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Megaherbivores modify forest structure and increase carbon stocks through multiple pathways.

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Abstract

Megaherbivores have pervasive ecological effects. In African rainforests, elephants can increase aboveground carbon, though the mechanisms are unclear. Here we combine a large unpublished dataset of forest elephant feeding with published browsing preferences totaling > 120,000 records covering > 700 plant species, including nutritional data for 145 species. Elephants increase carbon stocks by: 1) promoting high wood density plants via preferential browsing on leaves from low wood density species, which are more palatable and digestible; 2) dispersing seeds of trees that are relatively large and have the highest average wood density among tree guilds based on dispersal mode. Loss of forest elephants could cause a 6-9% decline in aboveground carbon stocks due to regeneration failure of elephant-dispersed trees and an increase in abundance of fast-growing low wood density plants. These results show the major importance of megaherbivores in maintaining diverse, high-carbon tropical forests. Successful elephant conservation will contribute to climate mitigation at a scale of global relevance.

Significance Statement

Very large herbivores (body mass >1000 kg), also known as megaherbivores, can significantly influence the structure and functioning of ecosystems. Most of our knowledge on the ecological role of megaherbivores is based on the African savanna; much less is known about forest-dwelling megaherbivores. We show that forest elephants can promote higher aboveground

carbon through browsing preferences and seed dispersal. Forest elephants browsing promotes high carbon density plants through the consumption of less carbon-dense plants. Elephant-dispersed trees are larger and have higher densities of carbon compared to trees with other dispersal modes. These results highlight the importance of forest elephants and other megaherbivores for maintaining biodiversity and high carbon stocks in tropical forests.

Main text

Introduction

Megaherbivores (body mass > 1000 kg) can have profound effects on vegetation, carbon stocks, and nutrient cycling[1–3]. However, knowledge on the ecosystem role of megaherbivores comes predominantly from African savanna ecosystems[1,4]. In tropical forests, initial evidence suggests that these large herbivores might also have profound effects[2,5–7]. Until the late Pleistocene, tropical forests hosted a variety of large- and megaherbivores playing critical roles in seed dispersal networks and in the dynamics and functioning of tropical forest communities due to their unique combination of ecological traits[2,8,9]. Today, Asian elephants (*Elephas maximus*) and African forest elephants (*Loxodonta cyclotis*) are the only forest-dwelling megaherbivores with extensive ranges and unique ecological traits: large size, diverse behaviors, and highly varied diets. Examples of “ecosystem engineering” have been observed in forest elephants (“elephants”) through seed dispersal[6,10] and disturbance, which includes consumption, breakage, and trampling[11–13]. Results from a process-based vegetation model suggested that by reducing tree density, elephants could promote the growth of larger trees with consequent drop in light and water availability in the understory. As a result, forests with elephants hold more aboveground carbon (AGC) because of a greater abundance of large late-successional tree species which have high wood density (WD)[5]. The same study reported that the average WD of smaller trees (diameter < 30 cm) was lower compared to larger trees at a site where elephants were extirpated 30 years ago. However, these results have not been validated experimentally. Also, Berzaghi et al. (2019) evaluated the effect of elephants in terms of a generic elephant-induced mortality not associated with any particular behavior. We aim to explore empirically the other pathways through which megaherbivores' interactions with ecosystems might influence forest structure and AGC, notably via more delicate processes such as herbivory and seed dispersal[6,14,15]. The high daily food consumption (100-200 kg[16,17]) and broad diet (over 350 species[18]) of elephants suggest that feeding preferences could drive shifts in tree species composition by promoting growth and survival of less-desirable browse species. Folivores prefer leaves high in protein and minerals and low in fiber and chemical defenses (e.g., phenolics and tannins)[17]. Among woody plants, slow-growing shade-tolerant species invest more in structural and chemical defenses compared to fast-growing gap-colonizing species[19]. Because WD is negatively correlated with growth rate[20], we hypothesize that high WD species are less palatable and less digestible compared to low WD species. As a result, elephants would promote high AGC by preferentially browsing leaves of low WD plants.

We also investigate the connection between trees dispersed exclusively by elephants ("Obligate" trees *sensu*[6]) and AGC. Large-seeded animal-dispersed trees have relatively large diameters, high WD, and contribute significantly to AGC[21]. Forest elephants are prodigious seed dispersers, moving more seeds of more species than any other animal species[6], but the contribution of Obligate trees to forest structure and AGC has not been evaluated. We hypothesize that the combined effects of elephant browsing, which *decreases* fitness of preferred food species, and seed dispersal, which *increases* fitness of dispersed species, are likely to have profound effects on forest structure and AGC. If supported, these two hypotheses would confirm the ecosystemic role of elephants in promoting high carbon stock forests by increasing the fitness of large, high WD trees[5]. To test these hypotheses, we combined forest inventories and elephant feeding data collected in Ndoki (Republic of Congo) and forest inventories in LuiKotale (Democratic Republic of Congo) with published diet preferences data across the Afrotropics. We analyzed nutritional properties of leaves and fruit as a function of elephant browsing preferences and WD to investigate the mechanisms driving elephant feeding choices and the influence of these choices on AGC. We then synthesized, based on literature, quantitative measures of the effects of elephants on forest properties and processes and schematically organized these findings. This synthesis identifies research gaps and provides input for modeling the ecological impacts of elephants using statistical and process-based models. Our results greatly enhance our understanding of the contribution of elephants to forest functioning and are key to evaluating the consequences of past megaherbivore extinctions and to informing conservation and management policy.

Results

Nutritional properties influence elephant food choices

We investigated the mechanisms that influence food preferences by combining data from a global database of plant nutritional values[22] with forest elephant feeding data from seven different sites across tropical Africa: West (N = 4), Central (2), and East (1 site from two separate studies). The nutritional data covered 145 plant species and 1343 records of essential biomolecules (crude proteins, minerals, fat, and carbohydrates), structural and defensive compounds (fibers, tannins, and phenols), which reduce food palatability and digestibility (% of assimilated food), and gross energy. Results from the ordinal logistic regression suggest that elephants prefer to feed on leaves low in fibers, tannins, and phenols (Fig. 1A). We found moderate to strong evidence that less-preferred species are more likely to contain higher percentage of these defensive compounds compared to highly preferred plants ($p = 0.004$-0.063). As the percentage of defensive compounds of leaves increases from 0-10% to 30-70%, the probability of a tree to be least preferred by elephants increases from ~37% to ~65-90%, depending on the defensive property (Fig. 1A). Protein and minerals increase the probability of a tree species being in the high-preference category compared to medium preference ($P \leq 0.001$), whereas nonstructural carbohydrates and fat decrease this probability ($P \leq 0.05$). We found no consistent pattern across preference groups in the other nutritional properties of leaves (Figs. 1A and S1). It appears that the main determinants of elephant preferences are defensive structural properties rather than essential biomolecules. These choices do not appear to be dictated by the relative abundance of plant species. Both at Ndoki NP and Kibale NP, very strong evidence suggests that preference is inversely correlated to availability with very similar slopes and fit in the linear model of both sites (Fig. S2, $R^2 = 0.51$-62, $P < 0.001$). The analysis of fruit properties consumed and not consumed by elephants also provides very strong evidence that elephant-consumed fruits are larger ($P < 0.0001$) and contain more fiber and minerals ($P < 0.01$) compared to non-consumed fruits (Fig. 1B). We found moderate evidence for differences between the two groups in total tannins, sugars, and fat (Fig. 1B, $P < 0.05$), the latter being the only property that was higher in non-consumed fruit. No statistical differences were found in crude tannins and proteins across the two groups. At Ndoki, the analysis of the relationship between total diameter at breast height (DBH), a possible proxy for total fruit availability, and percentage of detection in dung did not reveal any significant relationship (Fig. S3A). However, the correlation between presence of seeds in dung and fruit volume revealed a positive correlation (Fig. S3B, $R^2 = 0.16$, $P = 0.003$). This may suggest that larger fruit are selected for their size and not for their abundance. However, detectability of seeds during dung sampling might be biased by other factors (see discussion). Overall, the analysis of nutritive properties suggests that elephant seek more palatable and less fibrous leaves and large fruits, which are also high in sugars and minerals but have the drawback of being more fibrous (i.e., less digestible) and less fatty.

The comparison between nutritional properties of fruits and leaves consumed by elephants revealed very strong evidence that, compared to fruit, leaves contain roughly twice as much protein ($P < 0.0001$) and minerals ($P < 0.0001$), but six times less sugars and non-structural carbohydrates ($P < 0.0001$) (Figs. 1C and S4). Moderate evidence suggests that fruits contain less phenols and more protein compared to leaves. There were no significant differences in gross energy content between the two organs (Fig. 1C). Thus, fruits provide short-term usable energy, although gross energy content is similar to leaves, which instead contain biomolecules useful for longer-term physiological processes. Forest elephants are making deliberate choices that are mostly independent of plant availability and more dependent on nutritional or morphological (i.e., fruit) properties.

Wood density is related to nutritional quality of leaves and fruits

We then investigated if WD is a good predictor of leaf and fruit nutritional properties. Results from linear regression models revealed strong to very strong evidence that for leaves, WD is positively correlated with fibers ($R^2 = 0.11$, $P < 0.001$) and phenolics ($R^2 = 0.12$, $P = 0.007$) (Fig. 2A). There was weak to moderate evidence of a negative correlation between WD and fat ($R^2 = 0.14$, $P = 0.025$) and a positive correlation with gross energy ($R^2 = 0.07$, $P = 0.057$) and tannins ($R^2 = 0.04$, $P = 0.084$). We found no evidence of a correlation between WD and protein or minerals, and little to weak evidence of a negative correlation with total nonstructural carbohydrates (Fig. 2A and S5). Whereas leaves from higher WD plants had higher content of structural and defensive properties, we found strong evidence that fruits from higher WD plants were lower in essential biomolecules compared to fruits produced by lower WD species (Fig. 2). In particular, we observed a negative correlation between WD and minerals, proteins, and fat ($R^2 = 0.07\text{-}0.15$, $P < 0.001$) and a positive correlation with sugars ($R^2 = 0.16$, $P = 0.014$) (Fig. 2B). Note however that total nonstructural carbohydrates (sugars plus starches) did not show any significant correlation with WD (Fig. S5B). The data revealed weak to moderate evidence of WD being positively correlated with fruit phenols and fiber content ($R^2 = 0.03\text{-}0.10$, $P = 0.043\text{-}0.085$) (Fig. 2B). No other statistically-significant relationship was found for the other nutritional properties (Fig. S5B).

Forest elephants browse most frequently on low wood density species

The elephant feeding data and browsing preferences included 197,557 feeding records from 730 plant species for which WD could be determined (eight total studies, Table S1). The actual number of feeding records is higher because three studies did not report their total sample size (Table S1). At all sites, except Bia National Park and Santchou Wildlife Reserve, feeding preference metrics were reported in terms of relative preference for single species in relation to all consumed plants. These metrics could be assimilated into three groups indicating high, intermediate, and low preference (Methods). Data from Ndoki included number of feeding events and quantity consumed, and, along the two sites mentioned above, were not included in the global analysis. Results from the ordinal logistic regression provided strong evidence that globally the probability of a species being more preferred decreases as WD increases across all and between low and medium groups (Fig. 3, P = 0.003-0.027); in the aggregated model, the average WD was systematically lower in higher preference groups but statistically different only between the low and high groups (Fig. 3, T-test - P < 0.01). At Ndoki, the only site where both feeding frequency and quantity consumed were available, we also found very strong evidence that higher probability of preference was associated with decreasing WD (Fig. 3, P <0.0001). We found very significant differences between medium and high (Ordinal regression, P <0.0001) and low and high (T-test, P <0.0001) preference groups at Ndoki. At Tai and Kibale (1996 study) similar patterns were found with strong to weak evidence, respectively (Fig. S6). Data from Bia provided moderate evidence that the probability for high preference increases with WD (P = 0.026). However, this study did not report site-relative preferences and many species were only recorded as browsed once, resulting in a large number of species in the low preference group (see Methods and discussion for further considerations). At Satchou Wildlife Reserve, there was no correlation between preference rank and WD based on 16 species (Fig. S6). In five out of seven studies, there was moderate to very strong evidence that the high preference group had the lowest WD compared to the intermediate and/or low preference groups (Fig. 3 and S6). Only at Bossematie there was no significant trend. The aggregated sites, Ndoki, and Tai analyses provided moderate to very strong evidence that the WD of trees dispersed by elephants was higher compared to the WD of species browsed by them (Fig. 3). No other statistical differences between WD of fruit and browse were found at Bia where comparisons were possible. Overall, these results are compatible with the hypothesis that elephants increase tree community WD through dispersal of higher WD species and browsing of lower WD species.

Our data from Ndoki (understory and overstory) and LuiKotale (overstory) showed moderate to strong evidence that high WD species are slightly more abundant than low WD ones with abundance measured as a percentage of total stems or total DBH (R^2 = 0.05-06, P = 0.003-0.019); the linear model explains however only a small fraction of the variability (Fig. S7-S8). As shown previously for nutritive properties of leaves, elephants seem to make specific choices regardless of the abundance of species. For example, in Ndoki understory vegetation plots, *Rinora welwitschii* and *Diospyros bipindensis* were recorded 559 and 468 times respectively (from a dataset of 6548 tree stems from at least 151 species, see Methods). Yet, of 5458 feeding events, only two involved *D. bipindensis* and *R. welwitchii* was never browsed.

Elephant-dispersed trees are larger and have higher wood density compared to trees with other dispersal modes

We identified five dispersal modes in Ndoki and LuiKotale: Gravity/dehiscence (GD), wind, elephants and other animals (Non-Obligate), elephants (Obligate), and Other-Animals[6,23] (total of 307 species, complete list in Dataset S1). The analysis of the variation of WD as a function of dispersal mode revealed that Obligate species had the highest average WD in both sites (Fig. 4A). However, at LuiKotale, only GD, Obligate and Non-obligate species had statistically different WD (P ≤ 0.05). At Ndoki, data showed moderate to very strong evidence that Obligate species had statistically higher WD compared to Non-obligate, Other animal and wind dispersed but not GD species. Wind-dispersed (Ndoki) and Non-obligate (LuiKotale) species had the lowest WD. The total number of species identified at LuiKotale (n = 103) was almost half that of Ndoki (n = 204), we thus urge more caution when interpreting these results from LuiKotale.

The distribution of stem size classes by dispersal mode was similar at the two sites (Fig.4B). Obligate and wind-dispersed tree communities were characterized by few smaller trees, a higher number of larger trees, and are overrepresented in the 125-250 cm range compared to trees with other dispersal modes (Fig. 4B). Obligate trees represent the largest proportion of stems with diameter > 150 cm in LuiKotale (35-75%) and second largest of stems with diameter 125-225 cm in Ndoki, 18-38%, depending on size class. The proportion of wind-dispersed trees also increased with size class at both sites. Gravity-dispersed, Non-obligate and Other-animals trees are most abundant in the lower size classes between 40-125 cm (Fig. 4B). This distribution of stem size across dispersal modes might reveal the long-term history of these forests emerging after the recolonization of savannas as late as 800-250 year ago[24].

Contribution of elephant-dispersed trees to aboveground carbon

The distribution of aboveground carbon in trees (diameter ≥ 40 cm) grouped by dispersal mode reveals diverse patterns in Ndoki and LuiKotale (Fig. 5). In Ndoki, AGC is more evenly distributed among dispersal modes. Abiotically-dispersed trees account for ~50% and Obligate for ~15% of AGC. In LuiKotale, trees dispersed by Other-animals store 52% of AGC and ~19% is stored in Obligate trees (second largest biomass pool). At Ndoki, our sampling of vegetation was slightly biased toward the monodominant *Gilbertiodendron dewevrei* forest, which occupies a proportion of Ndoki[18] following watercourses, as do forest elephants. If *G. dewevrei* forest was removed from the analysis, and only mixed species *terra firma* forest considered, the contribution of Obligate species would increase by ~2-3% in DBH classes > 40 cm and > 70 cm, respectively. When considering only larger trees (diameter ≥ 70 cm), the percentage of AGC stored increases in Obligate (23% LuiKotale and 19% Ndoki) and abiotically-dispersed trees (57% Ndoki) (Fig. 5). Notably, at both sites the few Obligate species have the highest relative contribution to AGC, despite their low stem count (i.e. highest AGC to stem ratio represented by bar widths in Fig. 5). This is explained by their high WD, highest AGC per cm of diameter, and high relative abundance in the large size classes (diameter > 125 cm) (Fig. 4B). The loss of forest elephants likely greatly diminishes or prevents the recruitment of Obligate trees in addition to negatively affecting Non-Obligate species[6,23]. We quantified the loss of AGC by simulating a replacement of Obligate trees with random trees with other dispersal modes proportionally to their relative total DBH (Methods). The loss of AGC was estimated to be 9.2% (s.d. ± 0.07) at LuiKotale and 5.8% (s.d. ± 0.02) at Ndoki. Thus, the "other" trees cannot completely compensate the contribution of Obligate trees to AGC. The important role of large trees in AGC[25,26] and the widespread decline of forest elephants make the plight of Obligate species critical for the future of AGC in African tropical forests.

Ecological processes influenced by elephants

Both savanna and forest elephants are the largest megavertebrates in their respective ecosystems, and there are similarities in their ecological roles in the physical and trophic structuring of ecosystems. The effects of savanna elephants on their environment have been heavily studied[1], yet few studies have quantified the impacts of forest elephants. We synthesized the literature and selected studies that provided quantifiable measures of the mechanisms of ecosystem engineering by elephants expressed in terms of rates, equations, or data. Of all the possible ecological processes influenced by elephants[27], only a few have been quantified and most of them only once or twice. Many other studies exist on seed dispersal or browsing preferences but we could not quantify, or generalize with equations, their consequences on ecosystem properties. Savanna and forest elephants alike topple small trees to access foliage, scar and debark trunks but the impacts of these foraging effects on mortality in forests are poorly quantified (Table 1). Data on debarking and scarring and forest properties (forest openness, stem density, AGC, and WD) come from single studies (Table 1). Only one study quantified forest properties as a function of elephant trails[28]. However, a few general conclusions can be drawn from our synthesis. The annual mortality rate inflicted by elephants to large trees (DBH >10 cm) is between 1-2% which is similar to the background mortality of African tropical forests[20]. The mortality of seedling and saplings is several times higher compared to large trees. Distance from trails is a key parameter when assessing the effect of elephants on forest properties. There is also a clear relationship between canopy openness, reduced regeneration, and elephant preference, however this has not been estimated in more quantitative terms such as visitation frequency or biomass consumption. Less robust conclusions can be drawn on forest elephant impacts on the density of small trees and the mortality rate of large trees due to debarking.

Discussion

We have shown that elephant browsing preferences are likely driven by leaf nutritive values rather than plant abundance. Low WD and frequently-browsed plants produced more digestible leaves containing less structural and defensive properties. Fruit preferences were tightly associated with fruit–size and possibly mineral and sugar content; fruit from high WD plants appeared to contain more sugars and less fat, which are important nutritional properties in fruits. Seed surveys in dung do not provide a quantitative measure to completely assess if fruit preferences are also affected by fruit abundance. Across their range, African forest elephants browse most frequently on tree species with low WD and consume fruit from high WD species (Fig. 3). Our results at Ndoki accounted also for quantity consumed, a critical parameter for assessing browsing preferences, and confirmed this general trend. The exception of Bia NP could be due to the history of the forests in this park as it was extensively logged around the middle of the 20th century. Bia NP has abundant presence of woody lianas and climbers both in the forest and in elephant diets (more than 60% of all species consumed[29]) compared to the other side where trees dominate the diet. Probably the intense opening of the canopy changed drastically the composition of plant species. These results strongly support our hypothesis that elephant browsing increases the AGC of central African forests by reducing the fitness of preferred fast-growing species and by promoting the survival and growth of slow growing high WD species. Previous studies also suggested that if elephants are extirpated from forests, the community average WD declines and composition might shift towards an alternative state dominated by lianas, fast-growing and abiotically-dispersed species[5,6,30]. The slightly higher abundance of high WD species and low abundance of elephant-preferred plants might suggest that elephants contribute in keeping a balance between low and high WD species within the forest. Another study reported that the abundance of elephant-preferred species did not decline overtime[31], which might explain why elephant-preferred species remain at low abundance but do not disappear.

Elephants also influence AGC by dispersing seeds of high WD tree species which are also over-represented in large sizes (Fig. 4). The reason for a higher relative abundance of Obligate trees in larger size classes is unclear, but may be due to the combination of life history traits of large seeded species, phylogenetic signal, and forest succession history. Wood density is correlated with structural strength, low mortality, and resistance to decay which favor large size and longevity (though slow growth means that attaining large size takes longer for these species)[32,33]. However, some of the largest trees in the forest are also fast growing, wind dispersed species of low WD (e.g. *Triplochiton scleroxylon* and *Ceiba pentandra*). Whatever the underlying reasons for their large size and high WD, Obligate trees contribute significantly to AGC. Declines in abundance or the complete extirpation of forest elephants will therefore reduce recruitment[6] and result in an important reduction in AGC, estimated at 6-9% at our two study sites. Many other Non-Obligate tree species might also experience reduced recruitment rates because elephants contribute to a large proportion of their seed dispersal[6].

The current knowledge base on the processes and properties of forest that are influenced by elephants is better developed in the early stages of plant development (Table 1). Elephant density (individuals/km^2) is not always reported; this parameter is useful when evaluating the magnitude of elephant effects on forest properties and processes, particularly when extrapolating results to other areas. We suggest that studies should report the equations of fitted regressions, which would be useful for modelling approaches. In light of the important relations between nutritive properties, feeding preferences, and WD, we also suggest that feeding studies of forest-dwelling herbivores also consider these plant properties. These data will help better understand the contribution of species to tropical forests carbon cycling. Many processes and properties have received less attention or have been evaluated in more qualitative terms. For example, trampling, unrooting, and other mechanical non-feeding processes may have profound effects on forest structure, light regimes, soil compaction, etc.[34] . There is a lack of repeated experiments in different sites to verify if locally-observed effects are consistent across sites and to evaluate the relation between elephant density and the magnitude of the observed change.

Yet the current knowledge provides a good starting point to better characterize elephant effects in modeling studies.

Our results add further evidence that megaherbivores contribute to enhance AGC in tropical forests through a variety of mechanisms. Until the late Pleistocene, many large herbivores inhabited Amazonian and southeast Asian tropical forests and could have had a significant effect on the functioning of those ecosystems[2,4,7]. The low protein and mineral content of fruit might limit the maximum body mass attainable by obligate frugivores, who might not be able assimilate enough of these nutrients to sustain all bodily functions over the long-term[17]. This information might help to estimate diet composition of (extinct) forest-dwelling megaherbivores based on maximum daily dry matter intake and nutritional requirement[17].

The consequences of the loss of elephants we describe on AGC will take place over multiple generations of trees. However, the combination of climate change, extreme climatic events (e.g., droughts) and land use change are occurring over years and decades and could accelerate changes in AGC. Logging is systematically removing the largest elephant- and wind dispersed (*Entandrophragma* spp.) trees across the entire Congo Basin outside of protected areas. When they are not being hunted, forest elephants preferentially use light gaps in secondary forest because they can find abundant secondary, fast growing, vegetation. If a functional elephant population fills disturbed areas and light gaps with elephant-dispersed high WD species, then the carbon sequestration begins immediately; if the gaps are filled with fast-growing species the opportunity is lost. Maintenance of forest elephants in logged and naturally-disturbed forest will be critical in an immediate wildlife-driven mitigation response to climate change[35,36] by encouraging the regeneration of high WD and removal of low WD species. Process-based vegetation models based on our findings and the processes shown in Table 1 will help better estimate the time scale and long-term consequences of elephants decline or repopulation[37]. The significant contribution of forest elephants to carbon stocks and biodiversity should be accounted to prioritize conservation of the species and their habitat, implemented in climate change mitigation policy, and leveraged to promote and finance nature-based solutions in tropical Africa[35,38].

Material and Methods

Study sites

The Ndoki Forest (“Ndoki” 1.5–3° N, 16–17° E) lies in the northern Republic of Congo. The climate is transitional between the Congolo-Equatorial and sub-equatorial zones with a mean annual rainfall of ca. 1400 mm (Ndoki Forest records) [6,18]. Topography varies from *terra firma* uplands and flat plateaus to the northwest to the extensive floodplain of the Likouala aux Herbes River to the southeast. Soils are of three main types: arenosols to the north and west, ferrasols to the southeast in the Likouala aux Herbes basin on *terra firma*, and gleysols in the swamps further southeast. Ndoki is embedded in wet Guineo-Congolian lowland rainforest, transitioning to the north into dry Guineo-Congolian lowland rainforest, and into swamp forests to the south. *Terra firma* is dominated by Sterculiaceae-Ulmaceae semi-deciduous forest, with large patches of mono-dominant *Gilbertiodendron dewevrei* forest along watercourses and upland plateaus, and swamp forests[18]. The Ndoki fauna includes several large charismatic species such as forest elephants, western lowland gorillas (*Gorilla gorilla gorilla*), common chimpanzees *(Pan troglodytes troglodytes*), forest buffalo (*Syncerus caffer nanus*), bongo (*Tragelaphus eurycerus*), and leopards (*Panthera pardus*). The human population density is low (<1 inhabitant/ km^2) and the immediate study area contains no permanent human settlement.

The LuiKotale research site is located within the equatorial rainforest (2°470S, 20°210E), at the south-western fringe of Salonga National Park in the Democratic Republic of the Congo[23]. The study site covers >60 km2 of primary evergreen lowland tropical forest. The climate is equatorial with abundant rainfall (>2000 mm/yr) and two dry seasons, a short one around February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21 °C and 28 °C with a minimum of 17 °C and a maximum of 38 °C (2007–2010). Two major habitat types can be distinguished. The dry (*terra firma*) forest and the wet temporarily and permanently inundated forest. The dry habitat dominates with heterogeneous species composition covering 73% and patches of mono-dominant *Gilbertiodendron* spp. covering 6% of the site. The wet habitat consists of heterogeneous forest temporarily (17%) and permanently (4%) inundated[23]. The LuiKotale fauna includes several large species such as elephants (almost extinct), bonobos (*Pan paniscus*), forest buffalo, bongo (*Tragelaphus eurycerus*), and leopards (*Panthera pardus*). Similarly to Ndoki, the human population density is low (<1 inhabitant/ km^2) and the immediate study area contains no permanent human settlement.

Elephant food selection at Ndoki

Fresh elephant trails were followed opportunistically over the course of two years in Ndoki across a range of habitat types including permanent swamps, seasonally inundated forests, and *terra firma* open and closed canopy forest. In the case of woody species, a single feeding event was defined as all fresh feeding signs on an individual plant, regardless of plant parts consumed, though all parts consumed were also recorded. At each feeding site data were collected on location (using a handheld Garmin GPS) estimated age (fresh [<24 hrs] or recent [24-48hrs]), plant species, plant part consumed (leaf, stem, bark, wood, roots, etc.), estimated amount consumed on a 1-4 scale (rare, few, moderate, and abundant). Five thousand six hundred and forty-eight feeding events were recorded. Quantifying diet selection based on secondary evidence is open to several sources of bias – for example, one cannot detect a feeding event of a sampling that was completely consumed. In an attempt to reduce and standardize observation bias, we quantified feeding events based on identifiable remains (e.g. a terminal branch stripped of its leaves) in close association with fresh elephant prints, and feel confident we captured gross trends on diet selection.

Over a 3-yr period throughout the Ndoki Forest, the seed content of 855 piles of fresh intact elephant dung was quantified. Dung piles were broken apart with sticks, and fibers were thoroughly teased apart. In each dung pile, all seeds were identified to species and the percentage of presence of each species was calculated based on all sampled dung piles..

Elephant feeding preference data

Our data of forest elephant feeding preferences at Ndoki were combined with data from the MegaFeed database, which contains feeding preferences of all elephant species including the forest elephant. We only retained data from studies that quantified feeding preferences per plant species through ordinal ranking, count of browsing events, selection ratio, or browsing frequency. We excluded studies providing only a list of consumed species. Our Ndoki data and the data from MegaFeed included a total of eight studies. Five out of eight studies classified feeding preference in three categories: rare, medium, high. The Ndoki data contained four categories that were recategorized in three by combining the rare and medium categories into “low”. The remaining two studies had different data compared to the other five. The data from Bia National Park[29] reported the number of browsing events per tree species. We assigned species to three categories (low, medium, high browsing preference) based on the frequency distribution of browsing events. Species with less than three browsing events were assigned to the "low" category, species with more than six were assigned to the "high" category, and the species in between to the "medium" category. Feeding preferences at Santchou Wildlife Reserve [39] were reported with an ordinal scale and thus are presented without using categories. The feeding preferences at Kibale also accounted for relative abundance of elephant-preferred species in relation to all plant availability. Dispersal mode of trees was determined following[6,10] and complemented with data collected at LuiKotale [23]. The Obligate elephant species were: *Ochna gilletiana, Omphalocarpum lecomteanum, Omphalocarpum procerum, Autranella congolensis, Balanites wilsoniana, Detarium macrocarpum, Drypetes gossweileri, Irvingia excelsa, Irvingia gabonensis, Irvingia grandifolia, Irvingia robur, Klainedoxa gabonensis, Mammea Africana, Maranthes sp., Omphalocarpum elatum, Panda oleosa, Tridesmostemon omphalocarpoides, Picralima nitida,* and *Strychnos aculeata*. The complete species list is provided in Dataset S1. Note that not all Obligate elephant species indicated by[23] were classified as such, as we found evidence in literature that some of those species can be dispersed also by other animals.

Tree inventory data and taxonomy harmonization

Tree inventory data were collected in Ndoki (along and perpendicularly from nine large elephant trails, 5674 trees DBH > 40 cm) and LuiKotale (16 1-ha plots, 6579 trees DBH >10 cm). In Ndoki, 1664 understory circular plots were enumerated, in which 6479 trees and shrubs were measured and identified. Tree species data (browsing preference plus forest inventories) from other sites spanned over several decades and species names were homogenized and updated following the taxonomy provided by World Flora Online through their associated R package.

Wood density data and AGC analysis

We used the R package “BIOMASS” to assign WD to each feeding record starting at the species level, to the genus, and finally to the site family average. If none of these were available, we assigned the plot-average WD for the inventory data. Feeding data records without WD were removed because the plot-average WD was not available. Aboveground carbon (AGC) was calculated using the “BIOMASS” package with the following equation:

$$AGC = \exp(-2.024- 0.896*E + 0.920*\log(WD) + 2.795*\log(DBH) - 0.0461*(\log(DBH)^2))$$

Where E is a measure of environmental stress estimated from site coordinates[40]. We simulated the loss of AGC due to the lack of recruitment of Elephant-obligate trees by adapting a methodology used to study the consequences of changes in tree species composition on AGC[41]. We replaced the total DBH of Obligate trees with new trees which were randomly sampled from the remaining trees proportional to their total DBH. The relative total DBH of trees of each dispersal mode was maintained. This process was repeated 10,000 times for each of the two sites and the difference between pre- and post-replacement calculated for each iteration. The mean and standard deviation of the 10,000 iterations were used to estimate the loss of Obligate trees on AGC.

Nutritional values of plants

We gathered nutritional values of plant species consumed by elephants from *PNuts*, a global database of plant nutritional values (Berzaghi et al. in prep). *PNuts* contained nutritional values of leaves, bark, roots, fruits, and stems. However, we retained only data for leaves and fruits because they were the most comprehensive and included data of several nutritional properties. We selected the nutritional properties for which more data were available, these properties were: crude protein (in the main text referred as "protein" or CP), acid detergent fiber ("fibers" or ADF), crude tannins ("Cr. tannins" or CT), total tannins ("Tot. Tannins" or TT), total phenols ("tot. Phenols" or TP), ash ("minerals"), water structural carbohydrates ("sugars" or WSC), total nonstructural carbohydrates (starch + sugars, TNC), and gross energy (GE). The retained data covered 1343 records (fruits and leaves) and 145 plant species included in the forest elephant diet and 45 species and 346 records of fruit not consumed by elephants. Fruit volume was calculated by multiplying fruit length and width found in the African Plant Database[42]. The same database was used to retrieve seed length.

Analysis of effects of forest elephants on ecosystems

We researched the literature using Google Scholar and Web of Science to find studies investigating the physical effect of forest elephants on the ecosystem. The following keywords were used: "forest elephant", "Loxodonta cyclotis", "ecosystem engineering", "ecosystem engineer", "regeneration", "mortality", "tree density", "stem density", "debarking", and "nutrients". We also examined any relevant publication within the references cited by the articles found during the systematic literature search.

Statistical analyses.

Linear regressions were performed with the R “stats” package function “lm”. For each regression, we checked for normality of the data with Q-Q plots. The homogeneity of variances was checked by examining the graphs of residuals vs. fitted values for each model. In the cases where a trend in the residuals was detected, the data were log-transformed and the homogeneity of the variances re-examined. The log-transformed variables are indicated in their respective figures’ descriptions. We used ordinal logistic regressions to analyze the association between wood density or nutritional properties and browsing preferences[43]. In our case, the ordinal logistic regression allows to calculate the probability of a species being in a certain feeding group. The results estimate the slope of the regression as well as the odds-ratio of being in successive categories (low, medium and high preference). For each estimate, a t-value along with a p-value were estimated. P-values were calculated by comparing t-value against the standard normal distribution. From these models, we calculated the specific probability of an observation being in each level of the ordinal category in our fitted model by simply calculating the difference between the fitted values from each pair of adjacent stratified binomial models[43]. The model slope is based on the low preference group as the “focal group” being compared with the other two preference groups. These analyses were performed with functions “polr” and “ggpredict” from R package “MASS” and “ggeffect”, respectively. The aggregated analysis of WD across preference groups on the four sites (five studies) was carried out by including a random effect to account for site effect. For this ordinal logistic regression with random effect, we used the function “clmm” from R package “ordinal”. In this analysis, the Ndoki, Santchou, and Bia sites were removed because the methodology used to quantify elephant food preferences was different from the other sites. The five studies aggregate and the Ndoki analysis were presented as the main results. The aggregate result allows to discern a general pattern beyond site-specific trends and the Ndoki data is ideal because it reports not only frequency of feeding but also quantity, which is critical when assessing the potential effects of biomass consumption. The single-site analysis of the relationships between WD and browsing preferences was conducted using an ordinal logistic regression model and are presented in the supplementary. Analysis of leaf nutritional properties across preference groups was performed following the same procedure. Given that ordinal logistic regression models do not provide any information on statistical differences between the low and high categories, we compared the means of these two groups using additional t-tests. The normality of the distributions was verified and if this was not verified (only in data from Ndoki) a non-parametric Wilcoxon test was used. The same procedure was followed to compare the means of other categories (fruit eaten or not eaten by elephants, fruit vs leaf constituents). Complete test results are included in the supplementary material. We report our scientific findings by following recently suggested methodology that avoids interpreting P-values with arbitrary cutoff point but instead through evidence language associated to ranges of P-values[44]. Evidence language include: very strong, strong, moderate, weak, and little or no evidence according to P-value ranges[44].

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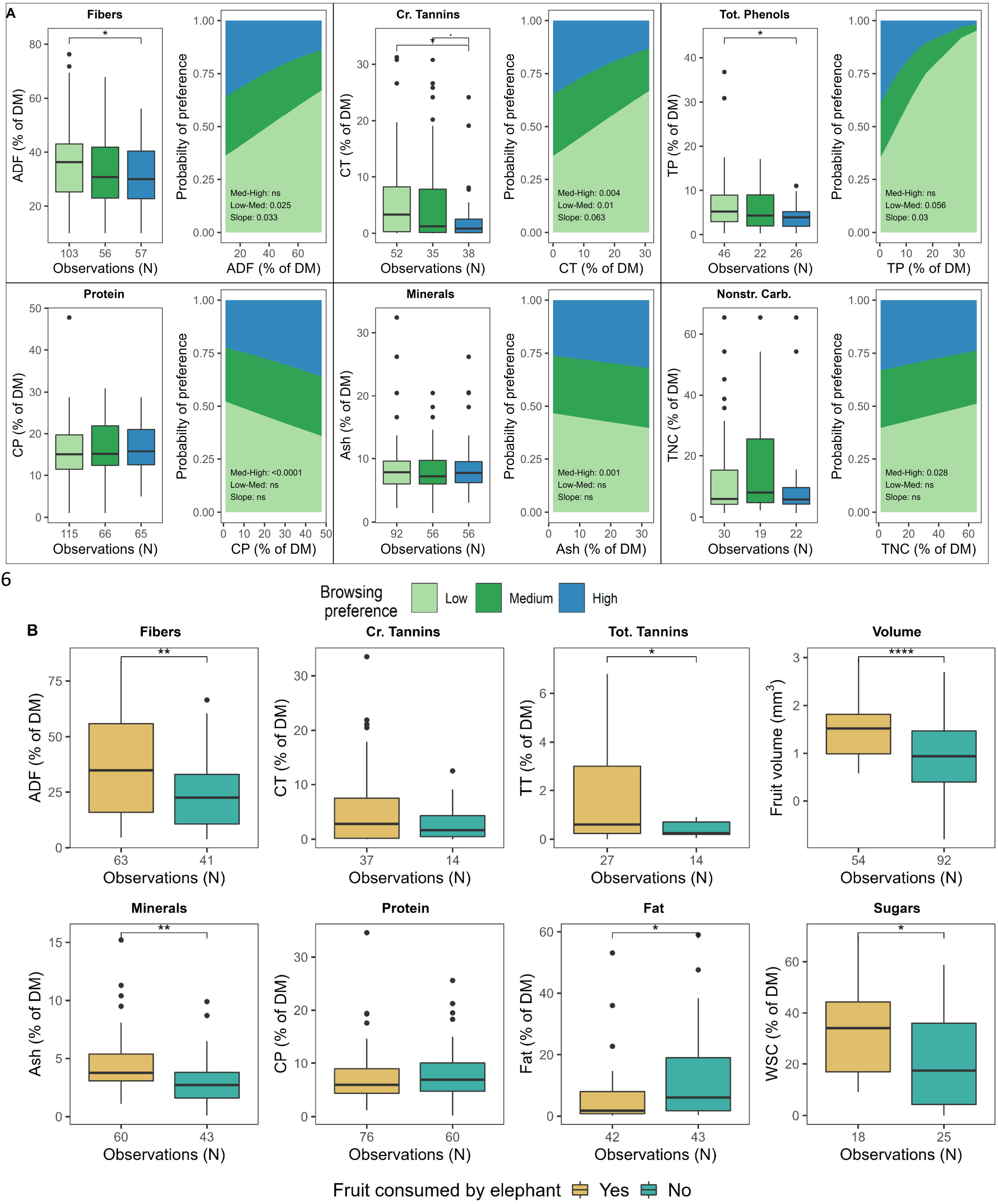
Data availability: LuiKotale and Ndoki vegetation plot data are available at ForestPlots.net; all other data are available from their respective sources list in Table S2.

Figures and Tables



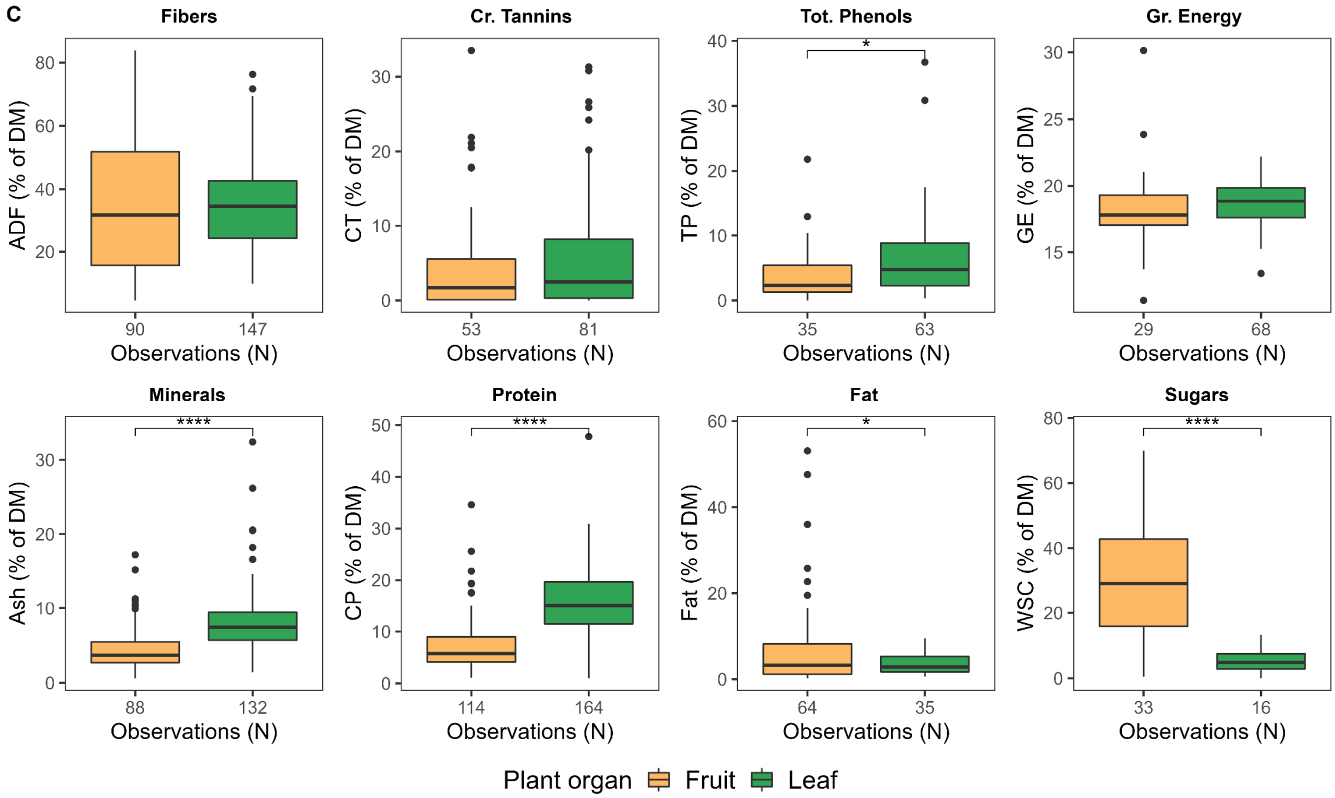


Fig. 1 Nutritional and morphological characteristics of leaves and fruit according to elephant food preferences (low, medium, high) and elephant fruit consumption or avoidance. (A) box plot (left panel) and predicted probability of preference based on results from ordinal logistic regression (right panel) indicating the probability of a plant falling within a preference category with increasing abundance of each nutritional property. For fibers, for example, the figure shows that as fibers increase there is a higher probability of a species being in the low preference category. The P-values shown in the right panels indicate whether the slope differs significantly from zero and is calculated based on the ordinal logistic regression results (Material and Methods). Acid Detergent Fiber (ADF); Crude Tannins (CT); Total Phenols (TP); Total Non-structural Carbohydrates (sugars + starches, TNC); Crude Protein (CP); Ash (minerals); Total Tannins (TT); Water Soluble Carbohydrates (sugars, WSC); Gross Energy (GE). (B) Comparison of fruit consumed or not consumed by elephants at Ndoki; these include Obligate and Non-Obligate trees (see text). (C) Comparison of fruit and leaves consumed by elephants. In box-plots, P-values calculated using t-test indicate statistical significance between the mean of the two groups. Significance levels: ˙P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001; ****P < 0.0001.

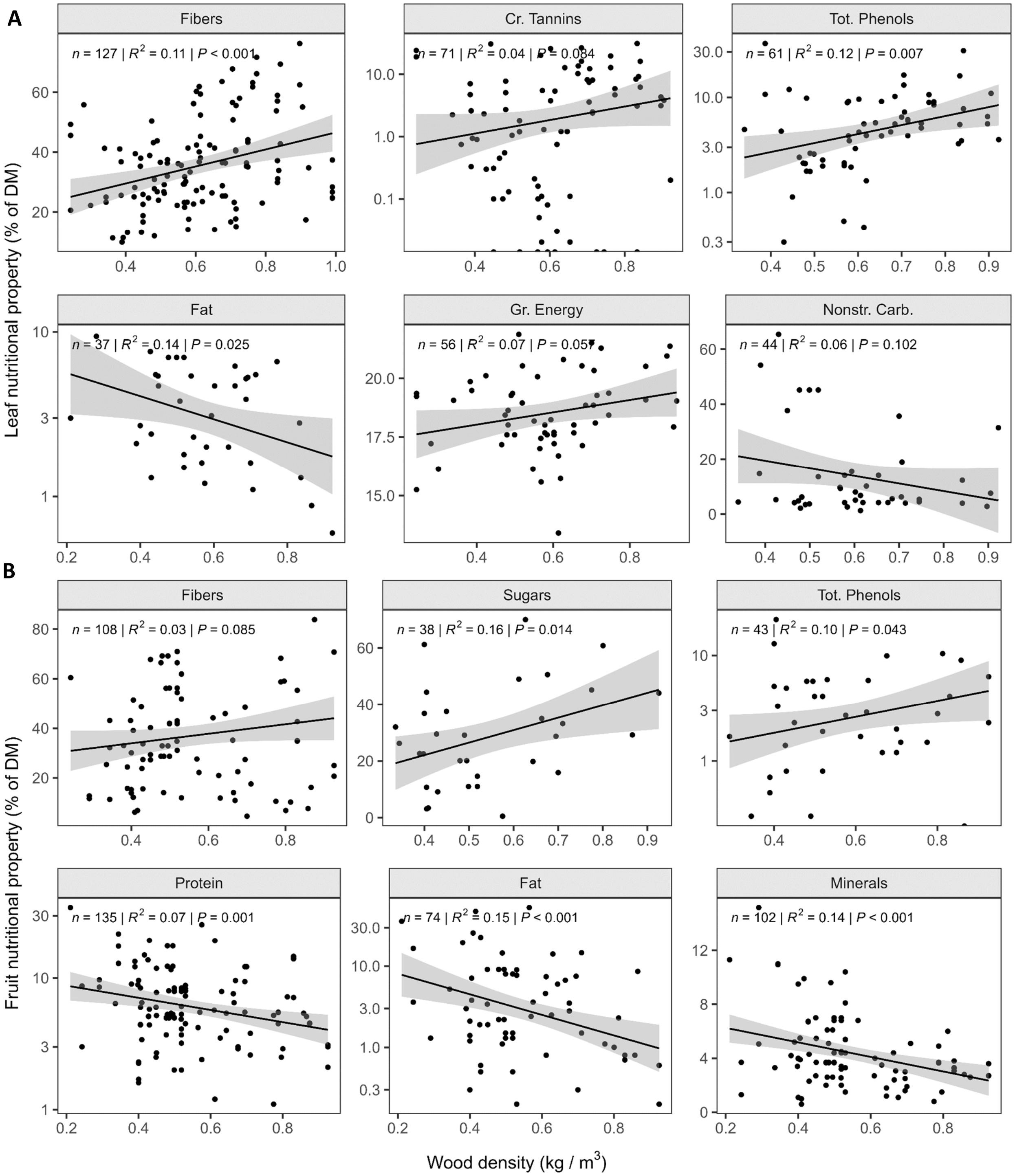


Fig. 2. Correlations between nutritional characteristics of leaves and fruits consumed by elephants and wood density. Each dot represents a tree species that is consumed by elephants. Gross Energy is expressed in MJ/kg. (A) Leaf and (B) fruit nutritional properties as a function of wood density. Crude tannins, total phenols, and Fat of leaves and fruit and were log transformed (see Materials and Methods).

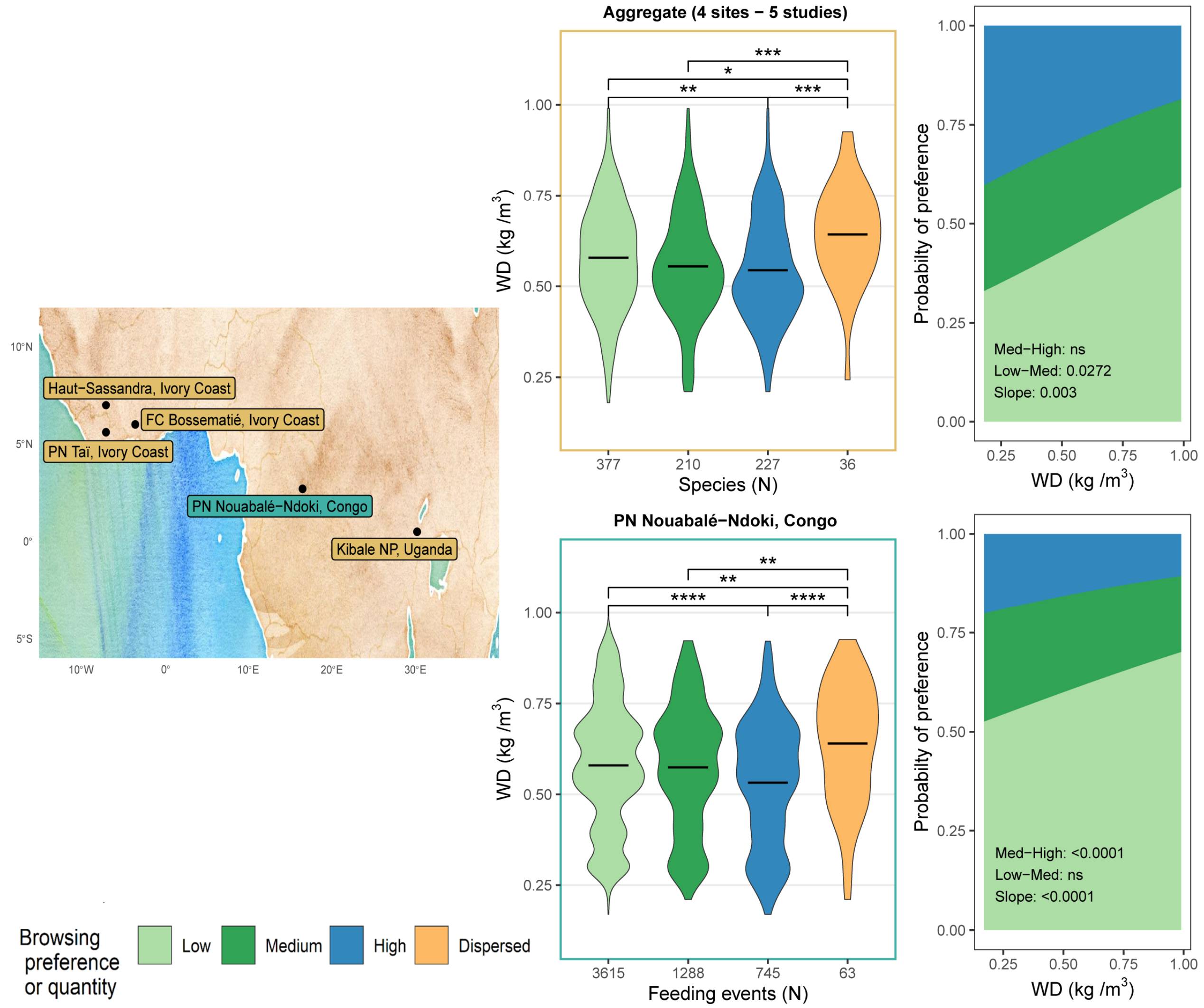


Fig. 3. Wood density in relation to elephant browsing preferences and elephant-dispersed plants in five sites across tropical Africa. Sites included in the aggregated analysis are highlighted in light yellow on the map. Variation of wood density across browsing preference groups and dispersed plants (left panels) and predicted probability of preference based on results from ordinal logistic regression (right panel) indicating the probability of a plant falling within a preference group with increasing wood density. In violin plots, P-values calculated using t-test indicate significance differences between the mean of the low and high groups and leaves vs. fruit groups. P-values in probability plots are based on the ordinal logistic regression. The elephant-dispersed group includes species dispersed by elephants and includes Obligate and Non-obligate species (see text). Significance level of pairwise statistical comparison: *P < 0.05; **P < 0.01; ***P < 0.001; ****P < 0.0001.

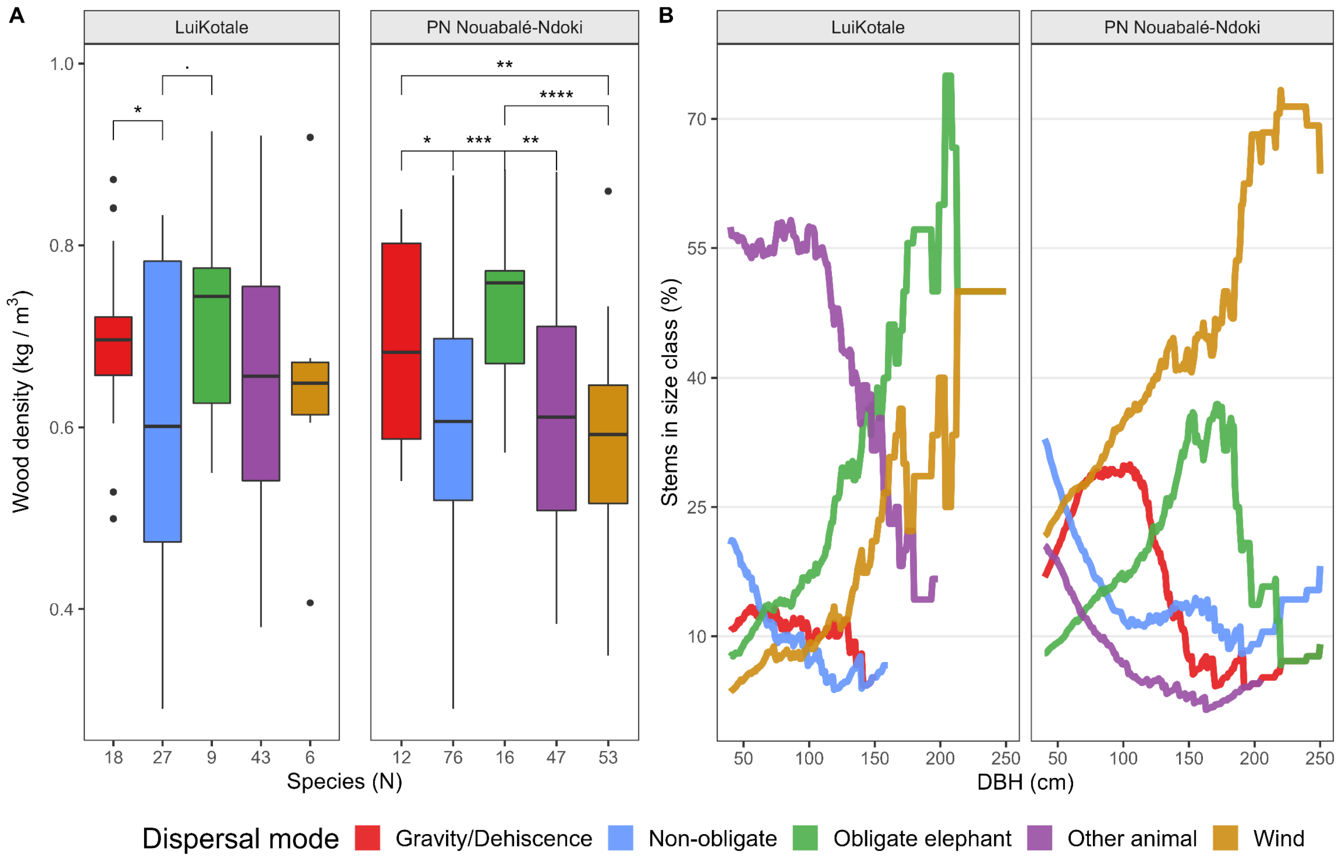


Fig 4. Wood density and forest structure at Ndoki and LuiKotale according to dispersal modes. (A) Variation in wood density in species with different dispersal mode. Significance level of pairwise statistical comparison: ˙P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001; ****P < 0.0001. (B) Relative percentage of stems for each dispersal guild in relation to total stems at each increase of 1 cm in diameter at breast height (DBH). Complete list of species with their respective dispersal mode in Dataset S1.

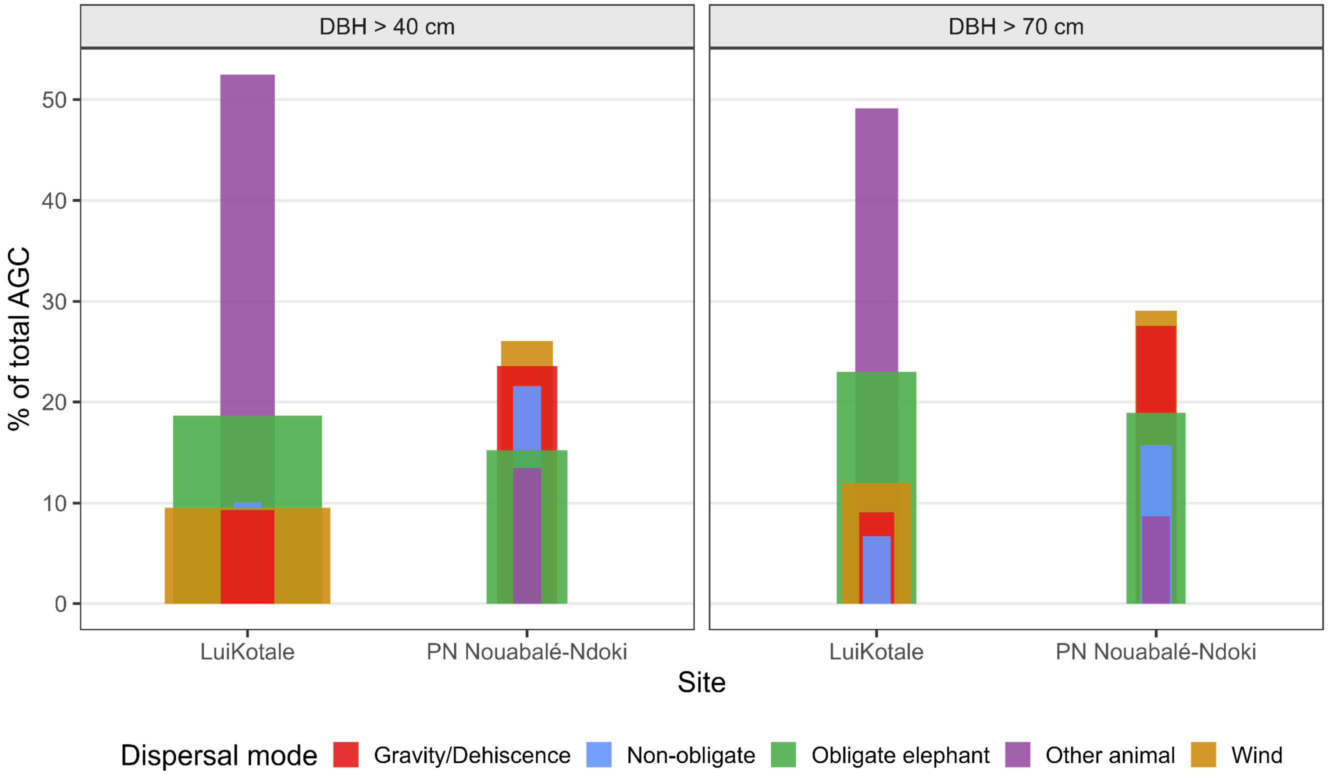


Fig. 5. Relative contribution of dispersal guilds to aboveground carbon at different size thresholds. The bar width is an indication of the relative importance of each guild for AGC in relation to the total number of stems in the forest. It is calculated for each guild by dividing the percentage of total AGC by the percentage of stems at each site. Larger ratios (wider bars) indicate a large contribution to AGC relative to a small number of stems.

Description	**Quantitative result**	**Qualitative result (if any)**	**Location, elephant density, and sampled area**	**Ref.**
Mortality - regeneration				
Mortality rate after elephant damage (DBH > 10 cm)	1.4% (Annual rate)		Kibale NP, Uganda, 5.3 ha	31
Recovery rate after elephant damage (DBH > 10 cm)	1.2% (Annual rate)		Kibale NP, Uganda, 5.3 ha	31
Sapling mortality rate	4% (Annual rate)		Kibale NP, Uganda, logged	12
Seedling and saplings mortality (height > 10 cm)	15-18%		Kibale NP, Uganda, logged	13
Tree toppling & branch breaking	2 - 9.9 cm DBH: - toppled 40.9% - broken branch 24% > 10 cm DBH - toppled 6.9% - broken branch 7%	Tree toppling and broken branches decline sharply for trees > 10 cm DBH. Larger trees suffer more bark stripping	Bwindi NP, Uganda, 0.97 ha	45
	68% breaks by elephants	Most breaks between 1 m and 3 m height, 2 cm and 6 cm DBH	Several sites, Gabon	11
Reduced regeneration	- Browsed species contained 19% saplings of canopy and 48% subcanopy species - Trampling, movement, and grubbing prevents regeneration in 25% of the sampled area		Shimba Hills National Reserve, Kenya (both forest and savanna elephants common in the part)	46
	- Canopy opening < 20% and forest gaps < 300 m^2 reduces elephant		Kibale NP, Uganda	47
Forest properties				
Mean DBH from trail (distance from trail)	52 cm (0-5m) 23 cm (21-25m)	Mean DBH decreases away from trails	Salonga, 0.05 ind/km^2, 100 km of transects	28
Understory openness & elephant encounter rate	$y = 0.2386x + 0.055$	Dung encounter rate increases linearly with understory openness	Salonga, 0.05 ind/km^2, 100 km of transects	28
Tree species composition & distance from trail		Distribution of fruit-preferred and browse-preferred trees varies as a function of distance from trails	Salonga, 0.05 ind/km^2, 100 km of transects	28
Seedling and sapling density and damage near elephant trees	Elephant presence increases chances of damage to seedlings (84%) and saplings (24%)		Ivindo NP, Gabon	48
Aboveground carbon	$y = -0.0841 + 0.3311x - 0.0630x^2$	Percentage change in aboveground carbon (y) as a function of elephant density (x)	Process-based vegetation model	5
Stem density	Reduced density of plants between < 1 cm and >= 1 m in height			11
Stem scarring (DBH > 10 cm)	16% of stems scarred		Rabongo, Uganda, 7ha	49
Debarking height	Species-specific results	Percentage of debarked trees, average diameter and debarking height		29,39

Table 1. Summary of literature review of the ecological effects of elephants in closed canopy forests across the Afrotropics. Only studies that provided a quantitative measure or a mathematical function were included in the table. DBH = diameter at breast height