Carbon stocks in central African forests enhanced by elephant disturbance

Fabio Berzaghi [1,2,3]*, Marcos Longo [4,5], Philippe Ciais [2], Stephen Blake[6,7], François Bretagnolle[3], Simone Vieira [8], Marcos Scaranello[4], Giuseppe Scarascia-Mugnozza[1] and Christopher E. Doughty [9]

Large herbivores, such as elephants, can have important effects on ecosystems and biogeochemical cycles. Yet, the influence of elephants on the structure, productivity and carbon stocks in Africa's rainforests remain largely unknown. Here, we quantify those effects by incorporating elephant disturbance in the Ecosystem Demography model, and verify the modelled effects by comparing them with forest inventory data from two lowland primary forests in Africa. We find that the reduction of forest stem density due to the presence of elephants leads to changes in the competition for light, water and space among trees. These changes favour the emergence of fewer and larger trees with higher wood density. Such a shift in African's rainforest structure and species composition increases the long-term equilibrium of aboveground biomass. The shift also reduces the forest net primary productivity, given the trade-off between productivity and wood density. At a typical density of 0.5 to 1 animals per km^2, elephant disturbances increase aboveground biomass by 26–60 t ha^{-1}. Conversely, the extinction of forest elephants would result in a 7% decrease in the aboveground biomass in central African rainforests. These modelled results are confirmed by field inventory data. We speculate that the presence of forest elephants may have shaped the structure of Africa's rainforests, which probably plays an important role in differentiating them from Amazonian rainforests.

Megaherbivores and large herbivores (terrestrial vertebrates with body mass greater than 1,000 kg and 45–1,000 kg, respectively) can have profound effects on ecosystems and biogeochemical cycles by consuming biomass, transporting nutrients and changing plant mortality[1–5]. The extinction of most megaherbivores at the end of the Pleistocene induced cascading effects on plant communities and ecosystem functioning[1–3,5]. Megaherbivores and most large herbivores are now endangered, and their disappearance may have important ecological repercussions[1–4]. Elephants, one of the last remaining megaherbivores, are classified as vulnerable (*Loxodonta*) or endangered (*Elephas*) by the International Union for Conservation of Nature Red List[6]. The ecosystem-engineering role of savannah elephants (*L. africana* Blumenbach, 1797) has been studied extensively[7] but much less is known about the role of forest elephants (*L. cyclotis* Matschie, 1900) in African rainforests. Forest elephants are rapidly declining in numbers[8] and have mostly received attention for their role as seed dispersers[9–11]. Forest elephants are found in west and central African forests; they are not found in Amazonia, nor is any comparable species. The presence of elephants in central African rainforests could partly explain some of their distinctive features compared with Amazonian forests. Despite similar climate and soil conditions, central African forests have a lower average stem density (426 ± 11 stems ha^{-1}), larger tree diameters (average ≈ 31 cm) and higher mean aboveground biomass (AGB) (~360–430 Mg ha^{-1} dry weight) compared to Amazonian forests (~600 ± 11 stems ha^{-1}, ~25 cm and ~260–340 Mg ha^{-1}, respectively)[12–14]. Although Amazonia has some high-AGB areas, elephants may contribute to biome-scale differences between the two continents over long timescales. Forest elephants kill and browse trees smaller than 30 cm in diameter that are located on and near trails used for movement; a size class subject to strong light competition[15]. We hypothesize that the chronic thinning of those small trees by elephants alleviates competition for resources in the low canopy strata, allowing surviving trees to attain large sizes—a process that gives rise to higher total AGB stocks at the stand level.

To test this hypothesis, elephant disturbance was incorporated into a mechanistic forest-stand model (ED2[16]; see Methods). The model simulations were evaluated against measurements of tree size and wood density at two Congo Basin sites (see Methods) with contrasting elephant disturbance[11,17]. The ED2 model simulates horizontal and vertical vegetation heterogeneity in long-term forest succession, plant competition for resources leading to mortality and stochastic disturbance events (for example, tree fall). Plant functional diversity in ED2 is represented by three plant functional types (PFTs): early-successional trees (shade-intolerant, fast-growing pioneers, low wood density), mid-successional trees (intermediate) and late-successional trees (shade-tolerant, slow-growing, canopy-dominant and high wood density) (see the PFT parameters in Supplementary Table 1). We represented elephant disturbance by increasing the mortality of trees with diameters <30 cm based on observations of plant survival rates from browsing or trampling[18,19]. Mortality was inversely proportional to tree size and proportional to animal population density[4]. We performed idealized site-level simulations to analyse the sensitivity of forest properties to different animal densities that are representative of central Africa. These densities ranged from 0.25 to 5 individuals km^{-2} (refs. [8,20]).

Here we show that elephant disturbance changes forest structure, increases AGB and average tree diameter, and reduces stem density,

[1]Dipartimento per la Innovazione nei sistemi Biologici, Agroalimentari e Forestali, University of Tuscia, Viterbo, Italy. [2]Laboratoire des Sciences du Climat et de l'Environnement, IPSL-LSCE CEA/CNRS/UVSQ, Gif-sur-Yvette, France. [3]Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, Dijon, France. [4]Embrapa Agricultural Informatics, Campinas, Brazil. [5]NASA Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA, USA. [6]Department of Biology, Saint Louis University, St. Louis, MO, USA. [7]Wildlife Conservation Society, New York, NY, USA. [8]Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Campinas, Brazil. [9]School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ, USA. *e-mail: fabio.berzaghi@lsce.ipsl.fr
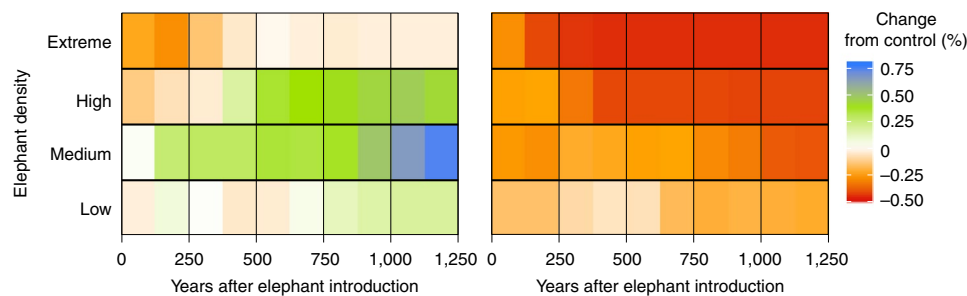
Fig. 1 | Simulated stand-scale AGB and NPP in response to different elephant population densities in the Congo Basin. The percentage changes in ABG (left) and NPP (right) were calculated relative to a control simulation (without elephants) with equilibrium values of 388 Mg ha^{-1} (AGB) and 33 Mg ha^{-1} yr^{-1} (NPP). Elephants were introduced at $t=0$, after the control simulation. Elephant densities (individuals km^{-2}) have been aggregated into bins: low (0.25), medium (0.5, 0.75, 1 and 2), high (3 and 4) and extreme (5).

consistent with the hypothesis that megaherbivores may have contributed to the differences between African and Amazonian rainforests[14]. These findings have implications for carbon policy and elephant conservation and demonstrate the transformative role of forest elephants and large herbivores and the far-ranging ecological consequences of their past and present extinctions.

Modelled effects of elephant disturbance

We found that, starting from an initial steady state with no elephants (see Methods), the introduction of elephants causes a temporary (125–250 yr) reduction in AGB that is caused by the increase in small tree mortality. This transient reduction is then reversed and higher, long-term AGB than without elephants is obtained at low, medium and high elephant densities (Fig. 1). This new long-term equilibrium is reached between 250 and 1,000 yr after elephants are introduced (Supplementary Fig. 1). Intermediate and high elephant densities lead to the highest increase in equilibrium AGB (77% and 43% higher than without elephants, respectively; Fig. 1). At low elephant density, however, the increase in AGB is only about 18%. At extreme densities, the equilibrium AGB is similar (−4%) to the control forest. In contrast to AGB, simulated net primary productivity (NPP) at the stand level is systematically lower when elephants are present (Fig. 1).

This reduction in NPP ranges between 42% and 48% below the control value at medium, high and extreme elephant densities, and 22% at low density. Within the stand, however, the NPP of large trees (diameters >50 cm) is 90 kg C yr^{-1} compared to 65 kg C yr^{-1} without elephants (Supplementary Fig. 2). Thus, the reduction in stem density due to thinning by elephants clearly favours the growth of large trees by reducing competition for light, water and space (Fig. 2a). Changes in AGB and NPP are also associated with changes in the relative amounts of the different PFTs (Fig. 2b and Supplementary Fig. 1). Elephant disturbance reduces (and in the extreme case suppresses) the recruitment of early- and mid-successional PFTs. These two PFTs are suppressed directly by elephants and indirectly by changes in understory environmental conditions (light and water used by larger trees; Fig. 2a). Conversely, late-successional trees become dominant and eventually account for 47–100% of the total basal area (Fig. 2b). Late-successional trees in ED2 are prescribed on the basis of observations to be less productive and to have a higher wood density than the other two PFTs[21]. Consequently, the high abundance of late-successional trees in forests appropriated by elephants reduces NPP, but also increases the equilibrium AGB. Figure 2a summarizes the directional changes in the processes that affect the relative amounts of PFTs, forest structure and, ultimately, NPP and AGB. At medium and high elephant densities, the fraction of large trees increases but the fraction of 30–50 cm diameter trees is conversely reduced by half (Fig. 2c). Overall, stem density is lower in elephant-disturbed

forests (Supplementary Fig. 3). With elephants, the total leaf area index (LAI, a measure of canopy cover) is within 5% of the control, but the LAI of large trees is ~70% higher than without elephants; this leads to ~50% less light reaching the understory, which further inhibits the growth of small trees (Supplementary Fig. 2). Large trees capture more water and water stress of seedlings (diameters <0.2 cm) increases by a factor of three with elephants, whereas the water stress of trees >10 cm is slightly alleviated (up to 2–4%) (Supplementary Fig. 2). These modelled responses of LAI and light availability have been observed in experimentally thinned plots[22]. Overall, elephants have a thinning effect that transforms the structure of tropical forests (Fig. 2c and Supplementary Fig. 4). This transformation creates environmental conditions that favour canopy-dominant, slow-growing, late-successional trees that can persist at low light and water levels until they emerge from the understory.

Observed effects of elephants from forest inventory data

We then evaluated the model predictions against inventory data from two sites. One site includes both elephant-disturbed plots (near or on elephant trails) and undisturbed plots (Ndoki, Republic of Congo[17]; 0.56 individuals km^{-2}). The other site is completely undisturbed (LuiKotale, Democratic Republic of Congo[11]). LuiKotale can be considered a valid reference site because of the relatively large surveyed area (15 ha) and because it has no logging or other disturbances, unlike the nearly all other surveyed sites that lack elephants[8]. The data summarized in Table 1 confirm key ED2 result that AGB and tree size are higher, and that stem density is lower, in the elephant-disturbed plots (Table 1, Fig. 2, Supplementary Figs. 3 and 5 and Supplementary Table 3). The AGB at Ndoki is 690 Mg ha^{-1} compared with 582 Mg ha^{-1} at LuiKotale (Table 1)—a relative difference of 16%, which is comparable to the model output shown at intermediate densities (Fig. 1, Fig. 3a and Table 1). The fraction of small trees with diameters of 10–30 cm is also lower at Ndoki compared with LuiKotale, which is comparable to the model results (Fig. 2c, Table 1 and Supplementary Fig. 3). At Ndoki we can also compare disturbed and undisturbed plots. The disturbed plots have a higher abundance of large trees (diameters >70 cm; $P=0.1$) contributing to the higher AGB (Supplementary Table 3). A significantly higher wood density of trees, particularly small ones (diameters <30 cm), is also observed in the Ndoki plots that have been disturbed by elephants (Table 1); this is consistent with the simulated effect of the dominance of the hardwood late-successional PFT (Fig. 2b and Table 1). The opposite is observed at LuiKotale, where both small trees (10–30 cm diameter) and poles (<10 cm diameter) have lower wood densities (0.69 kg m^{-3} and 0.72 kg m^{-3}, respectively) than larger trees (0.73 kg m^{-3} cm). These differences alone would lead to AGB gains of a similar magnitude to our modelled results (Fig. 3a) and are statistically significant (Wilcoxon test
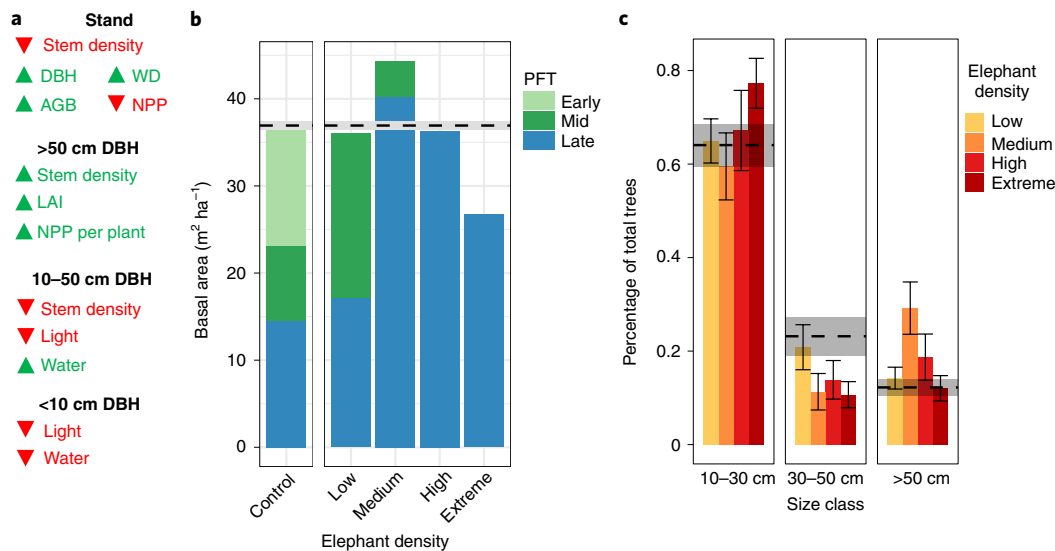
Fig. 2 | Stand-scale effect of elephant disturbance. a, Changes in stand properties and resource availability by size class. Gains (green) and losses (red) are relative to the control forest. DBH, diameter at breast height. **b**, Long-term effect of the prescribed density scenarios on equilibrium basal area and the composition of PFTs. **c**, Relative percentage of trees in each size class across density scenarios. Prescribed elephant densities have been aggregated as described in Fig. 1. The dashed lines and shaded areas represent the control (no elephants) at equilibrium and its standard deviation. The error bars indicate the standard deviation at equilibrium of the elephant-disturbed forests.

Table 1 | Comparison between sites disturbed and undisturbed by elephants

	AGB (Mg ha^{-1}) (CI)	Stem density (Ind. ha^{-1}) (CI)	Percentage of small trees (CI)	Mean tree size (m^2) (CI)	Mean wood density (kg m^{-3}) (median)		
Size class	All	All	<30 cm	All	All	<30 cm	≥30 cm
Disturbed							
Ndoki (4.6 ha)	690 (549–810)	372* (326–417)	72** (67–74)	0.114*** (0.086–0.142)	0.69 (0.69)	0.71*** (0.71)	0.64*** (0.67)
ED2 model (stand)	672 (659–700)	240 (207–277)	61 (55–65)	0.145 (0.110–0.18)	0.82 (0.81)	0.79 (0.79)	0.84 (0.88)
Undisturbed							
Ndoki (23 ha)	439 (424–454)	366 (359–373)	NA	NA	0.64 (0.64)	NA	NA
ED2 model (stand)	382 (377–387)	372 (329–415)	64 (59–69)	0.095 (0.087–0.103)	0.71 (0.71)	0.71 (0.71)	0.71 (0.71)
LuiKotale (15 ha)	582 (490–671)	436* (410–461)	80** (79–81)	0.076*** (0.074–0.078)	0.72 (0.71)	0.72*** (0.70)	0.73*** (0.75)
Central Africa[12]	429 (NA)	425 (414–436)	NA	0.074 (NA)	0.65 (NA)	NA	NA

The total area inventoried at each site is shown in parentheses. All refers to trees with diameter >10 cm (forest inventories usually do not measure trees <10 cm). Details on AGB calculation and reference datasets are provided in the Methods. The ED2 model with elephants is the average of stand-scale results at a prescribed elephant density of 0.5–1 individuals km^{-2}. Statistical comparisons are across sites (Ndoki disturbed versus LuiKotale only), except for wood density (within-site). Asterisks indicate significance level for statistical comparison: *$P < 0.001$; **$P < 0.0001$; ***$P < 0.00001$. CI, confidence interval (shown in parentheses).

P value < 0.0001), but note the wood density at Ndoki is not higher overall than that at LuiKotale. Given the inverse correlation between trees' individual growth rates and their wood densities[23], NPP at Ndoki may be reduced by elephants (as predicted by ED2), but we did not have woody NPP estimates from successive inventories to confirm this finding.

Long-term effects of elephant extirpation on biomass

After evaluating the ED2 results against the limited site-level inventories available, we then outlined a rough estimate of how elephants have altered the biomass of the entire central African forest (2.2 million km^2). In the real world, elephant density is unlikely to be uniform because individuals are localized near trails, like those at Ndoki, where they feed on fruits. Their migration results in small-scale gradients in disturbance and forest structure. This small-scale heterogeneity of elephant disturbance was not

explicitly modelled, but was instead parameterized (see Methods). We defined the elephant 'range' as the percentage of an area occupied by elephants. Inside the elephant range, even when they are endemic, there is always a fraction of undisturbed forest. The pre-hunting early-nineteenth-century forest elephant population in central African forests was estimated at 1 million individuals[24] (mean density of 0.5 individuals km^{-2}). At such a density, ~10% of the forest would have been disturbed by elephants—a reasonable assumption that matches observed heterogeneous elephant disturbance across the landscape[18] (see Methods). By the 1980s, elephant population dropped to 0.17–0.4 million and reached a density of 0.11–0.36 individuals km^{-2} (refs. [24,25]); by 2011 it had dropped to 0.1 million at a density of 0.16 individuals km^{-2} (ref. [8]) (Fig. 3b). This nearly complete extirpation of elephants is estimated to have caused a reduction in the equilibrium biomass of central African forests of ~7% (2.9 ± 0.06 PgC). This reduction may not be completely
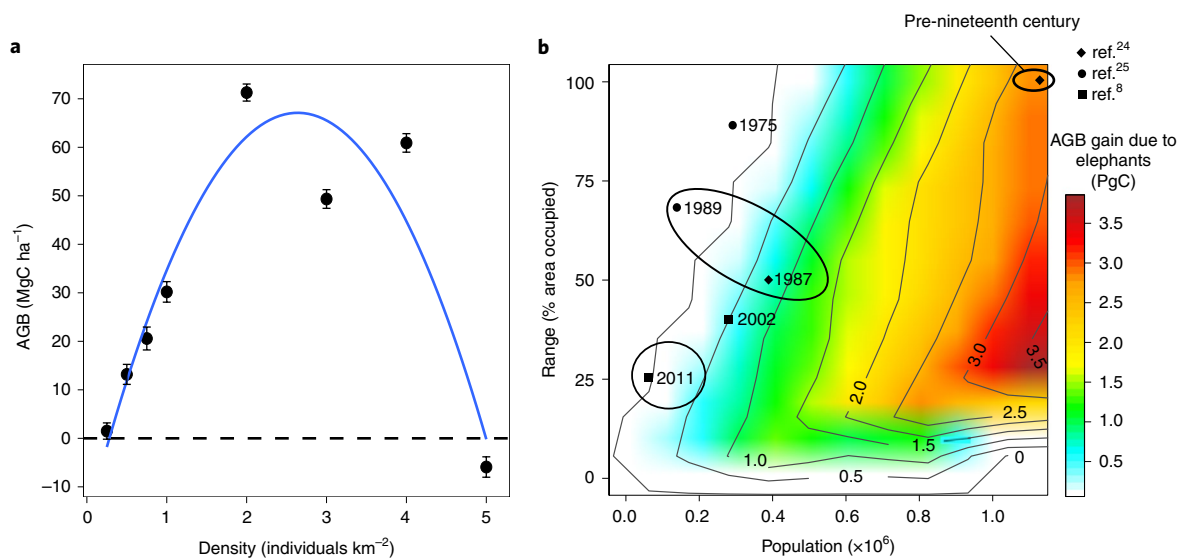
Fig. 3 | Summary of the regional effect of elephant disturbance on AGB. a, Change in AGB carbon (upscaled from stand to ha, see main text and Methods) compared with the control forest as a function of the prescribed elephant densities. The blue line is the fitted polynomial regression. Error bars represent confidence intervals. **b**, Elephant-induced increase in AGB across the central African rainforest zone (total area = 2.2 million km²) as a function of the total population and range occupied by elephants (see the main text and Methods). Historical population estimates from previous studies were used to calculate the (committed) loss of biomass carbon caused by progressive elephant extirpation[8,24,25].

realized yet, given the slow response of forests to changes in elephant densities (Fig. 1), but this estimate can be viewed as a committed change in AGB.

Ecological and conservation implications

The selective removal of young trees by elephants is similar to the ecological process of self-thinning, which empirically relates a decrease in tree density to an increase in biomass per unit area[26]. Elephants kill small trees and target light-demanding pioneer species that are more palatable and have fewer defenses against herbivores than slow-growing species[27]. Elephants thus by-pass the natural succession initiated by tree fall that creates the gaps that allow the recruitment of light-demanding species with low wood density—a process that constrains AGB[28]. Short-term (10–30 yr) variations in forest properties when elephant densities change are subtle and mainly involve the demography of young trees (Table 1), as reported previously[19]. The effect of elephants becomes more evident in the medium term (50–150 yr; Fig. 1). Modelled long-term changes (250–1,000 yr) are more difficult to evaluate because there is also interplay with climate disturbances (for example, drought, thunderstorm, and fire[29]) on such timescales. The field inventory data in Table 1 offer a snapshot of the short-term effect of elephants, which disappeared from Luikotake ~30 yr ago, and a window on future demographic changes. The effect on AGB could not be fully evaluated from the limited field data in Table 1. Elephants congregate around large fruiting trees, but we lack data from former trail intersections in LuiKotale to check whether the previous presence of elephants in those spots had favoured species with high wood densities. Other processes associated with elephants were not accounted for in ED2. Seed dispersal and nutrient transport may affect plant species composition, carbon stocks[10,30] and primary productivity at large scale and over very long periods[31]. Elephants may also further suppress tree recruitment and maintain light gaps through frequent visitations, although this mechanism has been observed more frequently in logged forests[19]. The large-scale effects over the entire African forest depend critically on the actual area under elephant disturbance, and on the spatial patterns of trails[17]; we accounted for this in our estimate in a highly simplified manner (see Methods).

More information is needed on the frequency and extent of this type of disturbance.

Elephant disturbance in ED2 was calibrated with observations from elephant studies, and evaluated against limited inventory measurements. Overall, the modelled impact of elephants is consistent with distinctive characteristics (low stem density, abundance of large trees and high AGB) of central African forests[12,14]. This suggests that, compared with Amazonian forests, megaherbivores may have played an important role in structuring African rainforests and increasing their biomass. It is interesting to note that in our simulations, elephants caused a transition from a closed canopy to slightly more open vegetation at only the highest density (Supplementary Fig. 1)—a finding that does not support the hypothesis that megaherbivores alone could convert forest to open woodlands[5]. Rather, at a typical density of 0.5–1 individuals km⁻², elephants induce higher equilibrium AGB. The projected decrease of ~7±0.1% of carbon stocks is more than the estimated loss in tropical America and Africa due to the disappearance of large-seeded trees and their dispersers[30], and comparable with future impacts of climate change[32]. Elephant conservation may reverse this trend, which would represent a carbon storage service of US$43 billion at a conservative carbon stock price of US$15 MgC⁻¹ (ref. [33]). The effect of elephants should also be considered when modelling climate–carbon–nutrient interactions using Earth system models. Our results also point out the need to consider the forest elephant as a separate species to the savannah elephant[18], given their different disturbance behaviour and diverging roles as ecosystem engineers. This study provides evidence for the wide-reaching impacts of forest elephants on rainforest ecosystem functioning and carbon cycling. In this context, the value of the ecosystem services provided by the forest elephant and other megaherbivores should be reassessed in relation to carbon storage policy, forest management and conservation.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at https://doi.org/10.1038/s41561-019-0395-6.

References

1. Gill, J. L. Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytol.* **201**, 1163–1169 (2014).
2. Bakker, E. S. et al. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl Acad. Sci. USA* **113**, 847–855 (2016).
3. Malhi, Y. et al. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl Acad. Sci. USA* **113**, 838–846 (2016).
4. Berzaghi, F. et al. Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles—the potential of vegetation models. *Ecography* **41**, 1934–1954 (2018).
5. Owen-Smith, N. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* **13**, 351–362 (1987).
6. *The IUCN Red List of Threatened Species* (IUCN, 2018); http://www.iucnredlist.org/
7. Guldemond, R. & Van Aarde, R. A meta-analysis of the impact of African elephants on savanna vegetation. *J. Wildl. Manage.* **72**, 892–899 (2008).
8. Maisels, F. et al. Devastating decline of forest elephants in Central Africa. *PLoS ONE* **8**, e59469 (2013).
9. Hawthorne, W. D. & Parren, M. P. E. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *J. Trop. Ecol.* **16**, 133–150 (2000).
10. Blake, S., Deem, S. L., Mossimbo, E., Maisels, F. & Walsh, P. Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468 (2009).
11. Beaune, D., Fruth, B., Bollache, L., Hohmann, G. & Bretagnolle, F. Doom of the elephant-dependent trees in a Congo tropical forest. *For. Ecol. Manage.* **295**, 109–117 (2013).
12. Lewis, S. L. et al. Above-ground biomass and structure of 260 African tropical forests. *Phil. Trans. R. Soc. Lond. B* **368**, 20120295 (2013).
13. Avitabile, V. et al. An integrated pan-tropical biomass map using multiple reference datasets. *Glob. Change Biol.* **22**, 1406–1420 (2016).
14. Terborgh, J. et al. The African rainforest: odd man out or megafaunal landscape? African and Amazonian forests compared. *Ecography* **39**, 187–193 (2016).
15. Farrior, C. E., Bohlman, S. A., Hubbell, S. & Pacala, S. W. Dominance of the suppressed: power-law size structure in tropical forests. *Science* **351**, 155–157 (2016).
16. Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y. & Moorcroft, P. R. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *J. Geophys. Res. Biogeosci.* **114**, G01002 (2009).
17. Blake, S. & Inkamba-Nkulu, C. Fruit, minerals, and forest elephant trails: do all roads lead to Rome? *Biotropica* **36**, 392–401 (2004).
18. Wing, L. D. & Buss, I. O. Elephants and Forests. *Wildl. Monogr.* **19**, 3–92 (1970).
19. Omeja, P. A. et al. Changes in elephant abundance affect forest composition or regeneration? *Biotropica* **46**, 704–711 (2014).
20. Poulsen, J. R. et al. Poaching empties critical Central African wilderness of forest elephants. *Curr. Biol.* **27**, R134–R135 (2017).
21. Reich, P. B., Walters, M. B. & Ellsworth, D. S. From tropics to tundra: global convergence in plant functioning. *Proc. Natl Acad. Sci. USA* **94**, 13730–13734 (1997).
22. Huang, S., Bartlett, P. & Arain, M. A. Assessing nitrogen controls on carbon, water and energy exchanges in major plant functional types across North America using a carbon and nitrogen coupled ecosystem model. *Ecol. Model.* **323**, 12–27 (2016).
23. Wright, S. J. et al. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* **91**, 3664–3674 (2010).
24. Milner-Gulland, E. J. & Beddington, J. R. The exploitation of elephants for the ivory trade: an historical perspective. *Proc. R. Soc. Lond. B* **252**, 29–37 (1993).
25. Michelmore, F., Beardsley, K., Barnes, R. F. W. & Douglas-Hamilton, I. A model illustrating the changes in forest elephant numbers caused by poaching. *Afr. J. Ecol.* **32**, 89–99 (1994).
26. Pillet, M. et al. Disentangling competitive vs. climatic drivers of tropical forest mortality. *J. Ecol.* **106**, 1165–1179 (2018).
27. Poorter, L. & Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**, 1733–1743 (2006).
28. Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *J. Ecol.* **98**, 106–116 (2010).
29. Maley, J. et al. Late Holocene forest contraction and fragmentation in central Africa. *Quat. Res.* **89**, 43–59 (2018).
30. Osuri, A. M. et al. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* **7**, 11351 (2016).
31. Doughty, C. E. et al. Global nutrient transport in a world of giants. *Proc. Natl Acad. Sci. USA* **113**, 868–873 (2016).
32. Friedlingstein, P., Cadule, P., Piao, S. L., Ciais, P. & Sitch, S. The African contribution to the global climate-carbon cycle feedback of the 21st century. *Biogeosciences* **7**, 513–519 (2010).
33. *State and Trends of Carbon Pricing 2018* (World Bank, 2018).

Author contributions

F. Berzaghi and C.E.D. conceived the study and S.V., M.L. and M.S. helped refine the design. F. Berzaghi led the writing with inputs from all co-authors. F. Berzaghi and M.L. developed the ED2 model. F. Berzaghi analysed data and created figures with inputs from P.C., C.E.D. and S.B.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41561-019-0395-6.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to F.B.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Methods

ED2 model of stand structure. We used the Ecosystem Demography 2 (ED2) model[16] to simulate the dynamics and structural properties of a tropical lowland forest within a grid cell 90×90 km^2. ED2 is a deterministic vegetation model that represents the heterogeneity of a forest by simulating plant ecophysiological processes and competition for resources among plants. The climate and soil within the simulated area (grid cell) are homogeneous and representative of the conditions around the LuiKotale area (Democratic Republic of Congo), but the microenvironment changes according to the horizontal and vertical structure of the vegetation. The simulated area is divided into patches (equivalent to a few hectares with similar disturbance history) to capture the heterogeneity of the vegetation, which is composed of cohorts of trees with similar properties (size, age, PFT and successional stage; for further model details see refs. [16,34]).

PFTs are commonly used in vegetation models to represent the functional diversity of plants present in the simulated domain in a simplified way. There are three evergreen tropical PFTs in ED2: early-successional, mid-successional and late-successional trees. Each PFT is defined by roughly 80 parameters that describe biomass and height allometry, leaf properties, mortality, growth rate and so on. The main differences among these tropical PFTs are highlighted in Supplementary Table 1. In brief, early-successional trees are fast-growing pioneer plants that thrive in light gaps, have low wood density and higher intrinsic mortality (aging mortality). Late-successional trees are canopy-dominant, shade-tolerant, slow-growing plants with high wood density and lower intrinsic mortality. Mid-successional trees are a compromise between the two, but slightly closer to the late-successional PFT.

Model integration and evaluation at LuiKotale. The model was driven by climate data from the National Centers for Environmental Prediction and National Center for Atmospheric Research[35] for 1979 to 2015 at a 6 h temporal resolution and 1.8° spatial resolution, with prescribed CO$_2$ concentrations. The soil type was set to xanthic ferrasol based on the FAO soil database[36]. We ran an initial spin-up simulation from bare ground (just seeds and a few seedlings for each PFT) for 500 yr to reach a steady state in which the number of plants, biomass, basal area and so on had minimal (<1%) year-to-year variation. We then compared the average of the last 100 yr of the model output with the forest inventory data from LuiKotale and published data from tropical African forests[12,37]. The model output compared reasonably well to the LuiKotale and central Africa data in terms of stems ha^{-1}, basal area, mean diameter and AGB (Supplementary Table 2). Some differences in the distribution of size classes can be observed (Supplementary Fig. 5). It should be noted that the forest inventory is only a snapshot in time of a small fraction of the landscape, whereas the model simulates transient vegetation and presents an average over a large area. The simulated relative amounts of each PFT comprise a realistic mix of early-, mid- and late-successional types (Supplementary Fig. 6). Modelled NPP (average 17.5 Mg ha^{-1} yr^{-1}) compares reasonably with field measurements in tropical Africa (13–16 MgC ha^{-1} yr^{-1}; ref. [37]).

Implementation and parameterization of elephant disturbance. Disturbances in ED2 trigger plant mortality according to specific plant properties. Disturbances are defined by survivorship (the fraction of plants surviving a disturbance event, S), and by the annual rate (λ) at which a disturbance is applied to a fraction of the simulated area (A). The survivorship of plants affected by a disturbance event is defined by:

$$S = 1 - (1 - \exp(-\mu)) / A \qquad (1)$$

where μ is the instantaneous mortality rate and A is the fraction of the area which is disturbed each year. The rate (yr^{-1}) at which disturbance is applied to the fraction of the simulated area is defined by:

$$\lambda = \ln(1 - A) \qquad (2)$$

We parameterized elephant disturbance by reviewing *L. cyclotis* literature that provides quantitative measurements of plant mortality caused by this species. We excluded other elephant species because their foraging behaviour differs from *L. cyclotis*[38]. Most studies agree that forest elephants feed and interact with trees of size <10 cm DBH (diameter at breast height; referred to as small trees) in more than 90% of the cases and up to 97% (refs. [18,39,40]). The effect of elephants on the mortality rate of small trees and their specific feeding behaviour is unknown in closed-canopy forests and observed stem breaks are not a reliable measure of tree mortality[19,39,41]. An estimate of small-tree survivorship due to foraging of highly destructive herbivores is reported from wild boar (*Sus scrofa*) in Malaysian forests, where 93.4% of saplings had resprouted after breakage[38]. This finding might suggest that the survival rate of dicot plants (the main diet of elephants in closed-canopy African forests) might be higher than 80%, as dicots can resprout after elephant browsing or trampling. Forest elephants also have a direct effect on trees with DBH between 10 and 30 cm, which are occasionally uprooted or pushed over. The mortality in this size class has been estimated to be between 1.0 and 1.4% (refs. [18,19]). Trees >30 cm DBH are mostly subject to debarking and no correlation has been found between debarking and tree mortality[42]. Thus, to model elephant disturbance we considered two separate size classes: 0–10 cm and 10–30 cm; these classes were given separate survivorship values. We implemented the new elephant disturbance

in ED2 by defining a size-dependent and PFT-independent survivorship with two parameters: S_{st}, survivorship of small trees (<10 cm DBH) and S_{lt}, survivorship of large trees ($\geq$10 and <30 cm DBH).

We also defined the elephant disturbance rate (λ_e) on the basis of the fraction of area disturbed by elephants (A_e). We calculated λ_e by substituting A with A_e in equation (2) for each prescribed elephant density. Elephant densities (expressed in individuals km^{-2}) and their corresponding A_e values (in parentheses) are: 0.25 (5), 0.5 (10), 0.75 (14), 1 (19), 2 (38), 3 (57), 4 (76) and 5 (95). The comprehensive study by Wing and Buss[18] is the only source of information to estimate A_e as a function of elephant density (ρ_{eph}). Wing and Buss estimated that during 1 yr, the elephant population in Kibale Forest Reserve (density of 0.75 individuals km^{-2}) interacted with 14% of all forest stems within the area occupied by elephants (their range). We assumed that $A_e = 14\%$ because 98% of stems used by elephants are less than 10 cm DBH and 75% are less than 2.5 cm DBH. As the vast majority of stems in a forest are <10 cm DBH (and with no other data available), 14% is a first approximation of A_e at a density $\rho_{eph} = 0.75$ individuals km^{-2}. The S_{st} value was set conservatively at 90%, which represents a 1.4% annual mortality at $\rho_{eph} = 0.75$—a reasonable estimate considering the destructive nature of elephant foraging. The S_{lt} value was set to 90%, calculated from the 1.4% annual mortality reported by Omeja et al.[19] (same Kibale population studied by Wing and Buss[18]). The data from Omeja et al.[19] were used because Wing and Buss did not report mortality rates, only the percentage of pushed-over trees (1.08%). The mortality and survivorship values we have chosen should be considered conservative; a view that is confirmed by comparison to another study[40]. The S_{st} estimation is uncertain and we performed a sensitivity analysis to evaluate its effect on model results (see the sensitivity analysis in the Supplementary Information).

Modelling protocol and runs at variable elephant densities. The initial 500 yr spin-up period without elephants was used to create a steady-state forest. This steady state set the initial conditions for the second phase, in which elephants were introduced. The second phase lasted for 1,500 yr and included a control simulation with zero elephant density and a set of simulations with variable densities. We chose to simulate 1,500 yr to evaluate long-term trends and identify any unstable states. We parameterized density scenarios on the basis of our initial assumption at a density of 0.75 individuals km^{-2} associated with a disturbed area of 14% by assuming a constant ratio between A_e and ρ_{eph}. This assumption implies that following a change in density, elephants will disturb a higher (or lower) fraction of the landscape but that the local effect, survivorship of plants (S_{st} and S_{lt}) will remain constant within the disturbed area. In other words, at any ρ_{eph}, the local effect will be the same (90% survivorship) but the disturbance is applied to an area proportional to the density of elephants. This is a reasonable assumption, given that the group size of forest elephants is usually small (between two and four individuals[43]) with minimal overlap between groups[44], except when they gather in forest clearings. Following this assumption, we created ρ_{eph} scenarios based on a range of previously reported ρ_{eph} across central Africa. The density scenarios include (in individuals km^{-2}): low (0.25), medium (0.5, 0.75, 1 and 2), high (3 and 4) and extreme (5). Low and medium densities are observed more often. When poaching is limited or absent, ρ_{eph} could be between 0.5 and 1.0 km^{-2} (refs. [8]). Higher densities have been documented less frequently than low and medium ones. Still, elephant densities of 2–3 km^{-2}, and in some periods up to 4–5 km^{-2}, appear in the literature for different parts of central Africa[20,45–47]. In the model, 5 individuals km^{-2} disturb 95% of the landscape, a limit scenario in which a population is constrained within a certain area. Given the assumption concerning the A_e:ρ_{eph} ratio, values farther away from the baselines of 14% for A_e and of 0.75 for ρ_{eph} should be interpreted with caution, because at higher densities the effect over a large area might deviate from this assumption. As the area simulated in ED2 is not tied to a specific geographic location, the results can be interpreted in terms of elephant density and extrapolated to any area (from the hectare to regional scale), assuming comparable environmental conditions and forest properties. However, elephant disturbance in the model is not spatially explicit, so the simulations are more representative of a stand-scale average effect. In reality, elephant movement in closed-canopy forests occurs along trails and is influenced by water and fruit availability[17]. Note that movement does not necessarily involve disturbance once elephant trails are defined. However, the continuous use of trails by elephants is needed to maintain them. To address this model limitation and scale up the model results to the regional scale, we use A_e values of 5, 10, 14, 19, 38, 57, 76 and 95 to calculate estimates of AGB at the regional scale (AGB$_{regional}$; in Mg ha^{-1}), using a weighted average based on ED2 results for each simulated elephant density:

$$\text{AGB}_{regional} = \text{AGB}_{elephant} \times (A_e) + \text{AGB}_{control} \times (1 - A_e) \qquad (3)$$

where AGB$_{elephant}$ (in Mg ha^{-1}) is the modelled AGB at steady state from the different elephant density simulations, and AGB$_{control}$ (in Mg ha^{-1}) is from the simulation without elephants. To calculate the effect on AGB across the whole central African rainforest zone (2.2 million km^2), we first calculated elephant density on the basis of historical estimates of elephant populations and elephant range[8,24,25]. We define the range as the fraction of central African rainforest occupied by elephants. We then multiplied AGB$_{regional}$ at the elephant density of interest by the range derived from each historical estimate, thus this calculation already accounts for the area disturbed/undisturbed within the total range.

Forest inventory data. We obtained forest inventory data from the Ndoki Forest (NF[17]) (1.5–3° N, 16–17° E) near the Nouabalé-Ndoki National Park, Republic of Congo, and from LuiKotale research site (LK[11]) (2°47′ S, 20°21′ E) at the edge of the Salonga National Park, Democratic Republic of the Congo. Both sites are located in lowland primary forest with very low human disturbance and no permanent human settlements nearby; they have comparable environmental conditions (climate and soil)[11,17]. Elephants have been absent from LK for more than 30 yr (ref. [11]), whereas NF is one of the last strongholds of forest elephants in the Congo Basin, with a population density of 0.56 individuals km^{-2} (ref. [17]). Forest inventory data include all trees with DBH ≥ 10 cm. LK data comprise 15 plots of 1 ha (ref. [11]), and NF data include 230 paired small plots of 200 m^2 at elephant trail intersections and at random locations between 50 and 100 m from the intersection[17]. LK data also include trees with DBH <10 cm and height >200 cm, referred to as elephant-disturbed in the main text. The high abundance of elephant-preferred adult trees in the Ndoki plots, particularly the ones on trail intersections[10,17], suggests that elephants have been visiting the trails areas for a long time and influenced plant recruitment and forest structure. Note that trail intersections tend to form near large fruiting trees, thus half of the Ndoki data contain some spatial bias in size-class distribution, but is not statistically significant from other datasets (Supplementary Table 3). We added to our comparison a set of 23 additional 1 ha plots from NF from other sources[48,49]. These plots (called Ndoki undisturbed in the main text and Table 1) were randomly sampled across NF, as opposed to the other NF plots that were chosen to be either on the trails or around them. We consider these 23 plots as undisturbed, although we acknowledge that some might contain elephant trails. However, as elephant disturbance applies to only a fraction of the landscape, these undisturbed plots may still contain a small proportion of disturbed trees but offer a contrasting view compared with the rest of the Ndoki plots. We classified forest inventory data according to their elephant disturbance history: no disturbance for the LK plots and NF undisturbed, and continuous disturbance (the NF disturbed plots from ref. [17]). The NF plots cover a relatively small area (4.6 ha), but their census gives one of the few datasets for pristine forest in the lowland Congo Basin[17] where the effect of elephants can be measured. For comparison, Omeja et al.[19] surveyed 5 ha to estimate tree mortality due to elephants. As elephant poaching is highly correlated with roads, most forests where elephants have disappeared have been logged or have been under concession[8,48] (Supplementary Section B). Compared to sites where biomass and forest structure is impacted by anthropogenic effects, LK is far away from roads and has not been disturbed by fire or logging, offering an ideal reference site for the absence of elephants. Forest plots are rare in undisturbed forests without elephants. We found only two sites across central Africa with conditions similar to LK, but could not confirm the timing of elephant disappearance (Supplementary Section B).

Statistical analysis. We compared results from the variable elephant density simulations against the control (no elephant disturbance). We aggregated elephant density simulations with similar results in terms of AGB/NPP dynamics and new steady-state values. Simulations were grouped into four bins (individuals km^{-2}): low (0.25), medium (0.5, 0.75, 1 and 2), high (3 and 4) and extreme (5). We identified the periods of lowest variability in forest properties using a moving standard deviation with a window size of 100 yr for the medium-term effects (first 250 yr after elephant introduction) and a window size of 200 yr for the long-term effects. A moving standard deviation was necessary because vegetation changes through time. We also disentangled how alterations in ecological processes at the stand level contribute to variations in forest structure and function.

We calculated AGB following ref. [50] and used the Global Wood Density Database[51] to determine species wood density. Wood density data were assigned first by using data from tropical Africa, by species and then by genus. If no match was found, we used data from other tropical regions. Any unidentified species were assigned the plot-averaged wood density[52]. Previously published data from NF provided AGB, wood density and stem density[12,48,49]. To analyse the differences in forest structure across and within the two sites we used the Student's *t*-test (two-sided) for normally distributed data and the Wilcoxon sum-rank test (two-sided) for non-normally distributed data. Confidence intervals were calculated with non-parametric bootstrapping ($n = 10,000$ for both sites). For the ED2 model data and published central African data, we calculated confidence intervals with the standard deviation. We also fitted a Weibull function to the distribution of tree sizes to validate the model and compare model simulations. The parameters of the Weibull distribution are shape (β) and scale (α); these determine the form of the distribution: β is an index to represent the relative frequency of small trees, a higher β indicates a higher relative frequency of small trees and α is a close approximation of the median of the distribution[53].

Sensitivity analysis. We performed a sensitivity analysis on the parameter S_{st}, which represents the effect of disturbance on small plants, and was the parameter estimated with the highest uncertainty. The 0–10 cm DBH size class contains the greatest number of plants in a stand and mortality in this size class plays an important role in vegetation dynamics[15], including long-term legacy effects. The effect of λ_c is already shown through the prescribed density scenarios and the sensitivity analysis was performed including these scenarios. The analysis of sensitivity to S_{st} was run for 1,500 yr at each prescribed density, three values of S_{st}

were tested: 90% (baseline), 80% and 70%. The sensitivity analysis revealed that the model is rather insensitive to changes in small tree survivorship because most results are within 10% of each other (Supplementary Fig. 7). Prescribed elephant density and survivorship values can affect the path and time to reach a new steady state after introducing elephants. Overall, the differences among values of S_{st} affected the long-term trends after 250–300 years more strongly, indicating that long-term results are more sensitive to different survivorship values than medium-term results (Supplementary Fig. 7). High survivorship, the one used as our main parameterization, produced slightly lower AGB at low elephant densities and slightly higher AGB at high elephant densities compared with other survivorship values. These results reinforce our findings that at low elephant densities thinning increases AGB, whereas at higher densities, more intense thinning produces the opposite effect. In the 0.5 individuals km^{-2} scenario, a typical elephant density, the variability due to a lower survivorship of small trees is between 3% and 7%, which indicates a low sensitivity of the model and minimal uncertainty in our stand-scale and regional results. Further considerations and results for S_{st} are presented in Supplementary Section A.

Data availability
Forest data are available for NF upon request to S.B. and for LK at www.forestplots.net. Central Africa forest data are available in the supplementary material of Lewis et al.[12] and Slik et al.[49] and in the main text of Poulsen et. al.[48].

Code availability
The ED2 model code is available at https://github.com/fabeit/ED2/tree/master/ED/src.

References
34. Moorcroft, P. R., Hurtt, G. C. & Pacala, S. W. A method for scaling vegetation dynamics: the ecosystem demography model (ed). *Ecol. Monogr.* **71**, 557–586 (2001).
35. Kalnay, E. et al. The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteorol. Soc.* **77**, 437–471 (1996).
36. *Harmonized World Soil Database* Version 1.2 (FAO, accessed 29 August 2018); http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en
37. Moore, S. et al. Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. *Glob. Change Biol.* **24**, e496–e510 (2018).
38. Terborgh, J., Davenport, L. C., Ong, L. & Campos-Arceiz, A. Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity. *Biotropica* **50**, 84–89 (2017).
39. Blake, S. *The Ecology of Forest Elephant Distribution and its Implications for Conservation* PhD thesis, Univ. Edinburgh (2003).
40. Ssali, F., Sheil, D. & Nkurunungi, J. B. How selective are elephants as agents of forest tree damage in Bwindi Impenetrable National Park, Uganda? *Afr. J. Ecol.* **51**, 55–65 (2013).
41. Terborgh, J. et al. Megafaunal influences on tree recruitment in African equatorial forests. *Ecography* **39**, 180–186 (2016).
42. Struhsaker, T. T. et al. Tree mortality in the Kibale Forest, Uganda: a case study of dieback in a tropical rain forest adjacent to exotic conifer plantations. *For. Ecol. Manage.* **29**, 165–185 (1989).
43. White, L. J. T., Tutin, C. E. G. & Fernandez, M. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *Afr. J. Ecol.* **31**, 181–199 (1993).
44. Schuttler, S. G., Blake, S. & Eggert, L. S. Movement patterns and spatial relationships among African forest elephants. *Biotropica* **44**, 445–448 (2012).
45. Carroll, R. Status of the lowland gorilla and other wildlife in the Dzanga-Sangha region of southwestern Central African Republic. *Primate Conserv.* **7**, 38–41 (1986).
46. Morgan, B. J. Group size, density and biomass of large mammals in the Réserve de Faune du Petit Loango, Gabon. *Afr. J. Ecol.* **45**, 508–518 (2007).
47. White, L. J. T. Biomass of rain forest mammals in the Lopé Reserve, Gabon. *J. Anim. Ecol.* **63**, 499–512 (1994).
48. Poulsen, J. R., Clark, C. J. & Palmer, T. M. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* **163**, 122–130 (2013).
49. Slik, J. W. F. et al. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob. Ecol. Biogeogr.* **22**, 1261–1271 (2013).
50. Chave, J. et al. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* **20**, 3177–3190 (2014).
51. Chave, J. et al. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **12**, 351–366 (2009).
52. Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003–1006 (2009).
53. Lima, R. A. F., Muller-Landau, H. C., Prado, P. I. & Condit, R. How do size distributions relate to concurrently measured demographic rates? Evidence from over 150 tree species in Panama. *J. Trop. Ecol.* **32**, 179–192 (2016).