TROPICAL FOREST

Long-term collapse in fruit availability threatens Central African forest megafauna

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Afrotropical forests host much of the world’s remaining megafauna, although these animals are confined to areas where direct human influences are low. We used a rare long-term dataset of tree reproduction and a photographic database of forest elephants to assess food availability and body condition of an emblematic megafauna species at Lopé National Park, Gabon. Our analysis reveals an 81% decline in fruiting over a 32-year period (1986–2018) and an 11% decline in body condition of fruit-dependent forest elephants from 2008 to 2018. Fruit famine in one of the last strongholds for African forest elephants should raise concern about the ability of this species and other fruit-dependent megafauna to persist in the long term, with potential consequences for broader ecosystem and biosphere functioning.
Instead we consider it likely that climate changes experienced at the site have contributed to this shift in reproduction. Global warming has caused minimum daily temperature to increase, on average, by 0.25°C per decade at Lopé (23), which may be a key factor in reduced reproduction for some tree species that rely on a critical minimum temperature to trigger flowering (18). Rainfall has simultaneously decreased at the site by 75 mm per decade (23); thus, all tree species might be suffering because of water stress (24).

Given the decline in fruit since 1986, it is likely that fruit-dependent wildlife—such as forest elephants, great apes, monkeys, and many bird species—has been affected. Long-term population data are not available for these species at Lopé. Other measures of population health, such as body condition, can be used to gauge population responses to environmental change over relatively short periods. Forest elephants, the largest frugivores in the ecosystem (9), have been consistently photographed by researchers and visitors to the site since the late 1990s, resulting in a large photographic database (>80,000 photos). We used this database to evaluate annual and seasonal trends in the external body condition of forest elephants between 1997 and 2018, hypothesizing that elephant body condition has declined along with reduced food availability. Elephant body condition in photos was scored systematically by means of a custom-built web application and user interface (22). Scorers (n = 6 individuals) did not have access to the time and date of photographs, nor to the research question and hypothesis. Scoring effort (number of photos viewed per scorer) varied, but we found high agreement among scorers who used a standardized test database (mean intraclass correlation coefficient of 0.89, n = 200 photos). A total of 2823 photos met the strict image-quality criteria for scoring, and we used linear mixed effects models (LMMs) to quantify changes in elephant body condition (accounting for elephant age) over the full 21-year period, as well as separately for the first 11 years (1997 to 2007) and last 11 years (2008 to 2018) of data.

We detected long-term declines in forest elephant body condition at Lopé (LMM). For the period between 1997 and 2018, mean body condition of the population declined by 5.0% for all age classes. However, uncertainty was high, ranging from a small improvement in body condition to a large decline [LMM; 95% confidence interval (CI) = +0.9 to −11.2%; table S6]. The change was most pronounced in the second half of the time period (2008–2018) when body condition declined, on average, by 11.1% (LMM; 95% CI = −4.3 to −15.6%; Fig. 2A and table S6). Body condition varied seasonally in the first half of the time period (1997–2007), appearing to track fruit availability (dipping in June and peaking after the long dry season) without any obvious lag at the monthly resolution of this analysis (Fig. 1B). The sharp drop in body condition in November during 1997–2007 was inconsistent with fruit availability, but closer inspection of the data indicated that this finding was highly influenced by one very thin individual (body condition score = 2), recorded in November 1999, out of only three photos available for this calendar month during this period (table S7). In the 2008–2018 period, the peak in body condition after the long dry season had disappeared (Fig. 2B and table S6). However, the sparse data for 1997–2007 and high uncertainty in the CIs for seasonality in body

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**Fig. 1.** Changes in ripe fruit encounters and availability from 1986 to 2018 at Lopé National Park, Gabon. (A) Results from analysis with a binomial GLMM (table S4), showing the change in probability of encountering ripe fruit over time for any given tree in any given month (solid lines) and 95% CIs (dashed lines). Summed raw data are plotted in fig. S1. (B) Interannual changes in ripe fruit availability for all species monitored consistently throughout the time period. Fruit availability is calculated as a proportion of maximum theoretical fruit availability; ripe fruit availability equals 1 when all trees in a subset have 100% canopy cover of ripe fruit for 12 months in a year. (C) Results from analysis with a binomial GLMM (table S4), showing the seasonal change in probability of encountering ripe fruit for any given tree in each calendar month contrasted for the years 1987 and 2017 (points and solid lines) and accompanying 95% CIs (dashed vertical lines).
condition mean that comparisons between the early and late time periods should be made with caution (tables S6 and S7).

It is not known whether the changes observed in body condition in this study have affected forest elephant population health or dynamics in the study area. However, studies of African savanna elephants show that environmental stressors can have substantial long-term consequences for both individual fitness and population dynamics, with reproductive females and calves particularly affected (25). Reduced food availability could also act in synergy with other factors (such as disease) to magnify negative physiological consequences (table S8). Although the biological mechanisms and consequences of declining body condition are unclear at this point, the effects on forest elephant populations across the region are unlikely to be benign, particularly when coupled with illegal hunting, habitat loss, and habitat degradation (3).

These declines in both plant reproduction and elephant body condition are indicative of system-wide change and are expected to have disproportionate impacts on the functioning and metabolism of the ecosystem. A reduction or displacement of historic populations of large frugivores in this region, along with diminished availability of seeds, could lead to collapse of seed dispersal (8), landscape-level shifts in habitat structure (26), reduction of carbon stocks (27), and potential for increased competition with humans for food (28). However, long-lived plant and animal species are able to buffer environmental change to a certain extent (7), and the broad diet of forest elephants (9) means that alternative food sources could offer some relief. Nonetheless, environmental stress can have lifelong negative impacts on elephant survival and fitness (25), and the impacts of these changes should be closely monitored.

The long-term plant and animal datasets presented here are rare for the tropics, and it is possible that such changes may be occurring elsewhere, undocumented. These data serve as a reminder that even where direct human pressures are low, plant and animal communities may not be protected from the creeping influences of the Anthropocene. Coordinated international efforts to relieve direct human pressures and to halt and reverse climate change will be critical to saving the remaining megafauna and megaflora of the African tropics and preserving their specialized roles in the functioning of our biosphere.

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SUPPLEMENTARY MATERIALS
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Materials and Methods
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References (1–28)
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