Trait matching and sampling effort shape the structure of the frugivory network in Afrotropical forests

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Summary

• Frugivory in tropical forests is a major ecological process as most tree species rely on frugivores to disperse their seeds. However, the underlying mechanisms driving frugivore–plant networks remain understudied. Here, we evaluate the data available on the Afrotropical frugivory network to identify structural properties, as well as assess knowledge gaps.

• We assembled a database of frugivory interactions from the literature with > 10 000 links, between 807 tree and 285 frugivore species. We analysed the network structure using a block model that groups species with similar interaction patterns and estimates interaction probabilities among them. We investigated the species traits related to this grouping structure.

• This frugivory network was simplified into 14 tree and 14 frugivore blocks. The block structure depended on the sampling effort among species: Large mammals were better-studied, while smaller frugivores were the least studied. Species traits related to frugivory were strong predictors of the species composition of blocks and interactions among them. Fruits from larger trees were consumed by most frugivores, and large frugivores had higher probabilities to consume larger fruits.

• To conclude, this large-scale frugivory network was mainly structured by species traits involved in frugivory, and as expected by the distribution areas of species, while still being limited by sampling incompleteness.

Introduction

Biodiversity depends on multiple ecological interactions, and, in the last few decades, one of the chief goals of community ecology was to characterize the complex patterns of interactions among species and the factors shaping them (Olesen *et al.*, 2007; Coelho & Rangel, 2018). Such interaction network approaches are particularly relevant to understand the responses of communities to disturbances of anthropogenic or natural origins (e.g. Galetti *et al.*, 2006; Tylianakis *et al.*, 2007).

Bipartite mutualistic interaction networks, involving beneficial interactions between two categories of species such as plants and seed dispersers or pollinators, share consistent patterns in their topological structures (Bascompte & Jordano, 2007). These mutualistic networks have been mainly studied at local or community scale, in particular regarding the heterogeneity of species generalism, with few species being highly connected and most species being poorly connected (Jordano *et al.*, 2003). From this observation, nestedness in plant–frugivore networks was described as the overlap in interaction among species of increasing generalism (Bascompte *et al.*, 2003; Almeida-Neto *et al.*, 2008). By contrast, modularity arose as a term that identified groups of interacting species (modules) that are linked more densely than with other species of the network (Olesen *et al.*, 2007). Both nestedness and modularity are predicted to relate to community stability (Thebault & Fontaine, 2010), and several processes have highlighted both ecological patterns. These nonexclusive processes include filters that constrain the possibility of links, such as the spatial (distribution matching or distribution overlap), temporal species matching (phenological matching), trait-based processes (trait matching) and phylogenetic relationships (Vázquez *et al.*, 2009a,b; González-Varo & Traveset, 2016;

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Araujo *et al.*, 2018; Valdovinos, 2019). Most plant–frugivore relationships concerned local community or subset of organisms that restrict the interpretation of the structure of the networks. With the increasing availability of data on species interactions, mutualistic networks have also been studied at regional or biome scales (e.g. de Almeida & de Mikich, 2018; Redhead *et al.*, 2018; Windsor *et al.*, 2023). Such large-scale networks, based on the aggregation of observed interactions at different sites, often named metaweb (Maiorano *et al.*, 2020), provide more robust estimates of the topological descriptors of the networks (Quintero *et al.*, 2022). Additionally, the integration of large-scale data allows exploring ecological and biogeographical patterns (Redhead *et al.*, 2018; Galiana *et al.*, 2021) and the eco-evolutionary processes shaping them (Windsor *et al.*, 2023). Finally, large-scale networks are great tools for proposing conservation priorities or for restoring ecosystems (de Almeida & de Mikich, 2018; Windsor *et al.*, 2023).

The recent development of latent block models offers a new perspective to understand the structure of ecological networks (Leger *et al.*, 2015; de Manincor *et al.*, 2020; Bar-Hen *et al.*, 2022). Latent block models are parametric clustering methods that group species into blocks, according to their pattern of interaction, with distinct blocks of the two set of nodes of the bipartite network. Then, species in the same block of animals probabilistically share the same interactions with species from other blocks of plants and *vice versa*. Contrary to nestedness and modularity approaches that identify a single predefined architectural pattern, latent block models look for the structure that best explains the data. Species within blocks can therefore be considered as functionally redundant as they have a similar interaction pattern. Latent block models can not only reveal a modular or a nested structure but also highlight structures that are more complex, by allowing different numbers of blocks for each side of the network and estimating probabilities of interaction among each block couple (Fig. S1). The probabilities of interactions linking blocks identify whether a block, for example of trees, maintains a strong and/or specific relationship with a particular block of frugivores rather than with many blocks of frugivores. Therefore, the identification of the functional and taxonomic characteristics of the species within blocks appears promising to investigate (1) the relative role of functional convergence with potential associated syndromes (Ronce & Clobert, 2012; Valenta & Nevo, 2020) and (2) phylogenetic inertia with species sharing inherited traits (Olesen *et al.*, 2007).

Very few studies investigate the structure of tropical plant–frugivore networks (de Almeida & de Mikich, 2018), and this is particularly lacking in Afrotropical forests. These forests are particularly affected by the global decline in large wildlife – downsizing crisis – and plants due to the unsustainable human extraction (Abernethy *et al.*, 2013; Malhi *et al.*, 2016). Afrotropical forests are some of the last remaining areas where megafauna and megaflora persist at densities that maintain their ecological functions (Terborgh *et al.*, 2016; Berzaghi *et al.*, 2018), and their decline raises major concerns for the future functioning and resilience of tropical ecosystems (Markl *et al.*, 2012; Abernethy *et al.*, 2013; Beaune *et al.*, 2013; Effiom *et al.*, 2013; Galetti

et al., 2018). In these forests, most trees produce fleshy fruits that depend on frugivores to disperse their seeds (Abernethy *et al.*, 2013; Effiom *et al.*, 2013), while being important food resources for the forest fauna, particularly the megafauna (Gautier-Hion *et al.*, 1985; Beaune *et al.*, 2013; Bush *et al.*, 2020). At the continental scale, many site-scale studies on frugivory have documented diets of African frugivores, mostly on charismatic species (e.g. primates and elephants), but at a more regional level, interactions remain poorly sampled. Thus, the overall structure of tree–frugivore networks in Afrotropical forests is largely unexplored (Dugger *et al.*, 2019).

We know from other parts of the world that frugivory interactions are mostly governed by trait matching, with the size of fruits and seeds ingested constrained by the size of the fruit eaters (Kitamura *et al.*, 2002; Forget *et al.*, 2007; Donatti *et al.*, 2011; Dehling *et al.*, 2016). We also know that frugivore body mass is related to specialization, with the biggest species tending to be more generalist than the smaller ones, as they are able to ingest both small and large fruits and seeds (Trolliet *et al.*, 2019; Godínez-Alvarez *et al.*, 2020). These large-bodied species increase network cohesion and thereby network stability (Vidal *et al.*, 2014). Investigating such patterns related to body, fruit and seed size in Afrotropical forest frugivory networks is thus a priority to identify, understand and mitigate the consequences of the downsizing crisis in these forests.

Recently, de Almeida & de Mikich (2018) proposed an approach of concatenating local information to assemble a global network so that structural properties could be ascertained. Their approach, which advanced the understanding of ecological processes of network structure in Neotropical communities, inspired our study on Afrotropical frugivory networks. Here, we assemble and analyse a database aggregating the current knowledge on tree–frugivore interactions in Afrotropical forests. We quantify the database's sampling completeness and then analyse the structure of the corresponding interaction network using a latent block model. We investigated the relationships between the block structure of the network and species taxonomy, geographic distribution, trait and conservation status as well as sampling effort. More specifically, we answered two main questions: (1) What are the determinants of the species composition of blocks? In other words, do species from the same block share particular characteristics? (2) What are the determinants of the probability of interactions of tree and frugivore blocks? In other words, are block couples with high probability of interaction made of species with matching characteristics? Our analysis first indicates that the sampling of frugivory interactions in Afrotropical forests is still far from complete and that this affects the structure that our analysis highlights. Second, we found that despite this sampling effect, the blocks we identified species grouped together with similar traits rather than similar taxonomy and distribution. Third, we found that the probability of interactions among blocks was related to expected trait and distribution matching among species. In addition, to provide an overview of current knowledge on frugivory interaction in Afrotropical forests, our study brings evidence of the relevance of block models to relate network structure to ecological processes at regional scales. Unlike most studies on

mutualistic networks, which tend to have local scale focus (e.g. Donatti *et al.*, 2011; Schleuning *et al.*, 2011; Carreira *et al.*, 2020), the results from our study provide important conceptual ideas on network structure at large spatial scales, here on the broader Afrotropical forests.

Materials and Methods

Study sites and database

We assembled a tree–frugivore interaction dataset from literature by searching both the Web of Science and Google Scholar. The search terms used were frugivor*, seed dispers*, tree-frugivore interaction, and the genus or guild name of tree and vertebrate species that inhabit Afrotropical forests. We selected literature sources presenting data on endozoochory and synzoochory with trees, palms or shrubs taller than 3 m (hereafter tree).

A total of 256 literature sources were selected (Appendix A), listing 10 547 interactions – one interaction being the consumption of the fruit of a given tree species by a given vertebrate species. This involved 807 tree and 285 frugivore species and included forests across Africa (Fig. 1). We focused our study on the 6022 unique interactions, that is an interaction between one species of tree and one frugivore species. We removed duplicates to avoid the redundancy and bias towards certain interactions.

In addition to species' identity, we included their order, family, geographic distribution and conservation status. Distributional data were obtained from the African Plant Database of the Geneva Botanical Garden for trees, and for frugivores, these data were derived from IUCN (https://www.iucnredlist.org). Following Droissart *et al.* (2018), we considered three biogeographical regions as categorical variables: West Africa (W), Central Africa (C) and Albertine Rift montane (East Africa, E). Each species was assigned to one category: W, C, E, WC, WE, CE or A (whole geographical area). For conservation status, we used the species status given in the IUCN Red List of Threatened Species (2020) considering species with a critically endangered, endangered, vulnerable or near-threatened status as 'threatened' and species with a least concern status as 'not threatened'.

We derived species traits of trees and frugivores from the different literature sources (Appendix A). For frugivores, we recorded body mass (g). For trees, we recorded fruit and seed dimensions (length and width in cm), number of seeds per fruit, average height (m) and wood density (g cm^{-3}). Tree height and wood density reveal aspects of life strategy of trees, which impact their relationships with frugivores. For example, pioneer species have often low wood densities. The wood density values for each tree species were obtained in R (R Core Team, 2021) with the function *getWoodDensity* from the BIOMASS package (Réjou-Méchain *et al.*, 2017) using data from Chave *et al.* (2009).

Sampling completeness of the tree–frugivore interactions

To assess the sampling completeness of the dataset, we used accumulation curves for both species and interactions, examining the difference between the estimated richness calculated by the non-parametric estimator Chao 2, that is the asymptote of the accumulation curve, and the observed richness (Costa *et al.*, 2016).
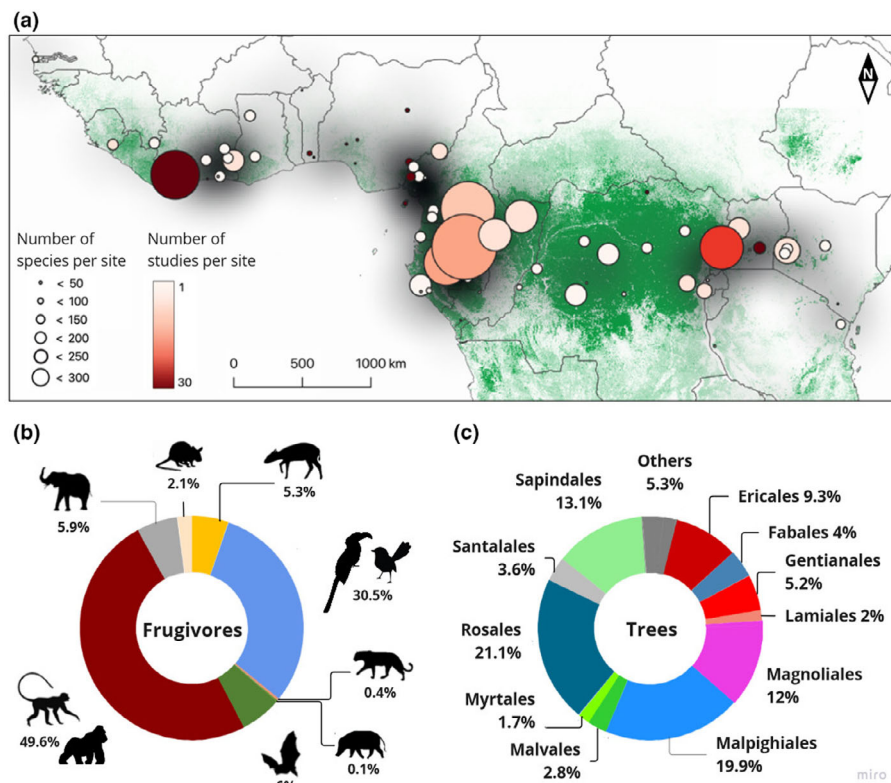
Fig. 1 (a) Location and contribution of the different study sites included in the database. Circles represent study sites, with their size being proportional to the number of species studied and their colour related to the number of studies per site. The green areas show forest cover > 30%. (b) Proportion of unique interactions involving the different frugivore groups included in the database, in clockwise order starting with ruminants, birds (large and small), carnivores, pigs, bats, primates (apes and monkeys), elephant and rodents. (c) Proportion of unique interactions involving the different tree orders included in the database (only orders involved in > 0.5% of unique interactions are presented).

We estimated the expected richness of tree and frugivore species using the full dataset of 10 547 interactions on the overall Afrotropical region and the three biogeographical regions separately. We considered one interaction record between a plant species and an animal species registered per site within each study. Similarly, we estimated the expected number of interactions per frugivore taxonomic group as in Fig. 1b, comparing it to the number of interactions included in our database. The expected Chao 2 estimator values were obtained with the *specpool* function from VEGAN package in R (R Core Team, 2021; Chao *et al.*, 2009).

Network structure: block model analysis

We used a latent block model to analyse the structure of the presence–absence interaction matrix between tree and frugivore species. This parametric method, based on regression models and latent variables, uses statistical inference to assign species with similar interaction patterns into groups called blocks and estimates probabilities of interaction among blocks. The number of blocks, the probabilities for species to belong to each block and the probabilities of species interaction between block couples are estimated by maximizing the integrated complete-data likelihood (Newman, 2016). This allows one to highlight network structure in a very flexible way, without predefining a structure beforehand, except the existence of blocks. We used the BLOCKMODELS R package (Leger, 2016) adapted for bipartite networks, with the Bernoulli family to match our binary adjacency matrix.

Relative contribution of sampling effort, species distribution area, traits and taxonomy to the block structure of the frugivory network

Several nonexclusive factors could originate the block structure or, in other words, could make pattern of interaction similar within groups of species. Among those, species could have a similar pattern of interaction because they share (1) the same distribution area and thereby the same pool of potential partners, or (2) traits involved in the choice of similar interacting partners due to a common evolutionary history. In addition, the sampling effort for each species might also affect the block structure of the network, for example species with low sampling effort having very few interactions being grouped in the same block, while species with high sampling effort having many interactions being grouped in other blocks.

To evaluate the relative contribution of these factors to the block structure of the network, despite the correlations among them, we performed a random forest model as implemented in the R package RANDOMFOREST (Liaw & Wiener, 2002). This classification method relies on building decision trees from bootstrap samples (Fox *et al.*, 2017) that allow one to incorporate categorical (taxonomy and distribution area) as well as continuous variables (species traits), and support possible interactions and collinearity among variables, as expected in our case among species traits and taxonomy (De & Fabricius, 2000; Loh, 2014). We quantified the variable importance by using the mean decrease in Gini index that measures how each variable contributes to the homogeneity of the classification resulting from a random forest model. For each variable, the mean decrease in Gini index is the average aggregative values of Gini index over all decision trees (Fox *et al.*, 2017). Higher the mean decrease in Gini index values, higher the importance of the variable.

We fitted one random forest classification model for frugivore blocks and another one for tree blocks. For frugivores, we included the effects of the body mass (log-transformed), the taxonomic group and the distribution area of species, as well as the number of publications in the database to account for sampling effort. For trees, we had pairs of highly correlated trait variables, such as fruit length and width or seed length and width. For these cases, we selected the trait with the highest variable importance in determining the blocks, that is fruit length and seed length. We further added tree height, wood density and seed number as well as the taxonomic order, its distribution area and the number of publications. For tree and frugivore models, we used the seven geographic categories described previously as descriptors of distribution area.

In a second step, to visualize potential differences in tree traits among blocks, we ran a principal component analysis (PCA) (FACTOMINER; Husson *et al.*, 2018). The variables used in the PCA were the seed length, seed width, fruit length, fruit width, tree size, number of seeds per fruit and wood density. The first dimension explained 38.26% of the variation and had a positive loading with the fruit size – width and length – and seed size – width and length – components. Dimension 2 explained 24.67% of the variance and had a positive loading with the number of seeds and a negative loading with wood density; it differentiated species with numerous seeds and low wood density from species with few seeds and high wood density. Dimension 3 explained 12.89% of the variation and had a positive loading with tree size.

Determinants of the summed-interaction-probability of blocks and average species traits

We used the summed-interaction-probability of blocks as the sum of the probabilities of interaction with other blocks estimated by the latent block model. A high summed-interaction-probability indicates strong interactions with many blocks it interacts with.

To investigate the relationships between block summed-interaction-probability and the average trait values of the species within blocks, we used a generalized linear model with a negative binomial family distribution. We included the summed-interaction-probability of blocks as the dependent variable and the average trait values of the species within blocks, as well as the number of publications that include species from the blocks, as covariates. The average trait values were average body mass (log-transformed) for frugivore blocks, and the average species coordinate from the PCA as described previously using dimensions 1–3 (Fig. S2). We selected the best models (Table S1), using the MUMIN package (Barton, 2019).

Determinants of the probability of interaction between block couples

The probability of interaction between species from one frugivore block and one tree block might be related to the overlap in distribution areas between the species belonging to this block couple (distribution matching). Similarly, this probability might also be affected by the match in the mean trait value of the species in each block (trait matching). We quantified the proportion of 'species couples' having some overlap in their distribution area as the number of tree–animal species couples with overlapping distribution areas over the total number of possible species pairs between the two blocks. We performed a linear mixed-model regression, with the probability of interaction between tree and frugivore blocks (logit transformed) as the dependent variable and with (a) the average body mass (log-transformed) per frugivore block, (b) the mean coordinate of the first dimension of the PCA, (c) the mean coordinate of the second dimension of the PCA, (d) the mean coordinate of the third dimension of the PCA, (e) the proportion of species with overlapping distribution areas, as well as (f) the mean number of studies by tree block and (g) the mean number of studies by frugivore blocks. We implemented interactions between (a) and (b), (a) and (c), (a) and (d). We included tree and frugivore block identity as random factors, to account for pseudo-replication. We selected the best model (Table S2), using the MuMIn package (Barton, 2019).

Results

Sampling completeness of the dataset

The sampling completeness for species richness reached 72% for frugivore species and 73% for tree species. Concerning the richness of interactions, our dataset only reached a sampling completeness of 42% (Fig. S3). The sampling completeness for interaction richness did not differ when considering the biogeographical region separately: 43% for Western Africa, 42% for Central Africa and 42% for Eastern Africa.

The sampling completeness of interactions by frugivore groups ranged from 3% to 66%, with elephants having the highest sampling completeness, followed by primates, bats, ruminants and birds with intermediate values, and pigs, carnivores and rodents having the lowest values (Table 1).

Structure of the tree–frugivore network: blocks and interaction probability

The latent block model found the best block combination with 14 tree blocks and 14 frugivore blocks (Fig. 2). Most species were attributed with high certainty to their respective blocks, with 95% of frugivores and tree species having a probability higher than 0.8 of belonging to their block (Fig. S4).

The number of species within each block was highly variable. In particular, one block of frugivores and one block of trees, respectively named F14 and T14, encompassed a much higher number of species than the others: respectively, 105 and 427

Table 1 Sampling completeness of interaction richness for frugivore groups.

	Number of species	Number of observed interactions	Estimated total number of interactions ± SE	Sampling completeness (%)
Rodents	21	199	6578.2 ± 3794.9	3 [1–4]
Carnivores	4	27	182.7 ± 127.1	15 [9–49]
Pigs	2	9	44.9 ± 25.4	20 [13–46]
Birds	141	2151	6354.5 ± 318.2	34 [32–36]
Ruminants	13	421	931.5 ± 81.2	45 [42–49]
Bats	20	341	734.0 ± 72.3	46 [42–51]
Primates	48	2767	5604.6 ± 192.1	49 [48–51]
Elephant	1	209	315.5 ± 28.9	66 [61–73]

The number of observed interactions corresponds to the number of unique interactions in our database. The estimated total number of interactions corresponds to the asymptotic values calculated by the Chao 2 estimator, with standard error (±SE). The sampling completeness represents the proportion of observed interactions over the estimation; the completeness range is presented in brackets.

species or 37% and 55% of the total number of species. The remaining 13 frugivore and tree blocks contained four to 33 species (mean = 14.6) and 12–84 species (mean = 40) respectively.

The probabilities of interactions between species of frugivore and tree blocks estimated by the latent block model were typically low (Fig. S5). Only 11% of the interactions had a probability > 0.5, while 63% had a probability lower than 0.1 (Fig. 2). The richest blocks F14 and T14 had probabilities of interactions < 0.1 with any other block, except for the interactions between T14 and F2 that reached 0.15 (Fig. 2). The average number of bibliographic sources per species and per block was 39.36 for tree blocks and 109.57 for frugivore blocks; this number was minimal for blocks T14 and F14, with on average 2.70 and 3.07 bibliographic sources per species respectively. The low probabilities of blocks T14 and F14 interacting with the other blocks were likely due to a lack of information regarding the interactions of their respective species.

Determinants of the species composition of tree and frugivore blocks

For both tree and frugivore blocks, the random forest model that best predicted the assignation of tree and frugivore species to their block included all traits, taxonomy, distribution area and sampling effort variables. These models had a 58% and 56% accuracy respectively for tree and frugivore blocks, indicating that nearly 60% of species were correctly assigned to their block with this set of predictors. To investigate the contribution of the predictor, we looked at the variable importance with the mean decrease in Gini index that quantifies how much the performance of the classification relies on the different variables included in the model (Fig. 3). For frugivores, the predictors with the highest importance were the body mass of the species, followed by the sampling effort, and subsequently by the distribution area and the frugivore taxonomic groups (Fig. 3a). For tree blocks, the pattern was different, with the sampling effort on tree species
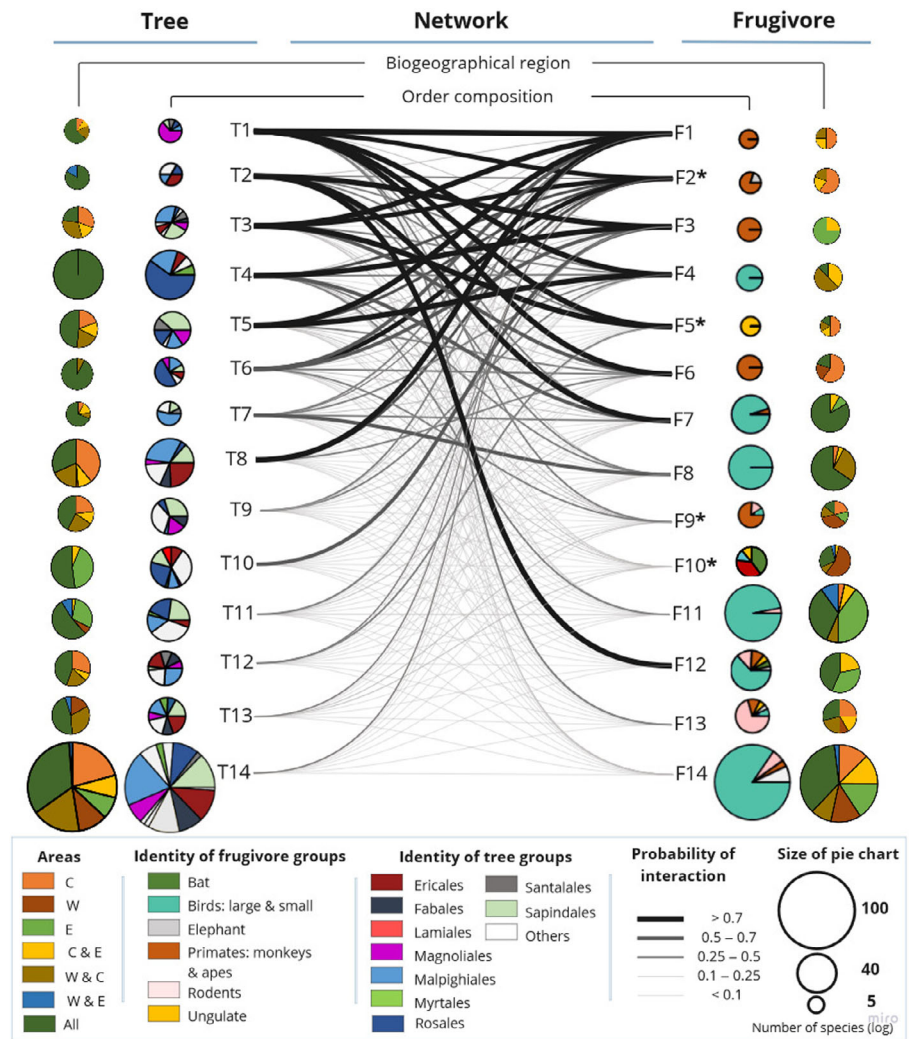
Fig. 2 Bipartite network between tree blocks (left) and frugivores blocks (right). Blocks are ordered by decreasing the sum of probabilities (see the Materials and Methods section). The probability of interactions between blocks or probability of a species from a block interacting with a species from the other block is represented by grey to black lines whose thickness is proportional to the interaction probability. The pie charts represent the composition in terms of taxonomic orders and distribution area in each block, with the size of the circles varying according to the number of species assigned to the block (log-transformed). For biogeographic regions (C, central Africa; E, eastern Africa; W, western Africa), the blocks represented by asterisk had an over-representation of globally threatened species, shown by a significant chi-squared test ($\chi^2 = 68.72$, df = 12, $P < 0.001$).

having the highest variable importance by far, followed by a set of four tree traits including fruit and seed sizes and by taxonomic order, distribution area and seed number (Fig. 3b).

We further illustrated the relatively high variable importance of fruit and seed size using a PCA (Figs 4, S6). Six blocks tended to have distinct trait values: blocks T2, T3, T4, T7, T10 and T11. Blocks T2 and T3 had, on average, larger seeds and fruits, and also larger trees than most of the other blocks. Blocks T4, T7, T10 and T11 had, on average, smaller fruits and seeds, but while T7 was composed of smaller trees, T4 and T11 had larger trees (Figs 4, S6). Blocks T1, T4, T5 and T6 had, on average, larger trees. The second dimension of the PCA, driven by the number of seeds and wood density, did not strongly discriminate the various blocks (Fig. S6).

Despite a rather low variable importance of taxonomy for both tree and frugivore blocks, there was some taxonomic clustering within blocks, with some blocks presenting a high proportion of one or two taxonomic groups of trees or frugivores (Fig. 2). For frugivore blocks, blocks F1, F2, F3, F6 and F9 were mostly composed of primates, blocks F4, F7, F8, F11, F12 and F14 were mostly composed of birds, and blocks F5 and F13 were mostly composed of ruminants and rodents, whereas block F10 was

mostly composed of bats and primates (Fig. 2). For tree blocks, block T1 was mostly composed of Magnoliales, whereas blocks T4 and T6 had the highest proportion of Rosales trees (Fig. 2).

Similarly, some blocks tended to group species according to their distribution areas (Fig. 2). For frugivore blocks, blocks F1, F2, F5 and F6 had a high proportion of species from Central Africa. Block F3 had a high proportion of species from East Africa, with blocks F11 and F12 that also had species widespread in all three regions. Blocks F9 and F10 were mostly composed of species from West Africa. Blocks F7, F8 and F14 had a high proportion of species widespread across all three regions (Fig. 2). Trees with wide distributions covering all three regions were present in all blocks in high proportion. In blocks T3 and T8, a high proportion of species were from central Africa, with some species also present in Central and West Africa. Blocks T10 and T11 had a high proportion of species from East Africa (Fig. 2).

Determinants of the summed-interaction-probability of blocks

The summed-interaction-probability of blocks, measured as the sum of the probabilities that species from a block have to interact
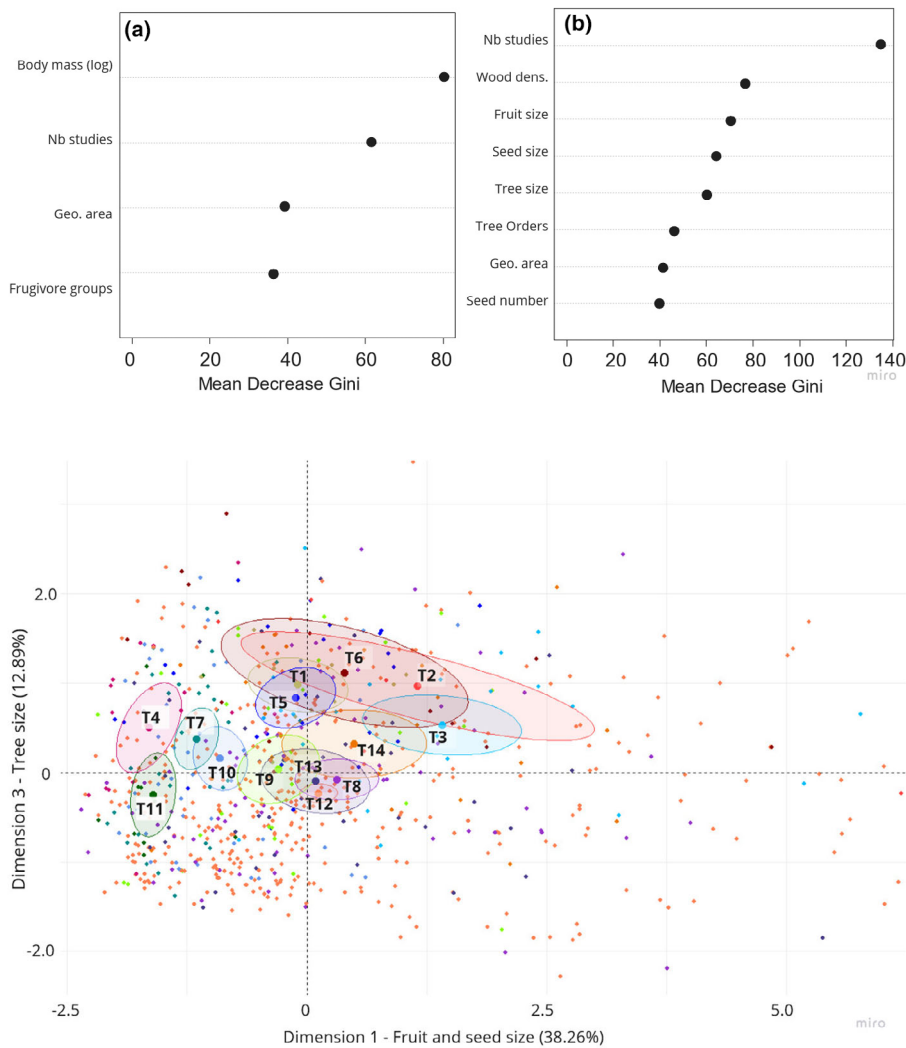
Fig. 3 Results of random forest models illustrating the relative importance of different model variables (measured by the mean decrease in Gini index) in predicting the assignment of species to their blocks. The greater the mean decrease in Gini index, the more the associated variable contributes to predicting the assignment of species in their block. (a) Frugivores species and (b) tree species. Nb studies, number of studies; Geo. area, biogeographical regions.

Fig. 4 Representation of the tree species through the first and third axes of the principal component analysis on tree traits, regarding their blocks. The first axis (dimension 1) is positively related to the size of fruits and seeds, with large fruits and seeds having positive values. The third axis (dimension 3) differentiates small and large trees, with large trees having positive values (see Fig. S2). The ellipses are confidence ellipses representing the mean value of the block around the barycentre. Blocks are represented by different colours.

with species from all other blocks, was for frugivores only related to the mean number of publications per species ($P = 0.002$; Table S3; Fig. 5a), and not to the mean body mass of frugivores (Table S3). For tree blocks, we found that block summed-interaction-probability was positively related to the third dimension of the PCA, related to tree size ($P = 0.002$; Table S3; Fig. 5b), but the other dimensions, as well as the number of publications by species, had no significant effect (Table S3).

Determinants of the probability of interaction between block couples

We found that the probability of interaction between tree and frugivore block couples was related to the statistical interaction between the mean value of dimension 1 of the PCA – representing the size of fruits and seeds of trees – over the species of the tree block and the mean body mass of the species of the frugivore block (Table S4). This indicated that while the probability to interact with small fruits and seeds was not affected by the mean body mass of the frugivore blocks, the probability to interact with larger fruit and seed increased with the mean body mass of the frugivore blocks (Figs 6a, S7). We also found a negative

relationship between the probability of interactions between block couples and the statistical interaction between the mean value of dimension 3 of the PCA over the species of the tree block and the mean body mass of the species of frugivore blocks. This indicated that small trees had a higher probability of interactions with larger frugivores, while large trees had similar probability of interactions with small and large frugivores (Fig. 6b). As expected, the higher the mean distribution overlap was among the species between block couples, the higher the probability for them to interact was (Table S4). The mean number of studies per species and per block of trees and frugivores was also positively related to the probability of interactions between block couples, suggesting that blocks with frequently studied species had a higher probability of interactions with each other. We also found a significant positive relationship with the mean body mass of frugivore blocks, suggesting that blocks containing large frugivores had higher probabilities of interactions with tree blocks (Fig. S8). We found a negative relationship with dimensions 1 and 2 of the PCA on tree traits and a positive relationship with dimension 3 (Fig. S8). This indicates that blocks containing trees with smaller seeds and fruits – dimension 1 – had higher probability of interactions with frugivore blocks, as well as blocks with

Fig. 5 Relationships between summed-interaction-probability for frugivore (a) and tree blocks (b) with (a) mean number of studies by frugivore species inside frugivore blocks and (b) mean coordinates of tree species on dimension 3 of the principal component analysis (PCA) related to tree size; where each dot represent a block. The grey shading represent the confidence intervals.
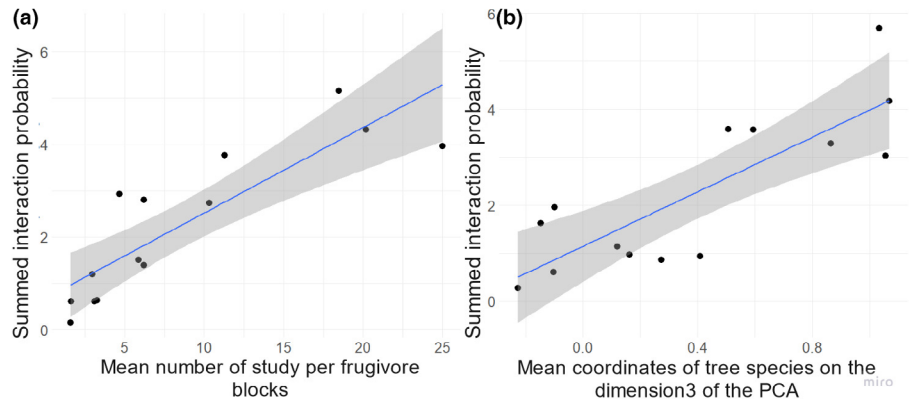

Fig. 6 Relationship between the probability of interactions between tree and blocks (logit), and mean biological traits of tree and frugivore species. (a) How the mean seed size and fruit size of trees (represented by dimension 1 of the principal component analysis (PCA)) and the mean body mass of frugivores affect the probability of interaction among blocks. (b) How the size of trees (represented by dimension 3 of the PCA) and the mean body mass of frugivores affect the probability of interaction among blocks. Each point represents one of the interactions between one frugivore and one tree block. The colour of the point indicates the mean body mass of the frugivores, from dark blue for large frugivores to red for small frugivores. Blue and red lines represent fitted values for a mean frugivore body mass of 11.71 and 3.61 respectively.
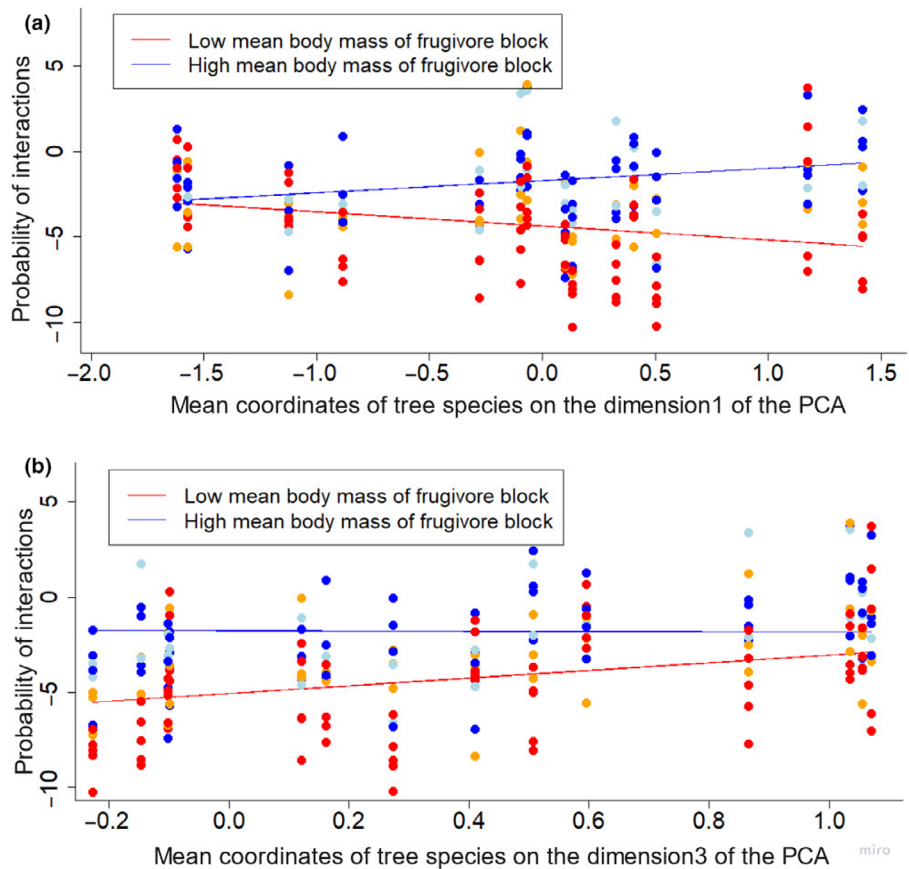
trees with high wood density and low number of seeds – dimension 2 – and blocks with taller tree species – dimension 3.

Overall, these results suggest that the structure of the network depends not only on the spatial distribution of species but also on species traits such as fruit and seed size and frugivore body mass making the imprint of trait matching visible in the block structure of the network.

Discussion

Here, we provide an assessment of current knowledge of frugivory interactions between trees and frugivores in a continent-wide scale of Afrotropical forests. Our analysis first emphasizes that we still have important gaps of information about frugivory interactions in this part of the world. Second, the latent block model approach allowed us to simplify the full network into a limited number of frugivore and tree blocks, that is groups of species with similar patterns of interaction. Third, we showed that this block structure is mainly related to both sampling effects and species traits linked to frugivory interactions. In what follows, we discuss these results in terms of the important drivers of structure in this network, and we also address how this analysis elucidates concerns about the ecological functioning of threatened Afrotropical forests.

The random forest analysis revealed that an important part of the block structure identified by the latent block model was related to variation in sampling effort among species. This was particularly evident for one block of frugivores and one block of trees that grouped together species that were poorly represented in the publications evaluated in this study. These two blocks are therefore more related to the absence of data rather than to the actual structure of the network. Importantly, these two blocks were the ones including the highest number of species, highlighting that we still miss data on the interactions of many species to fully uncover the structure of Afrotropical frugivory network (González-Varo & Traveset, 2016). The sampling completeness of our dataset was indeed moderate and varied substantially among vertebrate groups, with large frugivores reaching higher sampling completeness. However, even for primates, a very well-studied group, only half of the interactions were known. There are comparatively little data on small birds, bats, rodents and carnivores, although they can contribute significantly to frugivory and seed dispersal (Seltzer et al., 2013; Carreira et al., 2020; Godínez-Alvarez et al., 2020). To gain a deeper understanding of these networks, the bias towards large vertebrates should be compensated by additional sampling on lesser-known species and by tree-centred studies with systematic day and night observations of fruit eaters.

Species traits, in particular those related to frugivory interactions, such as frugivore body mass or seed and fruit length for trees also had high importance in the composition of blocks that was expected from long-term studies on frugivory interactions mostly outside Afrotropical forests (Gautier-Hion et al., 1985; Donatti et al., 2011; Bender et al., 2018; Ong et al., 2022). The structure highlighted by the latent block model further stresses the functional aspects of frugivory, making this approach very relevant to study networks of ecological interactions (Bar-Hen et al., 2022). Interestingly, the variable importance of such traits was higher than the ones of taxonomic groups or distribution areas. This suggests first that, despite known phylogenetic signal in frugivory interactions (Gautier-Hion et al., 1985; Donatti et al., 2011), these traits might not be fully conserved and that some convergences might be present. It is also possible that these traits contain more information on frugivory interactions than the taxonomic levels we used in our analysis. Finally, our analyses of frugivory interactions indicate that, despite the large area covered by our data, the species composition of the blocks we identified was more related to species traits than an imprint of the spatial distribution of species.

For frugivores, the mean body mass differed among blocks, and while it seems positively related to block summed-interaction-probability, the literature bias towards large frugivore species involved in this pattern did not allow us to confirm what was shown in previous studies (Donatti et al., 2011). For trees, their height as well as fruit and seed length differed among blocks, but tree height only was positively related to block summed-interaction-probability. The absence of relationships between block summed-interaction-probability and fruit or seed length was unexpected as a negative relationship was found in Asian forests (Kitamura et al., 2002). The increase in block summed-interaction-probability with tree height indicated that tall trees were consumed by most frugivore species, which also fit with previous findings showing that some frugivores, like birds and bats, prefer taller trees (Duncan & Chapman, 1999), a trait often associated with late-successional canopy species that primarily interact with generalist species (Schleuning et al., 2011).

In evaluating the probability of interactions among blocks, we found that they were related to the overlap in the distribution area of species between block couples. This was expected as species with nonoverlapping distributions cannot interact and our network data covered an area greater than the distribution area of most species. We also found that the match in the functional traits of species between block couples had great importance, with large-bodied frugivores interacting with a large spectrum of fruits and seed size and yet being the main disperser of large-seeded fruits. Such relationships between network structure and trait compatibility between frugivores and fruits and seeds of trees had already been highlighted in the forests of Gabon (Gautier-Hion et al., 1985), for African primates and hornbills (Poulsen et al., 2001, 2002) and in other tropical forests (Donatti et al., 2011; Hawes & Peres, 2014); all these examples are compatible with a nested structure (Balcomb & Chapman, 2003; Vidal et al., 2013).

Functional redundancy for frugivory interactions, an important concept in plant–animal interactions, could further be interpreted by the blocks identified by the latent block model. As species within blocks share similar patterns of interactions, blocks grouping many species may be considered as having a high redundancy. Trees inside blocks share similar frugivores, while frugivores of the same blocks feed on similar tree species. Therefore, the loss of one tree or frugivore species inside a block may have its ecological role substituted by another species in the block. However, our analysis does not account for variation in dispersal effectiveness among frugivores, which would be necessary to understand whether redundancy of species within blocks is actually realistic (Calviño-Cancela & Martín-Herrero, 2009; González-Castro et al., 2015, 2022). By contrast, blocks with few species and therefore low redundancy, or blocks grouping many globally threatened species might require particular conservation attention. This may be the case for four frugivore blocks (F2, F5, F9 and F10) with a high proportion of large species: apes, ruminants or monkeys that are threatened (Osuri et al., 2020). The loss of entire blocks could lead to the weakening of the network, and this could happen even before extinctions occur (Valiente-Banuet et al., 2015). In Afrotropical forests where large species are rapidly declining, due to hunting and logging, negative consequences on seed dispersal and thereby tree recruitment have been predicted and already shown by several studies (e.g. Vanthomme et al., 2010; Abernethy et al., 2013; Beaune et al., 2013; Effiom et al., 2013). Implications of their loss for Afrotropical forests are profound, even with an uneven sampling of frugivory interactions.

Our study exemplifies the relevance of latent block model to study the structure of ecological networks, showing the imprint of ecological processes on the revealed block structure despite the incompleteness of the data. The processes we highlighted

were mainly related to the species traits involved in frugivory, as well as to overlap in distribution areas that could be expected given the spatial scale of our study. However, the full understanding of the structure of the network and associated processes is still limited by sampling incompleteness. Information on the role the different frugivores play in seed dispersal, particularly of poorly studied groups such as small birds, bats, rodents and carnivores, is also needed to improve our understanding of changes that will result from defaunation and deforestation and, at the same time, improve future conservation strategies.

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Author contributions

FB conceived the study. CF and CD-B took part in designing the study. CD-B and CF performed data analysis. FB assembled the dataset. CD-B wrote the first draft of the manuscript. NC, CC, KA and P-MF contributed substantially to the ideas and writing of the manuscript. CF and FB contributed equally to this work.

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Data availability

The data that support the findings of this study are available in the following doi: 10.5281/zenodo.7313425.

References

Abernethy KA, Coad L, Taylor G, Lee ME, Maisels F. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 368: 20120303.

de Almeida A, de Mikich SB. 2018. Combining plant–frugivore networks for describing the structure of neotropical communities. *Oikos* 127: 184–197.

Almeida-Neto M, Guimarães P, Guimarães PR Jr, Loyola RD, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117: 1227–1239.

Araujo AC, Martín González AM, Sandel B, Maruyama PK, Fischer E, Vizentin-Bugoni J, de Araújo FP, Coelho AG, Faria RR, Kohler G et al. 2018. Spatial distance and climate determine modularity in a cross-biomes plant–hummingbird interaction network in Brazil. *Journal of Biogeography* 45: 1846–1858.

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

Bar-Hen A, Barbillon P, Donnet S. 2022. Block models for generalized multipartite networks: applications in ecology and ethnobiology. *Statistical Modelling* 22: 273–296.

Barton K. 2019. *R package MuMIn: model selection and model averaging based on information criteria (AICc and alike)*. R package v.1.47.1 [WWW document] URL https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bascompte J, Jordano P. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38: 567–593.

Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences, USA* 100: 9383–9387.

Beaune D, Bretagnolle F, Bollache L, Hohmann G, Surbeck M, Fruth B. 2013. Seed dispersal strategies and the threat of defaunation in a Congo forest. *Biodiversity and Conservation* 22: 225–238.

Bender IMA, Kissling WD, Blendinger PG, Böhning-Gaese K, Hensen I, Kühn I, Muñoz MC, Neuschulz EL, Nowak L, Quitián M et al. 2018. Morphological trait matching shapes plant–frugivore networks across the Andes. *Ecography* 41: 1910–1919.

Berzaghi F, Verbeeck H, Nielsen MR, Doughty CE, Bretagnolle F, Marchetti M, Scarascia-Mugnozza G. 2018. Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential of vegetation models. *Ecography* 41: 1934–1954.

Bush ER, Whytock RC, Bahaa-el-din L, Bourgeois S, Bunnefeld N, Cardoso AW, Dikangadissi JT, Dimonda P, Dimoto E, Ndong JE et al. 2020. Long-term collapse in fruit availability threatens Central African forest megafauna. *Science* 370: 1219–1222.

Calviño-Cancela M, Martín-Herrero J. 2009. Effectiveness of a varied assemblage of seed dispersers of a fleshy-fruited plant. *Ecology* 90: 3503–3515.

Carreira DC, Dáttilo W, Bruno DL, Percequillo AR, Ferraz KMPMB, Galetti M. 2020. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. *Scientific Reports* 10: 10594.

Chao A, Colwell RK, Lin C-W, Gotelli NJ. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90: 1125–1133.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Coelho MTP, Rangel TF. 2018. Neutral community dynamics and the evolution of species interactions. *The American Naturalist* 191: 421–434.

Costa JM, da Silva LP, Ramos JA, Heleno RH. 2016. Sampling completeness in seed dispersal networks: when enough is enough. *Basic and Applied Ecology* 17: 155–164.

De'ath G, Fabricius KE. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81: 3178–3192.

Dehling DM, Jordano P, Schaefer HM, Böhning-Gaese K, Schleuning M. 2016. Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proceedings of the Royal Society B: Biological Sciences* 283: 20152444.

Donatti CI, Guimarães PR, Galetti M, Pizo MA, Marquitti FMD, Dirzo R. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters* 14: 773–781.

Droissart V, Dauby G, Hardy OJ, Deblauwe V, Harris DJ, Janssens S, Mackinder BA, Blach-Overgaard A, Sonké B, Sosef MSM et al. 2018. Beyond trees: biogeographical regionalization of tropical Africa. *Journal of Biogeography* 45: 1153–1167.

Dugger PJ, Blendinger PG, Böhning-Gaese K, Chama L, Correia M, Dehling DM, Emer C, Farwig N, Fricke EC, Galetti M et al. 2019. Seed-dispersal

networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography* 28: 248–261.

Duncan RS, Chapman CA. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9: 998–1008.

Effiom EO, Nuñez-Iturri G, Smith HG, Ottosson U, Olsson O. 2013. Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130246.

Forget PM, Dennis AJ, Mazer SJ, Jansen PA, Kitamura S, Lambert JE, Westcott DA. 2007. Seed allometry and disperser assemblages in tropical rain forests: a comparison of four floras on different continents. In: *Seed dispersal: theory and its application in a changing world*. Wallingford, UK: CABI, 5–36.

Fox EW, Hill RA, Leibowitz SG, Olsen AR, Thornbrugh DJ, Weber MH. 2017. Assessing the accuracy and stability of variable selection methods for random forest modeling in ecology. *Environmental Monitoring and Assessment* 189: 316.

Galetti M, Donatti CI, Pires AS, Guimarães P, Jordano P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society* 151: 141–149.

Galetti M, Moleón M, Jordano P, Pires MM, Guimarães PR, Pape T, Nichols E, Hansen D, Olesen JM, Munk M *et al.* 2018. Ecological and evolutionary legacy of megafauna extinctions. *Biological Reviews* 93: 845–862.

Galiana N, Barros C, Braga J, Ficetola GF, Maiorano L, Thuiller W, Montoya JM, Lurgi M. 2021. The spatial scaling of food web structure across European biogeographical regions. *Ecography* 44: 653–664.

Gautier-Hion A, Duplantier J-M, Quris R, Feer F, Sourd C, Decoux J-P, Dubost G, Emmons L, Erard C, Hecketsweiler P *et al.* 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324–337.

Godínez-Alvarez H, Ríos-Casanova L, Peco B. 2020. Are large frugivorous birds better seed dispersers than medium- and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution* 10: 6136–6143.

González-Castro A, Calviño-Cancela M, Nogales M. 2015. Comparing seed dispersal effectiveness by frugivores at the community level. *Ecology* 96: 808–818.

González-Castro A, Morán-López T, Nogales M, Traveset A. 2022. Changes in the structure of seed dispersal networks when including interaction outcomes from both plant and animal perspectives. *Oikos* 2022: e08315.

González-Varo JP, Traveset A. 2016. The labile limits of forbidden interactions. *Trends in Ecology & Evolution* 31: 700–710.

Hawes JE, Peres CA. 2014. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. *Journal of Tropical Ecology* 30: 381–399.

Husson F, Josse J, Le S, Mazet J. 2018. *FactoMineR: multivariate exploratory data analysis and data mining*. R package v.2.6 [WWW document] URL https://cran.r-project.org/web/packages/FactoMineR/FactoMineR.pdf.

IUCN. 2020. *The IUCN Red List of Threatened Species. v.2020-2*. [WWW document] URL www.iucnredlist.org [accessed 13 February 2020].

Jordano P, Bascompte J, Olesen JM. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* 6: 69–81.

Kitamura S, Yumoto T, Poonswad P, Chuailua P, Plongmai K, Maruhashi T, Noma N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133: 559–572.

Leger J-B. 2016. BLOCKMODELS: a R-package for estimating in Latent Block Model and Stochastic Block Model, with various probability functions, with or without covariates. *arXiv*. doi: 10.48550/arXiv.1602.07587.

Leger J-B, Daudin J-J, Vacher C. 2015. Clustering methods differ in their ability to detect patterns in ecological networks. *Methods in Ecology and Evolution* 6: 474–481.

Liaw A, Wiener M. 2002. Classification and regression by RANDOMFOREST. *R News* 2: 18–22.

Loh W-Y. 2014. Fifty years of classification and regression trees. *International Statistical Review* 82: 329–348.

Maiorano L, Montemaggiori A, Ficetola GF, O'connor L, Thuiller W. 2020. TETRA-EU 1.0: a species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography* 29: 1452–1457.

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW. 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences, USA* 113: 838–846.

de Manincor N, Hautekèete N, Mazoyer C, Moreau P, Piquot Y, Schatz B, Schmitt E, Zélazny M, Massol F. 2020. How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks. *Acta Oecologica* 105: 103551.

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

Newman MEJ. 2016. Equivalence between modularity optimization and maximum likelihood methods for community detection. *Physical Review E* 94: 52315.

Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences, USA* 104: 19891–19896.

Ong L, McConkey KR, Campos-Arceiz A. 2022. The ability to disperse large seeds, rather than body mass alone, defines the importance of animals in a hyper-diverse seed dispersal network. *Journal of Ecology* 110: 313–326.

Osuri AM, Mendiratta U, Naniwadekar R, Varma V, Naeem S. 2020. Hunting and forest modification have distinct defaunation impacts on tropical mammals and birds. *Frontiers in Forests and Global Change* 2: 87.

Poulsen JR, Clark CJ, Connor EF, Smith TB. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83: 228–240.

Poulsen JR, Clark CJ, Smith TB. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787–808.

Quintero E, Isla J, Jordano P. 2022. Methodological overview and data-merging approaches in the study of plant–frugivore interactions. *Oikos* 2022: e08379.

R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Redhead JW, Woodcock BA, Pocock MJ, Pywell RF, Vanbergen AJ, Oliver TH. 2018. Potential landscape-scale pollinator networks across Great Britain: structure, stability and influence of agricultural land cover. *Ecology Letters* 21: 1821–1832.

Réjou-Méchain M, Tanguy A, Piponiot C, Chave J, Hérault B. 2017. BIOMASS: an r package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution* 8: 1163–1167.

Ronce O, Clobert J. 2012. Dispersal syndromes. In: *Dispersal ecology and evolution*. Oxford, UK: Oxford University Press, 119–138.

Schleuning M, Blüthgen N, Flörchinger M, Braun J, Schaefer HM, Böhning-Gaese K. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology* 92: 26–36.

Seltzer CE, Ndangalasi HJ, Cordeiro NJ. 2013. Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. *Biotropica* 45: 450–456.

Terborgh J, Davenport LC, Niangadouma R, Dimoto E, Mouandza JC, Schultz O, Jaen MR. 2016. The African rainforest: odd man out or megafaunal landscape? African and Amazonian forests compared. *Ecography* 39: 187–193.

Thebault E, Fontaine C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329: 853–856.

Trolliet F, Bauman D, Forget P-M, Doucet J-L, Gillet J-F, Hambuckers A. 2019. How complementary are large frugivores for tree seedling recruitment? A case study in The Congo Basin. *Journal of Tropical Ecology* 35: 223–236.

Tylianakis JM, Tscharntke T, Lewis OT. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445: 202–205.

Valdovinos FS. 2019. Mutualistic networks: moving closer to a predictive theory. *Ecology Letters* 22: 1517–1534.

Valenta K, Nevo O. 2020. The dispersal syndrome hypothesis: how animals shaped fruit traits, and how they did not. *Functional Ecology* 34: 1158–1169.

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, García MB, García D, Gómez JM, Jordano P *et al.* 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* 29: 299–307.

Vanthomme H, Bellé B, Forget P-M. 2010. Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. *Biotropica* 42: 672–679.

Vázquez DP, Blüthgen N, Cagnolo L, Chacoff NP. 2009a. Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany* 103: 1445–1457.

Vázquez DP, Chacoff NP, Cagnolo L. 2009b. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90: 2039–2046.

Vidal MM, Hasui E, Pizo MA, Tamashiro JY, Silva WR, Guimarães PR. 2014. Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology* 95: 3440–3447.

Vidal MM, Pires MM, Guimarães PR. 2013. Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation* 163: 42–48.

Windsor FM, van den Hoogen J, Crowther TW, Evans DM. 2023. Using ecological networks to answer questions in global biogeography and ecology. *Journal of Biogeography* 50: 50–62.

Appendix A

Literature sources used in the study

Agmen FL, Chapman HM, Bawuro M. 2010. Seed dispersal by tantalus monkeys (*Chlorocebus tantalus tantalus*) in a Nigerian montane forest. *African Journal of Ecology* 48: 1123–1128.

Alexandre DY. 1978. Le rôle disséminateur des éléphants en forêt de Tai, Côte-d'Ivoire. *Revue d'Ecologie, Terre et Vie* 1: 47–72.

Alexandre DY. 1980. Caractère saisonnier de la fructification dans une forêt hygrophile de Côte-d'Ivoire. *Revue d'Écologie, Terre et Vie* 34: 335–360.

Astaras C, Mühlenberg M, Waltert M. 2008. Note on drill (*Mandrillus leucophaeus*) ecology and conservation status in Korup National Park, Southwest Cameroon. *American Journal of Primatology* 70: 306–310.

Astaras C, Waltert M. 2010. What does seed handling by the drill tell us about the ecological services of terrestrial cercopithecines in African forests? *Animal Conservation* 13: 568–578.

Babweteera F. 2009. *Cordia millenii*: on the risk of local extinction? *African Journal of Ecology* 47: 367–373.

Babweteera F, Brown N. 2010. Spatial patterns of tree recruitment in East African tropical forests that have lost their vertebrate seed dispersers. *Journal of Tropical Ecology* 26: 193–203.

Badrian N, Badrian A, Susman RL. 1981. Preliminary observations on the feeding behavior of *Pan paniscus* in the Lomako forest of central Zaire. *Primates* 22: 173–181.

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

Barlow C, Wacher T. 2005. *A field guide to birds of The Gambia and Senegal*. New Haven, CT, USA: Yale University Press.

Basabose AK. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology* 58: 1–21.

Beaune D, Bretagnolle F, Bollache L, Bourson C, Hohmann G, Fruth B. 2013. Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest. *Journal of Tropical Ecology* 29: 367–380.

Berrod B, Bonnel L, Schmidt Q. 2010. *Préservation du singe Zinkaka dans l'environnement de Togbota*. Rapport non publié d'Urgence Afrique, Bénin.

Blake S. 2002. *The ecology of forest elephant distribution and its implications for conservation*. PhD thesis, University of Edinburgh, Edinburgh, UK.

Boesch C. 1978. New observations on chimpanzees of Tai forest, Ivory Coast. *Terre et la Vie-Revue d'écologie Appliquée* 32: 195–201.

Bourliere F. 1985. Primate communities: their structure and role in tropical ecosystems. *International Journal of Primatology* 6: 1–26.

Bousquet B. 1978. Un parc de forêt dense en Afrique: Le parc national de TAI (Côte D'ivoire): 1re partie. *Bois et forêts Des Tropiques* 179: 27–46.

Bradbury JW. 1977. Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie* 45: 225–255.

Bretagnolle F. Personnal_observation

Brosset A, Erard C. 1986. Les Oiseaux des Régions Forestières du nord-est du Gabon. Volume 1. Écologie et Comportement des Espèces. In: *Société nationale de protection de la nature et d'acclimatation de France*. Paris, France: FRA.

Bryson-Morrison N, Matsuzawa T, Humle T. 2016. Chimpanzees in an anthropogenic landscape: examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology* 78: 1237–1249.

Buzzard PJ. 2004. *Interspecific competition among Cercopithecus campbelli, C. petaurista, and C. diana at Tai Forest, Cote d'Ivoire*. PhD thesis, Columbia University, New York, NY, USA.

Calvert JJ. 1985. Food selection by western gorillas (*G.g. gorilla*) in relation to food chemistry. *Oecologia* 65: 236–246.

Chancellor RL, Rundus AS, Nyandwi S. 2017. Chimpanzee seed dispersal in a montane forest fragment in Rwanda. *American Journal of Primatology* 79: e22624.

Chapman CA, Chapman LJ. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491–504.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133: 861–875.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. 2003. Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* 24: 317–333.

Chapman CA, Struhsaker TT, Skorupa JP, Snaith TV, Rothman JM. 2010. Understanding long-term primate community dynamics: implications of forest change. *Ecological Applications* 20: 179–191.

Chapman LJ, Chapman CA, Wrangham RW. 1992. Balanites wilsoniana: elephant dependent dispersal? *Journal of Tropical Ecology* 8: 275–283.

Charles-Dominique P. 1978. Ecologie et vie sociale de *Nandinia binotata* (Carnivores, Viverrides): comparaison avec les pro simiens sympatriques du Gabon. *Revue d'Ecologie, Terre et Vie* 32: 477–528.

Chatelain C, Kadjo B, Koné I, Refisch J. 2001. Relations Faune-Flore Dans le Parc National de Taï: Une étude Bibliographique, *vol. 3*: 1–166.

Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* 86: 2684–2694.

Cooke CA. 2012. *The feeding, ranging, and positional behaviors of Cercocebus torquatus, the red-capped mangabey. Sette Cama Gabon: a phylogenetic perspective*. Doctoral dissertation, Ohio State University, Columbus, OH, USA.

Cordeiro NJ, Howe HF. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences, USA* 100: 14052–14056.

Cordeiro NJ, Munisi BJ. 2008. Fruit-eating at *Celtis gomphophylla* (Ulmaceae) by Bandedgreen Sunbirds Anthreptes rubritorques and other species. *Scopus: Journal of East African Ornithology* 28: 37–40.

Cordeiro NJ, Ndangalasi HJ, McEntee JP, Howe HF. 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90: 1030–1041.

Cordeiro NJ, Patrick DA, Munisi B, Gupta V. 2004. Role of dispersal in the invasion of an exotic tree in an East African submontane forest. *Journal of Tropical Ecology* 20: 449–457.

Daïnou K, Laurenty E, Mahy G, Hardy OJ, Brostaux Y, Tagg N, Doucet JL. 2012. Phenological patterns in a natural population of a tropical timber tree species, *Milicia excelsa* (Moraceae): evidence of isolation by time and its interaction with feeding strategies of dispersers. *American Journal of Botany* 99: 1453–1463.

Daru BH, Yessoufou K, Nuttman C, Abalaka J. 2015. A preliminary study of bird use of fig *Ficus* species in Amurum Forest Reserve, Nigeria. *Malimbus* 37: 1–15.

Database Global Species. [WWW document] URL http://globalspecies.org [accessed 25 April 2019].

Davies AG, Oates JF, Dasilva GL. 1999. Patterns of frugivory in three West African colobine monkeys. *International Journal of Primatology* 20: 327–357.

Djaha K. 2000. Analyse des effets secondaires du braconnage sur la régénération des plantes à mode de dissémination zoochore dans le Parc National de Taï, Côte d'Ivoire. *Etat Des Recherches en Cours Dans le Parc National de Taï (PNT)* 102.

Djègo-Djossou S, Koné I, Fandohan AB, Djègo JG, Huynen MC, Sinsin B. 2015. Habitat use by white-thighed colobus in the Kikélé Sacred Forest:

activity budget, feeding ecology and selection of sleeping trees. *Primate Conservation* **2015**: 97–105.

Djossa BA, Fahr J, Kalko EK, Sinsin BA. 2008. Fruit selection and effects of seed handling by flying foxes on germination rates of Shea trees, a key resource in northern Benin, West Africa. *Ecotropica* **14**: 37–48.

Djoufack SD, Nkongmeneck BA, Dupain J, Bekah S, Bombome KK, Epanda MA, Van Elsacker L. 2007. Manuel d'identification des fruits consommés par les gorilles et les chimpanzés des basses terres de l'Ouest. *Espèces de l'écosystème du Dja (Cameroun).*

Doran-Sheehy DM, Shah NF, Heimbauer LA. 2006. Sympatric western gorilla and mangabey diet: re-examination of ape and monkey foraging strategies. *Cambridge Studies in Biological and Evolutionary Anthropology* **48**: 49.

Doran-Sheehy D, Mongo P, Lodwick J, Conklin-Brittain NL. 2009. Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. *American Journal of Physical Anthropology* **140**: 727–738.

Doran-Sheehy DM, Boesch C. 2004. Behavioral ecology of western gorillas: new insights from the field. *American Journal of Primatology* **64**: 139–143.

Dowsett-Lemaire F, Dowsett RJ. 2008. The avifauna of Mole National Park, Ghana. *Malimbus* **30**: 93–133.

Dowsett-Lemaire F. 1983. Studies of a breeding population of Waller's red winged starlings in montane forests of South-Central Africa. *Ostrich* **54**: 105–112.

Dowsett-Lemaire F. 1988. Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Revue d'écologie, Terre et vie* **43**: 251–285.

Dowsett-Lemaire F. 1996. Avian frugivore assemblages at three small-fruited tree species in the forests of northern Congo. *Ostrich* **67**: 88–89.

Dowsett-Lemaire F, Dowsett RJ. 2011. Ornithological expedition to Togo 2010–2011. *Dowsett-Lemaire Miscellaneous Report* **78**: 1–33.

Dowsett-Lemaire F, Dowsett RJ. 2015. The birds of Ghana. *British Birds* **108**: 114–116.

Dubost G. 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. *Journal of Mammalogy* **65**: 298–316.

Dudley JP. 2000. Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. *Biotropica* **32**: 556–561.

Duncan RS, Chapman CA. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* **9**: 998–1008.

Dutton P, Chapman H. 2015. Dietary preferences of a submontane population of the rare Nigerian-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Ngel Nyaki Forest Reserve, Nigeria. *American Journal of Primatology* **77**: 86–97.

Eckardt W, Zuberbühler K. 2004. Cooperation and competition in two forest monkeys. *Behavioral Ecology* **15**: 400–411.

Ejidike BN, Salawu A. 2009. Food and feeding habits of mona monkey *Cercopithecus mona* in Ayede/Isan forest reserve, Ekiti State. *Journal of Research in Forestry, Wildlife and Environment* **1**: 56–59.

Engel TR. 1998. Seeds on the roundabout–tropical forest regeneration by *Genetta rubiginosa. Small Carnivore Conservation* **19**: 13–20.

Etiendem DN, Funwi-Gabga N, Tagg N, Hens L, Indah EK. 2013. The Cross River gorillas (*Gorilla gorilla diehli*) at Mawambi Hills, south-west Cameroon: habitat suitability and vulnerability to anthropogenic disturbance. *Folia Primatologica* **84**: 18–31.

Evrard Q, Hardy OJ, Tagg N, Doucet JL. 2019. Removal and predation of aril-covered seeds: the case of Afzelia bipindensis (Fabaceae–Detarioideae). *Plant Ecology and Evolution* **152**: 460–469.

Fahr J. 2013. AfriBats – a citizen-science project documenting bat distributions in Africa and surrounding islands. *African Bat Conservation News* **30**: 2.

Fairgrieve C, Geresomu M. 2003. Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *African Journal of Ecology* **41**: 141–149.

Fashing PJ et al. 2007. Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. *International Journal of Primatology* **28**: 529–550.

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

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

Fimbel C. 1994. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. *Biological Conservation* **70**: 277–286.

Fils EMB, Anong ABA, Fohouo FNT. 2012. First record of the Giant House Bat *Scotophilus nigrita* (Schreber, 1774) in Cameroon (Mammalia, Chiroptera). *Biodiversity Journal* **3**: 55–58.

Fleury MC. 1999. *Ecologie et organisation sociale du colobe satan (Colobus satanas).* PhD thesis, Université de Rennes 1, France.

Flörchinger M, Braun J, Böhning-Gaese K, Schaefer HM. 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia* **164**: 151–161.

Fourrier. 2013. *The spatial and temporal ecology of seed dispersal by gorillas in Lopé National Park, Gabon: linking patterns of disperser behavior and recruitment in an Afrotropical forest.* PhD thesis, Washington University in St Louis, MO, USA, 242.

Fuh T. 2013. Western lowland gorilla (*Gorilla gorilla gorilla*) diet and activity budgets: effects of group size, age class and food availability in the Dzanga-Ndoki National Park, Central African Republic. Gestural head movements in captive bonobos (*Pan paniscus*); use, function and evolutionary, 21.

Fujita MS, Tuttle MD. 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology* **5**: 455–463.

Furuichi T, Hashimoto C, Tashiro Y. 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *International Journal of Primatology* **22**: 929–945.

Gartlan JS, Thomas TS. 1972. Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *Journal of Zoology* **168**: 221–265.

Gautier-Hion A. 1971. L'écologie du talapoin du Gabon. *Revue d'Écologie, Terre et Vie* **4**: 427–490.

Gautier-Hion A. 1977. Données sur le régime alimentaire de Cercocebus albigena albigena dans le Nord-Est du Gabon. *Revue d'Ecologie, Terre et Vie* **4**: 579–585.

Gautier-Hion A, Emmons LH, Dubost G. 1980. A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). *Oecologia* **45**: 182–189.

Gautier-Hion A, Gautier JP, Quris R. 1981. Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Revue d'Ecologie, Terre et Vie* **35**: 511–536.

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

Gibbs D, Barnes E, Cox J. 2001. Pigeons and doves: a guide to the pigeons and doves of the world. *British Birds* **94**: 336–338.

Grassham AM. 2012. *The role of the tantalus monkey (*Chlorocebus tantalus tantalus*) in forest restoration via seed dispersal in a West African montane forest.* PhD Thesis, University of Canterbury, School of Biological Sciences, Canterbury, UK.

Gross-Camp ND, Kaplin BA. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica* **37**: 578–586.

Gross-Camp ND, Masozera M, Kaplin BA. 2009. Chimpanzee seed dispersal quantity in a tropical montane forest of Rwanda. *American Journal of Primatology* **71**: 901–911.

Gross-Camp ND, Mulindahabi F, Kaplin BA. 2009. Comparing the dispersal of large-seeded tree species by frugivore assemblages in tropical montane forest in Africa. *Biotropica* **41**: 442–451.

Gunderson V. 1977. Some observations on the ecology of *Colobus badius temmincki*, Abuko Nature Reserve, The Gambia, West Africa. *Primates* **18**: 305–314.

Harris TR, Chapman CA. 2007. Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates* **48**: 208–221.

Harrison MJS, Hladik CM. 1986. Un primate granivore: le Colobe noir dans la forêt du Gabon: potentialité d'évolution du comportement alimentaire. *Revue d'écologie, Terre et Vie* **41**: 281–298.

Haurez B, Daïnou K, Tagg N, Petre CA, Doucet JL. 2015. The role of great apes in seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in Gabon. *Journal of Tropical Ecology* 31: 395–402.

Haurez B, Brostaux Y, Petre CA, Doucet JL. 2015. Is the western lowland gorilla a good gardener? Evidence for directed dispersal in Southeast Gabon. *Bois et Forêts Des Tropiques* 324: 39–50.

Head JS, Boesch C, Makaga L, Robbins MM. 2011. Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology* 32: 755–775.

Helbig-Bonitz M, Rutten G, Kalko EK. 2014. Fruit bats can disperse figs over different land-use types on Mount Kilimanjaro, Tanzania. *African Journal of Ecology* 52: 122–125.

Hicks TC. 2004. *Chimpanzee* (Pan troglodytes) *tool use in the Ngotto Forest, Central African Republic.* PhD thesis, Central Washington University, Ellensburg, WA, USA.

Hladik CM. 1973. Alimentation et activité d'un groupe de chimpanzés réintroduits en forêt gabonaise. *La Terre et la Vie* 27: 343–413.

Hofmann T, Roth H. 2003. Feeding preferences of duiker (*Cephalophus maxwelli, C. rufilatus,* and *C. niger*) in Ivory Coast and Ghana. *Mammalian Biology* 68: 65–77.

Holbrook KM, Smith TB. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* 125: 249–257.

Hongo S. 2016. Socioecology of mandrills (*Mandrillus sphinx*): mating and feeding tactics in a primate with extremely large group.

Horn AD. 1987. The socioecology of the black mangabey (*Cercocebus aterrimus*) near Lake Tumba, Zaire. *American Journal of Primatology* 12: 165–180.

Hoshino J. 1985. Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo animal reserve, Cameroon. *Primates* 26: 248–273.

Houle A, Chapman CA, Vickery WL. 2010. Intratree vertical variation of fruit density and the nature of contest competition in frugivores. *Behavioral Ecology and Sociobiology* 64: 429–441.

Hovestadt T, Yao P, Linsenmair KE. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1–25.

Idani G. 1986. Seed dispersal by pygmy chimpanzees (*Pan paniscus*): a preliminary report. *Primates* 27: 441–447.

Idani G. 1994. Flora and vegetation of Wamba forest, central Zaire with reference to bonobo (*Pan paniscus*) foods. *Tropics* 3: 309–332.

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

Janmaat KR, Boesch C, Byrne R, Chapman CA, Goné Bi ZB, Head JS, Robbins M, Wrangham RW, Polansky L. 2016. Spatio-temporal complexity of chimpanzee food: how cognitive adaptations can counteract the ephemeral nature of ripe fruit. *American Journal of Primatology* 78: 626–645.

Jensch D, Ellenberg H. 1999. The Hornbill (*Tockus semifasciatus*) as a seed-disperser and ecological indicator, and forest rehabilitation in eastern Ivory Coast. *La Terre et la Vie* 54: 333–350.

Jerome I, Chapman H, Iyiola T, Calistus A, Goldson S. 2011. Guild of Frugivores on three fruit-producing tree species Polyscias fulva, Syzyguim Guineensis SUBSP. Bamensdae and Pouteria Altissima in Ngel Nyaki Forest Reserve, a Montane Forest Ecosystem in Nigeria. *Journal of Research in Forestry, Wildlife and Environment* 3: 1–11.

Kagoro-Rugunda G, Hashimoto C. 2015. Fruit phenology of tree species and chimpanzees' choice of consumption in Kalinzu Forest Reserve, Uganda. *Open Journal of Ecology* 5: 477.

Kane EE, McGraw WS. 2017. Dietary variation in Diana monkeys (*Cercopithecus diana*): The effects of polyspecific associations. *Folia Primatologica* 88: 455–482.

Kane EE. 2012. *The context of dietary variation in Cercopithecus diana in the Ivory Coast's Tai National Park.* Thesis. The Ohio State University, Columbus, OH, USA.

Kankam BO, Oduro W. 2009. Frugivores and fruit removal of *Antiaris toxicaria* (Moraceae) at Bia Biosphere Reserve, Ghana. *Journal of Tropical Ecology* 25: 201–204.

Kano T. 1983. An ecological study of the pygmy chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology* 4: 1–31.

Kaplin BA, Moermond TC. 2000. Foraging ecology of the mountain monkey (*Cercopithecus l'hoesti*): implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology* 50: 227–246.

Kaplin BA, Moermond TC. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45: 83–101.

Kendrick EL, Shipley LA, Hagerman AE, Kelley LM. 2009. Fruit and fibre: the nutritional value of figs for a small tropical ruminant, the blue duiker (*Cephalophus monticola*). *African Journal of Ecology* 47: 556–566.

Kirika JM, Farwig N, Böhning-gaese K. 2008. Effects of local disturbance of tropical forests on frugivores and seed removal of a small-seeded Afrotropical tree. *Conservation Biology* 22: 318–328.

Klaus-Hügi C, Klaus G, Schmid B, König B. 1999. Feeding ecology of a large social antelope in the rainforest. *Oecologia* 119: 81–90.

Kock D, Barnett L, Fahr J, Emms C. 2002. On a collection of bats (Mammalia: Chiroptera) from The Gambia. *Acta Chiropterologica* 4: 77–97.

Koné I, Lambert JE, Refisch J, Bakayoko A. 2008. Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: implications for the conservation of forest fragments. *Tropical Conservation Science* 1: 293–305.

Kouamé D, Yao CYA, Nandjui A, N'guessan EK. 2010. Le rôle de l'éléphant dans la germination des graines de *Irvingia gabonensis* (Irvingiaceae), *Balanites wilsoniana* (Balanitaceae), *Parinari excelsa* (Chrysobalanaceae) et *Sacoglottis gabonensis* (Humiriaceae) en forêt tropicale: cas du Parc National d'Azagn. *International Journal of Biological and Chemical Sciences* 4: 1442–1454.

Kunz BK, Hovestadt T, Linsenmair KE. 2008. Variation of dispersal agents? Frugivore assemblages and fruit handling in a typical 'bird-dispersed' tree (*Lannea acida*, Anacardiaceae). *Ecotropica* 14: 101–112.

Lahm SA. 1986. Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications of foraging strategy. *American Journal of Primatology* 11: 9–26.

Lambert JE, Garber PA. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9–28.

Lambert J. 1998. Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *African Journal of Ecology* 36: 234–240.

Lambert JE. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and red tail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology* 109: 365–386.

Lambert JE. 2001. Red-tailed guenons (*Cercopithecus ascanius*) and Strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology* 22: 189–201.

Lambert JE. 2011. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *American Journal of Primatology* 73: 9–24.

Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology* 125: 363–368.

Lamperti AM, French AR, Dierenfeld ES, Fogiel MK, Whitney KD, Stauffer D et al. 2014. Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa. *Journal of Tropical Ecology* 30: 273–290.

Langevin P, Barclay RM. 1990. *Hypsignathus monstrosus. Mammalian Species* 357: 1–4.

Lehouck V, Spanhove T, Demeter S, Groot NE, Lens L. 2009. Complementary seed dispersal by three avian frugivores in a fragmented Afromontane forest. *Journal of Vegetation Science* 20: 1110–1120.

Lehouck V, Spanhove T, Vangestel C, Cordeiro NJ, Lens L. 2009. Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? *Ecography* 32: 789–799.

Lehouck V, Spanhove T, Colson L, Adringa-Davis A, Cordeiro NJ, Lens L. 2009. Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos* 118: 1023–1034.

Lehouck V, Spanhove T, Lens L. 2011. Avian fruit ingestion differentially facilitates seed germination of four fleshy-fruited plant species of an Afrotropical forest. *Plant Ecology and Evolution* 144: 96–100.

Lehouck V. Unpublished data.

Lieberman D, Lieberman M, Martin C. 1987. Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* 19: 365–369.

Lovette IJ, Fitzpatrick JW. 2016. *Handbook of bird biology. 3rd edn*, UK: John Wiley & Sons.

Luef EM, Breuer T, Pika S. 2016. Food-associated calling in Gorillas (*Gorilla g. gorilla*) in the Wild. *PLoS ONE* 11: e0144197.

Lumpkin S, Kranz KR. 1984. *Cephalophus sylvicultor. Mammalian Species* 225: 1–7.

Magloire NC, Blaise K, Noël DD, Inza K. 2017. Preliminary study on *Eidolon helvum* (Kerr, 1792) population dynamic in Cote d'Ivoire, West Africa. *Journal of Experimental Biology* 5: 6.

Maisels F, Gautier-Hion A, Gautier JP. 1994. Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. *International Journal of Primatology* 15: 681–701.

Marshall AG, William ANM. 1982. Ecological observations on epomorphorine fruit-bats (Megachiroptera) in West African savanna woodland. *Journal of Zoology* 198: 53–67.

Marshall AG. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society* 83: 351–369.

Masette M, Isabirye-Basuta G, Baranga D, Chapman CA, Rothman JM. 2015. The challenge of interpreting primate diets: mangabey foraging on *Blighia unijugata* fruit in relation to changing nutrient content. *African Journal of Ecology* 53: 259–267.

Masi S, Mundry R, Ortmann S, Cipolletta C, Boitani L, Robbins MM. 2015. The influence of seasonal frugivory on nutrient and energy intake in wild western gorillas. *PLoS ONE* 10: e0129254.

Matsumoto-Oda A, Hayashi Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica* 70: 154–162.

Maurois C, Chamberlan C, Marechal C. 1997. Aperçu du régime alimentaire de l'éléphant de forêt, Loxodonta africana cyclotis, dans le Parc National d'Odzala, République du Congo. *Mammalia* 61: 127–130.

Mbelli HM. 2000. *Plant animal relations: effects of disturbance on the regeneration of commercial tree species*. The Tropenbos-Cameroon Programme, Kribi, Cameroon. Tropenbos-Cameroon Documents.

McGraw WS, Vick AE, Daegling DJ. 2011. Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 144: 140–153.

Menke S, Böhning-Gaese K, Schleuning M. 2012. Plant–frugivore networks are less specialized and more robust at forest–farmland edges than in the interior of a tropical forest. *Oikos* 121: 1553–1566.

Merz G. 1981. Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt. *Loxodonta Africana Cyclotis Matschie* 45: 1900–1981.

Mickleburgh SP, Hutson AM, Racey PA. 1992. *Old World fruit bats. An action plan for their conservation*. Gland, Switzerland: IUCN, 263.

Mitani M. 1989. *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. *Primates* 30: 307–323.

Mitani M. 1991. Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. *Primates* 32: 137–151.

Molloy L, Hart JA. 2002. Duiker food selection: palatability trials using natural foods in the Ituri Forest, Democratic Republic of Congo. *Zoo Biology* 21: 149–159.

Morgan D, Sanz C, Onononga JR, Strindberg S. 2006. Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology* 27: 147–179.

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

Morgan BJ. 2007. Group size, density and biomass of large mammals in the Reserve de Faune du Petit Loango, Gabon. *African Journal of Ecology* 45: 508–518.

Moupela C, Doucet JL, Daïnou K, Tagg N, Bourland N, Vermeulen C. 2014. Dispersal and predation of diaspores of *Coula edulis* Baill. in an evergreen forest of Gabon. *African Journal of Ecology* 52: 88–96.

Mulotwa EM, Louette MB, Dudu A, Upoki A. 2011. Contribution à la connaissance du régime alimentaire du Paon congolais *Afropavo congensis* (Chapin, 1936). *Numéro Spécial* 14: 73–83.

Muscarella R, Fleming TH. 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews* 82: 573–590.

Mwenja I. 2007. A new population of De Brazza's monkey in Kenya. *Primate Conservation* 22: 117–122.

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

Newton-Fisher NE. 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology* 37: 344–354.

Niamien M, Yaokokore-beibro H, Koné I, Yao S, N'goran, E. 2009. Données préliminaires sur les habitudes alimentaires des chauves-souris paillées, *Eidolon helvum* (Kerr, 1972) (Pteropodidae) de la commune d'Abidjan Plateau (Côte D'ivoire). *Agronomie Africaine* 21: 231–240.

Nishihara T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates* 36: 151–168.

Norris J. 1988. Diet and feeding behavior of semi-free ranging mandrills in an enclosed Gabonais forest. *Primates* 29: 449–463.

Nsi Akoue G, Mbading-Mbading W, Willaume E, Souza A, Mbatchi B, Charpentier MJ. 2017. Seasonal and individual predictors of diet in a free-ranging population of mandrills. *Ethology* 123: 600–613.

Nyiramana A, Mendoza I, Kaplin BA, Forget PM. 2011. Evidence for seed dispersal by rodents in tropical montane forest in Africa. *Biotropica* 43: 654–657.

Oates JF, Whitesides GH. 1990. Association between olive colobus (*Procolobus verus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *American Journal of Primatology* 21: 129–146.

Oates JF. 1978. Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica* 10: 241–253.

Oates JF. 1988. The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. *International Journal of Primatology* 9: 457–478.

Oates JF, Swain T, Zantovska J. 1977. Secondary compounds and food selection by colobus monkeys. *Biochemical Systematics and Ecology* 5: 317–321.

Oelze VM, Head JS, Robbins MM, Richards M, Boesch C. 2014. Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. *Journal of Human Evolution* 66: 95–106.

Ogogo AU, Enieng EA, Etta US. 2013. Habitat utilization and conservation of the Cross River gorilla (*Gorilla gorilla diehli*) in Afi Mountain Wildlife Sanctuary of Cross River State, Nigeria. *International Journal of Biological and Chemical Sciences* 7: 1579–1585.

Okekedunu JO, Ogunjemite BG, Adeyemo IA, Olaniyi OE. 2014. Daily activity budget of Mona monkey (*Cercopithecus mona* schreber) in Ibodi Monkey Forest, Osun State, Nigeria. *FUTA Journal of Research in Sciences* 2: 218–227.

Olaleru F. 2017. Seasonality and nutrient composition of the plant diets of mona monkeys (*Cercopithecus mona*) in University of Lagos, Nigeria. *Zoologist* 15: 13–21.

Osmaston HA. 1965. Pollen and seed dispersal in *Chlorophora excelsa* and other Moraceae, and in Parkia filicoidea (Mimosaceae), with special reference to the role of the fruit bat, Eidolon Helvum. *The Commonwealth Forestry Review* 44: 96–104.

Owens JR, Honarvar S, Nessel M, Hearn GW. 2015. From frugivore to folivore: altitudinal variations in the diet and feeding ecology of the Bioko Island drill (*Mandrillus leucophaeus poensis*). *American Journal of Primatology* 77: 1263–1275.

Pendje G. 1994. Frugivory of *Civettictis civetta* and its role in seed dispersal at Mayombe. *Revue d'Ecologie (la Terre et la Vie)* 49: 107–116.

Petre CA, Tagg N, Beudels-Jamar RC, Haurez B, Doucet JL. 2015. Western lowland gorilla seed dispersal: are seeds adapted to long gut retention times? *Acta Oecologica* 67: 59–65.

Petre CA, Tagg N, Beudels-Jamar R, Haurez B, Salah M, Spetschinsky V, Doucet JL. 2015. Quantity and spatial distribution of seeds dispersed by a western lowland gorilla population in south-east Cameroon. *Journal of Tropical Ecology* 31: 201–212.

Potts KB, Watts DP, Wrangham RW. 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology* 32: 669–690.

Poulsen JR, Clark CJ, Smith TB. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787–808.

Poulsen JR, Clark CJ, Connor EF, Smith TB. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83: 228–240.

Poulsen JR, Clark CJ, Bolker BM. 2012. Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. *Ecology* 93: 500–510.

Prota_Database. [WWW document] URL https://prota4u.org/database/ [accessed 17 December 2018].

Quris R. 1975. Ecologie et organisation sociale de Cercocebus galeritus agilis dans le Nord-Est du Gabon. *Revue d'Ecoloie, Terre et vie* 3: 337–398.

Remis MJ, Dierenfeld ES, Mowry CB, Carroll RW. 2001. Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *International Journal of Primatology* 22: 807–836.

Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *American Journal of Primatology* 43: 87–109.

Richter HV, Cumming GS. 2006. Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology* 268: 35–44.

Rode KD, Chiyo PI, Chapman CA, McDowell LR. 2006. Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of Tropical Ecology* 22: 441–449.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJ, Tutin CE. 1996. Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. *American Journal of Primatology* 40: 297–313.

Rogers ME, Voysey BC, McDonald KE, Parnell RJ, Tutin CEG. 1998. Lowland gorillas and seed dispersal: the importance of nest sites. *American Journal of Primatology* 45: 45–68.

Rogers ME, Maisels F, Williamson EA, Fernandez M, Tutin CE. 1990. Gorilla diet in the lope reserve, Gabon. *Oecologia* 84: 326–339.

Royal botanic garden of Edinburgh database. [WWW document] URL https://data.rbge.org.uk/search/livingcollection/ [accessed 6 October 2019].

Sabater-Pí J. 1979. Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). *Zeitschrift Fuer Tierpsychologie* 50: 265–281.

Sam MK, Danquah E, Oppong SK, Bosu ED. 2006. Elephant survey in the Bia Conservation Area, western Ghana. *Pachyderm* 40: 42–50.

Sawyer SC. 2012. *The ecology and conservation of the critically endangered Cross River gorilla in Cameroon*. Berkeley, CA, USA: University of California.

Schleuning M, Blüthgen N, Flörchinger M, Braun J, Schaefer HM, Böhning-Gaese K. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology* 92: 26–36.

Seltzer CE, Ndangalasi HJ, Cordeiro NJ. 2013. Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. *Biotropica* 45: 450–456.

Serckx A, Kühl HS, Beudels-Jamar RC, Poncin P, Bastin JF, Huynen MC. 2015. Feeding ecology of bonobos living in forest-savannah mosaics: diet seasonal variation and importance of fallback foods. *American Journal of Primatology* 77: 948–962.

Shanahan M, So S, Gompton SG, Gorlett R. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76: 529–572.

Short L, Horne J, Horne JF. 2001. *Toucans, barbets, and honeyguides: Ramphastidae, Capitonidae and Indicatoridae, vol. 8*. Oxford, UK: Oxford University Press.

Short J. 1981. Diet and feeding behaviour of the forest elephant. *Mammalia* 45: 177–185.

Sourd C, Gautier-Hion A. 1986. Fruit selection by a forest guenon. *The Journal of Animal Ecology* 55: 235–244.

Struhsaker TT. 2017. Dietary variability in redtail monkeys (*Cercopithecus ascanius schmidti*) of Kibale National Park, Uganda: the role of time, space, and hybridization. *International Journal of Primatology* 38: 914–941.

Sun C, Moermond TC. 1997. Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *The Auk* 114: 396–404.

Tashiro Y. 2006. Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates* 47: 170–173.

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

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

Tolo CU, Baranga J, Kagoro-Rugunda G. 2008. Dietary selection of L'Hoest monkeys in Kalinzu forest reserve, southwestern Uganda. *African Journal of Ecology* 46: 149–157.

Tosso DNF. 2018. *Évolution et adaptation fonctionnelle des arbres tropicaux: le cas du genre Guibourtia Benn*. Doctoral dissertation, Université de Liège, Liège, Belgique.

Trolliet F, Serckx A, Forget PM, Beudels-Jamar RC, Huynen MC, Hambuckers A. 2016. Ecosystem services provided by a large endangered primate in a forest-savanna mosaic landscape. *Biological Conservation* 203: 55–66.

Tsuji Y, Yangozene K, Sakamaki T. 2010. Estimation of seed dispersal distance by the bonobo, Pan paniscus, in a tropical forest in Democratic Republic of Congo. *Journal of Tropical Ecology* 26: 115–118.

Tutin CE, Fernandez M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology* 30: 195–211.

Tutin CE. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates* 40: 249–265.

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

Tutin CE, White LJ, Williamson EA, Fernandez M, McPherson G. 1994. Floral lists from five study sites of apes in the African tropical forests. List of plant species identified in the northern part of the Lope Reserve, Gabon. *Tropics* 3: 249–276.

Tutin CE, Parnell RJ, White F. 1996. Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 12: 371–384.

Tutin CE, Ham RM, White LJ, Harrison MJ. 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42: 1–24.

Tutin CE, Fernandez M. 1985. Foods consumed by sympatric populations of *Gorilla G. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. *International Journal of Primatology* 6: 27.

Tweheyo M, Lye KA. 2003. Phenology of figs in Budongo Forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology* 41: 306–316.

Tweheyo M, Obua J. 2001. Feeding habits of chimpanzees (*Pan troglodytes*), red-tail monkeys (*Cercopithecus ascanius schmidti*) and blue monkeys (*Cercopithecus mitis stuhlmanii*) on figs in Budongo Forest Reserve, Uganda. *African Journal of Ecology* 39: 133–139.

Twinomugisha D, Basuta GI, Chapman CA. 2003. Status and ecology of the golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda. *African Journal of Ecology* 41: 47–55.

Uwimbabazi M, Eilu G. 2014. Avian frugivore assemblages on *Celtis gomphophylla*, Baker, in Budongo Forest Reserve, Uganda. *African Journal of Ecology* 52: 97–102.

Van Cakenberghe V, Seamark EC. 2009. African Chiroptera Report 2014.

Voysey BC, Mcdonald KE, Rogers ME, Tutin CE, Parnell RJ. 1999. Gorillas and seed dispersal in the Lope Reserve, Gabon. I: gorilla acquisition by trees. *Journal of Tropical Ecology* 15: 23–38.

Wahome JM, Rowell TE, Tsingalia HM. 1993. The natural history of de Brazza's monkey in Kenya. *International Journal of Primatology* 14: 445–466.

Wang BC. 2008. *Impacts of hunting on seed dispersal in a Central African tropical forest*. PhD thesis, University of California, Los Angeles.

Wang BC, Sork VL, Leong MT, Smith TB. 2007. Hunting of mammals reduces seed removal and dispersal of the afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica* 39: 340–347.

Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology* 72: 650–659.

Webala PW, Musila S, Makau R. 2014. Roost occupancy, roost site selection and diet of straw-coloured fruit bats (Pteropodidae: *Eidolon helvum*) in western Kenya: the need for continued public education. *Acta Chiropterologica* **16**: 85–94.

Watts DP, Potts KB, Lwanga JS, Mitani JC. 2012. Diet of chimpanzees (*Pan troglodytes* schweinfurthii) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American Journal of Primatology* **74**: 114–129.

White L, Abernethy K. 1996. *Guide de la végétation de la Réserve de la Lopé.* Libreville, Gabon: Ecofac.

White LJ, Tutin CE, Fernandez M. 1993. Group composition and diet of forest elephants, *Loxodonta africana* cyclotis Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology* **31**: 181–199.

Whitney KD, Fogiel MK, Lamperti AM, Holbrook KM, Stauffer DJ, Hardesty B *et al.* 1998. Seed dispersal by *Ceratogymna hornbills* in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* **14**: 351–371.

Williamson EA, Tutin CE, Rogers ME, Fernandez M. 1990. Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology* **21**: 265–277.

Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP. 1993. The value of figs to chimpanzees. *International Journal of Primatology* **14**: 243–256.

Wrangham RW, Chapman CA, Chapman LJ. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* **10**: 355–368.

Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance, I. Antifeedants. *International Journal of Primatology* **19**: 949–970.

Yamagiwa J, Basabose AK. 2006. Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi–Biega National Park. *Primates* **47**: 74–90.

Yamagiwa J, Basabose AK. 2009. Fallback foods and dietary partitioning among Pan and Gorilla. *American Journal of Physical Anthropology* **140**: 739–750.

Yamagiwa J, Mwanza N, Yumoto T, Maruhashi T. 1994. Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* **35**: 1–14.

Yamagiwa J, Basabose AK, Kaleme K, Yumoto T. 2005. Diet of Grauer's gorillas in the montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology* **26**: 1345–1373.

Yamagiwa J, Basabose AK, Kaleme KP, Yumoto T. 2008. Phenology of fruits consumed by a sympatric population of gorillas and chimpanzees in Kahuzibiega National Park, Democratic Republic of Congo. *African Study Monographs* **39**: 3–22.

Yumoto T, Maruhashi T, Yamagiwa J, Mwanza N. 1995. Seed-dispersal by elephants in a tropical rain forest in Kahuzi-Biega National Park, Zaire. *Biotropica* **27**: 526–530.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Example of the treatment of plant–animal interactions networks by modularity and latent block model.

Fig. S2 Results showing the correlation among tree traits from the principal component analysis.

Fig. S3 Accumulation curves showing the sampling completeness of the frugivory network.

Fig. S4 Graphs of the probability of each tree and frugivore species belonging to its block.

Fig. S5 Graph of the probability of interaction between tree blocks and frugivore blocks.

Fig. S6 Clustering of species by blocks regarding their trait values on the principal component analysis.

Fig. S7 Matrix showing the probability of tree and frugivore blocks interacting following species traits.

Fig. S8 Graphs showing the relationships between the probability of interactions between blocks and species traits.

Table S1 Result from the model selection of models including the sum of probabilities by blocks and species traits and number of studies by blocks.

Table S2 Results of the selection of model including the probabilities of interaction between tree and frugivore blocks.

Table S3 Results from the generalized linear model showing the relationships with the sums of probability between tree and frugivore blocks.

Table S4 Results from the linear mixed regression showing the relationships between the probability of interactions between blocks and species traits.

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