaluamos el papel de los elefantes del bosque en la dispersión de semillas, reciclaje de nutrientes, herbivoría, y daño físico para predecir los efectos ecológicos en cascada de la declinación de sus poblaciones. La falta de la dispersión de semillas realizada por elefantes favorecerá a las especies de árboles dispersadas abióticamente y por agentes dispersores más pequeños, y la composición de las especies de árboles dependerá de los efectos derivados de los cambios en el pastoreo y circulación de nutrientes de los elefantes. La ausencia de pisoteo y de la herbivoría de brotes y retoños resultará en una alta densidad de árboles conforme estas especies sean liberadas de la presión del pastoreo. La disminución en la dispersión de semillas por los elefantes y la alta densidad de tallos probablemente reduzcan el reclutamiento de árboles grandes, lo que incrementará la homogeneidad de la estructura del bosque y disminuirá las reservas de carbono. La pérdida de servicios ecológicos generados por elefantes probablemente implique que los bosques*

*email john.poulsen@duke.edu
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del centro de África sean más como los bosques neotropicales, en los que la megafauna fue extirpada hace miles de años. Sin una intervención, hasta el 96% de los bosques del centro de África tendrán una composición y estructura modificadas conforme los elefantes son restringidos dentro de las áreas protegidas. Detener la caza furtiva de elefantes es un primer paso urgente para mitigar estos efectos, pero la conservación a largo plazo requerirá una planeación de uso de suelo que incorpore al hábitat del elefante dentro de los paisajes boscosos que están siendo transformados rápidamente por la industria agrícola y maderera.

Palabras Clave: África Central, bosque tropical, dispersión de semillas, herbivoría, *Loxodonta cyclotis*, reciclaje de nutrientes

摘要: *偷猎正在导致非洲森林象 (Loxodonta cyclotis) 从它们大部分的历史分布区消失, 留下大片没有大象的热带森林。大象是创造和维持森林生境的生态工程师, 因此它们的消失会对非洲热带界森林的组成和结构产生很大影响。通过全面的文献综述, 我们评估了森林象在种子传播、营养循环、食草作用以及对森林的直接破坏中的作用, 以预测它们种群下降产生的生态级联效应。失去了大象对种子的传播, 将有利于树种通过非生物途径和更小型的传播者来传播种子, 而树木种类的组成将取决于大象的营养循环和食草作用变化的下游效应。没有大象来踩踏、取食幼苗和小树会导致树木密度增大, 因为树木不再受到被取食的压力。大象对种子传播作用的下降和树木密度的增高可能减少森林中大树的补充, 因此增加了森林结构的均质性, 减少了碳储量。森林象带来的生态服务功能衰退可能意味着中非森林将变得像几千年前巨型动物群灭绝了的新热带界森林。在没有干预的情况下,随着大象的分布区收缩到剩余的保护区中, 高达 96% 的中非森林的物种组成和结构会发生改变。要减缓这些影响, 刻不容缓的第一步是停止偷猎, 但长期的保护还需要土地利用规划将大象的生境纳入到正在因农业产业化和伐木而快速转化的森林景观中。*【**翻译: 胡怡思; 审校: 胡义波**】

关键词:*Loxodonta cyclotis*, 中非, 种子传播, 食草作用, 营养循环, 热带森林

Elephants as Ecological Engineers in a Time of Crisis

The worldwide loss of large animals is perhaps the most perceptible ecological consequence of anthropogenic disturbance on Earth (Dirzo et al. 2014). In the late Pleistocene, extinctions of megafauna (animals with body masses ≥1000 kg) reduced herbivory and caused large-scale shifts in vegetation patterns that contributed to global warming (e.g., Gill et al. 2009; Johnson 2009; Malhi et al. 2016). Today, humans are causing equally dramatic reductions in large animals: 60% of remaining large-bodied herbivores (animals with body masses ≥100 kg) are threatened with extinction, and nearly all suffer from range reduction due to overhunting, anthropogenic climate change, and habitat loss (Ripple et al. 2015). In particular, poaching for ivory is driving elephants, the largest terrestrial animals on Earth, to the brink of extinction (Wittemyer et al. 2014). If the ecological effects of past megafaunal extinctions are indicators of future changes, the decimation of elephants is likely to have far-reaching consequences.

Although human activities have reduced the distribution and abundance of elephants worldwide (Wittemyer et al. 2014; Chaiyarat et al. 2015; Ripple et al. 2015), the most precipitous declines have occurred among African forest elephants (*Loxodonta cyclotis*) (Fig. 1). These reductions have been driven by poaching, habitat loss, and fragmentation (Underwood et al. 2013). In West Africa, forest elephant populations are restricted to 6–7% of their 1984 range and survive in small, fragmented populations (e.g., Roth & Douglas-Hamilton 1991; Chase et al. 2016; Thouless et al. 2016). In Central Africa, forest elephant numbers plummeted 62% from 2002 to 2011, and current populations persist at 10% of their potential size and occupy <25% of their potential range (Maisels et al. 2013). Even sites regarded as the last bastions of forest elephants have lost over 80% of their populations to poaching in roughly the last 10 years (Poulsen et al. 2017).

Despite the threat of extinction, African forest elephants remain understudied (Breuer et al. 2016). Knowledge of their ecological impacts on tropical forests is limited, and most studies of forest elephants have been concentrated in several protected areas (Fig. 2). Although the better-studied savanna elephant (*Loxodonta africana*) is a major driver of vegetation structure, tree recruitment, and plant community composition (e.g., Laws et al. 1970; Guldemond & Aarde 2008; Asner & Levick 2012), studies of savanna elephants provide limited inference for understanding how forest elephants interact with their environment because the 2 taxa have demonstrable differences in morphology, ecology, reproduction, and social structure (e.g., Roca et al. 2001; Schuttler et al. 2014; Turkalo et al. 2017). This is a problematic knowledge gap because forest elephants are ecosystem engineers that control, directly or indirectly, the availability of resources to other organisms by causing physical state changes in biotic and abiotic materials. For example, forest elephants can be powerful filters of tree recruitment and survival (Terborgh et al. 2015*a*), generate extensive path networks, create and maintain forest clearings (Blake & Inkamba-Nkulu 2004), and shape tropical forest vegetation communities (Hawthorne & Parren 2000). These ecological interactions are hypothesized to

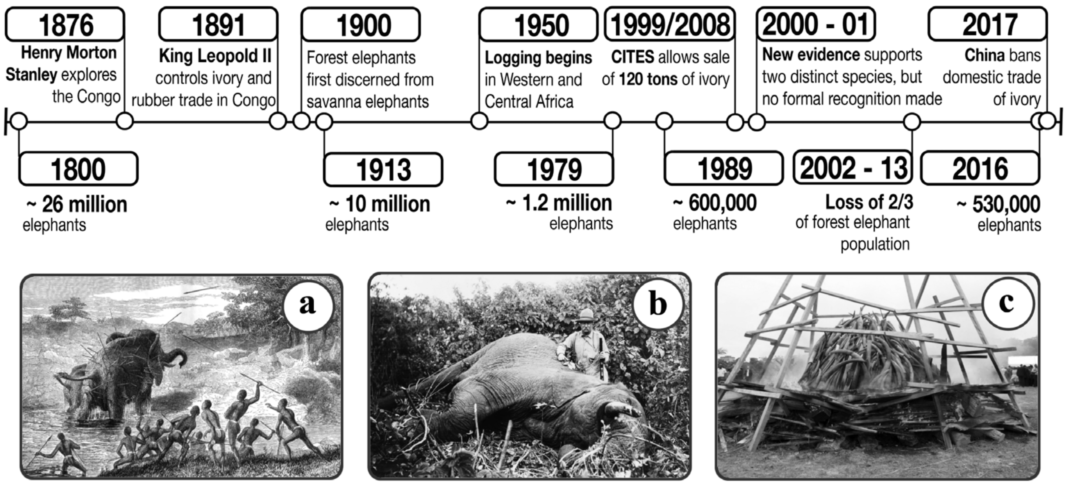

Figure 1. Timelines of historic threats to and declines (population estimates include savanna and forest elephants) in forest elephants: (a) indigenous peoples in Central Africa hunting elephants with spears before guns went into widespread use to hunt big game in the 19th century, (b) President Theodore Roosevelt with 1 of 11 elephants killed on the Smithsonian-Roosevelt African Expedition of 1909, and (c) burning of Gabon's ivory stocks in 2012.

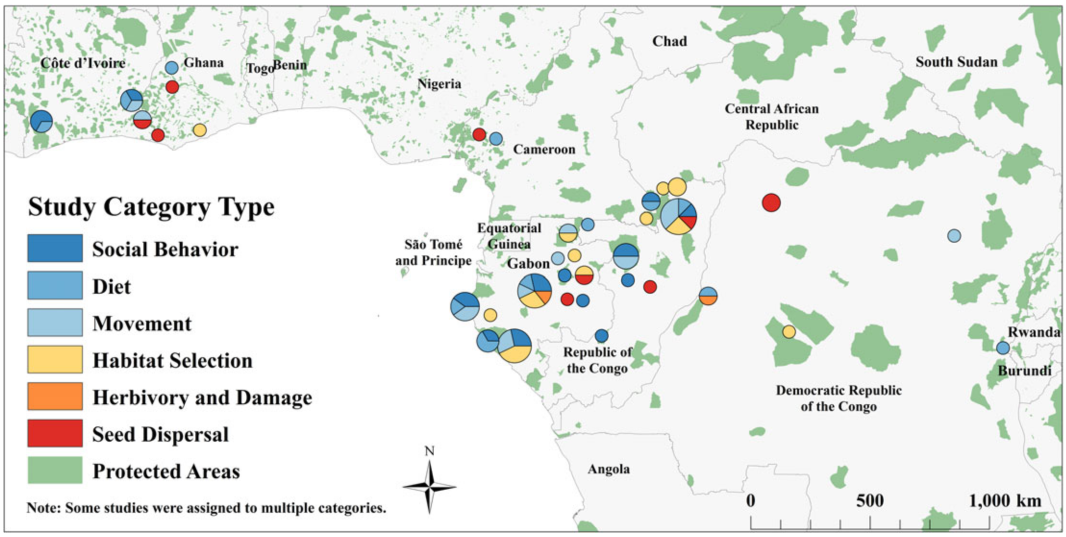

Figure 2. Distribution and focus (category) of ecological studies on forest elephants in Central Africa. The size of the pie charts represents the number of studies conducted at a given location (range 1–6).

drive patterns of forest structure and diversity that distinguish Afrotropical from Neotropical forests—where megafauna have been absent for 10,000 years (Cristoffer & Peres 2003; Terborgh et al. 2015*b*).

With elephants in crisis from poaching and anthropogenic change (Breuer et al. 2016), the area of elephant-free forest is expanding in Central Africa, raising the question of how the reduction or loss of forest elephants will affect the diversity, composition, and structure of forests. We synthesized current knowledge of the effects of African forest elephants on tropical forests to infer how their loss may affect forest functioning. We conducted a comprehensive literature search of the Web of Science and Scopus for the keywords "forest elephant," "Loxodonta africana cyclotis," "Loxodonta cyclotis," "L. cyclotis," and combinations of "ecology," "seed dispersal," "herbivory," "browsing," "damage," "social behavior," "habitat," "diet," "movement," "seed dispersal," and "Central Africa." We identified 158 peer-reviewed publications (Supporting Information). Of these papers, 66 (79 studies) focused on the ecology of forest elephants. We categorized these articles into 6 broad subject classes: social behavior, diet, movement, habitat selection, herbivory and damage, and seed dispersal. Of the 79 studies, most focused on the behavior and biology of forests elephants. In a minority of studies, the ecological effects of elephants were assessed, including 13.9% focused on seed dispersal and 2.5% focused on herbivory and damage.

We posit that declines in forest elephant populations will greatly modify ecological processes and thus affect plant community composition, forest structure, and ecosystem function. First, we reviewed the role of forest elephants in three principal ecological processes: seed dispersal, nutrient recycling, and herbivory and physical damage. Second, we assessed the consequences of these processes to predict the cascading ecological effects of the loss of elephants for tropical forests. Third, we devised recommendations and research priorities for mitigating the negative effects of declining populations of forest elephants.

Ecological Effects of Forest Elephants on Tropical Forests

Seed Dispersal

Elephants, the largest fruit-eating animals on the planet, may consume higher abundances of seeds from a wider variety of species than any other large vertebrate (Campos-Arceiz & Blake 2011). They transport large fruits and seeds with fibrous pulp, hard seed coverings, and chemical defenses (Feer 1995; Yumoto et al. 1995), resulting in the dispersal of a greater number of intact seeds than smaller-bodied vertebrates (Blake et al. 2009). Elephants are keystone dispersers for numerous tree species: 30 plant species in Taï National Park, Ivory Coast (Alexandre 1978), and 13 species in the Nouabalé-Ndoki National Park, Republic of Congo (Blake et al. 2009), are dispersed solely or predominantly by elephants. Elephants travel much greater distances than most other dispersers (Sekar et al. 2015), yielding a higher proportion of seeds that escape heavy seed predation near parent plants (Yumoto et al. 1995). In a study of 4 GPS-collared elephants in Congo, 88% of dispersed seeds were transported over 1 km and some were dispersed up to 57 km from the parent tree (Blake et al. 2009).

Elephant feeding ecology and digestive physiology enhance seed survival and recruitment. Seeds that pass through the digestive tract of elephants demonstrate reduced time to germination, increased early growth rates, and improved seedling survival due in part to the protective and nutrient-rich growth environment provided by elephant dung (Nchanji & Plumptre 2003; Jothish 2013; Spanbauer & Adler 2015). Elephant browsing and movement opens dense vegetation, creating suitable establishment sites for dispersed seeds (Yumoto et al. 1995). As a result, seed dispersal by elephants promotes seedling survival and growth (Nchanji & Plumptre 2003; Jothish 2013; Spanbauer & Adler 2015) and high diversity of forest species (Campos-Arceiz & Blake 2011).

Nutrient Recycling

By chewing, digesting, and defecating, elephants redistribute the macro- and micronutrients stored in plant material (Hobbs 2006). Due to their high dietary diversity (Blake 2002), elephants may play a critical role in the cycling of a broad range of nutrients and secondary compounds. Elephants facilitate rapid nutrient cycling by digesting recalcitrant plant matter and releasing nitrogen, sodium, and other nutrients into the soil (McNaughton et al. 1997). Elephants excavate termite mounds and salt licks—mineral hotspots where concentrations can be up to seven times higher than in topsoil—unearthing previously inaccessible nutrients (e.g., sodium, potassium, calcium, and magnesium [Metsio Sienne et al. 2014]).

Elephants also influence the spatial heterogeneity of nutrient availability and cycling rates through long-distance movements. By transporting nutrients away from fertile, nutrient-rich areas, large mammals create a relatively homogeneous nutrient distribution across the landscape (Doughty et al. 2013; Wolf et al. 2013). This diffusion of nutrients has been likened to that of blood flow in the human body: large animals act as arteries of ecosystems, transporting nutrients long distances, and smaller animals act as capillaries, distributing nutrients to smaller subsections of the ecosystem (Doughty et al. 2013).

Herbivory and Physical Damage

Elephants are considered ecosystem engineers because of their destructive feeding behaviors, large body size, and herd movement. Savanna elephants break and uproot trees up to 40–60 cm in diameter (Kortlandt 1984); annual elephant-induced tree mortality is 40–1500 trees/elephant (Cumming 1981). Although tree uprooting and destruction is less common in tropical forests, few stems escape damage by elephants (Terborgh et al. 2015*a*). Elephants damage trees by pollarding (clipping top branches), breaking limbs, and peeling or ripping bark (Rode et al. 2006), which increase plant susceptibility to damage by parasites, pathogens, and fire (Beuchner & Dawkins 1961). In addition to browsing, elephants modify the environment by trampling vegetation, killing seedlings and saplings, and denuding the ground of plants. Elephant trampling creates and maintains forest clearings and trail systems several meters wide and tens of kilometers long (Blake & Inkamba-Nkulu 2004).

Forest elephants are requisite generalists, consuming over 500 species of plants and a wide range of plant parts (Blake 2002); thus, through herbivory they may affect community-level vegetation structure and species composition. In savannas high rates of elephant disturbance suppress woody vegetation (Cumming et al. 1997; Shannon et al. 2008), which stalls succession, prevents development of the shade canopy (Laws et al. 1970), and allows herbs and grasses to colonize disturbed areas (Omeja et al. 2014). Elephants also alter the composition of the plant community through preferential browsing, which selects for browsing-tolerant plants that invest in chemical or physical defenses (Höft & Höft 1995). The ubiquitous damage to saplings in forest, however, may indicate elephants benefit fast-growing, light-demanding species that can recruit via escape in space and time by growing quickly through the size range of vulnerability to breakage (Poulsen et al. 2013; Osuri et al. 2016).

A World without Forest Elephants

Forest elephants have already been extirpated from large parts of their range (Maisels et al. 2013; Poulsen et al. 2017). Unless poaching is halted, a world without forest elephants is possible, and the effects of their loss will cascade through the ecosystem due to decreased rates of seed dispersal, nutrient recycling, herbivory and physical damage, and indirect ecological effects (Fig. 3). Based on the ecological roles of elephants, we examined how the loss of forest elephants will alter ecological processes to influence forest composition and structure.

Seed Dispersal

The loss of seed dispersal by forest elephants—the "megagardeners of the forest" (Campos-Arceiz & Blake 2011)—will reduce seed movement for many plant species, particularly those with large fruits or seeds (Guimarães et al. 2008; Blake et al. 2009). These plant species will become "Anthropocene anachronisms"—species with fruit traits and phenological patterns unmatched in the existing disperser community (Janzen & Martin 1982). Where forest elephant populations are extirpated, elephant-dispersed seedlings are likely to be less evenly distributed across the landscape and more susceptible to density-dependent mortality (Beaune et al. 2013). Furthermore, the reduction in long-distance dispersal by elephants will likely reduce genetic diversity and impede colonization of new habitats (Nathan 2006; Jordano et al. 2007). Without elephant seed dispersers, the composition of the forest could shift toward a greater relative abundance of species dispersed abiotically and by smaller animals (Terborgh et al. 2008). Because tropical forests are predominately composed of animal-dispersed tree species (Howe & Smallwood 1982) and larger-seeded species attain larger sizes than smaller-seeded trees, the loss of large animals such as elephants is expected to reduce the carbon storage potential of the forest (Poulsen et al. 2013; Bello et al. 2015; Osuri et al. 2016).

Nutrient Recycling

The extirpation of forest elephants will reduce the flow of nutrients at the landscape scale and have potentially global effects on the flux of phosphorous and sodium, as occurred following Pleistocene extinctions (Doughty et al. 2016). Reductions in elephant-mediated nutrient cycling can be expected to reduce soil fertility and tree growth because tropical trees are generally nutrient limited, particularly at younger life stages (Wright et al. 2011; Santiago 2015). Specifically, the loss of elephants may increase the relative abundance of slow-growing species because nitrogen deposition is hypothesized to shift community composition toward early-successional, fast-growing species (Tilman & Lehman 2001). Understory tree seedlings also show greater growth responses to nutrient addition when light availability increases (Thompson et al. 1988); thus, without elephant disturbance to open vegetation, seedlings may be less efficient at nutrient uptake, which compounds the consequences of elephant loss.

Herbivory and Physical Damage

The ecological consequences of declining herbivory and physical damage by elephants may mirror those that followed Pleistocene extinctions: increased abundance of woody plants and shifts in plant structure and composition favoring shade-tolerant (Bakker et al. 2016) and palatable plant species (Gill et al. 2009). In tropical forests specifically, reduced elephant browsing and damage is likely to increase understory stem density of tree seedlings, saplings, and herbaceous vegetation. The loss of understory thinning, particularly of woody saplings, could increase root competition among surviving trees, perhaps slowing tree growth and reducing their eventual size. With a higher density of understory stems, we expect lower light availability and higher competition for resources will limit the emergence of large, carbon-dense trees.

Summary and Hypothesized Long-Term Effects

Through changes in ecological processes, we hypothesize that the absence of forest elephants will Neotropicize tropical forests in Central Africa. Afrotropical forests generally support lower species diversity and lower tree density but greater numbers of large trees and higher aboveground biomass than Neotropical forests (Slik et al. 2013). Thus, we predict the loss of elephants from African tropical forests will reshape species composition, increase stem density, and lower the abundance of large trees (and carbon stocks). Such conditions will have the following broad effects: alter plant community composition, increase stem density, and decrease abundance of large trees.

Plant community composition will be altered via multiple processes. Lower dispersal of large-fruited tree species will result in higher proportions of species dispersed abiotically or by smaller animals. Lower rates of

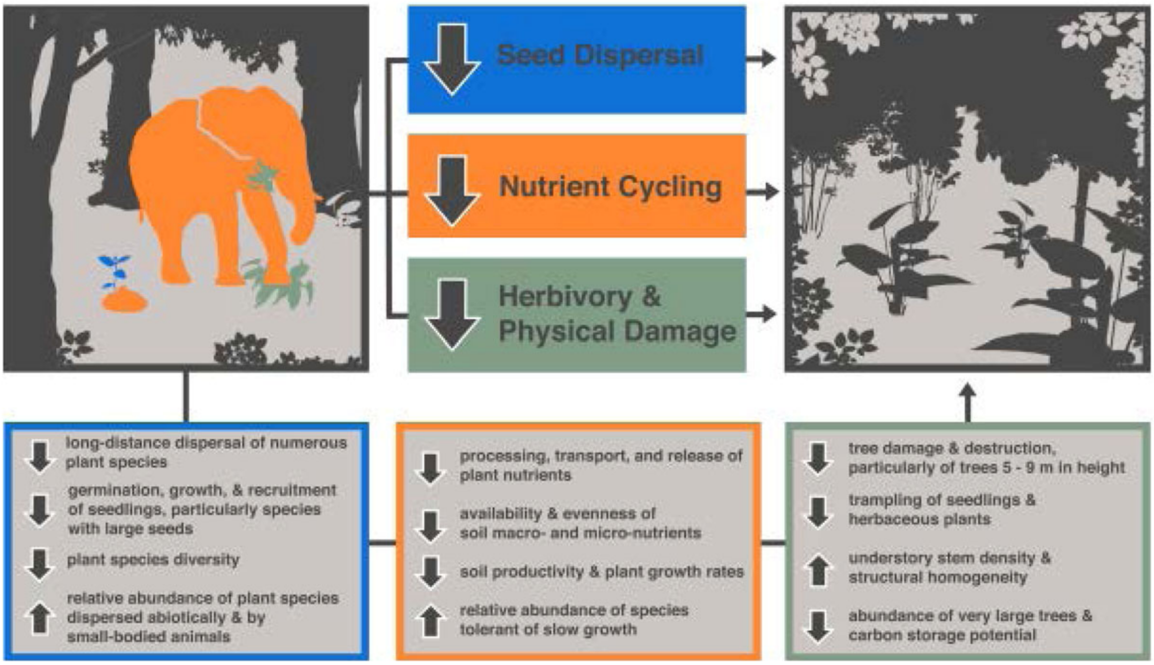

Figure 3. Ecological features (listed in rectangles) of tropical forests that are affected by elephants and the effects of elephant removal on these features (arrows, increase or decrease; top 2 factors in rectangles, immediate changes that will occur with the loss of elephants; bottom 2 factors, long-term changes that will occur with the loss of elephants).

nitrogen recycling and lower rates of vegetation disturbance (reduced light availability) may favor the regeneration of slow-growing, shade-tolerant seedling species. In contrast, undefended, palatable species—which tend to be fast growing and light loving—may also be released from elephant browsing.

Stem density will increase in elephant-free forests as a result of low rates of browsing, trampling of seedlings, and removal of saplings and small adult trees by elephants. Saplings will be released from the "browse trap" (Staver & Bond 2014) and be free to grow past the size at which they are vulnerable to browsing.

Abundance of large trees will be decreased by the loss of seed dispersal by elephants: seed diameter is positively associated with maximum tree height of animal-dispersed trees (Bello et al. 2015). Defaunation of seed dispersers can also increase the spatial aggregation of trees and result in smaller population size and decreased median basal area (Caughlin et al. 2015). At the same time, high stem density in the absence of elephant browsing will lessen the recruitment of emergent wind-dispersed species that require small gaps (Hall et al. 2003). With fewer large trees, carbon storage will likely fall over time (Poulsen et al. 2013; Bastin et al. 2015), particularly because mass growth rate increases continuously with tree size so that large trees fix large amounts of carbon relative to smaller trees (Stephenson et al. 2014).

Understanding Elephant-Free Tropical Forests

Forest elephants are increasingly being compressed into well-protected parks and reserves (Breuer et al. 2016). Assuming a minimum viable population of 100 elephants, with an average home range of 546.8 km^2 (Blake et al. 2008), and an average overlap in home range of 78% (ANPN, unpub. data), elephant populations would only be maintained in protected areas larger than 12,030 km^2. Approximately, 96% of the Central African forest (forest outside protected areas at least 12,030 km^2 in size [UNEP-WCMC 2016]) would be elephant-free and susceptible to our predicted changes. To know with confidence how the loss of elephants will affect forests, multiple questions urgently need answers. To what extent do forest elephants determine forest species composition and structure through seed dispersal, nutrient recycling, herbivory, or indirect effects? Which of these mechanisms most strongly affects forest composition and structure? Are plant species susceptible to extinction from loss of seed dispersal by elephants, or can other animals provide redundant services? How does anthropogenic land use (e.g., roads, timber concessions, agriculture) alter the ecosystem services provided by elephants? Do forest elephants facilitate the recruitment and survival of large trees and thus contribute to carbon sequestration? What is the necessary size of a forest elephant population to maintain its ecological role? What is the optimal configuration (size, distance, etc.) of forest patches and corridors to maintain forest elephant populations and their ecosystem services?

Safeguarding the Future of Forest Elephants

Although our predicted outcomes of elephant declines are probably underway in some places, there is hope for the conservation of forest elephants across part of their range. Recent studies call for recognizing African forest elephants as a unique species (Roca et al. 2001), which could lead to listing them on CITES Appendix 1 and an upgraded IUCN Red List status of critically endangered—an essential step to their conservation. And, international will exists to save the forest elephant. In 2014 several African governments launched the Elephant Protection Initiative to remove stockpiles of ivory from economic use and to ban ivory trade until elephant populations are no longer threatened. Multiple countries have burned their ivory stocks. Encouragingly, in early 2017 China announced a future ban on all domestic ivory trade. Closure of the Chinese market should greatly reduce demand for ivory and lower rates of poaching – remaining markets should be pressured to follow suit.

Preserving the ecological services of forest elephants will entail conservation of the largest area of forested habitat possible. But elephants and forests are caught in the countercurrent of expanding land development in Central Africa. Large-scale land-use planning (e.g., Austin et al. 2017) that maximizes economic development while sustaining elephant populations will be required to conserve functional elephant-inhabited forests. As the last wilderness areas are being attributed to logging, agricultural, and mining concessions (Abernethy et al. 2016), biodiversity corridors need to be equally prioritized to link protected areas and reserves. Corridors can be multiuse areas if settlements are prohibited and roads are policed (Blake et al. 2008; Clark et al. 2009; Poulsen et al. 2011). Planning for elephant conservation must be transboundary (CITES 2010) because poaching leaks across borders, (UNODC 2016). In the vein of Forest Stewardship Council (FSC) and Roundtable for Sustainable Palm Oil (RSPO) certifications, we propose an elephant-friendly habitat certification be awarded to logging concessions, agricultural plantations, ecotourism ventures, and carbon projects that take extra steps to protect elephants from poaching and maintain their habitat. Now is the time to secure a future for elephant-inhabited forests in Central Africa.

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Supporting Information

A list of the articles included in our literature search (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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