Mutualistic tree-frugivore interactions in Afrotropical forests : from local ecological knowledge to the identification of network interaction patterns

Clementine Durand Durand-Bessart

THESE DE DOCTORAT DE L'ETABLISSEMENT UNIVERSITE BOURGOGNE FRANCHE-COMTE

Préparée à l'Unité Mixte de Recherche Biogéosciences (UMR 6282) et au CESCO (MNHN)

Ecole doctorale n°554, Environnement - Santé

Doctorat en Ecologie

Mutualistic tree-frugivore interactions in Afrotropical forests: from local ecological knowledge to the identification of network interaction patterns

Par

DURAND-BESSART Clémentine

Thèse présentée et soutenue à DIJON, le 28 juin 2022

Composition du Jury:

McCONKEY, Kim, Assistant Honorary Professor – University of Nottingham	Rapportrice
THEBAUD, Christophe, Professor – Universite de Toulouse Paul Sabatier	Rapporteur
GOURLET-FLEURY, Sylvie, Chargée de recherche, CIRAD	Examinatrice
CARRIERE, Stéphanie, Directrice de Recherche IRD	Examinatrice
BRETAGNOLLE, François, Professeur – Université de Bourgogne	Directeur de thèse
FONTAINE, Colin, Chargé de Recherche, CNRS	Co-directeur de thèse

Titre : Interactions mutualistes arbres-frugivores dans les forêts Afrotropicales : des connaissances écologiques locales à la mise en évidence des patrons d'interaction du réseau de frugivorie

Mots clés : Interactions mutualistes, latent block model, communauté forestière, interview

Dans les forêts tropicales la frugivorie est un processus écologique majeur, car la plupart des espèces d'arbres dépendent des frugivores pour leur dispersion, et de nombreux animaux utilisent les fruits comme principales sources de nourriture. Cependant, les réseaux de frugivorie sont peu décrits dans les forêts Afrotropicales et les mécanismes qui les façonnent restent largement inexplorés. Cette thèse de doctorat aborde une approche structurelle du réseau de frugivorie, une approche plantes-communautés et une approche méthodologique utilisant les connaissances locales et les caméras.

Le chapitre 1 décrit le réseau de frugivorie des forêts Afrotropicales, basé sur une compilation des interactions de frugivorie issues de la littérature avec >10 000 interactions. La structure du réseau a été analysée avec un *latent block model*, une méthode probabiliste qui groupe des espèces présentant des schémas d'interaction similaires. Les grands frugivores étaient les principaux disperseurs de la plupart des arbres et les grands arbres étaient les principales sources de fruits de la plupart des frugivores. Nos résultats montrent aussi la vulnérabilité de ce réseau de frugivorie et l'intégrité fragile des forêts Afrotropicales.

Le chapitre 2 s'est concentré sur les variations des traits des communautés d'arbres dans les forêts du Bassin du Congo en relation avec les interactions frugivores. Nos résultats ont montré des différences dans les traits liés à la frugivorie selon les types floristiques, les forêts atlantiques offrant de plus gros fruits, tandis que les forêts du Nord présentaient une plus grande abondance de petits fruits. Nous avons constaté que les chimpanzés et les calaos interagissent avec les fruits les plus abondants, les éléphants consomment toujours les plus gros fruits offerts par la communauté, tandis que les petits oiseaux consomment les plus petits fruits.

Le chapitre 3 portait sur les connaissances écologiques locales (LEK) en rapport avec les interactions de frugivorie. Un socle commun d'arbres et de frugivores a été utilisé, pour comparer les informations provenant des LEK et les connaissances académiques. Les populations locales avaient une connaissance substantielle des relations entre arbres et frugivores, avec 39% de nouvelles interactions, modifiant également la structure du réseau de frugivorie, en attribuant en moyenne de plus petits frugivores aux espèces d'arbres.

Dans le chapitre 4, l'utilisation de caméras pour enregistrer les interactions entre arbres et frugivores de la communauté forestière des frugivores terrestres du Gabon, a permis d'ajouter plus de 30% de nouvelles interactions. La plupart de ces interactions concernaient les petits frugivores comme les rongeurs, mais aussi certains grands mammifères. Ces résultats montrent la nécessité de poursuivre les recherches sur les interactions arbres-frugivores mais aussi d'intégrer d'autres sources complémentaires pour apprécier la complexité des réseaux mutualistes.

Ce travail de thèse a permis de comprendre les différents mécanismes qui régissent les interactions entre les arbres et les frugivores, notamment l'importance de la distribution spatiale des espèces et leurs traits biologiques. Nous avons également mis en évidence des biais concernant les données, la plupart des études portant sur des espèces emblématiques et certaines zones, et concernant les différentes méthodes, les caméras se concentrant sur les frugivores terrestres et le LEK étant borné par les connaissances académiques. Ces résultats nous permettent de faire des recommandations pour contrer ces biais, dont la diversification des méthodes d'échantillonnage, notamment en collaborant avec les populations locales dans diverses zones Afrotropicales.

Title : Mutualistic tree-frugivore interactions in Afrotropical forests: from local ecological knowledge to the identification of network interaction patterns

Keywords : Frugivory interactions, latent block model, forest community, interview

Frugivory in tropical forests is a major ecological process, as most tree species rely on frugivores for their dispersion, and numerous animal species used fruits as their principal sources of food. However, frugivory networks between plants and animals in Afrotropical forests are poorly described, and the mechanisms shaping them remain largely unexplored. This PhD thesis addresses a structural approach of the frugivory network, a plant-community approach and a methodological approach using local ecological knowledge and cameras.

The first chapter describes the frugivory network of Afrotropical forests, based on a compilation of frugivory interactions from the literature that comprised >10,000 links. We analysed the network structure with a latent block model that groups species with similar interaction patterns and estimates interaction probabilities among them. Larger frugivores were the main dispersers of most trees and larger and/or low wood density trees were the primary fruit sources of most frugivores. Our findings show the vulnerability of this frugivory network and the fragile integrity of Afrotropical forest composition.

The second chapter focused on the trait variations of tree communities within Central African forests in relation to frugivory interactions. Our findings showed differences in frugivory traits offered among the floristic type, with Atlantic forests offering larger fruits, while Northern forests presented a greater abundance of smaller fruits with smaller seeds. Moreover, we found that while chimpanzees and calaos interact with the fruits that are more abundant, elephants always consume the largest fruits and seeds offered by the community, while smaller birds consume the smallest fruits and seeds.

The third chapter focused on local ecological knowledge on tree-frugivore interactions. We used a common set of trees and frugivores species, to compare information gathered by local people, academic knowledge. Local people had substantial knowledge on tree-frugivore relationships, with 39% of unique interactions. LEK also changed our understanding of the frugivory network, by assigning on average smaller frugivores to tree species and smaller seeded plants to frugivore species.

In the chapter four, we used camera traps to monitor frugivory interactions of terrestrial species of Gabonese forests. We compared the records of cameras with the LEK and academic dataset, and showed that camera added more than 30% of new interactions Most of these interactions concerned smaller frugivore like rodents, but also large mammals like elephants and gorillas. These results show the necessity to continue the investigation on tree-frugivore interactions but also to integrate other complementary sources to appreciate the complexity of mutualistic networks.

This PhD work gave insight on the different mechanisms governing frugivory interactions, regarding the importance of overlap in distribution areas and match between biological traits. We also highlighted biases concerning the dataset with most studies on emblematic species and certain areas, and concerning the different methods with cameras focus on ground frugivores, and LEK restricted by academic knowledge. These results allowed us to give recommendations to increase our knowledge on frugivory interactions. One of the recommendations was to diversify the methods to sample interactions, by collaborating with local people in diverse areas of the Afrotropical forests, or by using arboreal cameras to record smaller frugivores.

Remerciements

First, I would like to thank the members of the jury that kindly accepted to evaluate my work, Kim McConkey, Christophe Thébault, Sylvie Gourlet-Fleury and Stéphanie Carrière.

En premier lieu, je remercie chaleureusement Colin et François qui en encadrant cette thèse ont partagé avec moi cette passionnante aventure riche en rebondissements ! Cette thèse est le fruit d'un grand travail collaboratif, et je suis ravie d'avoir fait équipe avec vous. François merci de m'avoir fait découvrir le Gabon, ces forêts incroyables et les animaux qui les peuplent : éléphants, gorilles et pangolins géants. Merci d'avoir partagé ton enthousiasme, tes connaissances et ta passion pour cet écosystème si particulier qu'est la forêt tropicale africaine. Je garde de précieux souvenirs des quelques jours de mission ensemble à Doussala, le taxi bus des enfers, le curry de mangues, le crocodile et bien d'autres choses improbables. Colin, merci d'avoir fait preuve d'une grande patience, de pédagogie malgré les (nombreuses) questions et analyses sans trop de sens. Merci aussi pour les échanges sur les doutes que l'on rencontre dans ce monde de la recherche si particulier et compétitif, je crois que ça m'a bien aidé et beaucoup soulagé, je garderai ces précieux conseils pour les nombreuses futures fois où je vais encore douter et hésiter.

Je souhaite également remercier Elisa, Pierre-Michel et Doyle pour leur participation aux comités de thèse, merci pour vos conseils avisés ! Doyle, tes cours ont été les plus passionants, et sont certainement pour beaucoup dans mon envie de poursuivre dans la recherche en ethno-écologie, merci beaucoup !

Merci aux co-auteurs et co-autrices pour leur précieuse contribution aux différents manuscrits: Kate Abernethy, Colin Chapman, Norbert Cordeiro, Pierre-Michel Forget, Maxime Réjou-Méchain, Cyrille Violle ; et également à Etienne et Ghislain, chercheurs de l'IRET qui m'ont aidé et accompagné pendant ma mission de terrain au Gabon. Un merci particulier à Ghislain qui a veillé sur moi pendant mon séjour à Doussala, pour les discussions sur les traditions Fang, pour m'avoir fait découvrir le vin de palme ! Merci à Yannick qui a été un grand moteur de ce projet au Gabon, j'ai été ravie de passer ces quelques semaines dans ta famille à Libreville.

Une pensée particulière à tous les participants aux enquêtes à Libreville comme à Doussala, je les remercie de m'avoir donné de leur temps, ainsi que d'avoir accepté de me léguer une partie de leur savoir sur la faune et la flore gabonaise, j'en serai toujours très honorée. Merci aux guides/interprètes/traducteurs qui m'ont accompagnée, j'ai beaucoup appris grâce à vous, donc merci à Giovanni qui m'a permis de parcourir Libreville sans encombre et de manger de délicieux Mafé; et puis à Roy d'avoir arpenté avec moi les forêts denses, tout en échappant aux éléphants, et en contemplant les gorilles.

Remerciements

En restant en Doussala, merci à Masaya et Mayuko, d'avoir illuminé les sombres heures d'attente dans la station, en m'apprenant le Japonais, et puis aussi pour les essais culinaires, je retiendrai les ebi-fri, les ramens, moins les poissons de rivières par contre … Merci Masaya d'avoir tenté de m'apprendre le base-ball, et m'avoir permis de rencontrer Nidaii (ci-dessous) et son groupe. J'ai pu m'imaginer le temps de quelques heures dans la peau de Dian Fossey ou Jane Goodall, et penser moi aussi pendant quelques instants que j'avais trouvé ma place dans ce monde.

« A sense of calm came over me. More and more often I found myself thinking,

"This is where I belong. This is what I came into this world to do."

Jane Goodall

Le magnifique Nidaii, prenant la pause. Photo de Masaya.

De retour en France, j'aimerais particulièrement remercier mes co-bureaux à Dijon : Antoine, Nico (l'orage dans le champ de cassis est gravé dans ma mémoire) & Corentin ; puis à Paris : Alice, Milena et Robin ; merci d'avoir supporté mes complaintes, mais surtout merci pour ces moments de rires et de partage et puis de m'avoir soutenu tout ce temps !

Belle ~~Milena~~ et Bulle ~~Alice,~~ on a été le meilleur trio (!), j'emporte avec moi toute votre bonne humeur, notre girl-power, les fous rires et les mèmes – je resterai productive mais asymptomatique à vie ! Alice je suis très heureuse d'avoir partagée ces derniers mois/semaines/jours de thèse en binôme avec toi, pensée spéciale à nos derniers soirs au CESCO à chasser la souris. Milena, merci d'être un modèle d'organisation de vie (!), pour les conseils stats et cette magnifique carte de dernière minute ! J'espère qu'on t'a pas fait trop peur avec Alice !

Merci au CESCO de m'avoir si bien accueilli pour ces derniers mois de thèse, particulièrement aux « habitants » du 135 qui m'ont permis de découvrir qu'on pouvait être super sérieux et studieux mais aussi et surtout faire super la fête ! Donc un grand merci à vous tous pour les (très ~~trop~~) nombreuses soirées : Anne-Christine – créatrice de Légendes, Charles, Martin (déso pour le vélo ^^'), Romain, Simon – pour les clit-origamis. Au Go du team roller-derby SexCocide of course : Suzanne, Camille, Dianicool, Anya, Mathilde, Nora – on va tout casser !! Mais aussi aux autres doctorants : Clément (compagnons de la BES), Ludo, Jean, Tanguy ; et la team Vigie nature : Anne, Benoit, Greg, Jérôme, Marine, Seb, Victor. Désolée aux oublié.e.s.

Un grand merci à Gabrielle, Nico & Solène, Corentin, et Antoine, pour les parties de GarticPhone pendant les confinements et puis après ! Merci aux autres Dijonnais.e.s, pour le soutien pendant la première partie de cette thèse: Adrien, Charlie, Yannick, Remi (je te dois toute ma connaissance sur les escargots !), Thierry. Merci à l'équipe de l'Expérimentarium, particulièrement Coralie et Robin, pour votre enthousiasme, votre écoute, et ce magnifique projet, auquel j'ai été ravie de prendre part.

Gabrielle – merci pour tout le Girl Power !, le soutien et les encouragements pendant ces derniers jours de thèse comme pendant l'ascension du Mont Aigoual ! J'espère pouvoir te rejoindre bientôt sous le soleil martiniquais.

Merci aux ami.e.s de Montpellier qui ont toujours été là, même en étant si loin: Lulu & Thomas, Mira & Maik, Cécilia, Michel, Joan. Merci aux ami.e.s d'ailleurs, Léna, Miléna, Magali (bon courage c'est bientôt fini !), Claire, Manon & Clémentine (merveilleuses colocs).

Remerciements

Merci à toutes celles et ceux que j'oublie, mais qui ont contribué de près ou de loin, au bon déroulement de ces années de thèse.

Vincent, nos conversations passionnantes, et notre amour commun pour les bizarreries des tropiques m'ont aidé à garder cette petite flamme qui m'anime quand je pense aux forêts tropicales. Je crois qu'un peu grâce à toi, j'ai quand même toujours envie d'y retourner malgré ~~tout~~ les éléphants.

Aurore un petit bout de cette thèse t'es dédiée, pour toute l'aide et le soutien apportés durant ces ~~trois~~ quatre années de thèse ! On y sera arrivé, malgré les nombreux obstacles rencontrés ! Je suis ravie de pouvoir continuer à tes côtés cette vie de bébé chercheuse ! Tu vois le radeau continue de flotter, sans trop d'effort, on se laisse porter, et on patiente.

Merci à mon incroyable famille pour le soutien sans faille ! À mes sœurs Marie-Lou et Macha, vous êtes les meilleures (Marie-Lou un grand merci pour cette relecture-correction de thèse finale). À mes parents de m'avoir toujours supporté et aidé pendant toute la thèse (et la vie aussi) et particulièrement pendant les longs mois de confinement. À Djaïpour d'incarner à lui seul la liberté, et de m'avoir permis de m'évader !

TABLE OF CONTENTS

PUBLICATIONS & COMMUNICATIONS

Durand-Bessart, C., Tixier, P., Quinteros, A., Andreotti, F., Rapidel, B., Tauvel, C., & Allinne, C. (2020). Analysis of interactions amongst shade trees, coffee foliar diseases and coffee yield in multistrata agroforestry systems. *Crop Protection*, *133*, 105137.

Durand-Bessart, C., Fontaine, C., Abernethy, K., Chapman, C., Cordeiro, N., Forget, P-M. & Bretagnolle, F. (in review). Big trees, large seeds, and frugivorous megafauna best explains structure of Afrotropical tree-frugivore networks. *Submitted to New Phytologist*

Berzaghi, F., Bretagnolle, F., **Durand-Bessart, C**., & Blake, S. (2021). Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. *bioRxiv*.

Talk

Durand-Bessart et al. (2021) – Complementarity of local ecological knowledge and academic studies on frugivory networks: case study of Afrotropical forests – British Ecological Society – Ecology Across Borders Liverpool 2021

Durand-Bessart et al. (2019) - Analysis of the interactions of shade trees on coffee leaf diseases and coffee yield in complex agroforestry systems. World Congress of Agroforestry – Montpellier 2019

Poster

Durand-Bessart et al. (2019) - Using blockmodel to analyse the hyper-diverse seed dispersal network of tropical African forests. Symposium of network ecology – Paris

INTRODUCTION

One of the largest tree of the Moukalaba-Doudou forests, an incredible source of food for numerous frugivores. Picture Clémentine Durand-Bessart

PART 1: PLANT-ANIMAL MUTUALISTIC INTERACTIONS

Mutualistic interactions between plants and animals have been a major axis of ecological studies since the beginning of ecological research (May, 1982; Bronstein, 1994; Holland and Bronstein, 2008). They stressed the huge impact mutualism had on Earth biodiversity with pollination inducing the diversification of insects and Angiosperms and dispersal by animals influencing fruit plants diversity (Ehrlich and Raven, 1964). Mutualism interactions between plants and animals are organised in networks, where each plant or animal species evolves in a community and interacts with one or more species (Bascompte and Jordano, 2006). The large number of studies on plant-animal interactions carried out over the last fifty years, with various methods, now facilitates research on interaction networks. The challenge of network studies was then to understand the functioning of these networks of mutualistic interactions and also to apprehend and anticipate the cascading effects resulting from perturbations (Bascompte et al., 2006; Thebault and Fontaine, 2010). For this purpose, diverse network analysis helped understand the structural organisation as well as the mechanisms behind interaction patterns.

A. Mutualistic plant-animal interactions: focus on the frugivory and seed dispersal

Mutualistic interactions between plant and animal species have been the centre of attention of the research community since the beginning of ecological and evolutionary studies (Box 1), beginning with Darwin's fascination for *Angraecum* orchids and its "untraceable" moth pollinator (Darwin, 1862). From then on, numerous examples of these species-specific interactions have been described, particularly the coevolution dynamic between some plant and animal species, such as figs and wasps (Wiebes, 1979; Michaloud et al., 1996; Cook and Rasplus, 2003), or yuccas and moths (Macior, 1971; Pellmyr, 2003). These examples applied only to a small minority of plant-animal interactions, based on an almost exclusive and obligatory relationship between both partners. Later on, studies have extended their focus to multi-specific approaches, by investigating small groups of interacting species, to describe a larger aspect of plant-animal interactions (Gautier-Hion et al., 1985; Parchman and Benkman, 2002). Today, studies and methods have changed to take into account hundreds of species, from diverse groups and to analyse their interaction dynamics through space and time (Poisot et al., 2015; Timóteo et al., 2018). Moving from interactions between species couples to complex multi-species interactions was made possible by approaching these multi-interactions partnerships as a network of interactions (Bascompte, 2019).

Box 1 – Definition of mutualism

Mutualism, i.e. the mutualistic interactions between individual of different species, is by definition beneficial to both parts, with positive effects on their fitness: reproduction and/or survival (Holland and Bronstein, 2008). Species involved in this mutualistic partnership must benefit from this interaction, being goods or services. In mutualism, the benefit received does not come without a cost for species (Bronstein, 1994), and mutualistic interactions are not altruistic: they do not imply the equitability between benefits and costs between interacting partners.

Benefits and costs come in various forms and depend on the organisms involved in this mutualism. In plant-animal interactions, such as pollination and seed dispersal, plants produce goods, here food resources, to attract pollinator or frugivore-dispersers, being nectar or fleshy-fruits. The cost of this production is non-negligible for the plant, while animals spend time and energy on fetching the goods. These costs and benefits also relate to the dependence of the species to this mutualistic interaction. Mutualism can be facultative or obligatory for both species, but also facultative for one and obligatory for the other. Interactions are facultative when the species population persists without the interactions, and are obligatory if the disappearance of the partnership causes the extinction of the population (Holland and Bronstein, 2008). This dependency can also vary in space and time, as a plant could have an obligatory interaction with an animal species to persist in one geographic area, but not throughout all its geographic range. In plant-animal interactions, obligatory interactions are rare.

Considering mutualistic interactions as an ensemble allowed to express their importance as a key process in the diversity dynamic of plants and animals – particularly insects – biodiversity on Earth, particularly through pollination and seed dispersal (Ehrlich and Raven, 1964). Indeed, the diversification of Angiosperms, i.e. flowering plants, is strongly linked to their increasing mutualistic interactions with insects for their pollination, a phenomenon that accelerated during the mid-Cretaceous (120 million years ago) (Labandeira et al., 2002). The diversification of plants with fruits and small mammals and birds also coincides with the evolution of fruit with structures involved in attracting animals for seed dispersal, which appeared in the Tertiary period (66-2.6 million years ago) (Tiffney, 2004). Also, strong evidences lead to a diversification of primate as a result of mutualism with plant species (Gómez and Verdú, 2012).

Box 2 – Definition of frugivory and seed dispersal

Dispersal is the departure of a diaspore – seed or fruit – from the parent plant. **Establishment** is the process during which a germinating seed takes root, uses up parental provisioning, and assumes independent growth as a seedling. A **fruit** is the matured gynoecium with or without other floral organs or parts of organs. Loosely, it is the ripened ovary including the embryo, seed nutrient (endosperm), and other parental tissues (Howe and Smallwood, 1982).

Zoochory is the seed dispersal of plants by animals as a vector of the dispersal, these animals help the dissemination of plants by consuming and defecating the seed elsewhere, or carrying it away from the parental tree, mostly through fleshy-fruits. Recent studies showed the importance of pulp removal, rather than digestion, for the seed to germinate. In seed dispersal by animals, fleshy-fruits are often composed of a soft, edible and nutritive tissue called pulp, located around the seeds, that is a substantial food resources for numerous frugivorous animals, such as mammals, birds, but also reptiles and insects (Howe, 1986; Jordano, 2000). There are multiple ways animals can disperse seeds: epizoochory where animals carry the seeds on their fur or feathers; endozoochory when animals consume the seeds through fruit consumption and the seeds is split or digested and rejected in the faeces; synzoochory when seeds are dispersed by caching animals, these animals often being seeds predators too (Gómez et al., 2019). In seed dispersal and frugivory plant-animal interactions, studies focus on endoozoochory and synzoochory.

The dispersal phenomenon is often divided in two or three phases (Vander Wall and Longland, 2004). Primary dispersal corresponds to the dispersion phase from the moment the fruit is detached from the mother tree and consumed directly on the plant or after it falls and is eaten on the ground. Secondary dispersal occurs when the seed has already been moved or consumed by another individual or species, and another species will consume it or move it. This dispersal is then assured by terrestrial dispersers that will eat or cache the seed (Kurten, 2013). Both dispersal phases benefit differently for the plant, phase 1 helps avoid the density-dependency mortality by the fact that the seed is moved away from the mother tree, and helps to colonize a new environment, but not automatically with a great establishment success. Phase 2 increases seeds establishment and survival by being placed in hides or safe sites.

B. Methods to monitor frugivory and seed dispersal

This extensive research on plant-animal networks dynamic was possible thanks to the effort allowed in recording and monitoring these interactions through diverse methods. Recording and monitoring plant-animal relationships has been a great challenge in ecology, as they take multiple form, change through space and follow phenological changes.

a. Developing tools to monitor frugivory and seed dispersal interactions

Frugivory interactions have been the focus of numerous studies for decades and various methods have been developed to monitor plant-animal mutualistic partnerships. The methods are often divided in two categories: i) visitation of animal on plant, based on direct observation by observant or cameras; or ii) dissemination, where information are collected indirectly mostly through faeces analysis (Fig. 1).

In the direct observation methods, species interactions monitoring is centered on the focal tree species: after identification of the tree species, the animal feeding on its fruits are recorded. The first method used to record plant-animal frugivory interactions was the direct observation of animals feeding directly on the trees bearing fruits (Levey et al., 1986). While being efficient, this method has several limits: the difficulty to detect shy or cryptic animals, the difficulty to identify the species involved and the cost that it represents in terms of sampling time. From this method, camera-trapping has been developed, still centered on specific plant or tree species. Cameras are helpful as they can detect shy and cryptic animals as well as nocturnal animals. Also, cameras have been useful to go further in monitoring interactions, by allowing a quantification of some animal feeding behaviour (Trolliet et al., 2014). Among other advantages, cameras can stay on study sites for a few weeks and even more with batteries replacement. A recent extension of this method is the possibility to place cameras in the canopy (Moore et al., 2021), as most studies were based on terrestrial species, creating a bias toward these species, mostly large mammals. Canopy cameras, while more technical and labor intensive, have been successful in recording interactions involving birds and bats (Zhu et al., 2021).

Indirect methods mostly use animal faeces, by identifying the remaining seeds or through DNA-based molecular analysis. They allow to monitor indirect and delayed interactions, and have opened new possibilities in this research area (González-Varo et al., 2014). They give details on the number of seeds ingested, and their viability after digestion. However, it is difficult and expensive to apply this method on a large scale, as most of them focus on one species of animal.

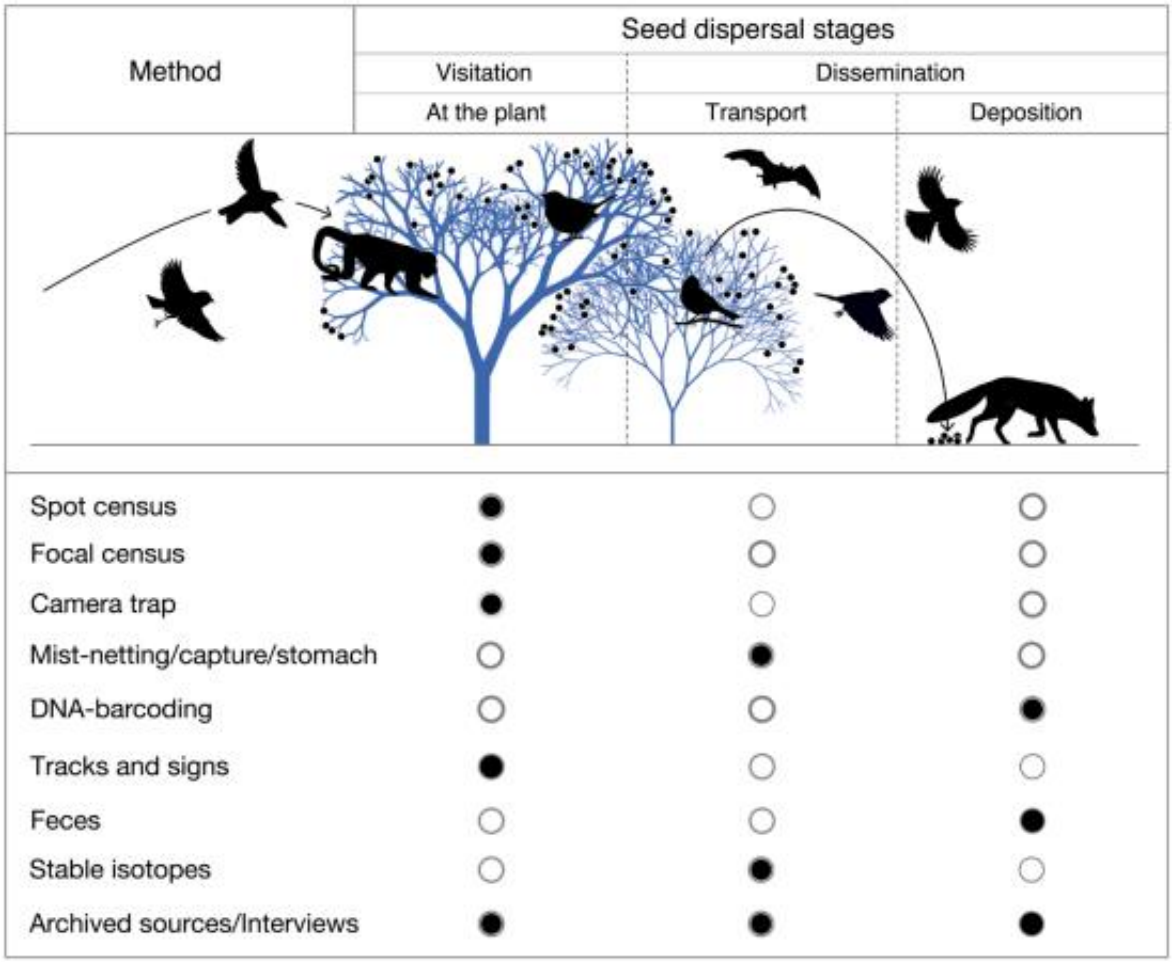

Figure 1. Most frequently used methods for recording plant–frugivore interactions. Sampling methods are classified according to the seed dispersal stage in which they are most frequently applied: 'visitation', 'transport' and 'deposition'. Extracted from Quintero el al. (2021).

b. Local ecological knowledge on plants and animals and their interactions

Along with the recent development of new tools to record plant-animal interactions, studies increasingly integrate local ecological knowledge (LEK), i.e. knowledge of indigenous peoples and local communities, on ecological processes. The knowledge of indigenous people and local communities about their surrounding environments on multiple ecological aspects ranging from the species composition of ecosystems to the services they provide, has recently been incorporated to ecological studies (Asselin, 2015; Cámara-Leret et al., 2019). Research efforts initially focused on the expertise of indigenous peoples and local communities on plants, mostly for pharmaceutical or conservation purposes, in different ecosystems (Schultes and Raffauf, 1990; Gadgil et al., 1993; Schultes, 1994; Sheng-Ji, 2001; Marie et al., 2009; Brondízio et al., 2021). Recently, local ecological knowledge has helped monitor species abundances (Anadón et al., 2010) and assess animal diversity trends (Azzurro et al., 2011).

From this assement, further studies focus on local ecological knowledge on more complex ecological processes such as species interactions. The combination of local ecological knowledge and academic studies has proven useful to understand the perturbation caused by invasive species on fisheries trophic networks (Rosa et al., 2014; Farr et al., 2018). Regarding frugivore-plant interactions, insights into frugivory and seed dispersal interactions in Amazonian forests (Hawes and Peres, 2014), and Asian tropical forests (Ong et al., 2021) have been consolidated and increased by including the knowledge of local people.

Network of interactions between plant and animal emerged from each study of plant-animal interaction, regardless of the methods. The compilation of different methods, such as camera trap, DNA barcoding, and interview with local people to monitor plant-animal interactions has proven effective in increasing the completeness of interaction networks and compensating for the bias of each method, e.g., the reduced sample size used for DNA barcoding and the ground animal bias for cameras (Quintero et al., 2021). Also, merging different data set from different methods induces the merging of multiple local networks, which has recently shown its efficiency to work on large scale networks (de Almeida and Mikich, 2018).

C. Network analysis

Network approaches in mutualistic interactions studies help unravel the link, i.e. the interactions between species at the community scale and help understand their dynamics (Bascompte, 2019). Plant-animal mutualistic networks exhibit a bipartite structure, meaning that there are two levels of species – here plants and animals – one level interacting with the other. In this framework, there are no interactions within each level, plants do not interact with plants, and the same goes for animals (Figure 2). In network studies, the distinct elements from a level (here, species) are also named “nodes”, while interactions, i.e., links between species, are named “edge”.

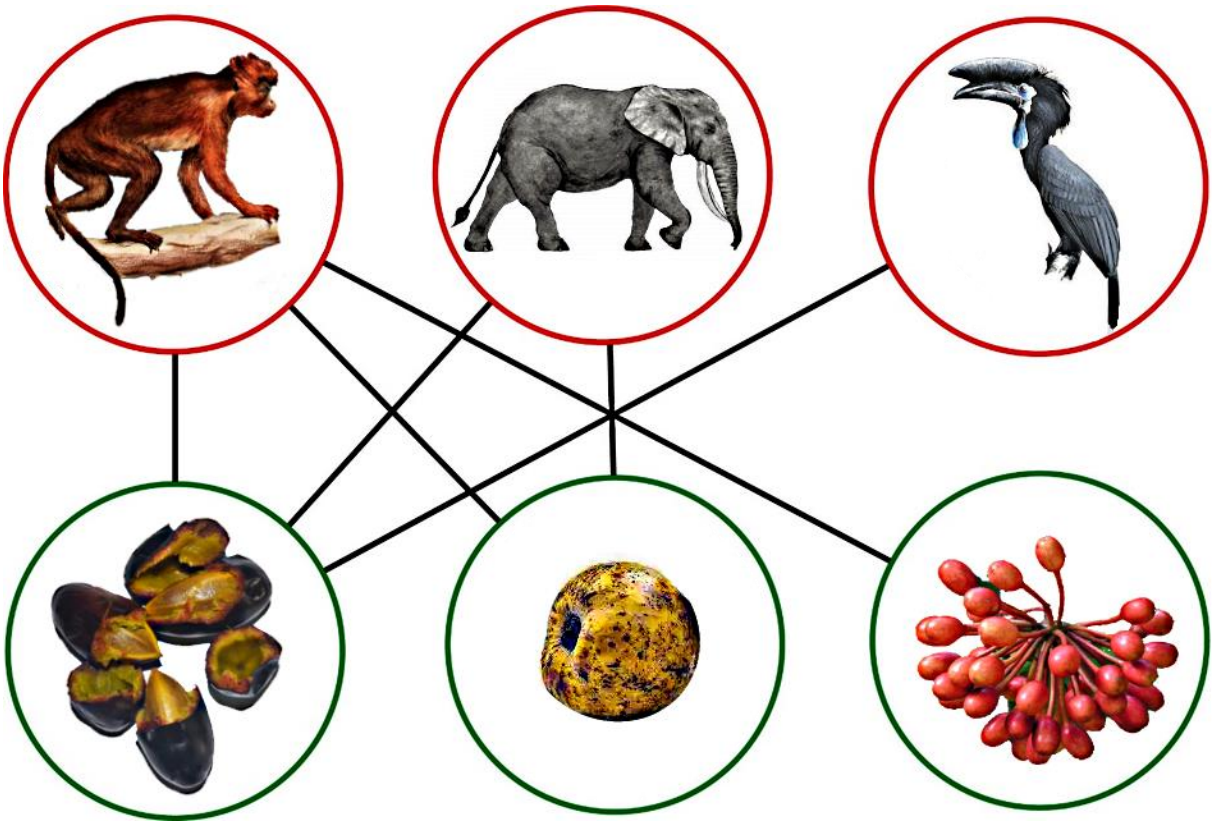

Figure 2. Networks of mutualistic interactions, between fruit plants and animal dispersers. Adapted from Bascompte (2019).

The structure of these bipartite networks depends on the diversity of species in the network, the number of links between species and the organisation of those links that create patterns of interactions. The diversity of species corresponds to the number of species integrated in the network, both for plants and animals. The number of links between species depends on how many species are connected inside this network, a property called connectance (Thebault and Fontaine, 2010). Connectance is defined as the number of observed interactions over the total number of possible interactions between species: if all species from one level, for example all animals, are interacting with all species from the other level – plants – the connectance is 1 (Jordano, 1987). Network diversity impacts connectance and an increase in the number of species will result in a decrease in connectance, as species do not perform all possible interactions.

The structural study of mutualistic networks of pollination and seed dispersal highlights the heterogeneity of interactions between plants and animals (Bascompte et al., 2006). Indeed, most species, called specialist species, interact with few species of such network, while some generalist species interact with most species of the network. In the Figure 2, the generalist animal is the monkey, and the bird is the specialist. This heterogeneity of interactions was repeatedly associated with a nested structure of the network, represented by a small number of generalist species that interact strongly with each other

– the core of the network – and a large number of specialist species that interact with the generalist species (Bascompte et al., 2003). After the discovery of nested structures in mutualistic networks, research focused on the explanation of such structures and their consequences for plant-animal networks. The dynamic of these networks was studied by testing their resilience to perturbations using simulations of species extinction. These studies showed that the degree of nestedness influences the stability of the network, as an increased nestedness raised the stability of the network. These results were obtained with different extinctions scenario, showing that the extinction of specialist species did not affect the network structures as long as generalist species – the core of the network – was maintained and allowed to continue most of the mutualistic partnerships (Memmott et al., 2004). This indicates that bipartite nested networks are more robust to habitat loss and extinction. Also, the nested structure seems to reduce the interspecific competition and increases the number of species that can coexist (Bastolla et al., 2009).

Another structure described in bipartite networks was the presence of subset of species highly connected, forming groups of species – called modules – having many interactions, but with few connections with species out of their modules (Jordano, 1987; Olesen et al., 2007). The investigation of the dynamic impact of perturbations on modular network structures showed that modularity – the presence of modules – in network increases its stability, because the effects of perturbations are mostly restrained inside a module (Olesen et al., 2007). However, some studies showed no or a negative correlation between resilience to perturbation and modularity, in complex mutualistic networks with high connectance (Thebault and Fontaine, 2010). Modularity and nestedness structure are non-exclusive and numerous mutualistic networks presented modular and nested structures (Olesen et al., 2007; Valdovinos et al., 2009). Still, future research has to focus on the links between different structural properties of mutualistic networks: connectivity, nestedness and modularity (Fortuna et al., 2010). The degree of nestedness has been arguably related to ecological stability (Bascompte et al., 2007; Thébault and Fontaine, 2010), while modularity has mostly been linked to species traits and functional diversity, with module expressing coevolutionnary units (Olesen et al. 2007; Tylianakis et al., 2010).

A new approach in network ecology is to use latent block models that are based on statistical inference to assign species with similar interaction patterns into groups called blocks (Leger et al., 2015). This approach has only recently been adapted to mutualistic networks (de Manincor et al., 2020a, 2020b). The development of latent block models offers a new perspective for the description of network structures (Leger et al., 2015; de Manicor et al., 2020; Bar-Hen et al, 2020). Indeed, latent block model is a clustering method that groups species into blocks – here distinct blocks for plants and animals – according to their patterns of interactions and estimates the probabilities of interaction among species from all plant-animal block couples. Compared to the modularity analysis, the latent block model is more flexible as it allows different numbers of blocks for plant and animals and allows each block, for example plant ones, to be linked to several animal blocks with links of variable intensity (Figure 3). Species within blocks might be considered as functionally redundant as they have a similar interaction

pattern, while the functional complementarity among blocks can be assessed from the estimated interaction probabilities among blocks (de Manincor et al., 2020; de Manincor et al., 2020). Then, the relationship between functional redundancy inside blocks and phenotypic traits or taxonomic signal of the species can be explored. Likewise, the probability of interactions between blocks allows to test different mechanisms behind interaction patterns between plant and animal blocks. Such mechanisms include for instance, the phenotypic hypothesis, where species interactions are defined by their phenotypic traits, or the encounter hypothesis, which relies only on the probability of one frugivore species to encounter a given tree species.

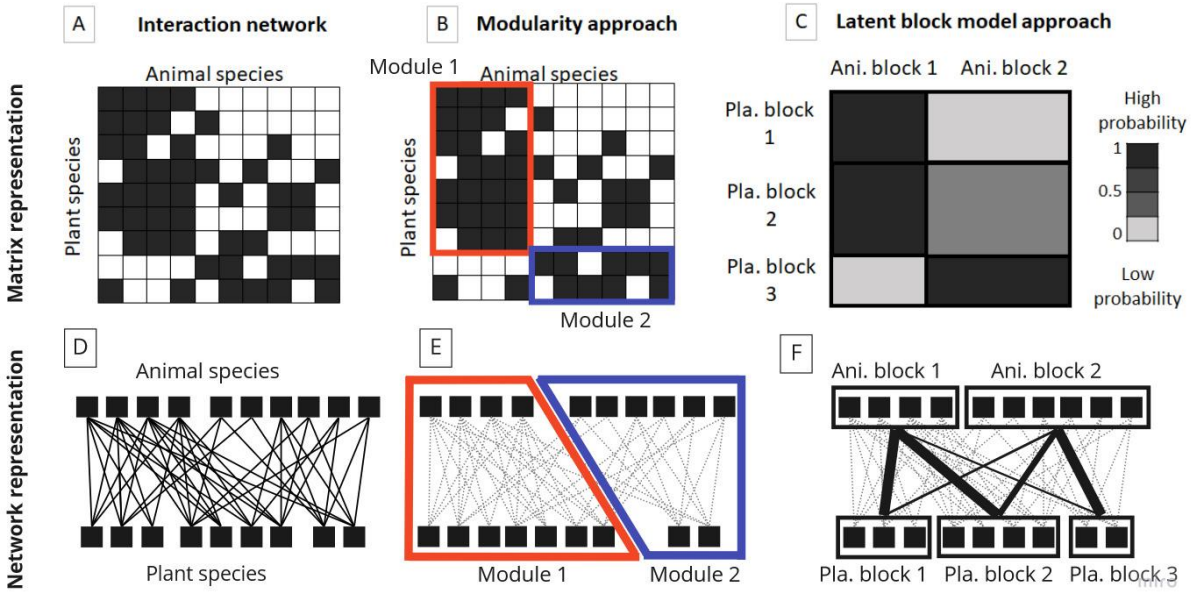

Figure 3. Interactions between species from two levels – here plants and animals – represented in matrix form (above) or network (below), and treated by two different analysis: modularity (B and E) and latent block model (C and F). The modularity analysis, clusters species in module composed of plants and animals having dense connections (B and E). The latent block model clusters species into blocks of two levels – here plants and animals separated according to their similar pattern of interactions, links between blocks are the probability of interactions and are illustrated by different intensities of grey (C) or different thickness of lines (F).

PART 2: FRUGIVORY AND SEED DISPERSAL NETWORKS IN TROPICAL FORESTS

Frugivory and seed dispersal are a central process in the ecosystems structure, particularly in tropical forests where 60 to 90% of tree species depend on animal for the dispersal of their seeds in favourable environments. Interactions between plants and animals are governed by a multiplicity of processes such as spatial and temporal species distribution, trait-based processes and phylogenetic relationships. These interactions patterns influence communities' assemblages in tropical forests. However, these key

interactions are threatened by deforestation and defaunation, leading to cascading effects on whole communities of plants and animals.

A. Interactions patterns between plant and animals

Network studies of plant-animal interactions gave new insight on the importance of mutualism to communities' structure and assemblage. First, frugivore species are consuming various fruits, depending on the season and their diet. These mutualistic interactions come from long co-evolution processes, where plant species traits evolved to be attractive to animals, and where frugivores increased their fruit diet (Jordano et al., 2011). Second, plants are often dispersed by different frugivore species, where each disperser has its own dispersing efficiency, following its living cycle, and transit (Fuzessy et al., 2016). These complex networks of interactions involve different factors that constrain the possible interactions, such as the spatial distribution of species, or their phenological timing, as well as trait-based processes or trait-matching, and phylogenetic relationships (Vázquez et al., 2009; Valdovinos, 2019).

Trait-based processes, mostly related to animals' body mass and seeds' size were shown as a determinant factor in the number of interactions between animal and plants (Jordano et al., 2011; Bender et al., 2018). Indeed, the size of the jaw or beak is highly correlated with the size of the animal and these are limiting factors in the ingestion of seeds (Sivault et al., 2020). However, frugivory and in some cases seed dispersal, is not only dependent on the body mass parameters, as dispersal methods can differ (Box 2). Then, smaller animals like rodents or bats are able to disperse larger fruits and seeds than predicted for their size (Ong et al., 2022). Biotic factors governing plant and animal relationships are not confined to animals' and seeds' size: different studies underlined the importance of fruit type e.g., drupe, berry or pods, or fruit color and smell (Valenta and Nevo, 2020). The description of syndrome of frugivory or seed dispersal represents specific fruits traits that attract different groups of frugivores, like the colors red and black attract birds, while green, orange and brown colors attract more mammals. This effect described in the early 90s is now being discussed (Valenta et al., 2018), as the prevalence of more cryptic colored fruits related to mammals is high in tropical areas, while birds are the most diverse frugivorous group (Fleming et al., 1987). Indeed, the correlation between large fruits and seeds with cryptic colors may be the results of an adaptation to the shaded environment of tropical forests (Willson and Whelan, 1990; Mack, 2000). Moreover, recent studies showed the importance of abiotic condition in selecting fruit traits, with the importance of temperature and season in the coloring patterns of fruits (Sinnott-Armstrong et al., 2021). Also, birds' beak sizes are positively correlated to temperature for thermoregulation purposes (Tattersall et al., 2017). Therefore, plants and animal traits are also linked to their taxonomic groups and phylogenetic effects while tenuous often plays a role in frugivory and seed dispersal networks (Rezende et al., 2007; Donatti et al., 2011). Indeed, some frugivores' group will preferentially be associated with other groups of plants and recent study showed that primates' evolution

and diversification could be linked to that of some tree families (Fuzessy et al., 2022), like Fabaceae and Moraceae. For example, the capacity of Moraceae species, like figs, to produce fruits year-round has an influence on the spatial distribution of primates species (Gautier-Hion and Michaloud, 1989; Shanahan et al., 2001; Ramos-Robles et al., 2018; Lim et al., 2021). The temporal parameters play an important role in seed dispersal efficiency, e.g. through species phenology, particularly fruiting peak – mast fruiting strategies (Norden et al., 2007), especially in seasonally dry forests (van Schaik et al., 1993). Fruits selection by birds depend on the abundance of the fruit species but also on the composition and abundance of co-fruiting species (Blendinger et al., 2016).

The overlapping in species spatial distribution and temporal factors, such as species distribution and abundance or phenology and fruit abundance, discriminate forbidden links from possible interactions (Olesen et al., 2011; González-Varo and Traveset, 2016; Ramos-Robles et al., 2018). Then, the asymmetric structure of bipartite mutualistic networks is related to species abundance, where abundant species have more symmetric interactions – having strong interactions with other abundant species, while rare species have asymmetric interactions as they depend more on abundant species (Vázquez et al., 2007). Showing that species generalism is strongly linked to their relative abundance. In addition, generalist species having large geographic distribution have proven to increase the connectivity between multi-layer networks in close localities, by guaranteeing the continuity of seed dispersal processes throughout a gradient of different landscapes (Timóteo et al., 2018). The temporal availability of plant and animal species also influences the network structures, with species of plant fruiting every years and frugivores' presence regularly forming a core of interacting partners – having more symmetric interactions – from which transient species of the network are related, independently of their relative abundance (Costa et al., 2020).

Then, plant-animal interactions depends on abundance and distribution of species, at local and regional scales, and these frugivory and seed dispersal interactions also influence abundance and distribution of species, particularly in tropical species.

B. Importance of frugivory in tropical forests

Tropical forests are widespread in South America, Africa and South-East Asia, covering about 18 million of km^2 (Keenan et al., 2015) and hosting the greatest species diversity on Earth (Schemske and Mittelbach, 2017). This high biodiversity closer to equatorial latitudes has been the subject of numerous hypotheses that can be summed up with three processes: the ecological hypothesis focusing on mechanisms of species' coexistence and the maintenance of species diversity, the evolutionary hypothesis focusing on rates of diversification, and the historical hypothesis focusing on the duration and extent of tropical environments in Earth's history (Mittelbach et al., 2007). The ecological

hypothesis linked the coexistence of species and the maintenance of high species richness to the heterogeneity of ecological niches. For plants in general and woody species in particular – that are fixed organisms – local occurrence depends on the suitability of the environment – the ecological niche – and on the dispersal success of the seeds. Then, the mechanism explaining species coexistence is the niche partitioning caused by interspecific competition.

The heterogeneity of available environments is thus a main factor determining the organisation of plant communities in rainforests (Flores et al., 2006). Disparities in abundance are common among plant species between different habitats or localities, but also on broader biogeographic scales, between different regions. The abundance and spatial distribution of species are intimately linked, with species having broader environmental tolerances achieving higher local densities and having a wider distribution range (Gaston and Kunin, 1997; Davidar et al., 2008). Some plant species tends to have aggregative patterns at a local scale, with the rarest species that tend to be more aggregated than the most common ones (Condit et al., 2000; Réjou-Méchain et al., 2011). Biological traits of plant species play a role in this aggregative pattern, with some plant families being more locally aggregated than other, mostly species without dispersal agents, or pioneer species, with low wood density and rapid growth (Condit et al., 2000). However, at a landscape scale (> 10km2) these aggregation patterns are not visible, implying other mechanisms such as sites' history or environmental conditions (Réjou-Méchain et al., 2011).

Plant assemblages of tropical forests are then highly linked to animal dispersal, as 50 to 90 % of tree species produce fleshy fruits and depend on fruit consumption and seed dispersal by animals (Howe and Smallwood, 1982; Bleher and Böhning-Gaese, 2001; Bascompte and Jordano, 2007). Seed dispersal diversifies potential habitats where a seed can be disseminated, and allows plant to move and colonize new environments (Vander Wall and Longland, 2004), or habitats after perturbation (Carlo and Yang, 2011). Compared to anemochory or barochory, only animals species, particularly vertebrates species, ensure the most efficient dispersal (Beaudrot et al., 2013).

Plant communities are differently impacted by long distance seed dispersal and short distance dispersal by animals. For most plant species, the majority of seeds are first dispersed to a short distance from the mother tree (Willson, 1993). Seed dispersal events thus have direct impact on the local population and the communities' dynamics (Howe and Smallwood, 1982). The fact that animals increase distance between seedlings or saplings, and parental trees, helps reduce their mortality and the intra-specific competition (Janzen, 1970; Connell, 1971). Indeed, the higher mortality of seeds, seedlings and saplings closer to the mother trees is due to their higher densities or in conspecific aggregates, mostly because of the highest rates of pests, pathogens, and herbivores or seed predators, which have a negative impact on tree recruitment (Connell, 1971; Janzen, 1970; Augspurger, 1984; Gonzalez et al., 2010). This phenomenon, known has the density and distance dependence mortality, promotes species diversity by decreasing seed and tree seedling density (Janzen 1970; Connell 1971). This negative density

dependence also affects conspecific species in plant assemblages, where population growth decreases with high densities, implying a higher species richness in the different communities (Johnson et al., 2012). Thus, dispersal is a strategy for plants to colonise a larger number of vacant sites, escape natural enemies present in concentrated sites around mother trees and reduce intraspecific competition.

The long distance dispersal performed by animals also allows distant plant populations to be connected which then has an effect on a larger scale (Levine and Murrell, 2003; Nathan, 2007). The organisation of communities on a local scale, even though they may be due to distinct processes, then contributes to global patterns observed at regional scale (Flores et al., 2006). These variation in tropical forests communities implied variation in community traits compositions that influence different ecological processes, such as the mutualistic relationship between plants and animals (de Bello et al., 2010; Dias et al., 2013). In pollination networks, the functional diversity of plants – their phenotypic differences – and their abundance, was positively correlated with the richness of pollinators and their visit frequency (Fontaine et al., 2005; Fornoff et al., 2017). These effects of the community traits on the ecosystem functioning have been explained by two non-exclusive mechanisms: the functional diversity and the mass-ratio effect. The functional diversity effect looks into the dissimilarities of traits values between co-existing species in a given community, regarding morphological traits such as petal color or fruit size; and also the non-additive effects due to the complementarity of traits in communities (Petchey et al., 2004; Mouillot et al., 2011; Dias et al., 2013). The mass-ratio effects explain this difference by integrating the abundance of species and expresses the traits of dominant species inside the community (Grime, 1998; Hector, 1998; Dias et al., 2013). In plant-frugivore assemblages, the abundance and dominance of large fruits would be related to the presence of large frugivore species, as they assume more of their dispersal. In community where megafaunal species have declined or disappeared, consequences on the plant assemblage is already visible, with a decrease of large seed establishment (Effiom et al., 2013).

C. Threats on tropical forests and consequences on plant-animal interactions

Tropical forests are threatened by defaunation (Fig 2) and deforestation (Box 3), resulting from the unsustainable activities of humans (Dirzo et al., 2014; Young et al., 2016). Deforestation impacts directly the resources available for animals, due to a decrease in tree diversity and density (Melito et al., 2021), affecting particularly plant-animal mutualistic interactions (Cowlishaw, 1999; Kinnaird et al., 2003; García-Morales et al., 2016; Morante-Filho et al., 2018). A loss of forest's cover greater than 30% causes important disruption in the functional diversity of forests, with an impact on reproductive and dispersal traits (Rocha-Santos et al., 2020). Some studies nonetheless suggest that communities are more resilient to forest degradation when relying more on plant-animal interactions (Montoya et al., 2008;

Camargo et al., 2022). In addition to deforestation problems, the defaunation crisis heavily impacts tropical ecosystems, creating "empty and silent" forests (Redford, 1992; Wilkie et al., 2011).

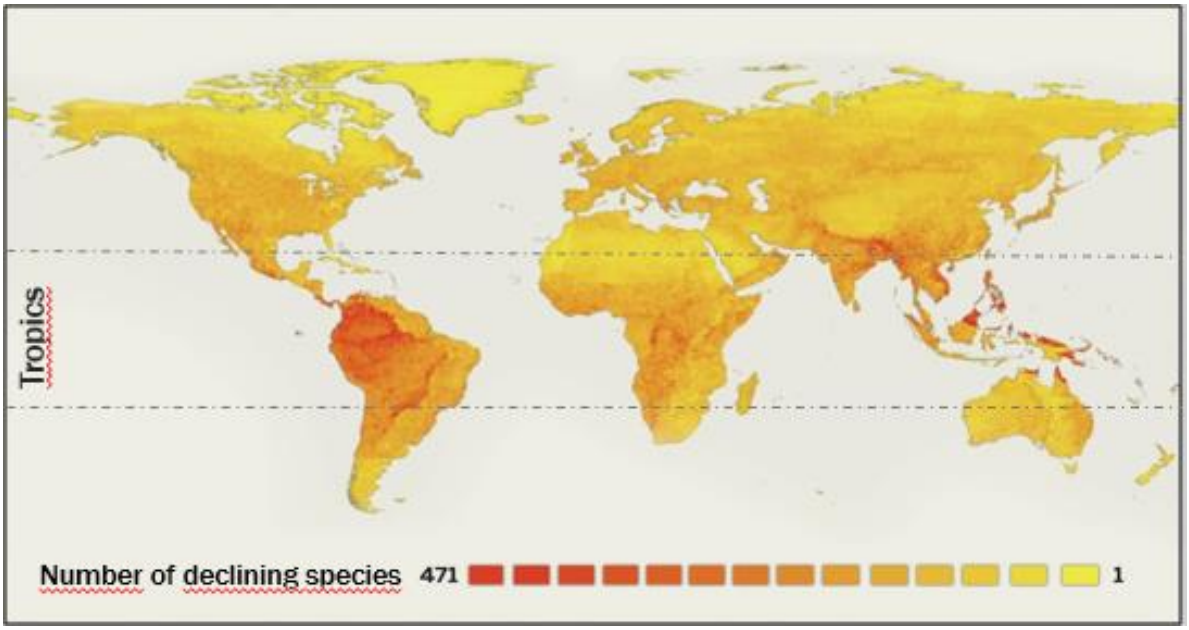

Figure 4. Number of declining species in the word. Extracted from Dirzo et al. (2014).

Disruption in forests communities are direct consequences of defaunation in tropical forests, where forest functioning relies heavily on plant-animal interactions (Gardner et al., 2019; Fricke et al., 2022). The negative effect on forest communities will have ecological and evolutionary consequences in the short and long term and at plot scales as well as global scales (Galetti and Dirzo, 2013).

Indeed, forest regeneration is impacted by the disturbance of functional structure processes such as seed predation (Galetti et al., 2015), herbivory (Jia et al., 2018), pollination (Anderson et al., 2021) and seed dispersal (Gardner et al., 2019). The changes in seed predation and/or herbivory lead to higher or lower seed recruitment, depending on tree species, inducing shifts in tree communities (Kurten, 2013). Moreover, the majority of tropical trees relies on animal for their dispersal, and in addition to the global decline of animal having important consequences on the downsizing crisis due to the removal of mostly large animal greatly impacts large-seeded tree species (Beaune et al., 2013a; Donoso et al., 2017, 2020). Large frugivores are primary disperser of large-seeded trees, and, by performing a long distance dispersal, provide unique services not fully compensated by other secondary dispersers (Galetti et al., 2018). A disruption in large seed dispersal leads to an increase in the aggregation of seedling close to parents and then to a greater mortality due to the distance dependence effect (see Janzen-Connell hypothesis Part 1-B) (Kurten, 2013).

In addition, studies showed that interactions between frugivores and plants are at a higher risk of extinction than the species implied (McConkey and Drake, 2006; Valiente-Banuet et al., 2015). Indeed, in areas where dispersers have a low abundance, the number of seed dispersers decrease, and the frugivores become inefficient dispersers before becoming extinct in the area. Specialist tree species dependent on few dispersers are highly at risk of extinction, where more generalist species could rely on secondary and less important dispersers (Beaune et al., 2013a; Kurten, 2013).

This phenomenon is already visible with the declining regeneration of large-seeded trees, and the increased regeneration of trees dispersed abioticaly or by smaller vertebrates, causing shifts in the composition of woody plant communities (Cordeiro and Howe, 2001; Nuñez-Iturri and Howe, 2007; Terborgh et al., 2008; Vanthomme et al., 2010; Effiom et al., 2013; Gardner et al., 2019). Also, the modelling of defaunation and downsizing of smaller species, like birds, showed a negative impact on seed size and diversity (Donoso et al., 2017). The disappearance of birds and primates, two key groups in frugivory and seed dispersal, was shown to lead to great declines in forest regeneration (Terborgh et al., 2008; Gardner et al., 2019), and also in other functional processes like pollination (Anderson et al., 2011, 2021).

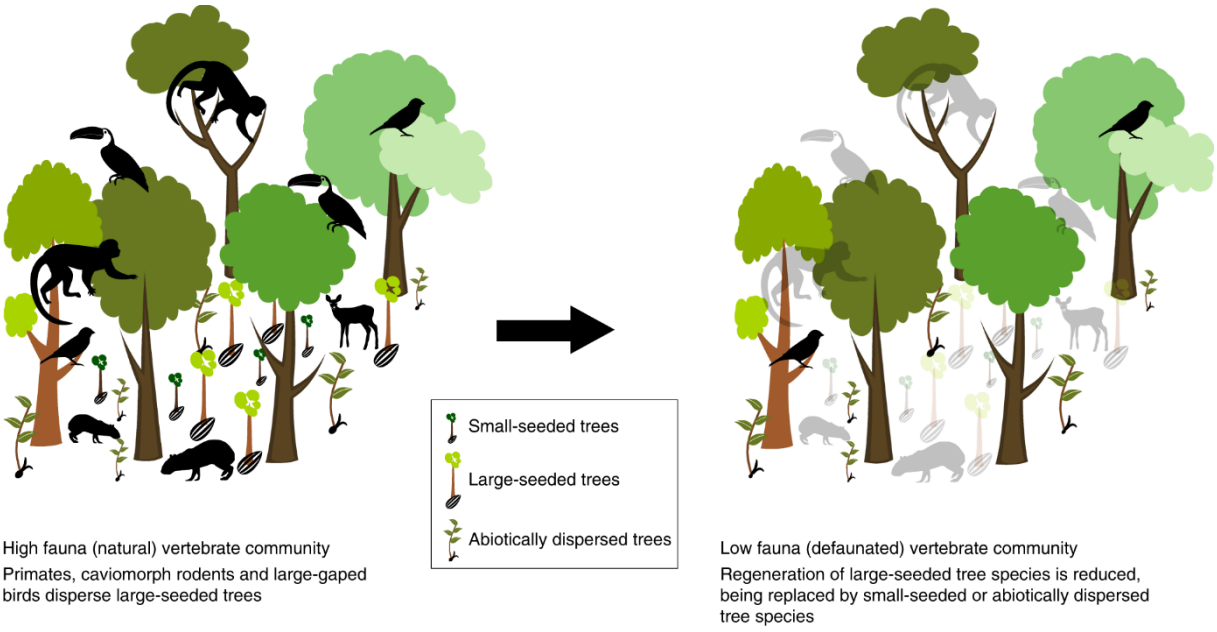

Figure 5. Schematic representation of forest regeneration in natural and defaunated forest communities. Extracted from Gardner et al (2019).

The prediction of the shifting of tree species toward smaller fruits and seeds, with the downsizing crisis was already recorded in the past, with the extinction of large mammals during the Late Pleistocene causing seeds to be smaller today than in the past (Lim et al., 2020). Moreover, a study of fossil records showed clearly that major extinctions of flowering plants were congruent with the decline of insects that

happened during the Cretaceous/Tertiary boundary (Labandeira 2002). In the Anthropocene, these deforestation and defaunation events are combined with climate change, and some studies suggest that the conjuncture of both phenomenon would only exacerbate the predicted effects (Abernethy et al., 2013; Fricke et al., 2022).

Box 3 - Definition of defaunation and deforestation

Defaunation is the loss of animals, due to direct human activities such as hunting and poaching, but also indirect such as deforestation, habitat loss and habitat fragmentation (Redford, 1992).

The removal of the largest species is creating a downsizing effect on animal communities, as large animals are hunted for food but are also more vulnerable to ecological and demographic changes caused by deforestation and habitat fragmentation (Peres and Palacios, 2007; Vidal et al., 2013).

Vertebrates populations of tropical forests have shown an important decline (estimated to reach 41 %) over the past 40 years (n=369) (WWF, 2016).

The definition of **deforestation** has changed throughout the years (Fernández-Montes de Oca et al., 2021), from complete transformation of forests to lands without a single tree (Myers, 1991), to a conversion of forests to other land uses, or to the long-term reduction of the tree canopy cover below the minimum 10% threshold (FAO, 2015). However, in the FAO definition, areas where trees were harvested or logged are not considered as deforested and the replacement of old-growth forests by plantations is not considered as deforestation.

PART 3: AFROTROPICAL FORESTS

Afrotropical forests have changed drastically in the past Quaternary (from 2.58 Ma to today), affecting their tree diversity that is today lower than that of South American and Asian tropical forests (Couvreur et al., 2021). Afrotropical forests are famous for their emblematic megafauna, with forests elephants, gorillas, chimpanzees and bonobos, species that are particularly threatened by defaunation due to poaching, and have already disappeared from certain areas, like in West Afrotropical forests. Despite their peculiarities, few studies have yet investigated their global mutualistic networks and tried to understand the functioning and structure of plant-animal interactions in these forests.

A. Afrotropical forests: tree composition and paleo history

Afrotropical forests are stretching discontinuously from Senegal in the West, to Kenya and Tanzania in the East. They can be subdivided in different bioregions, following the diversity of plant species, the

level of endemism with plant abundance, richness and distribution (Fig 6; Droissart et al., 2018). Tropical forests are mostly present in two of these regions: the Guineo-Congolian forests that are divided in three sub-bioregions: Upper Guinea, Lower Guinea and Congolia; and the Albertine Rift Montane forests (ARM) (Figure 6). These Afrotropical forests have a strong floral homogeneity, with differences between the Guineo-Congolian forests and the ARM forests. The higher plant species richness is located in the Lower Guinea forest, followed by the Upper Guinea, then the Congolia and the ARM forests, with the lower Guinea and Congolia bioregions having a greater proportion of shrubs and lianas than other regions.

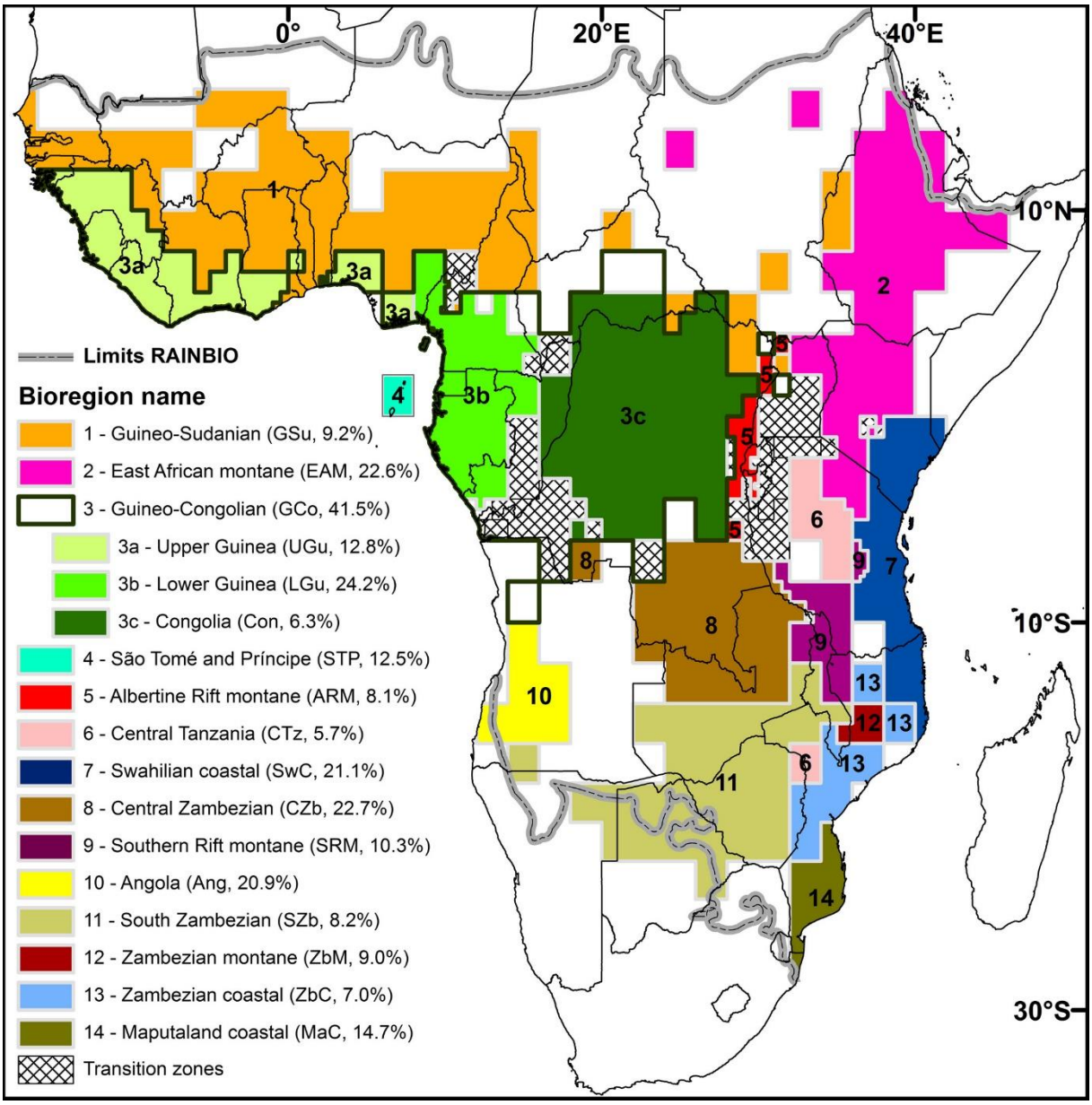

Figure 6. The main floristic bioregions and transition zones of tropical African forests, from Droissart et al (2018).

Compared to other tropical forests from South America and South-East Asia, African forests count fewer plant species (Couvreur, 2015; Slik et al., 2018). The different bioregions and this lower richness of Afrotropical forests can be explained by their evolution. A reconstruction of the past of these forests with palynology, carpology and paleo-botanic showed that Afrotropical forests shrank between the Eocene (55 Ma) where they covered 15-22 million km², the Pliocene (3 Ma, 10 million km²) and today, where they stretch over 3.4 million km² (Malhi et al., 2013). This general reduction in the area of African tropical forests over time, much greater in Africa than in the Amazon (Kissling et al., 2012) could explain current patterns of species diversity. The recent study of population dynamics (since the Pleistocene) of African tropical forests, using palynology analyses and climatic reconstruction models, shows an alternation during the Quaternary of long phases of cooling (glacial) and shorter phases of warming (interglacial) (Maley, 1996; Couvreur et al., 2021). The Ice Ages periods were characterised by a drier climate and one of the strongest hypotheses on the changes in vegetation that occurred during these periods, and notably during the last glacial Era (18000 BP), is the expansion of the savannah, that caused a contraction of forest in refuges areas (Robbrecht, 1996; Sosef, 1996). The location of these areas, distinguished by paleo-vegetation data and by current patterns of diversity and specific endemism, is controversial: there could either be several discrete refuges (Maley 1996), or a more continuous refuge area along the coasts of Cameroon and Gabon (Anhuf et al., 2006). Today, the advance of these savannahs during the last Glacial Era is still visible in South-West Gabon, where a mosaic of savannah and forests persisted, with human action, and where remnants of savannah fauna, like the waterbuck (*Kobus ellipsiprymnus defassa*), are still present.

B. Frugivory in Afrotropical forests: the lack of information

Afrotropical forests are mostly remarkable for the emblematic animals inhabiting the forests, particularly the remnant megafauna comprising forest elephants (*Loxodonta cyclotis*) and great apes like gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). These megafaunal species have tight interactions with woody species producing fleshy-fruits from whom they consume a large diversity of fruits and disperse their seeds (Malhi et al., 2016; Terborgh et al., 2016; Berzaghi et al., 2018). Elephants and apes are of the greater importance in frugivory and seed dispersal networks, but they are usually absent of most global network studies (Vidal et al., 2013). In general, Afrotropical forests are poorly studied, even if seed dispersal processes of some taxonomic groups like birds, bats or monkeys are well-documented, few researches focus on seed-dispersal networks on multiple taxonomic groups (Schleuning et al., 2012). However, to understand the mechanisms that fix seed-dispersal networks, there is a necessity to take into account all frugivores, from small birds to large mammals, even including secondary dispersers (Brocardo et al., 2013).

Elephants are presented as crucial for the proper functioning of Afrotropical forests, first because some tree species are elephant-dependent, mostly species with large seeds – like stone seeds – as well as late successional species (Beaune et al., 2013b; Berzaghi et al., 2021); second as they are the greatest seed consumers and long distance dispersers (Campos-Arceiz and Blake, 2011). Plant assemblages therefore depend on elephants, whose role was proven to influence tree diversity and distribution. Studies showed that a higher presence of elephants was correlated with lower tree aggregation, implying a reduction of the density dependence mortality (Blake et al., 2009; Berzaghi et al., 2019). On the primates side, apes and monkeys have been at the centre of numerous studies on frugivory and seed dispersal, showing their heterogeneous diet and their efficiency to disperse seeds on short to long distances (Balcomb and Chapman, 2003; Flörchinger et al., 2010). However, while being a great component of frugivory networks, megafauna species are often left out from structural network studies (Vidal et al., 2013), as most research are species-centre.

Megafauna species are greatly threatened by targeted hunting and poaching causing population scarcity (Abernethy et al., 2013; Bush et al., 2020). Indeed, some Central African forests showed a very striking rate of defaunation over the past decades, mainly due to increased poaching (Abernethy et al., 2013; Malhi et al., 2016). This practice has led to the decline of hundreds of animal species in Africa, with greater pressure on large animal, like forests elephants and apes (Abernethy et al. 2013). Recently, a long-term study showed a decline in fruiting offer of 80%, correlated with a decline in elephant body conditions, in a protected area of Gabon (Bush et al., 2020). Suggesting that the capacity of the ecosystem – here the offer in fruits – to support megafaunal species is decreasing, highlighting another threats for these communities. As interactions between seeds and their dispersal agents have a considerable influence on the dynamics of plant populations and communities, and their diversity (Jordano et al. 2011). This significant decline of African plant and animal species is likely to radically alter species assemblages and the communities that depend on interactions in which these species play a key role (Abernethy et al. 2013). The lack of data on community dynamic approach or network studies at large-scale including megafaunal species as well as other taxa prevent us from fully understanding the consequences of this disturbance on the Afrotropical forests.

OBJECTIVES, HYPOTHESIS & THESIS PLAN

In this context, where African forests are threatened by deforestation and defaunation, knowledge on ecological processes such as frugivory and seed dispersal interactions are essential to understand the consequence on these forests communities. However, Afrotropical ecosystems are largely understudied, and information on ecological processes are still lacking. Which is why, the goals of this PhD thesis were to:

(I) Reinforce our understanding of interaction patterns in frugivory networks and fill a gap in network studies in Afrotropical forests
(II) Evaluate our knowledge on plant-frugivore communities of Afrotropical forests
(III) Acquire new knowledge on frugivory network in Afrotropical forests by developing new methods

The first step of this PhD thesis (chapter 1) aims to uncover the structure of the network and test mechanism governing frugivory interactions and to develop our understanding of the frugivory networks in Afrotropical forests. Indeed, no extensive study was done in large scale in the area, or on diverse group of frugivore, despite numerous studies centered on species or specific taxonomic groups, like birds or monkeys. For that, we built a database compiling over 10,000 interactions between trees and frugivores species from all Afrotropical forests, extracted from 255 literature sources. Here, I contributed in the making of this database by adding interactions, but especially by adding traits related to tree and frugivore species. Thanks to this database, we were able to summarize and evaluate our knowledge on the Afrotropical frugivory network. We used the block model analysis to simplify our hyper-diverse network, a method recently applied to ecology that clusters species with similar interactions according to the identity of partner as well as the quantity. The use of latent block model analysis allowed us to work on the interactions patterns of frugivory, related to plants and animals biological traits, but also linked to their taxonomy and probability of encounter.
This first chapter was submitted as a paper in *New Phytologist*.
A collaborative work that focused on megafaunal species, has integrated data from the frugivory database, and this work was submitted to *PNAS* (Berzaghi F, Bretagnolle F., Durand-Bessart C., Blake S., in prep – APPENDIX 1).

The second part (chapter 2) focuses on variations in plant assemblages across afro-tropical forests, specifically the relationship between plant abundance and distribution over the Central African forests and their traits related to frugivory interactions. For this chapter, we had access to a database registering tree species composition and abundance from forestry inventories all over Central African forests (Réjou-Méchain et al., 2021). The aims of this study was to link the different forest types delimited in the study of Réjou-Méchain et al. 2020, to the frugivory interactions of our database. We compared the

plant communities of these different floristic types, in term of species composition and community traits, to understand the variation in the offer in fruits among the floristic types, by calculating community weighted means for each forests types.
This chapter is an ongoing chapter, and this work is in collaboration with Maxime Réjou-Méchain, Cyrille Violle, Lucie Mahaut, and Fabio Berzaghi. For this project, my work consist in linking the tree abundance and distribution database to the frugivory database, and analysed the mechanisms involved in the communities dynamic.

In the third chapter, my work consisted in developing a collaboration with Indigenous communities, to integrate local ecological knowledge on tree-frugivore interactions in our research study. Indeed, ethno-ecological approaches have received more attention since the past decade but remains poorly used despite promising results. To achieve this work, I developed a methodology to interview people and gather information on their knowledge about frugivory interactions, based on semi-structure interview using photographic guides of plant and animal species. I went to Gabon in 2019 for 10 weeks, and stayed at the scientific station of IRET (Research Institute on Tropical Ecology of Gabon) in Doussala, a small village neighbouring the southern border of Moukalaba-Doudou National Park. The population of Doussala is partly dependent on the forest, for hunting and gathering foods like fruits or tuber, and also for medicinal and construction purpose. This chapter also allowed us to evaluate academic knowledge on frugivory network by comparing the interactions from academic literature to the one gathered from local people. Also, we investigated the change brought by the new interactions from local ecological knowledge to interaction patterns.

This work is still an ongoing chapter but soon to be submitted.

Finally, the fourth chapter consisted in positioning cameras in Gabonese forests, on woody species with falling mature fruits, to record frugivory interactions of terrestrial vertebrate species. This chapter contributed to increase our knowledge on tree-frugivore interactions in Afrotropical forests. Linking this camera database to local ecological knowledge and academic literature allowed us to pinpoint where we still need to put effort to improve interactions knowledge.

This work is still an ongoing chapter but soon to be submitted.

CHAPTER 1

A latent block model approach reveals that species traits structure Afrotropical tree-frugivore networks

A young gorilla feeding on Lannea welwitchii. Picture by Clementine Durand-Bessart.

Context

In tropical forests, frugivory is a major ecological process, as 50 to 90 % of tree species rely on animals for their dispersal, and numerous groups of vertebrates rely on fruit as their primary source of food. Numerous studies focused on unraveling the structure of these mutualistic networks, looking into the diversity of species in the network, the number of links between species and the organisation of those links that create patterns of interactions. From there, different structures have been described such as nestedness (i.e. few species interacting strongly with each other and many species interacting with these strongly connected species), and modularity (i.e. structure forming groups of species called modules, with many interactions within a module but few between modules). This network structure highlighted that possible interactions between species are constrained by diverse filters, such as the spatial distribution of species or their phenology, but also their biological traits.

In Afrotropical forests, the mechanisms shaping frugivory interaction networks remain understudied. Here, we evaluate the data available on the Afrotropical frugivory interactions to identify structural properties of the network, as well as assessing knowledge gaps. To achieve this work, we compiled frugivory interactions from 255 literatures studies all over Afrotropical forests. This frugivory database comprised >10,000 links, between 807 tree and 285 frugivore species. We analysed the network structure, by using an approach recently incorporate in ecology studies, the latent block model. This clustering analysis groups species with similar interaction patterns into blocks and estimates interaction probabilities among them. We investigated the species traits related to this grouping structure and the relationship with the position of each block in the network.

Key results

The block model analysis simplified the Afrotropical frugivory network in 14 tree and 14 frugivore blocks. The block structure depended as expected on the overlap in species distribution, but also on the difference of sampling efforts among species, highlighting that further data is needed to fully assess the structure of the network.

Tree and frugivores blocks composition and the probability of interactions between them was also well predicted by biological traits of species related to frugivory. The composition of these blocks was mostly structured by species traits, with the frugivore body mass, and for trees: the mean wood density, fruit, seed, and tree size. We showed that larger trees were the primary fruit sources of most frugivores. Also, blocks with larger seeds and fruits had higher probabilities to be consumed by large frugivores.

A latent block model approach reveals that species traits structure Afrotropical tree-frugivore networks

Clementine Durand-Bessart [1,2], Colin Fontaine[2], Katharine Abernethy[3,4], Colin A. Chapman[5,6,7,8], Norbert J. Cordeiro[9,10], Pierre-Michel Forget[11], and François Bretagnolle[1]

[1] Biogeosciences, UMR 6282, Université Bourgogne Franche Comte-CNRS, Dijon, France

[2] Centre d'Ecologie et des Sciences de la Conservation, CESCO, UMR 7204, MNHN-CNRS-SU, Paris, France

[3] African Forest Ecology Group, School of Natural Sciences, University of Stirling, UK

[4] Institut de Recherches en Ecologie Tropicale, CENAREST, Gros Bouquet, Libreville, Gabon

[5] Wilson Center,1300 Pennsylvania Avenue NW, Washington, DC 20004

[6] Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington DC, USA, 20037

[7] School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, South Africa

[8] Shaanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an, China

[9] Department of Biology (mc WB 816), Roosevelt University, 430 S. Michigan Avenue, Chicago, Illinois 60605, United States of America

[10] Science & Education, The Field Museum, Chicago, 1400 S. Lake Shore Drive, Illinois 60605, United States of America

[11] Muséum National d'Histoire Naturelle, UMR 7179 MECADEV CNRS-MNHN, 1 avenue du Petit Château, 91800 Brunoy, France

Authors emails: clementine.durand-bessart@u-bourgogne.fr; colin.fontaine@mnhn.fr; k.a.abernethy@stir.ac.uk; colin.chapman.research@gmail.com; ncordeiro@fieldmuseum.org; pierre-michel.forget@mnhn.fr; Francois.Bretagnolle@u-bourgogne.fr

Corresponding author: Clementine Durand-Bessart, Biogéosciences UMR CNRS/uB 6282, Université de Bourgogne, 6 bd Gabriel, 21000 DIJON, France; + 33 (0)3 80 39 63 56; clementine.durand-bessart@u-bourgogne.fr

Keywords: Conservation, block models, downsizing crisis, functional redundancy, mutualism, tropical ecology, tropical forests

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 frugivory networks remain understudied. Here, we evaluate the data available on the Afrotropical frugivory network to identify structural properties of the network, as well as assessing knowledge gaps.
- We assembled a database of frugivory interactions from the literature that comprised >10,000 links, between 807 tree and 285 frugivore species. We analysed the network structure using a latent block model approach that groups species with similar interaction patterns and estimates interaction probabilities among them. We investigated the species traits related to this grouping structure and the relationship with the position of each block in the network.
- The Afrotropical frugivory network was simplified into 14 tree and 14 frugivore blocks. The block structure depended on the difference of sampling efforts among species, highlighting that further data is needed to fully assess the structure of the network. The block structure was also related to the overlap in species distribution areas.
- In addition, we found that species traits related to frugivory were strong predictors of both the specie composition of blocks and interactions among them. The composition of these blocks was mostly structured by species traits, with the frugivore body mass, and mean wood density, fruit, seed, and tree size. We found that larger trees were the primary fruit sources of most frugivores. Also, larger seeds and fruits had higher probabilities to be consumed by large frugivores. Although expected, these results are new at a large-scale for Afrotropical forests and exemplify the potential of latent block models to analyse network structure and the factors chapping it.
- As large frugivores are particularly threatened by hunting and logging, our findings show the vulnerability of this plant-frugivore network and the fragile integrity of Afrotropical forest composition.

INTRODUCTION

Biodiversity depends on multiple ecological interactions and, in the last decades, one of the goal of community ecology was to characterise the complex patterns of interactions among species and the factors shaping them (Olesen et al., 2007; Coelho and 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 plants and pollinators, share consistent patterns in their topological structures (Bascompte and Jordano, 2007). These patterns have been widely studied, in particular regarding the heterogeneity of species interactions, with few species being highly connected and most species being poorly connected (Jordano et al., 2003). From this observation, the nestedness was described as the overlap in interaction among species in the network (Bascompte et al., 2003; Almeida-Neto et al., 2008), and the modularity which seeks to identify 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 and Fontaine, 2010), and several processes originating them have been highlighted. These non-exclusive processes include filters that constrain the possibility of links, such as the spatial (distribution matching) or temporal (phenological matching) species matching, trait-based processes (i.e., trait-matching), and phylogenetic relationships (Vázquez et al., 2009b, 2009a; González-Varo and Traveset, 2016; Araujo et al., 2018; Valdovinos, 2019).

The recent development of latent block models offers a new perspective to understand the structure of ecological networks (Leger et al., 2015; Bar-Hen et al., 2018; de Manincor et al., 2020, 2020). Latent block models are parametric clustering methods that groups species into blocks – here distinct blocks for the two set of nodes of the bipartite network – according to their pattern of interaction; species in the same block probabilistically share the same interactions with species from other blocks. Species within blocks can therefore be considered as functionally redundant if they have a similar interaction pattern. Latent block model can not only reveal a modular or a nested structure, but also highlight structures that are more complex. This because the approach allows different numbers of blocks for each side of the network, and estimates the probabilities of interaction among each block couple (see Supplementary 1 Fig S1.1). Contrary to nestedness and modularity approaches that look for a single predefined architectural pattern, latent block models look for the structure that best explain the data. Further, the identification of the functional and taxonomic characteristics of the species within blocks appears promising to investigate the relative role of functional convergence with potential associated syndromes (Ronce and Clobert, 2012; Valenta and Nevo, 2020), and phylogenetic inertia with species sharing inherited traits (Olesen et al., 2007). Finally, as latent block model estimates

probabilities of interaction between all block couples, it is possible to investigate the factor affecting these interactions, such as spatial overlap or matching traits between block couples.

Few studies looked at the structure of tropical plant-frugivore networks (de Almeida and Mikich, 2018), and this is particularly lacking in Afrotropical forests. These forests are particularly affected by the global decline in large wildlife and plants due to the unsustainable human extraction and persecution, known as the downsizing crisis (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). The decline in megafauna and megaflora 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 and depend on frugivores to disperse their seeds (Abernethy et al., 2013; Effiom et al., 2013). These fruits are important food resources for much of the forest fauna, particularly the megafauna (Gautier-Hion et al., 1985; Beaune et al., 2013; Bush et al., 2020). Many studies on frugivory have documented diets of African frugivores, but there is a bias towards charismatic species (e.g., monkeys, apes, elephants) and general knowledge on plant-frugivore interactions in tropical Africa remains scattered. At the continental scale, a large amount of information about frugivory is available, but at 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 tree-frugivore interactions are mostly governed by trait-matching, with the size of fruits and seeds ingested by fruit-eaters constrained by the size of the fruit-eaters and their corresponding beak or jaw gape sizes (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 frugivory networks in Afrotropical forest is thus a priority to anticipate the consequences of the downsizing crisis in these forests.

Recently, de Almeida & 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 the ecological processes of network structure within the hyper-diverse Neotropical communities, inspired us to conduct a similar study on Afrotropical plant-frugivore 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. Finally, we investigate the relationships between network structure and species taxonomy, geographic distribution, trait, and

conservation status. Through the block model analysis, our findings advance our understanding of Afrotropical forest plant-frugivore networks, specifically the biological traits.

MATERIALS AND METHODS

Study sites and database

We assembled a tree-frugivore interaction dataset from literature by searching both Web of Science and Google Scholar using terms 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 (Table S1.2), 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, i.e., an interaction between one species of tree and one of frugivore, by removing duplicates, to avoid the redundancy and bias toward certain interactions.

In addition to species' identity, we included their Order and Family, geographic distribution, and conservation status. Distributional data was obtained from the African Plant database of the Geneva Botanical Garden for trees and, for frugivores this data was derived from IUCN (https://www.iucnredlist.org). Following Droissart et al., (2018), we considered three biogeographical regions as categorical variables: Guinea (West Africa, W), lower Guinea and central (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".

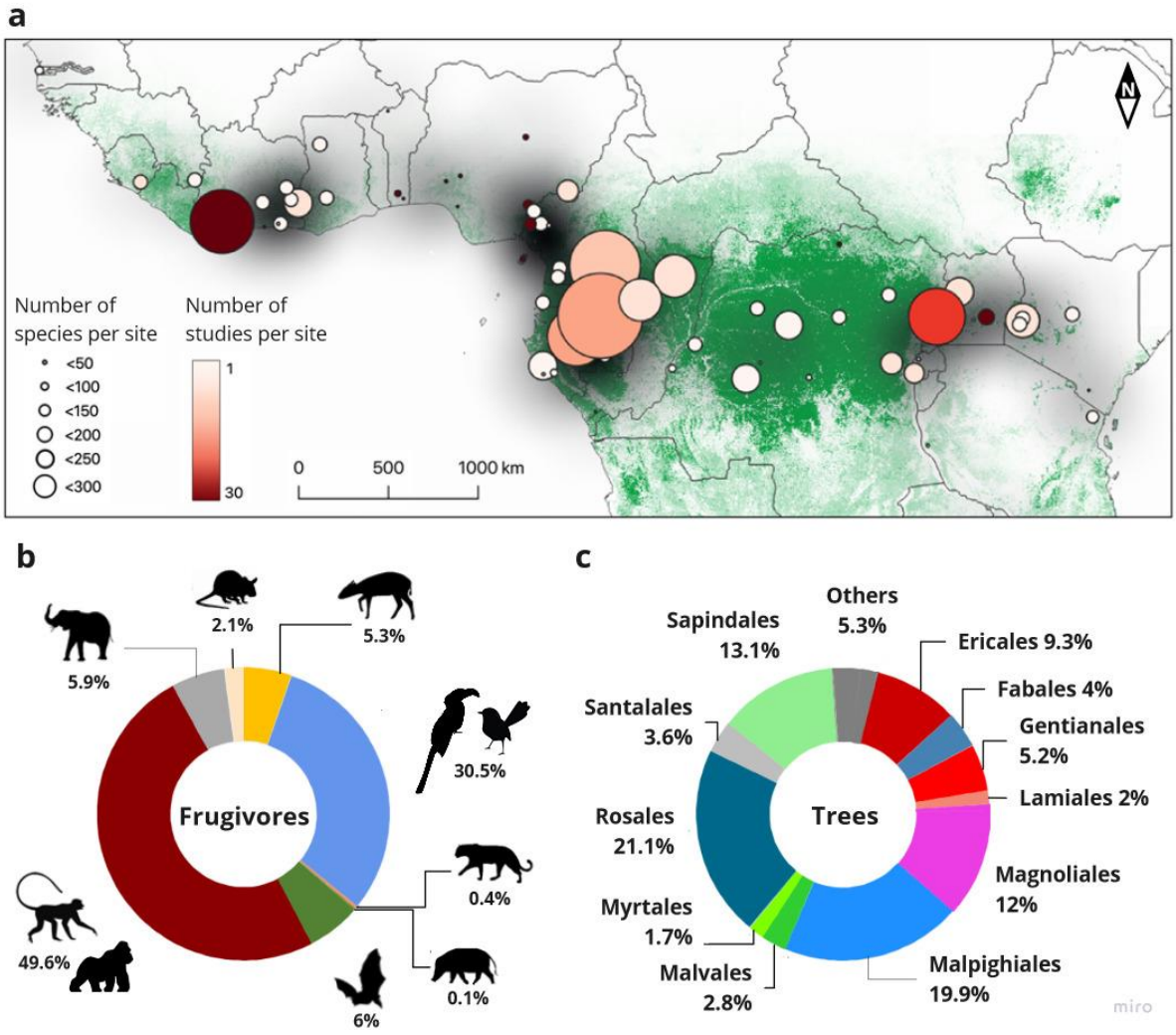

Figure 7. a) Location and contribution of the different study sites included in the database. Circles represent study sites, with their size being proportional to the number of species studied, and their colour related to the number of studies per site. The green areas show forest cover > 30%. b) Proportion of unique interactions involving the different frugivore groups included in the database, in order ungulates, birds (large and small), carnivores, pigs, bats, primates (apes and monkeys), elephant, rodents. c) Proportion of unique interactions involving the different tree orders included in the database (only orders involved in more than 0.5% of unique interactions are presented).

We derived species traits of trees and frugivores from the different literature sources (Table S1.2). For frugivores, we recorded body mass (g). For tree species traits, we recorded fruit and seed dimensions (length and width in cm), number of seeds per fruit, average height (m), and wood density ($g.cm^{-3}$). 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, i.e. the asymptote of the accumulation curve, and the observed richness (Costa et al., 2016). We estimated the expected richness of tree and frugivore species using the full dataset as well as the three biogeographical regions separately. Similarly, we estimated the expected number of interactions per frugivore taxonomic group as in Figure 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 maximising the integrated complete-data likelihood (ICL) (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 non-exclusive 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 similar pattern of interaction because they share the same distribution area and thereby the same pool of potential partners; or because they share traits involved in the choice of similar interacting partners, related or not to a common evolutionary history. In addition, the sampling effort on each species might also affect the block structure of the network, with for example species with low sampling effort having very few interactions could be grouped in the same block, while species with high sampling effort having many interactions could be grouped in other blocks.

To evaluate the relative contribution of these factors to the block structure of the network despite the correlations among them (Fig S2.1). We first performed a Random Forest model as implemented in the R package ‘randomForest’ (Liaw and Wiener, 2002). This classification method rely on building

decision trees from bootstrap samples (Fox et al., 2017) that allows one to incorporate categorical (taxonomy and distribution area), as well as continuous variable (species traits), and support possible interactions and collinearity among variables, as expected in our case among species traits and taxonomy (De'ath and Fabricius, 2000; Loh, 2014). We quantified the importance of each of the above-mentioned variables, that could affect the group structure of the network, by calculating for each of them the total decrease in node impurities from splitting on this variable over all trees, and using the Gini index to quantify node impurity (Archer and Kimes, 2008). The variable importance thus represents how much removing a variable reduces the accuracy of the Random Forest model.

We fitted one Random Forest classification models for frugivore blocks and another one for tree blocks. For Frugivores, we included the effects of the body mass (log transformed), of the taxonomic group, and of the distribution area of the species, as well as the effect of the number of publications in the database where the species is cited 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 highest variable importance in determining the blocks, i.e. 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 in the database where the species is cited. For both tree and frugivore models, we used the seven geographic categories described above 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 by 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.

Connectedness of blocks and average species traits

We evaluated the connectedness of blocks as the summed of the probabilities of interaction with other blocks estimated by the latent block model. A high connectedness or sum of probabilities for a block indicates strong interactions with many blocks it interact with.

To investigate the relationships between block connectedness 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 connectedness of blocks as dependant variable and the average trait values of the

species within blocks as well as the number of publication that include species from the blocks as covariates. The average trait values were average body mass for frugivore blocks and the average species coordinate from the PCA previously described using dimension 1 to 3 (Figure S2.1). The average frugivore body mass was log transformed to satisfy the model assumptions. We selected the best models (Table S2.2), using the muMIn package (Barton, 2019).

Determinants of the probability of interaction between blocks 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 couple 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 as the dependant variable and with (a) the average body mass 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 study by tree and (g) per 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. The probability of interactions between blocks was logit transformed to fulfil the assumption of the linear model. We selected the best model (Table S2.3), 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. S2.4). The sampling completeness for interaction richness did not differ when considering the biogeographical region separately: 43% for Western Africa and 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, ungulates, and birds, with intermediate values, and pigs, carnivores, and rodents having the lowest values (Table 1).

Table 1. Sampling completeness of interaction richness for frugivore groups. The number of observed interactions correspond to the number of unique interactions in our database. The estimated total number of interactions correspond to the asymptotic values calculated by the Chao 2 estimator, with standard error. The sampling completeness represents the proportion of observed interactions over the estimation; the completeness range is presented in brackets.

	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]
Ungulates	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]

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. S2.5).

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 species or 37% and 55% of the total number of species. The remaining 13 frugivore and tree blocks contained 4 to 33 species (mean = 14.6) and 12 to 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. S2.6). Only 11% of the interactions had a probability higher than 0.5, while 63 % had a probability lower than 0.1 (Fig. 2). The richest blocks F14 and T14 had probabilities of interactions lower than 0.1 with any other block, except for the interactions between T14 and F2 that reached 0.15 (Fig. 2). This low probability to interact with the other blocks was likely due to a lack of information regarding the interactions of their respective species. Indeed, while 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 the blocks T14 and F14, with on average 2.70 and 3.07 bibliographic sources per species, respectively.

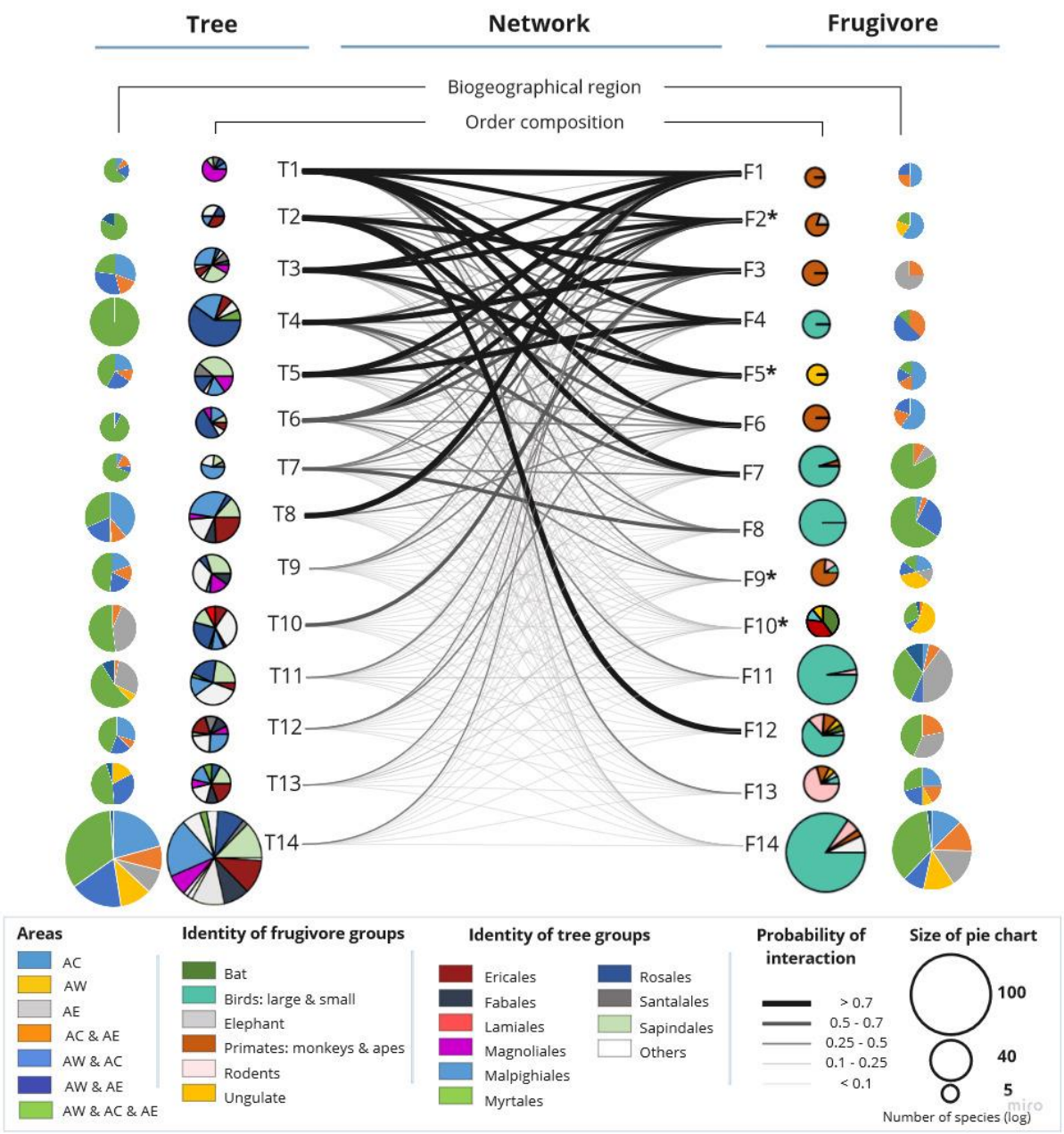

Figure 8. Bipartite network between trees blocks (left) and frugivores blocks (right). Blocks are ordered by decreasing sum of probabilities (see materials and methods). The probability of interactions between blocks or probability of a species from a block to interact with a species from the other block, are represented by grey to black lines whose thickness is proportional to the interaction probability. The pie charts represent the composition of in term 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 distribution areas: AC is for central Africa, AE: eastern Africa, AW: western Africa. The blocks represented by stars had an over-representation of threaten species, showed by a chi-square test.

Determinants of the species composition of tree and frugivore blocks

For both tree and frugivore blocks, the Random Forest model that best predicted the block of tree species 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 that quantify how much the performance of the classification rely on the different variables included in the model (Fig 3). For frugivores, the predictor with the highest importance were the body mass of the species, followed by the sampling effort, and subsequently by the distribution area and the taxonomic groups of frugivore (Fig 3a). The correlation between frugivore body mass and sampling effort suggests that part of the block structure may be related to the higher sampling effort on large frugivores (Fig S2.7). Turning to tree blocks, the pattern was different, with the sampling effort on tree species having the highest variable importance by far, suggesting that we still miss many data to elucidate fully the structure of afro-tropical frugivory network. Then a set of four tree traits including fruit and seed sizes, followed by taxonomic order, distribution area and seed number (Fig 3b).

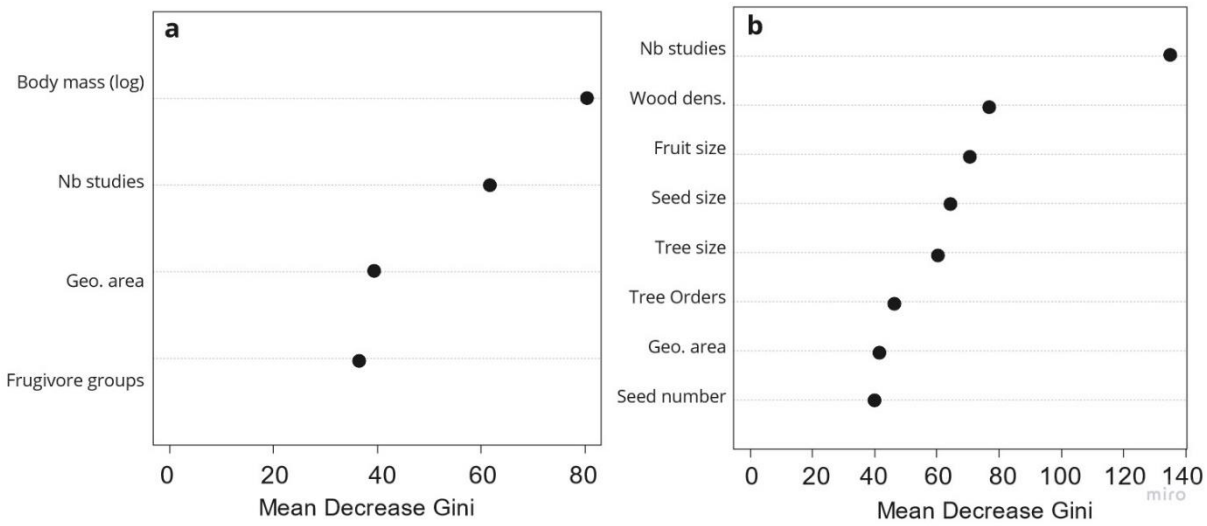

Figure 9. Results of random forest models illustrating the relative importance of different model variables (measured by the mean decrease of Gini coefficient) in predicting the assignment of species to their blocks. The greater the average decrease in the Gini coefficient, the more the associated variable contributes to predicting the assignment of species in their block. (a) frugivores species and (b) trees species. Note: Nb studies = number of studies; Geo. area = biogeographical regions.

We further illustrated the relatively high variable importance of fruit and seed size using a PCA (Fig. 4 & S2.8). Five blocks tended to have distinct traits values, the blocks T2, T3, T4, T7, T10, and

T11. The blocks T2 and T3 had, on average, larger seeds and fruits, and also larger trees than most of the other blocks. The blocks T4, T7, T10 and T11 had, on average, smaller fruits and seeds, but while T7 was composed of smaller trees T4 and T11 have larger trees (Fig. 4; Fig S2. 8). 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, was not discriminating strongly the various blocks (Fig S2.8).

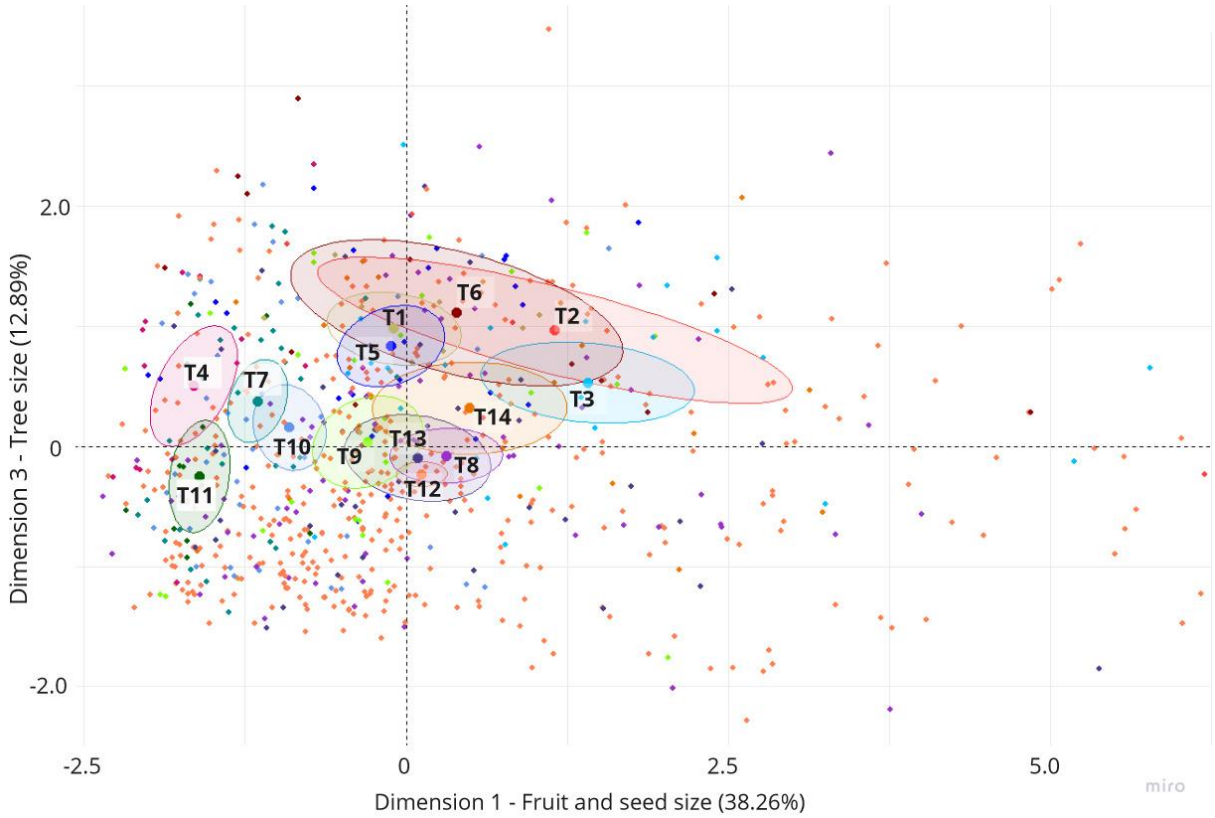

Figure 10. Representation of the species through the first and third axes of the PCA on tree traits, regarding their blocks. The first axis (Dimension 1) is driven by the size of fruits and seeds, while the third axis (Dimension 3) differentiates small and large trees (see Fig S2.1). The ellipses are confidence ellipses representing the mean value of the block around the barycentre. Blocks are represented by different colours.

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 ungulates and rodents, whereas the block F10 was mostly composed of bats and primates (Fig. 2). For the 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, the blocks F1, F2, F5, and F6 had a high proportion of species from Central Africa.

The block F3 had a high proportion of species from East Africa, with the 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 the block 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 connectedness of blocks

The connectedness of blocks, measured as the sum of the probabilities that species from a block have to interact with species from all other blocks, was for frugivores only related to the mean number of publication per species (p=0.002; Table S2.9; Fig. 5), and not to the mean body mass of frugivores (Table S2.2). For tree blocks, we found that block connectedness was positively related to the third dimension of the PCA, related to tree size (p=0.002; Table S2.9; Fig 5), but the other dimensions as well as the number of publication by species had no significant effect (Table S2.2). Suggesting that larger tree species tend to be food resources of most frugivore species.

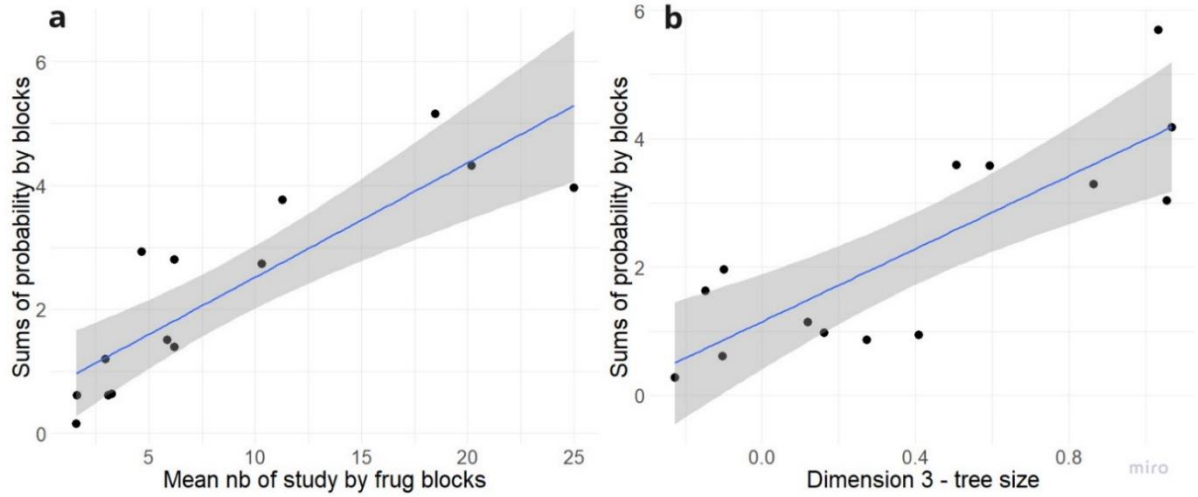

Figure 11. Relationships between sums of probabilities of blocks and the number of study by species by blocks: (a) mean number of study by frugivore species inside frugivore blocks, (b) mean number of study by tree species inside tree blocks.

Determinants of the probability of interaction between blocks 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 the 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 S2.10). 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 (Fig. 6a). 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 higher probability of interaction with larger frugivores, while large trees had similar probability of interactions with small and large frugivores (Fig 6b). As expected, the higher was the mean distribution overlap among the species between block couples, the higher was the probability for them to interact (Table S2.10). The mean number of studies per species and per block of trees and frugivores were also positively related to the probability of interactions between block couples, suggesting that blocks with well-studied species had 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 S2. 11). We found a negative relationship with the dimensions 1 and 2 of the PCA on tree traits and a positive relationship with the dimension 3 (Fig S2.11). 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 trees with high wood density and low number of seeds – dimension 2 – and blocks with taller tree species – dimension 3.

Overall, these results suggests that the structure of the network depends 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.

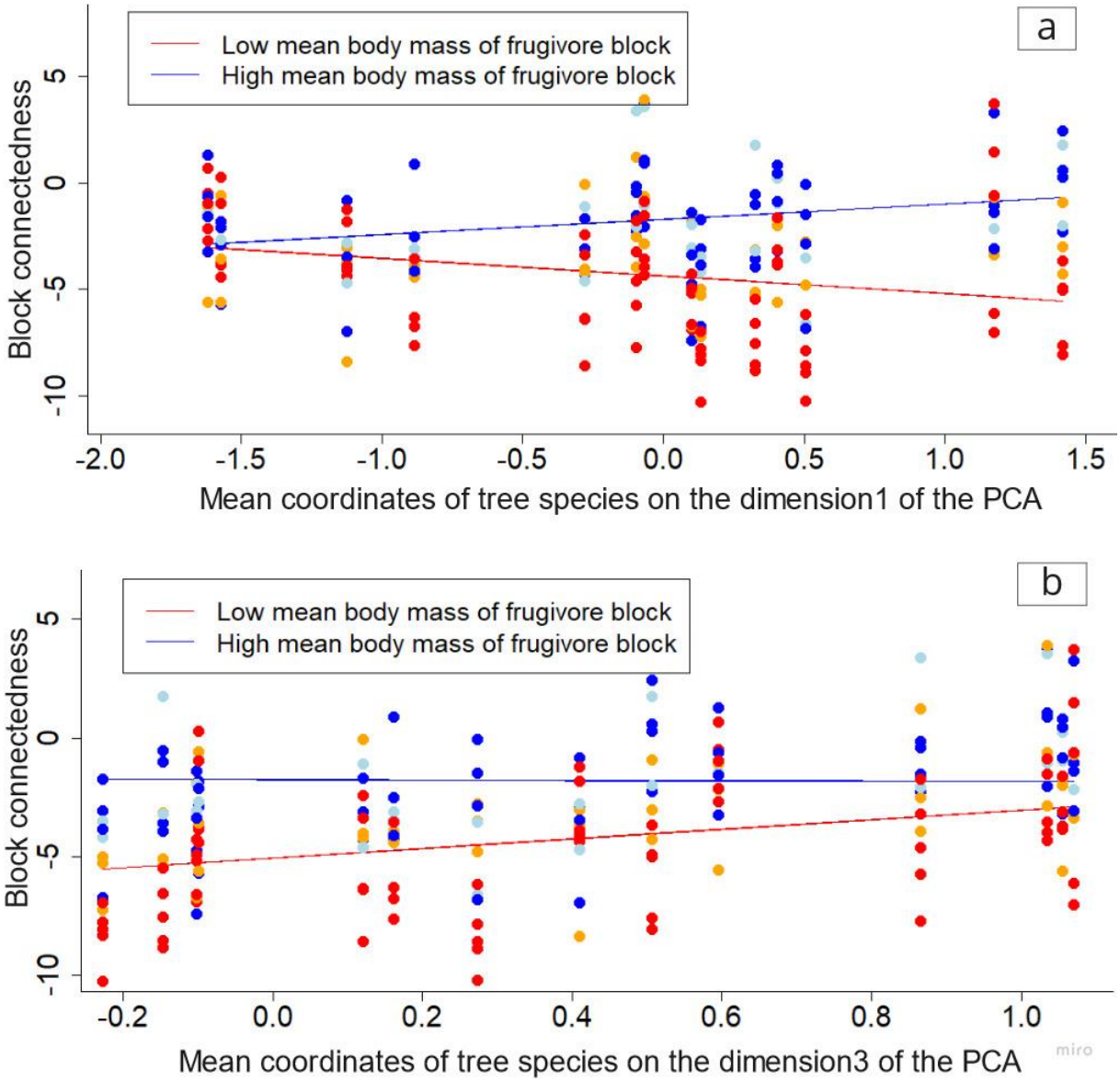

Figure 12. The relationship between the probability (logit) of interactions between blocks, and biological traits of tree and frugivore species. (a) How the mean seed size and fruit size of trees (represented by the dimension 1 of the PCA) and the mean body mass of frugivores affect the probability of interaction among blocks. (b) How the size of trees (represented by the 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 frugivore 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.

DISCUSSION

We provide here an assessment of current knowledge on frugivory interactions between trees and frugivores in Afrotropical forest. Our analysis of available data as an interaction network using the latent block model approach allowed us to highlight blocks for both frugivores and trees, i.e., groups of species

with similar patterns of interaction, and further showed that these blocks likely result from multiple non-exclusive processes.

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 frugivore and one block of trees that grouped together species that were little present in the publications originating the dataset. 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 and 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. Thus, despite a large effort, the network was under-sampled and biased to larger vertebrates. There is comparatively little data on small birds, bats, rodents, and carnivores, although they can contribute significantly to 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-charismatic 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 body mass for frugivore or seed and fruit length for trees, also had high importance, that was expected from extended studies on frugivory interactions mostly outside Afrotropical forests (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., 2018). 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, or at least that these traits contain more information on frugivory interactions than the taxonomic levels we used in our analysis. Also, it suggests 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 connectedness, the literature bias toward these large frugivore species involved in this pattern, did not allow us to confirm what was showed in previous studies (Donatti et al., 2011). For trees, their height as well as fruit and seed length differed among blocks, but trees height only was positively related to block connectedness. The absence of relationships between block connectedness and fruit or seed

length was unexpected as a negative relationship was found in Asian forests (Kitamura et al., 2002). The increase in block connectedness with tree height indicating blocks with tall trees were the more generalists also fit with previous findings showing that some frugivores, like birds and bats, prefer taller trees (Duncan and Chapman, 1999), a trait often associated with late successional canopy species that primarily interact with generalist species (Schleuning et al., 2011).

Looking at the probability of interactions among blocks, we found that they were related to the overlap in distribution area of species between block couples. This was expected as species with non-overlapping distribution areas cannot interact. We also found that the match in the functional traits of species between block couples had a 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 traits 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 and Peres, 2014), and is compatible with a nested structure (Balcomb and Chapman, 2003; Vidal et al., 2013).

The blocks identified by the latent block model can further be interpreted in term of functional redundancy. As species within blocks share similar pattern 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. On the contrary, blocks with few species and therefore low redundancy, or blocks grouping many threaten species might require particular conservation attention. This may be the case for three frugivore blocks with a high proportion of ungulates, monkeys, or bats species that are globally threatened and vulnerable to hunting (Osuri et al., 2020). Similarly, for the block F1 that was composed of the Endangered or Critically Endangered species, mostly apes (Vidal et al., 2014), the loss of this entire block could leads to the decline of tree and frugivore species by weakening the frugivore network, and this even before extinctions occur (Valiente-Banuet et al., 2015). For example, in south-eastern Nigeria a reduction in Endangered megafauna, like gorillas and chimpanzees, negatively impacted recruitment of dependent tree species, many of which were large-seeded species (Effiom et al., 2013). In Afrotropical forests where large megafauna are rapidly declining, due to hunting and logging, negative consequences on seed dispersal and thereby tree recruitment have been predicted by several studies (e.g. Vanthomme et al., 2010; Abernethy et al., 2013; Beaune et al., 2013).

Here, our large-scale study revealed that biological traits of both animals and plants played important roles in the network structure. In the future, our understanding of this network would be enhanced by more information on the role frugivores play in seed dispersal, particularly of poorly

studied groups, such small birds, bats, rodents, and carnivores. With this information, it would be possible to improve our predictions of structural changes that will result from defaunation and deforestation and, at the same time, improve future conservation strategies.

ACKNOWLEDGEMENTS

The authors thank Vincent Porcher for his help in data representation, Etienne Akomo-Okoue and Ghislain W. Ebang Ella, resarchers from the Institut de Recherches en Ecologie Tropicale (IRET) in Libreville for helpful discussion. The research project was supported by the Agence Universitaire de la Francophonie (AUF). Colin Chapman was supported by the Wilson Foundation while working on this project.

AUTHORS CONTRIBUTION

François Bretagnolle conceived the study, Colin Fontaine, and Clementine Durand-Bessart took part in designing the study. Clementine Durand-Bessart and Colin Fontaine performed data analysis. François Bretagnolle assembled the dataset. Clementine Durand-Bessart wrote the first draft of the manuscript, and all authors contributed substantially to the ideas and writing of the manuscript.

DATA ACCESSIBILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository.

REFERENCES

Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E., Maisels, F., 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120303–20120303. https://doi.org/10.1098/rstb.2012.0303

Almeida-Neto, M., Guimarães, P., Guimarães Jr, P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117, 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Araujo, A.C., Martín González, A.M., Sandel, B., Maruyama, P.K., Fischer, E., Vizentin-Bugoni, J., de Araújo, F.P., Coelho, A.G., Faria, R.R., Kohler, G., Las-Casas, F.M.G., Lopes, A.V., Machado, A.O., Machado, C.G., Machado, I.C., McGuire, J.A., Moura, A.C., Oliveira, G.M., Oliveira, P.E., Rocca, M.A., Rodrigues, L. da C., Rodrigues, M., Rui, A.M., Sazima, I., Sazima, M., Varassin, I.G., Wang, Z., Dalsgaard, B., Svenning, J.-C., 2018. Spatial distance and climate determine modularity in a cross-biomes plant–hummingbird interaction network in Brazil. Journal of Biogeography 45, 1846–1858. https://doi.org/10.1111/jbi.13367

Archer, K.J., Kimes, R.V., 2008. Empirical characterization of random forest variable importance measures. Computational Statistics & Data Analysis 52, 2249–2260. https://doi.org/10.1016/j.csda.2007.08.015

Balcomb, S.R., Chapman, C.A., 2003. Bridging the Gap: Influence of Seed Deposition on Seedling Recruitment in a Primate–Tree Interaction. Ecological Monographs 73, 625–642. https://doi.org/10.1890/02-4036

Bar-Hen, A., Barbillon, P., Donnet, S., 2018. Block models for multipartite networks.Applications in ecology and ethnobiology.

Barton, K., 2019. R package MuMIn: model selection and model averaging based on information criteria (AICc and alike).

Bascompte, J., Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 38, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. PNAS 100, 9383–9387. https://doi.org/10.1073/pnas.1633576100

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. Biodivers Conserv 22, 225–238. https://doi.org/10.1007/s10531-012-0416-x

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitián, M., Saavedra, F., Santillán, V., Töpfer, T., Wiegand, T., Dehling, D.M., Schleuning, M., 2018. Morphological trait matching shapes plant–frugivore networks across the Andes. Ecography 41, 1910–1919. https://doi.org/10.1111/ecog.03396

Berzaghi, F., Verbeeck, H., Nielsen, M.R., Doughty, C.E., 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. https://doi.org/10.1111/ecog.03309

Bush, E.R., Whytock, R.C., Bahaa-el-din, L., Bourgeois, S., Bunnefeld, N., Cardoso, A.W., Dikangadissi, J.T., Dimbonda, P., Dimoto, E., Ndong, J.E., Jeffery, K.J., Lehmann, D., Makaga, L., Momboua, B., Momont, L.R.W., Tutin, C.E.G., White, L.J.T., Whittaker, A., Abernethy, K., 2020. Long-term collapse in fruit availability threatens Central African forest megafauna. Science 370, 1219–1222. https://doi.org/10.1126/science.abc7791

Carreira, D.C., Dáttilo, W., Bruno, D.L., Percequillo, A.R., Ferraz, K.M.P.M.B., Galetti, M., 2020. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. Scientific Reports 10, 10594. https://doi.org/10.1038/s41598-020-67326-6

Chao, A., Colwell, R.K., Lin, C.-W., Gotelli, N.J., 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90, 1125–1133. https://doi.org/10.1890/07-2147.1

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecology Letters 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x@10.1111/(ISSN)1461-0248.conservation-management-forests

Coelho, M.T.P., Rangel, T.F., 2018. Neutral Community Dynamics and the Evolution of Species Interactions. The American Naturalist 191, 421–434. https://doi.org/10.1086/696216

Costa, J.M., da Silva, L.P., Ramos, J.A., Heleno, R.H., 2016. Sampling completeness in seed dispersal networks: When enough is enough. Basic and Applied Ecology 17, 155–164. https://doi.org/10.1016/j.baae.2015.09.008

de Almeida, A. de, Mikich, S.B., 2018. Combining plant–frugivore networks for describing the structure of neotropical communities. Oikos 127, 184–197. https://doi.org/10.1111/oik.04774

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. https://doi.org/10.1016/j.actao.2020.103551

De'ath, G., Fabricius, K.E., 2000. Classification and Regression Trees: A Powerful yet Simple Technique for Ecological Data Analysis. Ecology 81, 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

Dehling, D.M., Jordano, P., Schaefer, H.M., 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. https://doi.org/10.1098/rspb.2015.2444

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., Dirzo, R., 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters 14, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Droissart, V., Dauby, G., Hardy, O.J., Deblauwe, V., Harris, D.J., Janssens, S., Mackinder, B.A., Blach-Overgaard, A., Sonké, B., Sosef, M.S.M., Stévart, T., Svenning, J.-C., Wieringa, J.J., Couvreur, T.L.P., 2018. Beyond trees: Biogeographical regionalization of tropical Africa. Journal of Biogeography 45, 1153–1167. https://doi.org/10.1111/jbi.13190

Dugger, P.J., Blendinger, P.G., Böhning-Gaese, K., Chama, L., Correia, M., Dehling, D.M., Emer, C., Farwig, N., Fricke, E.C., Galetti, M., García, D., Grass, I., Heleno, R., Jacomassa, F.A.F., Moraes, S., Moran, C., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Piratelli, A., Pizo, M.A., Quitián, M., Rogers, H.S., Ruggera, R.A., Saavedra, F., Sánchez, M.S., Sánchez, R., Santillán, V., Schabo, D.G., Silva, F.R. da, Timóteo, S., Traveset, A., Vollstädt, M.G.R., Schleuning, M., 2019. Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. Global Ecology and Biogeography 28, 248–261. https://doi.org/10.1111/geb.12833

Duncan, R.S., Chapman, C.A., 1999. Seed Dispersal and Potential Forest Succession in Abandoned Agriculture in Tropical Africa. Ecological Applications 9, 998–1008. https://doi.org/10.1890/1051-0761(1999)009[0998:SDAPFS]2.0.CO;2

Effiom, E.O., Nuñez-Iturri, G., Smith, H.G., Ottosson, U., Olsson, O., 2013. Bushmeat hunting changes regeneration of African rainforests. Proceedings of the Royal Society B: Biological Sciences 280, 20130246. https://doi.org/10.1098/rspb.2013.0246

Forget, P.M., Dennis, A.J., Mazer, S.J., Jansen, P.A., Kitamura, S., Lambert, J.E., Westcott, D.A., 2007. Seed allometry and disperser assemblages in tropical rain forests: a comparison of four floras on different continents. Seed dispersal: theory and its application in a changing world 5–36.

Fox, E.W., Hill, R.A., Leibowitz, S.G., Olsen, A.R., Thornbrugh, D.J., Weber, M.H., 2017. Assessing the accuracy and stability of variable selection methods for random forest modeling in ecology. Environ Monit Assess 189, 316. https://doi.org/10.1007/s10661-017-6025-0

Galetti, M., Donatti, C.I., Pires, A.S., 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. https://doi.org/10.1111/j.1095-8339.2006.00529.x

Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimarães, P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., Mattos, J.S. de, Schweiger, A.H., Owen-Smith, N., Johnson, C.N., Marquis, R.J., Svenning, J.-C., 2018. Ecological and evolutionary legacy of megafauna extinctions. Biological Reviews 93, 845–862. https://doi.org/10.1111/brv.12374

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., Thiollay, J.-M., 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65, 324–337. https://doi.org/10.1007/BF00378906

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. https://doi.org/10.1002/ece3.6285

González-Varo, J.P., Traveset, A., 2016. The Labile Limits of Forbidden Interactions. Trends in Ecology & Evolution 31, 700–710. https://doi.org/10.1016/j.tree.2016.06.009

Hawes, J.E., Peres, C.A., 2014. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. Journal of Tropical Ecology 30, 381–399. https://doi.org/10.1017/S0266467414000261

Husson, F., Josse, J., Le, S., Mazet, J., 2018. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining.

Jordano, P., Bascompte, J., Olesen, J.M., 2003. Invariant properties in coevolutionary networks of plant–animal interactions. Ecology Letters 6, 69–81. https://doi.org/10.1046/j.1461-0248.2003.00403.x

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. https://doi.org/10.1007/s00442-002-1073-7

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:1602.07587 [stat].

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. https://doi.org/10.1111/2041-210X.12334

Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. R news 18–22.

Loh, W.-Y., 2014. Fifty Years of Classification and Regression Trees. International Statistical Review 82, 329–348. https://doi.org/10.1111/insr.12016

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proceedings of the National Academy of Sciences 113, 838–846. https://doi.org/10.1073/pnas.1502540113

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. Conservation Biology 26, 1072–1081. https://doi.org/10.1111/j.1523-1739.2012.01927.x

Newman, M.E.J., 2016. Equivalence between modularity optimization and maximum likelihood methods for community detection. Phys. Rev. E 94, 052315. https://doi.org/10.1103/PhysRevE.94.052315

Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. PNAS 104, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Ong, L., McConkey, K.R., 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. https://doi.org/10.1111/1365-2745.13809

Osuri, A.M., Mendiratta, U., Naniwadekar, R., Varma, V., Naeem, S., 2020. Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds. Front. For. Glob. Change 2. https://doi.org/10.3389/ffgc.2019.00087

Poulsen, J.R., Clark, C.J., Connor, E.F., Smith, T.B., 2002. Differential Resource Use by Primates and Hornbills: Implications for Seed Dispersal. Ecology 83, 228–240. https://doi.org/10.1890/0012-9658(2002)083[0228:DRUBPA]2.0.CO;2

Poulsen, J.R., Clark, C.J., Smith, T.B., 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. Journal of Tropical Ecology 17, 787–808. https://doi.org/10.1017/S0266467401001602

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. https://doi.org/10.1111/2041-210X.12753

Ronce, O., Clobert, J., 2012. Dispersal syndromes, in: Dispersal Ecology and Evolution. Oxford University Press, pp. 119–138.

Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H.M., Böhning-Gaese, K., 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. Ecology 92, 26–36. https://doi.org/10.1890/09-1842.1

Seltzer, C.E., Ndangalasi, H.J., Cordeiro, N.J., 2013. Seed Dispersal in the Dark: Shedding Light on the Role of Fruit Bats in Africa. Biotropica 45, 450–456. https://doi.org/10.1111/btp.12029

Terborgh, J., Davenport, L.C., Niangadouma, R., Dimoto, E., Mouandza, J.C., Schultz, O., Jaen, M.R., 2016. The African rainforest: odd man out or megafaunal landscape? African and Amazonian forests compared. Ecography 39, 187–193. https://doi.org/10.1111/ecog.01643

Thebault, E., Fontaine, C., 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science 329, 853–856. https://doi.org/10.1126/science.1188321

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. https://doi.org/10.1017/S026646741900018X

Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445, 202–205. https://doi.org/10.1038/nature05429

Valdovinos, F.S., 2019. Mutualistic networks: moving closer to a predictive theory. Ecology Letters 22, 1517–1534. https://doi.org/10.1111/ele.13279

Valenta, K., Nevo, O., 2020. The dispersal syndrome hypothesis: How animals shaped fruit traits, and how they did not. Functional Ecology 34, 1158–1169. https://doi.org/10.1111/1365-2435.13564

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29, 299–307. https://doi.org/10.1111/1365-2435.12356

Vanthomme, H., Bellé, B., Forget, P.-M., 2010. Bushmeat Hunting Alters Recruitment of Large-seeded Plant Species in Central Africa. Biotropica 42, 672–679. https://doi.org/10.1111/j.1744-7429.2010.00630.x

Vázquez, D.P., Blüthgen, N., Cagnolo, L., Chacoff, N.P., 2009a. Uniting pattern and process in plant–animal mutualistic networks: a review. Annals of Botany 103, 1445–1457. https://doi.org/10.1093/aob/mcp057

Vázquez, D.P., Chacoff, N.P., Cagnolo, L., 2009b. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. Ecology 90, 2039–2046. https://doi.org/10.1890/08-1837.1

Vidal, M.M., Hasui, E., Pizo, M.A., Tamashiro, J.Y., Silva, W.R., Guimarães, P.R., 2014. Frugivores at higher risk of extinction are the key elements of a mutualistic network. Ecology 95, 3440–3447. https://doi.org/10.1890/13-1584.1

Vidal, M.M., Pires, M.M., Guimarães, P.R., 2013. Large vertebrates as the missing components of seed-dispersal networks. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 42–48. https://doi.org/10.1016/j.biocon.2013.03.025

APPENDIX 1

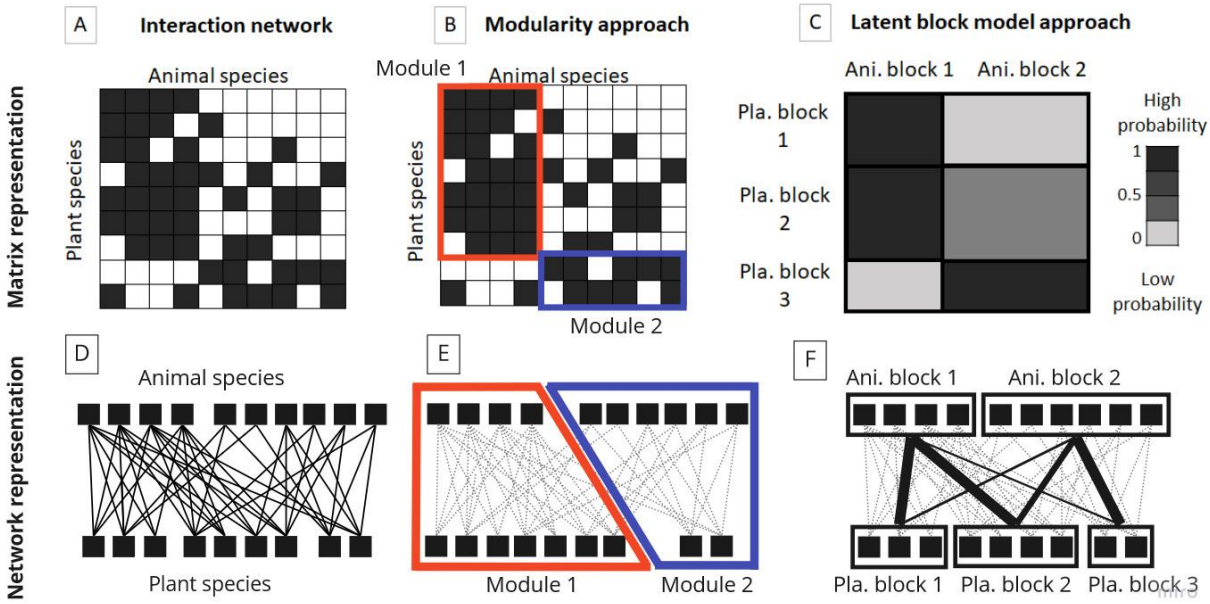

Figure S1.1. Interactions between species from two levels – here plants and animals – represented in matrix form (A) or network (D), and treated by two different analysis: modularity (B and E) and latent block model (C and F). The modularity analysis, clustering species in module composed of plants and animals having dense connections (B and E). The latent block model clusters species into blocks of two levels – here plants and animals separated - according to their similar pattern of interactions, links between block are probability of interactions and illustrated by different intensity of grey (C) or different thickness of lines (F).

Table S1.2. List of the literature sources on tree-frugivores interactions used to create the meta-network.

Agmen, F. L., Chapman, H. M., & Bawuro, M. (2010). Seed dispersal by tantalus monkeys (Chlorocebus tantalus tantalus) in a Nigerian montane forest. *African Journal of Ecology*, *48*(4), 1123-1128.
Alexandre, D. Y. (1978). Le rôle disséminateur des éléphants en forêt de Tai, Côte-d'Ivoire. *La Terre et la vie*.
Alexandre, D. Y. (1980). Caractère saisonnier de la fructification dans une forêt hygrophile de Côte-d'Ivoire. *Revue d'écologie*.
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*(6), 568-578.
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: Official Journal of the American Society of Primatologists*, *70*(3), 306-310.
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*, 193-203.
Babweteera, F. (2009). Cordia millenii: on the risk of local extinction?. *African Journal of Ecology*, *47*(3), 367-373.
Badrian, N., Badrian, A., & Susman, R. L. (1981). Preliminary observations on the feeding behavior ofPan paniscus in the Lomako forest of central Zaire. *Primates*, *22*(2), 173-181.
Balcomb, S. R., & Chapman, C. A. (2003). Bridging the gap: influence of seed deposition on seedling recruitment in a primate–tree interaction. *Ecological monographs*, *73*(4), 625-642.
Barlow, C., & Wacher, T. (2005). *A field guide to birds of The Gambia and Senegal*. Yale University Press.
Basabose, A. K. (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *58*(1), 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*, 367-380.
Berrod, B., Bonnel, L., & Schmidt, Q. (2010). Préservation du singe ZINKAKA dans l'environnement de Togbota. *Urgence Bénin*.
Blake, S. (2002). The ecology of forest elephant distribution and its implications for conservation.
Bourliere, F. (1985). Primate communities: their structure and role in tropical ecosystems. *International Journal of Primatology*, *6*(1), 1-26.
Bousquet, B. (1978). Un parc de forêt dense en Afrique: Le parc national de TAI (Côte d'Ivoire): 1re partie. *BOIS & FORETS DES TROPIQUES*, *179*, 27-46.
Bradbury, J. W. (1977). Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie*, *45*(3), 225-255.
Brosset, A., & Erard, C. (1986). *Les Oiseaux des Régions Forestières du nord-est du Gabon. Volume 1. Écologie et Comportement des Espèces*. Société nationale de protection de la nature et d'acclimatation de France, Paris (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*(12), 1237-1249.

Buzzard, P. J. (2004). Interspecific competition among Cercopithecus campbelli, C. petaurista, and C. diana at Tai Forest, Cote d'Ivoire. *PhD Thesis Columbia University*.
Calvert, J. J. (1985). Food selection by western gorillas (Gg gorilla) in relation to food chemistry. *Oecologia*, *65*(2), 236-246.
Chancellor, R. L., Rundus, A. S., & Nyandwi, S. (2017). Chimpanzee seed dispersal in a montane forest fragment in Rwanda. *American journal of primatology*, *79*(3), e22624.
Chapman, C. A., & Chapman, L. J. (1996). Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. Journal of Tropical Ecology, 491-504.
Wrangham, R. W., Chapman, C. A., & Chapman, L. J. (1994). Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, 355-368.
Chapman, C. A., & Chapman, L. J. (2002). Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *133*(3), 861-875.
Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology*, *24*(2), 317-333.
Chapman, C. A., Struhsaker, T. T., Skorupa, J. P., Snaith, T. V., & Rothman, J. M. (2010). Understanding long-term primate community dynamics: implications of forest change. *Ecological Applications*, *20*(1), 179-191.
Chapman, L. J., Chapman, C. A., & Wrangham, R. W. (1992). Balanites wilsoniana: elephant dependent dispersal?. *Journal of Tropical Ecology*, 275-283.
Charles-Dominique, P. (1978). Ecologie et vie sociale de Nandinia binotata (Carnivores, Viverrides): comparaison avec les pro simiens sympatriques du Gabon. *La Terre et la Vie*.
Chatelain, C., Kadjo, B., Koné, I., & Refisch, J. (2001). *Relations Faune-Flore dans le Parc National de Taï: une étude bibliographique* (Vol. 3, pp. 1-166).
Clark, C. J., Poulsen, J. R., Bolker, B. M., Connor, E. F., & Parker, V. T. (2005). Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, *86*(10), 2684-2694.
Bretagnolle. F _Personnal_observation
Cooke, C. A. (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*.
Cordeiro, N. J., Howe, H. F. (2003). Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences*, *100*(24), 14052-14056.
Cordeiro, N. J., Patrick, D. A., 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*, 449-457.
Cordeiro, N. J., & Munisi, B. J. (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, N. J., Ndangalasi, H. J., McEntee, J. P., Howe, H. F. (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology*, *90*(4), 1030-1041.
Daïnou, K., Laurenty, E., Mahy, G., Hardy, O. J., Brostaux, Y., Tagg, N., & Doucet, J. L. (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*(9), 1453-1463.

Sam, M. K., Danquah, E., Oppong, S. K., & Bosu, E. D. (2006). Elephant survey in the Bia Conservation Area, western Ghana. *IUCN*, 41.
Daru, B. H., 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 (http://globalspecies.org)
Davies, A. G., Oates, J. F., & Dasilva, G. L. (1999). Patterns of frugivory in three West African colobine monkeys. *International Journal of Primatology*, *20*(3), 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.
Boesch, C. (1978). New observations on chimpanzees of Tai forest, Ivory Coast. *Terre et la vie-Revue d'écologie appliquée*, *32*(2), 195-201.
Djègo-Djossou, S., Koné, I., Fandohan, A. B., Djègo, J. G., Huynen, M. C., & 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*(29), 97-105.
Djossa, B. A., Fahr, J., Kalko, E. K., & Sinsin, B. A. (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.
Djègo-Djossou, S., Koné, I., Fandohan, A. B., Djègo, J. G., Huynen, M. C., & 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*(29), 97-105.
Djoufack, S. D., Nkongmeneck, B. A., Dupain, J., Bekah, S., Bombome, K. K., Epanda, M. A., & 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, D. M., Shah, N. F., & Heimbauer, L. A. (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, N. L. (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: The Official Publication of the American Association of Physical Anthropologists*, *140*(4), 727-738.
Doran-Sheehy, D. M., & Boesch, C. (2004). Behavioral ecology of western gorillas: New insights from the field.
Dowsett-Lemaire, F., & Dowsett, R. J. (2008). The avifauna of Mole National Park, Ghana. *Malimbus*, *30*, 93-133.
Dowsett-Lemaire, F. (1983). STUDIES OF A BREEDING POPULATION OF WALLER'S REDWLNGED STARLINGS IN MONTANE FORESTS OF SOUTH-CENTRAL AFRICA. *Ostrich*, *54*(2), 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*.
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, R. J. (2011). Ornithological expedition to Togo 2010-2011. *Dowsett-Lemaire Misc. Rep*, *78*, 1-33.
Dowsett-Lemaire, F., & Dowsett, R. J. (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*(2), 298-316.
Dudley, J. P. (2000). Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. *Biotropica*, 556-561.
Duncan, R. S., & Chapman, C. A. (1999). Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological applications*, *9*(3), 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*(1), 86-97.
Eckardt, W., & Zuberbühler, K. (2004). Cooperation and competition in two forest monkeys. *Behavioral Ecology*, *15*(3), 400-411.
Ejidike, B. N., & 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*(1), 56-59.
Engel, T. R. (1998). Seeds on the roundabout–tropical forest regeneration by Genetta rubiginosa. *Small Carnivore Conservation*, *19*, 13-20.
Etiendem, D. N., Funwi-Gabga, N., Tagg, N., Hens, L., & Indah, E. K. (2013). The Cross River gorillas (Gorilla gorilla diehli) at Mawambi Hills, south-west Cameroon: habitat suitability and vulnerability to anthropogenic disturbance. *Folia Primatologica*, *84*(1), 18-31.
Evrard, Q., Hardy, O. J., Tagg, N., & Doucet, J. L. (2019). Removal and predation of aril-covered seeds: the case of Afzelia bipindensis (Fabaceae–Detarioidae). *Plant Ecology and Evolution*, *152*(3), 460-469.
Fahr, J. "AfriBats—a citizen-science project documenting bat distributions in Africa and surrounding islands." *African Bat Conservation News* 30.2 (2013).
Fairgrieve, Chris, and Geresomu Muhumuza. "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* 41.2 (2003): 141-149.
Fashing, Peter J., et al. "Activity and ranging patterns of Colobus angolensis ruwenzorii in Nyungwe Forest, Rwanda: possible costs of large group size." *International Journal of Primatology* 28.3 (2007): 529-550.
Feer, François. "Seed dispersal in African forest ruminants." *Journal of Tropical Ecology* (1995): 683-689.
Feer, F. (1995). Morphology of fruits dispersed by African forest elephants. *African Journal of Ecology*, *33*(3), 279-284.
Fimbel, Cheryl. "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* 70.3 (1994): 277-286.
Fleury, M. C. (1999). *Ecologie et organisation sociale du colobe satan (Colobus satanas)* (Doctoral dissertation, Rennes 1).
Flörchinger, Martina, et al. "Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds." *Oecologia* 164.1 (2010): 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. 242 pp.
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 Nationa l Park, Central African

Republic. *Gestural head movements in captive bonobos (Pan paniscus); use, function and evolutionary*, 21.

Fujita, Marty S., and Merlin D. Tuttle. "Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance." *Conservation Biology* 5.4 (1991): 455-463.

Furuichi, Takeshi, Chie Hashimoto, and Yasuko Tashiro. "Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods." *International Journal of Primatology* 22.6 (2001): 929-945.

Gartlan, J. Stephen, and Thomas T. Struhsaker. "Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa." *Journal of Zoology* 168.2 (1972): 221-265.

Gautier-Hion, A. (1971). L'écologie du talapoin du Gabon. *La terre et la vie*.

Gautier-Hion, A. (1977). Données sur le régime alimentaire de Cercocebus albigena albigena dans le Nord-Est du Gabon. *La Terre et la vie*.

Gautier-Hion, A., Emmons, L. H., & Dubost, G. (1980). A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). *Oecologia*, *45*(2), 182-189.

Gautier-Hion, A., Gautier, J. P., & 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*(4), 511-536.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., ... & Thiollay, J. M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, *65*(3), 324-337.

Gibbs, D., Barnes, E., & Cox, J. (2001). *Pigeons and doves: a guide to the pigeons and doves of the world* (Vol. 13). A&C Black.

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

Gross-Camp, N. D., & Kaplin, B. A. (2011). Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica*, *37*(6), 578-586.

Gross-Camp, N. D., Masozera, M., & Kaplin, B. A. (2009). Chimpanzee seed dispersal quantity in a tropical montane forest of Rwanda. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *71*(11), 901-911.

Gross-Camp, N. D., Mulindahabi, F., & Kaplin, B. A. (2009). Comparing the dispersal of large-seeded tree species by frugivore assemblages in tropical montane forest in Africa. *Biotropica*, *41*(4), 442-451.

Gunderson, V. (1977). Some observations on the ecology of Colobus badius temmincki, Abuko Nature Reserve, the Gambia, West Africa. *Primates*, *18*(2), 305-314.

Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, *48*(3), 208-221.

Harrison, M. J. S., & Hladik, C. M. (1986). Un primate granivore: le Colobe noir dans la forêt du Gabon: potentialité d'évolution du comportement alimentaire. *Revue d'écologie*.

Haurez, B., Daïnou, K., Tagg, N., Petre, C. A., & Doucet, J. L. (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*(5), 395-402.

Haurez, B., Brostaux, Y., Petre, C. A., & Doucet, J. L. (2015). Is the western lowland gorilla a good gardener? Evidence for directed dispersal in Southeast Gabon. *Bois et Forêts des Tropiques*, *324*(2), 39-50.
Lovette, I. J., & Fitzpatrick, J. W. (Eds.). (2016). *Handbook of bird biology*. John Wiley & Sons.
Head, J. S., Boesch, C., Makaga, L., & Robbins, M. M. (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*(3), 755-775.
Helbig-Bonitz, M., Rutten, G., & Kalko, E. K. (2014). Fruit bats can disperse figs over different land-use types on Mount Kilimanjaro, Tanzania. *African Journal of Ecology*, *52*(1), 122-125.
Hicks, T. C. (2004). *Chimpanzee (Pan troglodytes) Tool Use in the Ngotto Forest, Central African Republic* (Doctoral dissertation, Central Washington University).
Hladik, C. M. (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*(2), 65-77.
Holbrook, K. M., & Smith, T. B. (2000). Seed dispersal and movement patterns in two species of Ceratogymna hornbills in a West African tropical lowland forest. *Oecologia*, *125*(2), 249-257.
Horn, A. D. (1987). The socioecology of the black mangabey (Cercocebus aterrimus) near Lake Tumba, Zaire. *American journal of primatology*, *12*(2), 165-180.
Hoshino, J. (1985). Feeding ecology of mandrills (Mandrillus sphinx) in Campo animal reserve, Cameroon. *Primates*, *26*(3), 248-273.
Houle, A., Chapman, C. A., & Vickery, W. L. (2010). Intratree vertical variation of fruit density and the nature of contest competition in frugivores. *Behavioral Ecology and Sociobiology*, *64*(3), 429-441.
Hovestadt, T., Yao, P. & Linsenmair, K.E. 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 (1999). https://doi.org/10.1023/A:1009764031116
Idani, G. (1986). Seed dispersal by pygmy chimpanzees (Pan paniscus): a preliminary report. *Primates*, *27*(4), 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, B. I., 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, K. R., Boesch, C., Byrne, R., Chapman, C. A., Goné Bi, Z. B., Head, J. S., ... & 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*(6), 626-645.
Janmaat, K. R., Boesch, C., Byrne, R., Chapman, C. A., Goné Bi, Z. B., Head, J. S., ... & 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*(6), 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. *REVUE D ECOLOGIE-LA TERRE ET LA VIE*, *54*(4), 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*(2), 1-11.

Tolo, C. U., Baranga, J., & Kagoro-Rugunda, G. (2008). Dietary selection of L'Hoest monkeys in Kalinzu forest reserve, southwestern Uganda. *African Journal of Ecology*, *46*(2), 149-157.

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*(10), 477.

Kane, E. E., & McGraw, W. S. (2017). Dietary variation in Diana monkeys (Cercopithecus diana): The effects of polyspecific associations. *Folia Primatologica*, *88*(6), 455-482.

Kane, E. E. (2012). The context of dietary variation in Cercopithecus diana in the Ivory Coast's Tai National Park [thesis]. *Columbus, OH: The Ohio State University*.

Kankam, B. O., & Oduro, W. (2009). Frugivores and fruit removal of Antiaris toxicaria (Moraceae) at Bia Biosphere Reserve, Ghana. *Journal of Tropical Ecology*, 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), 1-31.

Kaplin, B. A., & Moermond, T. C. (2000). Foraging ecology of the mountain monkey (Cercopithecus l'hoesti): implications for its evolutionary history and use of disturbed forest. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *50*(4), 227-246.

Kaplin, B. A., & Moermond, T. C. (1998). Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology*, *45*(1), 83-101.

Kendrick, E. L., Shipley, L. A., Hagerman, A. E., & Kelley, L. M. (2009). Fruit and fibre: the nutritional value of figs for a small tropical ruminant, the blue duiker (Cephalophus monticola). *African Journal of Ecology*, *47*(4), 556-566.

Kirika, J. M., 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*(2), 318-328.

Klaus-Hügi, C., Klaus, G., Schmid, B., & König, B. (1999). Feeding ecology of a large social antelope in the rainforest. *Oecologia*, *119*(1), 81-90.

Kock, D., Barnett, L., Fahr, J., & Emms, C. (2002). On a collection of bats (Mammalia: Chiroptera) from The Gambia. *Acta Chiropterologica*, *4*(1), 77-97.

Koné, I., Lambert, J. E., 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*(3), 293-305.

Kouamé, D., Yao, C. Y. A., Nandjui, A., & N'guessan, E. K. (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*(5).

Kunz, B. K., Hovestadt, T., & Linsenmair, K. E. (2008). Variation of dispersal agents? Frugivore assemblages and fruit handling in a typical 'birddispersed'tree (Lannea acida, Anacardiaceae). *Ecotropica*, *14*, 101-112.

Lahm, S. A. (1986). Diet and habitat preference of Mandrillus sphinx in Gabon: implications of foraging strategy. *American Journal of Primatology*, *11*(1), 9-26.

Lambert, J. E., & Garber, P. A. (1998). Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology*, *45*(1), 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*(3), 234-240.
Lambert, J. E. (1999). Seed handling in chimpanzees (Pan troglodytes) and redtail monkeys (Cercopithecus ascanius): Implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *109*(3), 365-386.
Lambert, J. E. (2001). Red-tailed guenons (Cercopithecus ascanius) and Strychnos mitis: evidence for plant benefits beyond seed dispersal. *International Journal of Primatology*, *22*(2), 189-201.
Lambert, J. E. (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*(1), 9-24.
Lambert, J. E., Chapman, C. A., Wrangham, R. W., & Conklin-Brittain, N. L. (2004). Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *125*(4), 363-368.
Lamperti, A. M., French, A. R., Dierenfeld, E. S., Fogiel, M. K., Whitney, K. D., Stauffer, D. et al., (2014). Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa. *Journal of Tropical Ecology*, 273-290.
Langevin, P., & Barclay, R. M. (1990). Hypsignathus monstrosus. *Mammalian species*, (357), 1-4.
Lehouck, V., Spanhove, T., Demeter, S., Groot, N. E., Lens, L. (2009). Complementary seed dispersal by three avian frugivores in a fragmented Afromontane forest. *Journal of Vegetation Science*, *20*(6), 1110-1120.
Lehouck, V., Spanhove, T., Vangestel, C., Cordeiro, N. J., & Lens, L. (2009). Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest?. *Ecography*, *32*(5), 789-799.
Lehouck, V., Spanhove, T., Colson, L., Adringa-Davis, A., Cordeiro, N. J., & Lens, L. (2009). Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos*, *118*(7), 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*(1), 96-100.
Lehouck unpublished data
Lieberman, D., Lieberman, M., & Martin, C. (1987). Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica*, 365-369.
Luef, E. M., Breuer, T., & Pika, S. (2016). Food-associated calling in Gorillas (Gorilla g. gorilla) in the Wild. *PloS one*, *11*(2), e0144197.
Lumpkin, S., & Kranz, K. R. (1984). Cephalophus sylvicultor. *Mammalian Species*.
Magloire, N. C., Blaise, K., Noël, D. D., & Inza, K. (2017). PRELIMINARY STUDY ON Eidolon helvum (Kerr, 1792) POPULATION DYNAMIC IN CÔTE D'IVOIRE, WEST AFRICA. *Journal of Experimental Biology*, *5*, 6.
Maisels, F., Gautier-Hion, A., & Gautier, J. P. (1994). Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. *International Journal of Primatology*, *15*(5), 681-701.
Marshall, A. G., & William, A. N. M. (1982). Ecological observations on epomorphorine fruit-bats (Megachiroptera) in West African savanna woodland. *Journal of Zoology*, *198*(1), 53-67.

Marshall, A. G. (1985). Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society*, *83*(4), 351-369.

Masette, M., Isabirye-Basuta, G., Baranga, D., Chapman, C. A., & Rothman, J. M. (2015). The challenge of interpreting primate diets: mangabey foraging on Blighia unijugata fruit in relation to changing nutrient content. *African Journal of Ecology*, *53*(3), 259-267.

Masi, S., Mundry, R., Ortmann, S., Cipolletta, C., Boitani, L., & Robbins, M. M. (2015). The influence of seasonal frugivory on nutrient and energy intake in wild western gorillas. *PloS one*, *10*(7), e0129254.

Matsumoto-Oda, A., & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica*, *70*(3), 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*(1), 127-130.

Mbelli HM. 2000. p. 11. Plant animal relations: effects of disturbance on the regeneration of commercial tree species. The Tropenbos-Cameroon Programme, Kribi, Cameroon. Tropenbos-Cameroon Documents.

McGraw, W. S., Vick, A. E., & Daegling, D. J. (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*(1), 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*(10), 1553-1566.

Merz, G. (1981). Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt, Loxodonta africana cyclotis Matschie, 1900.

Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (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*(3), 307-323.

Mitani, M. (1991). Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. *Primates*, *32*(2), 137-151.

Fils, E. M. B., Anong, A. B. A., & Fohouo, F. N. T. (2012). First record of the Giant House Bat Scotophilus nigrita (Schreber, 1774) in Cameroon (Mammalia, Chiroptera). *Biodiversity Journal*, *3*(1), 55-58.

Molloy, L., & Hart, J. A. (2002). Duiker food selection: palatability trials using natural foods in the Ituri Forest, Democratic Republic of Congo. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *21*(2), 149-159.

Morgan, D., Sanz, C., Onononga, J. R., & Strindberg, S. (2006). Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology*, *27*(1), 147-179.

Morgan, B. J., & Lee, P. C. (2007). Forest elephant group composition, frugivory and coastal use in the Réserve de Faune du Petit Loango, Gabon. *African Journal of Ecology*, *45*(4), 519-526.

Morgan, B. J. (2007). Group size, density and biomass of large mammals in the Reserve de Faune du Petit Loango, Gabon. *African Journal of ecology*, *45*(4), 508-518.

Moupela, C., Doucet, J. L., Daïnou, K., Tagg, N., Bourland, N., & Vermeulen, C. (2014). Dispersal and predation of diaspores of C oula edulis B aill. in an evergreen forest of G abon. *African Journal of Ecology*, *52*(1), 88-96.

Mulotwa, E. M., Louette, M. B., Dudu, A., & Upoki, A. (2011). CONTRIBUTION A LA CONNAISSANCE DU REGIME ALIMENTAIRE DU PAON CONGOLAIS Afropavo congensis Chapin, 1936. *NUMERO SPECIAL*, *14*, 73-83.
Muscarella, R., & Fleming, T. H. (2007). The role of frugivorous bats in tropical forest succession. *Biological reviews*, *82*(4), 573-590.
Mwenja, I. (2007). A new population of De Brazza's monkey in Kenya. *Primate Conservation*, *22*(1), 117-122.
Nchanji AC, Plumptre AJ (2003) Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. J Trop Ecol 19:229–237
Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology*, *37*(3), 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)(Chiroptera: Pteropodidae) de la commune d'Abidjan Plateau (Côte d'Ivoire). *Agronomie Africaine*, *21*(3).
Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates*, *36*(2), 151-168.
Norris, J. (1988). Diet and feeding behavior of semi-free ranging mandrills in an enclosed Gabonais forest. *Primates*, *29*(4), 449-463.
Nsi Akoue, G., Mbading-Mbading, W., Willaume, E., Souza, A., Mbatchi, B., & Charpentier, M. J. (2017). Seasonal and individual predictors of diet in a free-ranging population of mandrills. *Ethology*, *123*(9), 600-613.
Nyiramana, A., Mendoza, I., Kaplin, B. A., & Forget, P. M. (2011). Evidence for seed dispersal by rodents in tropical montane forest in Africa. *Biotropica*, *43*(6), 654-657.
Oates, J. F., & Whitesides, G. H. (1990). Association between olive colobus (Procolobus verus), Diana guenons (Cercopithecus diana), and other forest monkeys in Sierra Leone. *American Journal of Primatology*, *21*(2), 129-146.
Oates, J. F. (1978). Water-plant and soil consumption by guereza monkeys (Colobus guereza): a relationship with minerals and toxins in the diet?. *Biotropica*, 241-253.
Oates, J. F. (1988). The diet of the olive colobus monkey, Procolobus verus, in Sierra Leone. *International journal of primatology*, *9*(5), 457-478.
Oates, J. F., Swain, T., & Zantovska, J. (1977). Secondary compounds and food selection by colobus monkeys. *Biochemical systematics and Ecology*, *5*(4), 317-321.
Kankam, B. O., & Oduro, W. (2009). Frugivores and fruit removal of Antiaris toxicaria (Moraceae) at Bia Biosphere Reserve, Ghana. *Journal of Tropical Ecology*, 201-204.
Oelze, V. M., Head, J. S., Robbins, M. M., 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, A. U., Enieng, E. A., & Etta, U. S. (2013). Habitat utilization and conservation of the Cross River gorilla (< i> Gorilla gorilla diehli</i.) in Afi Mountain Wildlife Sanctuary of Cross River State, Nigeria. *International Journal of Biological and Chemical Sciences*, *7*(4), 1579-1585.
Okekedunu, J. O., Ogunjemite, B. G., Adeyemo, I. A., & Olaniyi, O. E. (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 (The)*, *15*, 13-21.
Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (1992). Old World fruit bats. *An action plan for their conservation. Gland, Switzerland: IUCN*, *263*.
Osmaston, H. A. (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*, 96-104.
Owens, J. R., Honarvar, S., Nessel, M., & Hearn, G. W. (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*(12), 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*(2), 107-116.
Petre, C. A., Tagg, N., Beudels-Jamar, R. C., Haurez, B., & Doucet, J. L. (2015). Western lowland gorilla seed dispersal: are seeds adapted to long gut retention times?. *Acta Oecologica*, *67*, 59-65.
Petre, C. A., Tagg, N., Beudels-Jamar, R., Haurez, B., Salah, M., Spetschinsky, V., ... & Doucet, J. L. (2015). Quantity and spatial distribution of seeds dispersed by a western lowland gorilla population in south-east Cameroon. *Journal of Tropical Ecology*, *31*(3), 201-212.
Potts, K. B., Watts, D. P., & Wrangham, R. W. (2011). Comparative feeding ecology of two communities of chimpanzees (Pan troglodytes) in Kibale National Park, Uganda. *International Journal of Primatology*, *32*(3), 669-690.
Poulsen, J. R., Clark, C. J., & Smith, T. B. (2001). Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of tropical ecology*, 787-808.
Poulsen, J. R., Clark, C. J., Connor, E. F., & Smith, T. B. (2002). Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, *83*(1), 228-240.
Poulsen, J. R., Clark, C. J., & Bolker, B. M. (2012). Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. *Ecology*, *93*(3), 500-510.
Prota_Database (https://prota4u.org/database/)
Quris, R. (1975). Ecologie et organisation sociale de Cercocebus galeritus agilis dans le Nord-Est du Gabon. *La Terre et la vie*.
Remis, M. J., Dierenfeld, E. S., Mowry, C. B., & Carroll, R. W. (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*(5), 807-836.
Remis, M. J. (1997). Western lowland gorillas (Gorilla gorilla gorilla) as seasonal frugivores: use of variable resources. *American Journal of Primatology*, *43*(2), 87-109.
Richter, H. V., & Cumming, G. S. (2006). Food availability and annual migration of the straw-colored fruit bat (Eidolon helvum). *Journal of Zoology*, *268*(1), 35-44.
Rode, K. D., Chiyo, P. I., Chapman, C. A., & McDowell, L. R. (2006). Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of tropical ecology*, 441-449.
Rogers, M. E., Abernethy, K. A., Fontaine, B., Wickings, E. J., White, L. J., & Tutin, C. E. (1996). Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. *American Journal of Primatology*, *40*(4), 297-313.
Rogers, M. E., Voysey, B. C., McDonald, K. E., Parnell, R. J., & Tutin, C. E. G. (1998). Lowland gorillas and seed dispersal: the importance of nest sites. *American Journal of Primatology*, *45*(1), 45-68.

Rogers, M. E., Maisels, F., Williamson, E. A., Fernandez, M., & Tutin, C. E. (1990). Gorilla diet in the lope reserve, gabon. *Oecologia*, *84*(3), 326-339.
Royal botanic garden of Edinburgh database (https://data.rbge.org.uk/search/livingcollection/)
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*(3), 265-281.
Sawyer, S. C. (2012). *The ecology and conservation of the critically endangered Cross River gorilla in Cameroon*. University of California, Berkeley.
Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H. M., & Böhning-Gaese, K. (2011). Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology*, *92*(1), 26-36.
Seltzer, C. E., Ndangalasi, H. J., & Cordeiro, N. J. (2013). Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. *Biotropica*, *45*(4), 450-456.
Serckx, A., Kühl, H. S., Beudels-Jamar, R. C., Poncin, P., Bastin, J. F., & Huynen, M. C. (2015). Feeding ecology of bonobos living in forest-savannah mosaics: Diet seasonal variation and importance of fallback foods. *American journal of primatology*, *77*(9), 948-962.
Shanahan, M., So, S., Gompton, S. G., & Gorlett, R. (2001). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*, *76*(4), 529-572.
Short, L., Horne, J., & Horne, J. F. (2001). *Toucans, barbets, and honeyguides: Ramphastidae, Capitonidae and Indicatoridae* (Vol. 8). Oxford University Press.
Short, J. (1981). Diet and feeding behaviour of the forest elephant. *Mammalia*, *45*, 177-185.
Hongo, S. (2016). Socioecology of mandrills (Mandrillus sphinx): Mating and feeding tactics in a primate with extremely large group.
Sourd, C., & Gautier-Hion, A. (1986). Fruit selection by a forest guenon. *The Journal of Animal Ecology*, 235-244.
Struhsaker, T. T. (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*(5), 914-941.
Sun, C., & Moermond, T. C. (1997). Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *The Auk*, *114*(3), 396-404.
Tashiro, Y. (2006). Frequent insectivory by two guenons (Cercopithecus lhoesti and Cercopithecus mitis) in the Kalinzu Forest, Uganda. *Primates*, *47*(2), 170-173.
Tchamba, M. N., & Seme, P. M. (1993). Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *African Journal of Ecology*, *31*(2), 165-171.
Theuerkauf, J., Waitkuwait, W. E., 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*(4), 447-460.
Tolo, C. U., Baranga, J., & Kagoro-Rugunda, G. (2008). Dietary selection of L'Hoest monkeys in Kalinzu forest reserve, southwestern Uganda. *African Journal of Ecology*, *46*(2), 149-157.
Tosso, D. N. F. (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, P. M., Beudels-Jamar, R. C., Huynen, M. C., & 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*, 115-118.
Tutin, C. E., & 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*(3), 195-211.
Tutin, C. E. (1999). Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates*, *40*(1), 249-265.
Tutin, C. E., Williamson, E. A., Rogers, M. E., & 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*, 181-199.
Tutin, C. E., White, L. J., Williamson, E. A., 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*(3/4), 249-276.
Tutin, C. E., Parnell, R. J., & White, F. (1996). Protecting seeds from primates: Examples from Diospyros spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, 371-384.
Tutin, C. E., Ham, R. M., White, L. J., & Harrison, M. J. (1997). The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American journal of primatology*, *42*(1), 1-24.
Tutin, C. E., & Fernandez, M. (1985). Foods consumed by sympatric populations ofGorilla g. gorilla andPan t. troglodytes in Gabon: Some preliminary data. *International Journal of Primatology*, *6*(1), 27.
Tweheyo, M., & Lye, K. A. (2003). Phenology of figs in Budongo Forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology*, *41*(4), 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*(2), 133-139.
Twinomugisha, D., Basuta, G. I., & Chapman, C. A. (2003). Status and ecology of the golden monkey (Cercopithecus mitis kandti) in Mgahinga Gorilla National Park, Uganda. *African Journal of Ecology*, *41*(1), 47-55.
Uwimbabazi, M., & Eilu, G. (2014). Avian frugivore assemblages on C eltis gomphophylla, B aker, in B udongo F orest R eserve, U ganda. *African journal of ecology*, *52*(1), 97-102.
Van Cakenberghe, V., & Seamark, E. C. (2009). African Chiroptera Report 2014.
Voysey, B. C., Mcdonald, K. E., Rogers, M. E., Tutin, C. E., & Parnell, R. J. (1999). Gorillas and seed dispersal in the Lope Reserve, Gabon. I: Gorilla acquisition by trees. *Journal of Tropical Ecology*, 23-38.
Wahome, J. M., Rowell, T. E., & Tsingalia, H. M. (1993). The natural history of de Brazza's monkey in Kenya. *International journal of primatology*, *14*(3), 445-466.
Wang, B. C. (2008). *Impacts of hunting on seed dispersal in a Central African tropical forest* (Doctoral dissertation, University of California, Los Angeles).
Wang, B. C., Sork, V. L., Leong, M. T., & Smith, T. B. (2007). Hunting of mammals reduces seed removal and dispersal of the afrotropical tree Antrocaryon klaineanum (Anacardiaceae). *Biotropica*, *39*(3), 340-347.
Wasserman, M. D., & Chapman, C. A. (2003). Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology*, *72*(4), 650-659.

Webala, P. W., 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*(1), 85-94.
Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (Pan troglodytes schweinfurthii) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American Journal of Primatology*, *74*(2), 114-129.
White, L., & Abernethy, K. (1996). *Guide de la végétation de la Réserve de la Lopé*. Libreville: Ecofac.
White, L. J., Tutin, C. E., & 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*(3), 181-199.
Whitney, K. D., Fogiel, M. K., Lamperti, A. M., Holbrook, K. M., Stauffer, D. J., Hardesty, B. et al. (1998). Seed dispersal by Ceratogymna hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, 351-371.
Williamson, E. A., Tutin, C. E., Rogers, M. E., & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology*, *21*(4), 265-277.
Wrangham, R. W., Conklin, N. L., Etot, G., Obua, J., Hunt, K. D., Hauser, M. D., & Clark, A. P. (1993). The value of figs to chimpanzees. *International Journal of Primatology*, *14*(2), 243-256.
Wrangham, R. W., Chapman, C. A., & Chapman, L. J. (1994). Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, 355-368.
Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, *19*(6), 949-970.
Yamagiwa, J., & Basabose, A. K. (2006). Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi–Biega National Park. *Primates*, *47*(1), 74-90.
Yamagiwa, J., & Basabose, A. K. (2009). Fallback foods and dietary partitioning among Pan and Gorilla. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *140*(4), 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), 1-14.
Yamagiwa, J., Basabose, A. K., 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*(6), 1345-1373.
YAMAGIWA, J., BASABOSE, A. K., KALEME, K. P., & 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. Supplementary Issue.*, *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*, 526-530.

APPENDIX 2

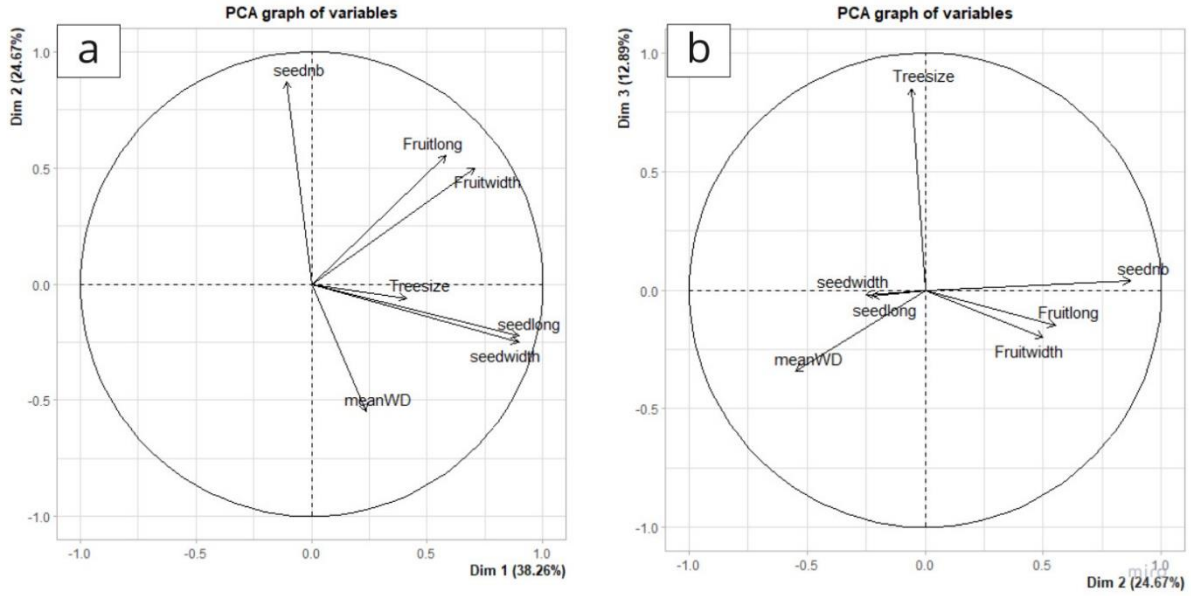

Figure S2.1. Representation of the three dimensions of the PCA, on traits of trees species. (a) The dimension 1 is positively loaded to the seed and fruit size (length or width), the dimension 2 is positively loaded to the number of seeds by fruits and negatively to the wood density of trees. (b) The dimension 3 is positively loaded to the tree size.

Table S2.2. Results from the model selection from the relationship between the sum of probabilities by blocks and species traits and number of study by blocks. For frugivore blocks, the covariates are mean body mass of frugivore by blocks and the number of study y blocks. For tree blocks, the dimension 1, 2 and 3 of the PCA, respectively representing the size of fruit and seeds, the seed number and wood density, and the tree size. The selection was realised on AICc from the dredge function in the MuMIN package.

Components	Df	logLik	AICc	delta	weight
Mean body mass (log)	3	-21.29	51.24	0.00	0.50
(NULL)	2	-23.18	51.55	0.31	0.42
Mean body mass (log) + number of studies (log)	4	-20.97	54.94	3.70	0.08
Dim 3	3	-20.04	48.49	0.00	0.37
Number of studies	3	-20.43	49.27	0.78	0.25
Dim 2 + Number of studies	4	-19.01	50.46	1.97	0.14
Dim 3 + Number of studies	4	-19.45	51.35	2.86	0.09
Dim 2 + Dim 3	4	-19.80	52.05	3.56	0.06

Table S2.3. Results from the model selection from the relationship between the probabilities of interaction between tree and frugivore blocks, and the dimension 1, the dimension 2 and the dimension 3 from the PCA on tree traits, and the proportion of overlapping areas between blocks, the number of study between blocks. With interaction between the dimension 1, 2, 3, and the body mass of frugivores. The selection was realised on AICc criteria with the function dredge from the MuMIN package. The first five models fitted are presented here.

Variables	Df	logLik	AICc	delta	weight
Dim1+ Dim2+ Dim3+ Bodymass+ overlapping + nb studies + Dim1 x bodymass + Dim3 x bodymass	12	-349.61	724.93	0	0.26
Dim2+ Dim3+ overlapping + nb studies	8	-354.91	726.60	1.67	0.11
Dim2+ Dim3+ Bodymass+ overlapping + nb studies	9	-353.82	726.61	1.68	0.11
Dim2+ Dim3+ Bodymass+ overlapping + nb studies + Dim3 x bodymass	10	-352.26	727.46	2.53	0.07
Dim1+ Dim3+ Bodymass+ overlapping + nb studies + Dim1 x bodymass + Dim3 x bodymass	11	-352.26	727.96	3.03	0.06

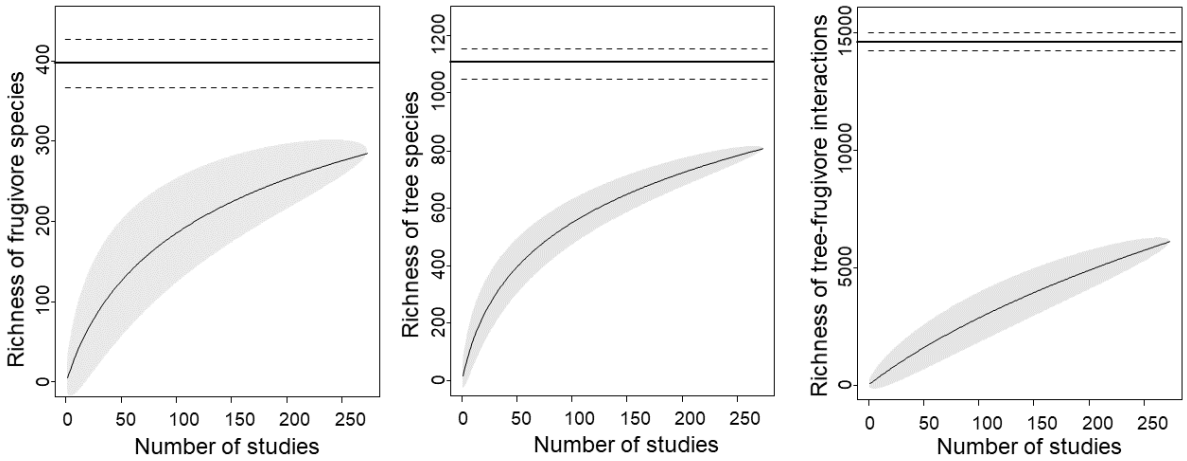

Figure S2.4. The accumulation curves of frugivore species (A), tree species (B) and tree-frugivore interactions (C) for the whole dataset. The estimated asymptotic of species or interactions richness based on the Chao 2 estimator is represented by the black straight line with standard errors as black dashed lines.

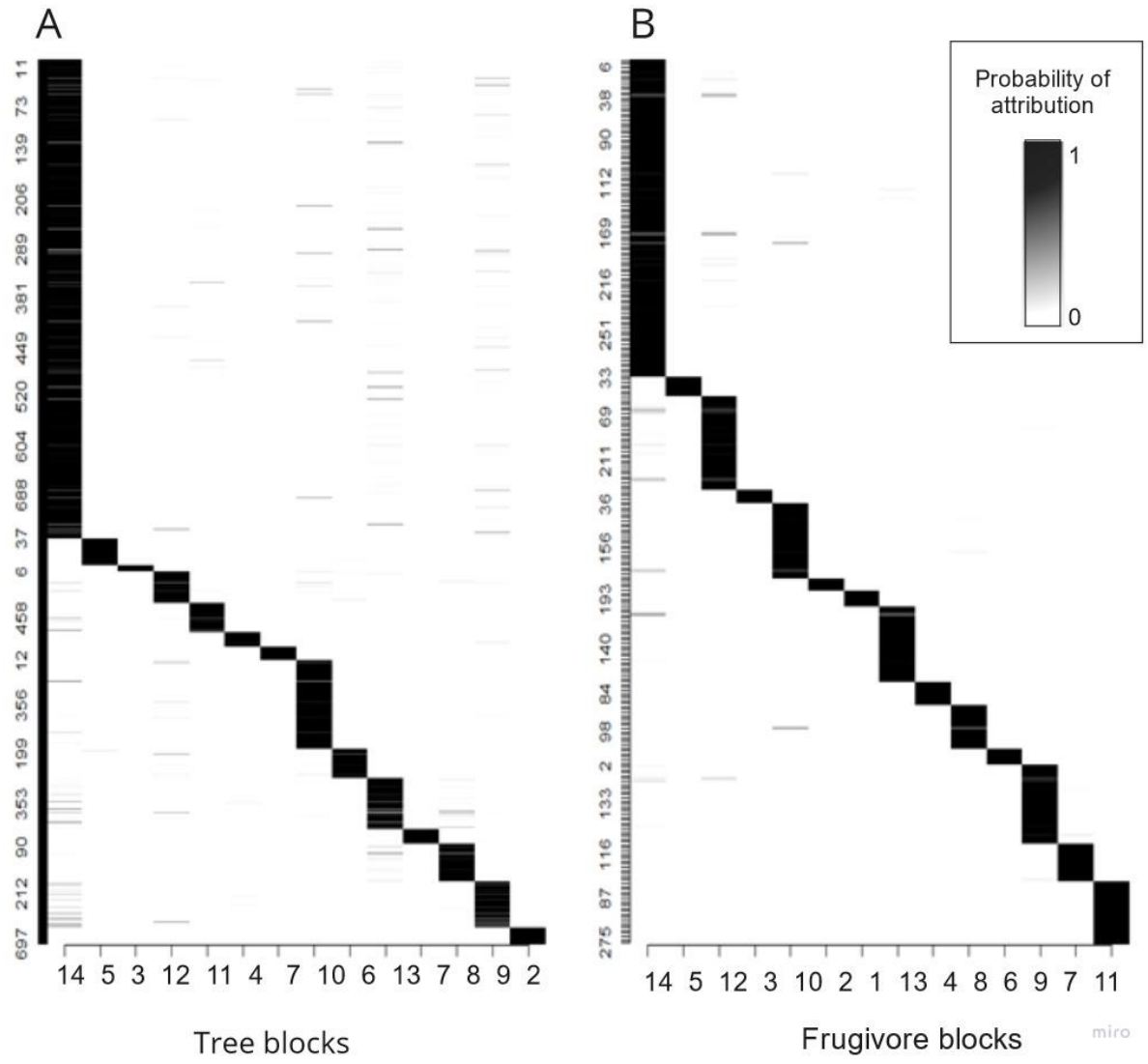

Figure S2.5. Probability of attribution of each tree species (A) and frugivore species (B) to their relevant blocks, from the latent block model result. Higher is the probability, darker is the color.

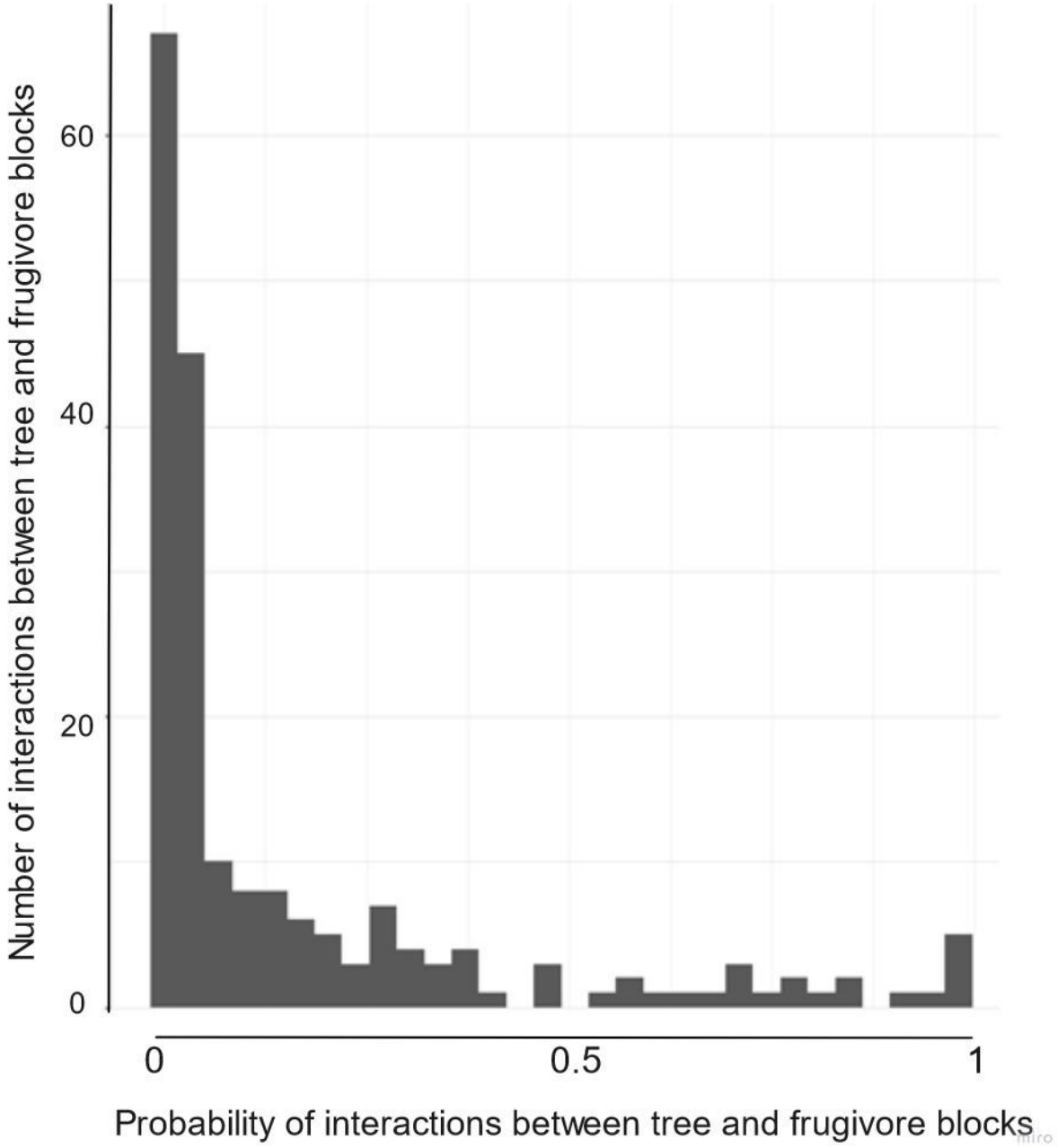

Figure S2.6. Distribution diagram of interactions probability between tree and frugivores blocks.

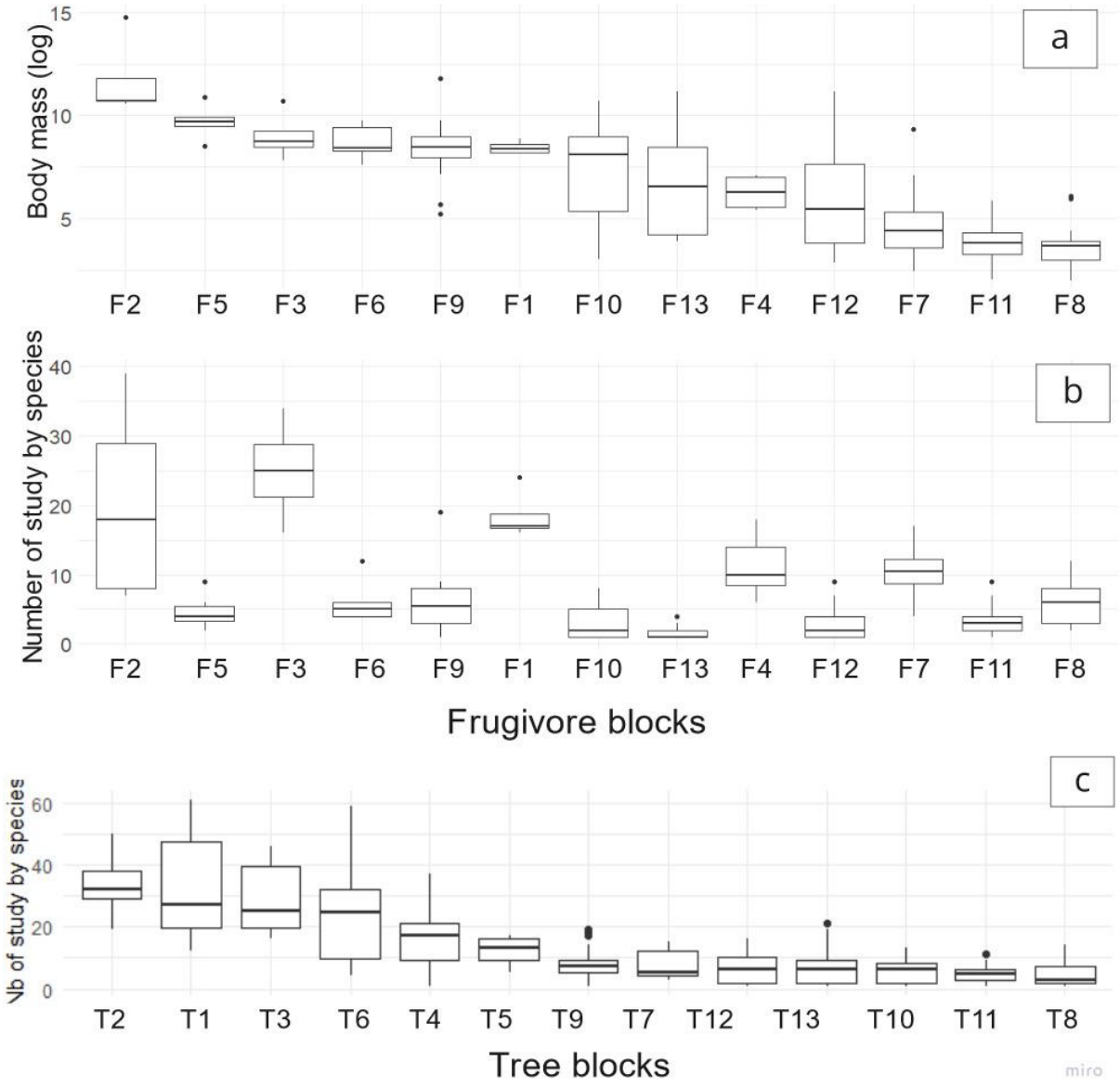

Figure S2.7. Species trait values by frugivore blocks (a) the body mass (log) of frugivore by blocks, (b) the number of study by species inside blocks. Frugivore blocks are ordered by frugivore mean body mass, from the larger (left) to the smaller (right).

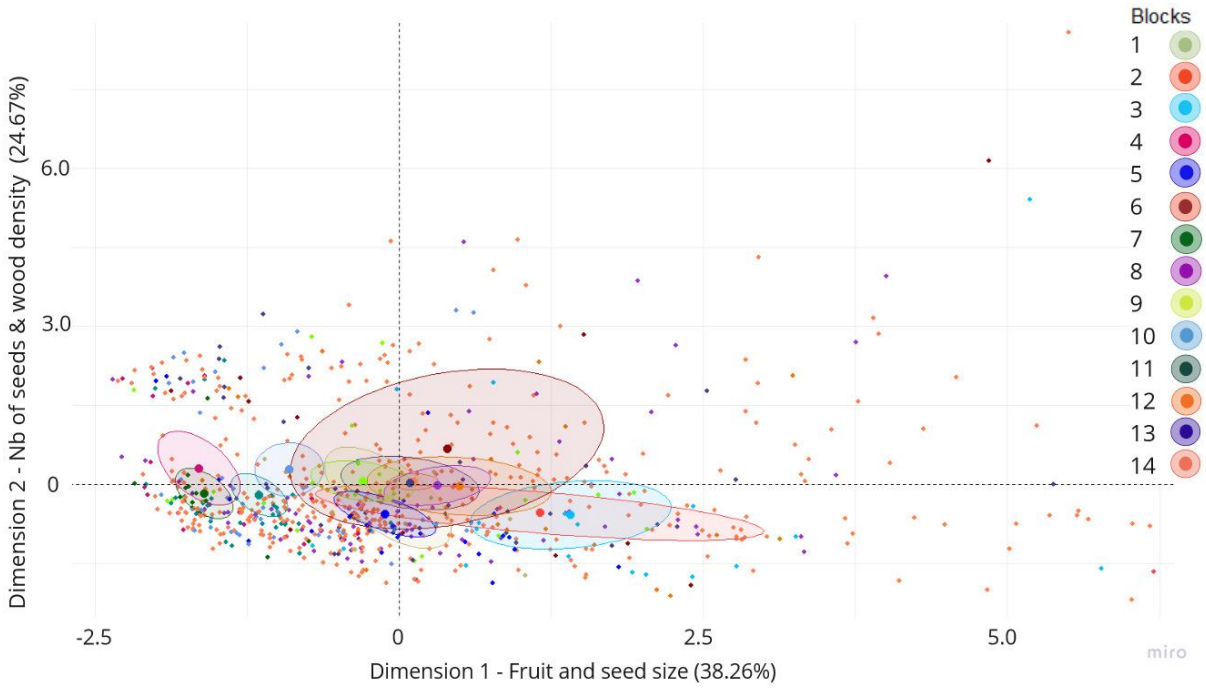

Figure S2.8. Representation of the species through the first and second axes of the PCA on tree traits, regarding their blocks. The first axes is driven by the size of fruits and seeds, while the second axes differentiate trees with numerous seeds and low wood density from seed with few seeds and high wood density (see Fig S2.1). The ellipses are confidence ellipses representing the mean value of the block around the barycentre. Blocks are represented by different colors.

Table S2.9. Generalized linear model results for the relationship between i) sums of probabilities and mean number of study by frugivore blocks; ii) sums of probabilities, and the dimension 3 representing tree size. P-values <0.05 are in bold.

Effects	Estimate	Std.error	DF	Z value	P > F
Intercept	0.10	0.32	/	0.33	0.741
Mean nb of study	0.07	0.02	13	3.19	**0.002**
Intercept	0.15	0.32	/	0.47	0.64
Dim 3 – tree size	1.27	0.41	13	3.08	**0.002**

Table S2.10. The linear mixed-model regression results with the probability of interaction between tree and frugivore blocks as the response variable and the average frugivore body mass per frugivore block, the average seed length per tree block, the interaction between body mass and seed length, the proportion of species with overlapping distribution between blocks, and the number of study between blocks as explanatory variables. The response variable was logit transformed to fulfil the assumptions of linear mixed-effects model. P-values <0.05 are in bold.

Effects	Sum sq	NumDf	DenDF	F-value	P > F
Dim 1	93.14	1	140.56	36.80	**<0.001**
Body mass (log)	75.99	1	20.42	30.02	**<0.001**
Dim 2	27.35	1	8.64	10.80	**0.010**
Dim 3	18.19	1	67.41	7.19	**0.009**
Distribution overlap (logit)	159.83	1	108.24	63.15	**<0.001**
Mean nb of study by frug blocks (log)	71.46	1	10.56	28.23	**<0.001**
Mean nb of study by tree blocks (log)	19.13	1	8.85	7.56	**0.023**
Dim 1 x Body mass (log)	83.45	1	164.36	32.97	**<0.001**
Dim 3 x Body mass (log)	12.93	1	164.35	5.11	**0.025**

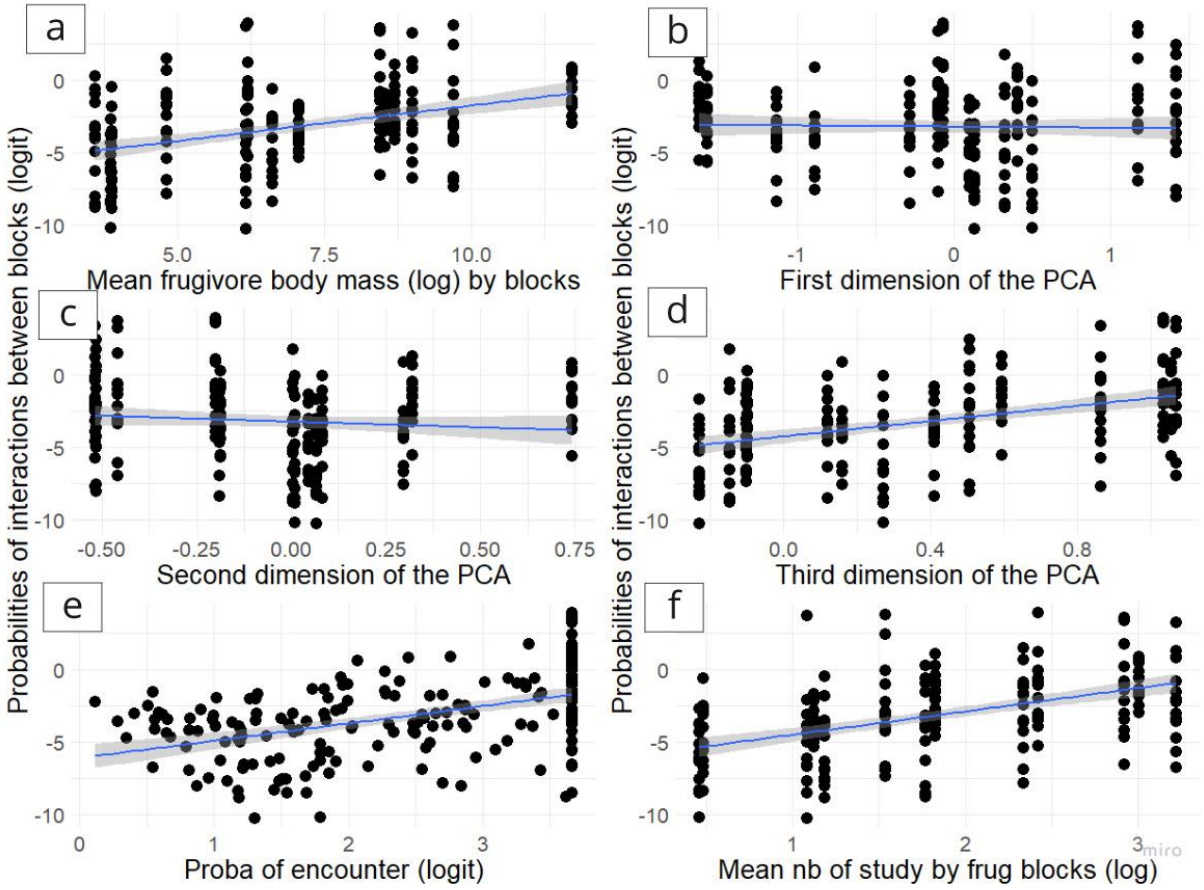

Figure S2.11. Relationships between the probability of interactions between tree and frugivore blocks, and (a) the mean frugivores body mass, (b) the first dimension of the PCA, representing fruit and seed size, (c) the second dimension of the PCA, representing seed number and wood density, (d) the third dimension of the PCA, representing tree size, (e) the proportion of overlapping areas between blocks (logit), and (f) the mean number of studies by frugivore species in frugivore blocks. The probability of interactions was logit transformed to fulfil the assumptions of the linear mixed model.

CHAPTER 2

Traits composition of tree communities differ among floristic types of Central African forests: relationship with frugivory

Small bird feeding on the rare Schummanniophyton hirsutum. Picture by Clementine Durand-Bessart.

Context

Tropical forests are characterized by their high species richness regarding tree and animal species. Abundance and distribution of tree species depend on abiotic – soil, precipitation, temperature – as well as biotic factors such as seed dispersal. Tree-frugivore interactions influence the patterns of abundance and distribution of trees species, due to the diversity of frugivores and their diverse seed dispersal effectiveness due to the different feeding strategies, mobility, digestion-time, etc. Each forest has different community traits due to the diversity of phenotype but also the abundance of the different species inside the community. Then, tree communities could differ regarding frugivory traits such as the composition of fruits types or the offer in particular fruits and seeds – small or large – influencing directly interactions with frugivore species.

In this study, we proposed to analyse the tree assemblage of different forests types across Central African forests, following Réjou-Méchain et al., (2021). We analysed the difference of fruits offering regarding species richness and abundance of the different forests, and by linking this plants community traits to the frugivory networks. Our study aims to describe the fruit offer of the different forests types, taking into account the abundance of species inside these forests.

Key results

The community weighted traits values changed among the different floristic types, coherently with the abundance and distribution profiles of fruits traits availability.

We observed a variation of tree traits following latitudinal and longitudinal gradients, with smaller fruits and seeds in the Northern plots.

The different frugivore species had different offers in fruits in each forest, showing their flexibility from frugivore in terms of the traits of fruits consumed.

The study also revealed that more frugivory studies occurred in three floristic types, mostly in Gabonese forests. These results showed a geographic bias of studies.

This chapter is still ongoing, and a work in progress. In the future, we would like to explore more the relationship between the different floristic type, and the frugivory network structure related.

Traits composition of tree communities differ among floristic types of Central African forests: relationship with frugivory

Durand-Bessart Clémentine[12], Bretagnolle François[1], Maxime Réjou-Méchain[3], Cyrille Violle[4], Lucie Mahaut[4], Fabio Berzaghi[6], Colin Fontaine[2]

[1] Biogeosciences, UMR 6282, Université Bourgogne Franche Comte-CNRS, Dijon, France

[2] Centre d'Ecologie et des Sciences de la Conservation, CESCO, UMR 7204, MNHN-CNRS-SU, Paris, France

[3]AMAP, Univ. Montpellier, IRD, CNRS, CIRAD, INRAE, Montpellier, France.

[4] CEFE, Univ Montpellier, CNRS, EPHE, IRD, F-34293 Montpellier, France

[5] Laboratory of Climate and Environmental Sciences (LSCE) – UMR CEA/CNRS/UVSQ; Gif-sur-Yvette, France.

Keywords: Tropical ecology, forest community, community weighted mean traits, mutualism

INTRODUCTION

Tree communities of tropical forests are characterized by their high species richness, with a low turnover in composition (i.e. beta-diversity) among closely related communities (Condit et al., 2000; 2002). The abundance and spatial distribution of species are intimately linked, with species having broader environmental tolerances achieving higher local densities and having a wider distribution range (Gaston and Kunin, 1997; Davidar et al., 2008). The heterogeneity of available environments have been presented as one of the main factor influencing the organisation of plant communities in tropical forests (Flores et al., 2006). However, some tree species expressed more spatially aggregated patterns at a local scale, like rare species, as well as pioneer species (Condit et al., 2000; Réjou-Méchain et al., 2011). Biotic interactions such as plant-animal mutualism have been recurrently advocated as key regulators of spatial distribution (Wisz et al., 2013; Uriarte et al., 2018), with an influence, for example, of dispersal process on patterns of abundance and distribution.

In tropical forests, dispersal mechanisms strongly affect diversity patterns of tree species and their cluster size, ballistic and gravity dispersal producing the most aggregated clusters, followed by wind, and finally animal dispersal (Seidler and Plotkin, 2006). However, in tropical forest communities, endozoochory is the major mechanisms of seed dispersal since 60-90% of species are frugivore-dependent for their seed dispersal (Howe, 1986; Beaudrot et al., 2013). This dispersal process has a direct effect on the composition of plant communities, helping to reduce density-dependent mortality (Janzen, 1970; Connell, 1971). Indeed, seeds and seedlings germinating and growing too close to the mother tree or in conspecific assemblage have a higher mortality, due to over mortality resulting from predators – eating seed or herbivores – pathogens, and also from competition (Johnson et al., 2012; LaManna et al., 2017). Plant-frugivore interactions are governed by multiple factors, such as biological traits, with the size of the jaw or beak of frugivores highly correlated with the size of the animal, representing a limiting factors in the ingestion of seeds (Sivault et al., 2020). The spatial distribution of species determines the possible interactions between species and the forbidden links (Olesen et al., 2011; González-Varo and Traveset, 2016), as well as temporal conditions such as phenology, are important filter on possible frugivory interactions (Ramos-Robles et al., 2018). In this context, the probability to interact between species also depends on the abundance of species, as local abundant species have an increase chance to encounter a potential partners (Vázquez et al., 2007; Timóteo et al., 2018).

Ecological communities of a given ecosystem have distinct traits compositions that influence the different ecological processes (de Bello et al., 2010; Dias et al., 2013). Two main mechanisms were proposed to explain traits effects on ecosystems functioning. First, the functional diversity effects that look into the degree of dissimilarities in traits values between co-existing species, and so the non-additive effects due to the complementarity of traits in communities (Petchey et al., 2004; Mouillot et al., 2011; Dias et al., 2013). Second, the mass-ratio effects that integrate the abundance of species and

expressed the traits of dominant species inside the community (Grime, 1998; Hector, 1998; Dias et al., 2013). In mutualistic networks – mostly pollination – the functional diversity of plants – their phenotypic differences – and their abundance – the mass ratio effect – is positively correlated with the richness of pollinators and their visit frequency (Fontaine et al., 2005; Fornoff et al., 2017). In plant-frugivore assemblages, the abundance and dominance of large fruits would be related with the presence of large frugivore species, as they assure more of their dispersal (Donatti et al., 2011). However, the plant traits composition has received less attention in frugivory assemblage, and studying the functional diversity and traits composition of plant communities will bring insight to the dynamic of plant-frugivore networks.

At different scales, the assemblage of plant and frugivore differ, creating different composition of fruits or dispersers, and then different networks. In this study, we proposed to analyse the tree assemblage of different forests types across Central African tropical forests, by looking into the difference of fruits offering regarding species richness and abundance of the different forests, and by linking this plants community traits to the frugivory networks. To achieve this analysis, we combined two large dataset, one giving tree species abundance and distribution from forestry inventories in the different forests types of Central African region, and one giving the actual knowledge of tree-frugivore interactions coupled to tree and frugivore species traits from all over Afrotropical forests. Our study aims to describe the fruit offer of the different forests types, taking into account the abundance of species inside these forests. Fruits traits are linked to frugivory interactions, and we investigated the relationships between each forest community, and local network of interactions between trees and frugivores.

MATERIAL & METHODS

VEGETATION DATA

Forestry inventories were conducted all over the forests of Central Africa (Réjou-Méchain et al., 2021), and transect data were aggregated in 10 x 10 km² grid cells across the area, representing 1571 grid cells. Each cell, included the composition and the relative abundance of each taxa – species or genus - representing 193 taxa, with 96 taxa identified at the species level, while the other 97 taxa were identified at the genus level.

The different floristic types were also extracted from the study of Réjou-Méchain et al. (2021), defining ten types of forests, all over the Central African region (Fig 1). The floristic type were defined following the difference in tree species composition, and abundance predicted by a model based on the forestry inventories. The floristic types covered areas from 2220 km² to 26550 km², for the type 5 and 7 respectively, and were illustrated by 8 to 283 inventory plots (Table S1). The floristic type 2 represented

the coastal forests of Gabon, was not sampled by forestry inventory plots, and was not included in the following analysis.

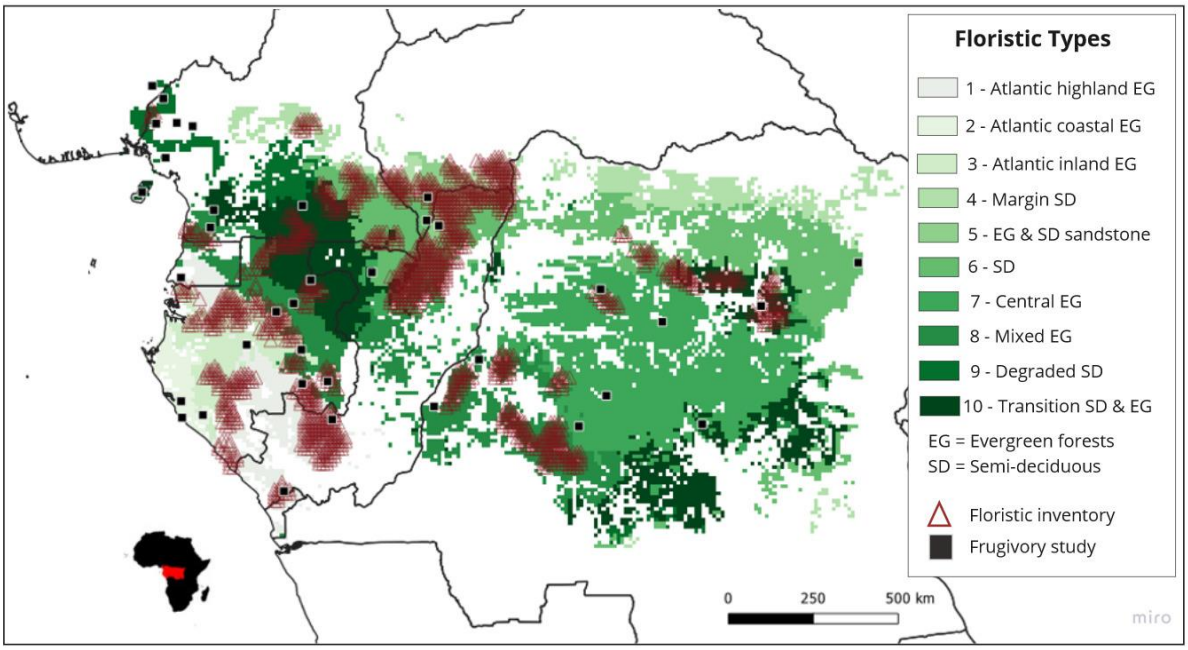

Figure 13. The different floristic types extracted from Réjou-Méchain et al (2021), as well as the floristic inventory plots. The site of floristic study took place, is extracted from the frugivory database (Durand-Bessart et al. in prep – Chapter 1).

FRUGIVORY INTERACTIONS DATA

The frugivory database was built from the compilation of 256 studies on frugivory interactions between 807 tree species and 285 vertebrate species, in all Afrotropical forests. The database recorded 10,547 interactions - one interaction being the consumption of the fruit of a given tree species by a given vertebrate species, comprising 6022 unique interactions, i.e. an interaction between one species of tree and one of frugivore, by removing duplicates, to avoid the redundancy and bias toward certain interactions.

The frugivory database included tree and frugivore species Order and Family, as well as biological traits and characteristics of each species. We derived species traits of trees and frugivores from the different literature sources (Durand-Bessart et al, *in prep*). For frugivores, we recorded the body mass (g). For tree species traits, we recorded fruit and seed dimensions (length and width in cm), number of seeds per fruit, average height (m), and wood density ($g.cm^{-3}$). 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)

STATISTICAL ANALYSIS

From the 193 taxa from the tree abundance dataset, 127 taxa were referenced, 56 at the species level and 71 at the genus level. For the 71 genus taxa, we aggregated the information on frugivory from the species of the genus present in the dataset. We selected the taxa only present in Central African forests, and to illustrate traits at the genus level we used the average traits of species.

Differences in the fruit offer among the floristic types

We tested the over-representation of tree Orders, in the different forests type, using Chi-square tests to assess differences from random expectation. We took into account the relative abundance of species in the different forests types.

We investigated the traits of the species inside the different forests types, and to avoid the collinearity among trees variables, we ran a principal component analysis (PCA) (FactoMineR; Husson et al., 2018). The variables used in the PCA are the seed length, fruit length, tree size, number of seeds by fruit, and wood density. From this PCA, we used the first three dimensions, later name dimension 1, dimension 2 and dimension 3 (Figure S1). The dimension 1 explained 31.56% of the variation, and had a positive loading with the seed size, tree size and tree wood density. The dimension 2 explained 29.06% of the variance and had a positive loading with the number of seed, and the fruit size. The dimension 3 explained 17.24% of the variation, and had a positive loading with wood density, but a negative loading with tree size, differentiating species with low wood density and small size or from tall trees with high density.

We used community weighted mean traits on the three dimension of the PCA, to study the difference in fruits offering and tree traits among the different forests type. The community weighted mean traits measure the average traits values of the community and shows the traits of dominant species, by taking into account the relative abundance of species inside a plot or a community (Dias et al., 2013). We firstly calculated the community weighted mean for each plot and used the mean value of plots for each forests types.

To investigate the relationships between the traits of tree species by plot and forests types, we used a linear model. The floristic types, the latitude and longitude of the plot were used as covariates, while the community weighted mean traits values by plot of the dimension 1, dimension 2 and dimension 3 were used as response variables for the three different models. We performed Duncan post-hoc tests for pairwise-comparisons between floristic types.

Number of studies on frugivory interactions per floristic type

We related the study recording tree-frugivore interactions from the global frugivory database, to the different forests types. We looked into the number of study by floristic types, the number of tree and frugivore species involved, and the availability of interaction data among the different forests types, regarding interaction with the different groups of frugivores.

Change in the fruit offer among the different floristic types for four examples of frugivore species

To test how the variations in tree abundance among floristic type may affect the availability of fruits for frugivores, we selected four frugivores species for which we had enough interactions data with the tree species targeted. We selected species coming from different taxonomic groups, with diverse body size, to maximize potential differences in their diet. The selected species are the forest elephant (*Loxodonta cyclotis)*, the chimpanzee (*Pan troglodytes troglodytes*), a large bird (*Ceratogymna atrata*) and a small bird (*Hylopsar purpureus*). From the interaction database, we extracted all interaction known for these species, making one sub-network per species.

In order to calculate the community traits based on the tree species that interact with each frugivore species, we calculated the community weighted mean traits for each plots only with the tree species that interact with one frugivore, and we did so for each sub-network. These values where related to the different floristic types, to give information on the species traits that the frugivore species depend on, but also to relate it with the global value of the community traits of the floristic type calculated above.

RESULTS

Plant composition of the different floristic types

The different forests types had taxonomic differences, where some Order where more abundant than what is randomly expected (X-squared = 848103, df = 136, p-value < 2.2e-16).

Ericales were over-represented in the floristic type 5, Malvales and Rosales were over-represented in the floristic types 4 and 6, while Urticales were only over-represented in the floristic type 6. Sapindales were over-represented in the floristic types 1 and 3, while Magnoliales were over-represented in the floristic type 3 and Malpighiales in the floristic type 1. Fabales and Santalales were over-represented in the floristic type 8. This result showed the variation in taxonomic composition among floristic type.

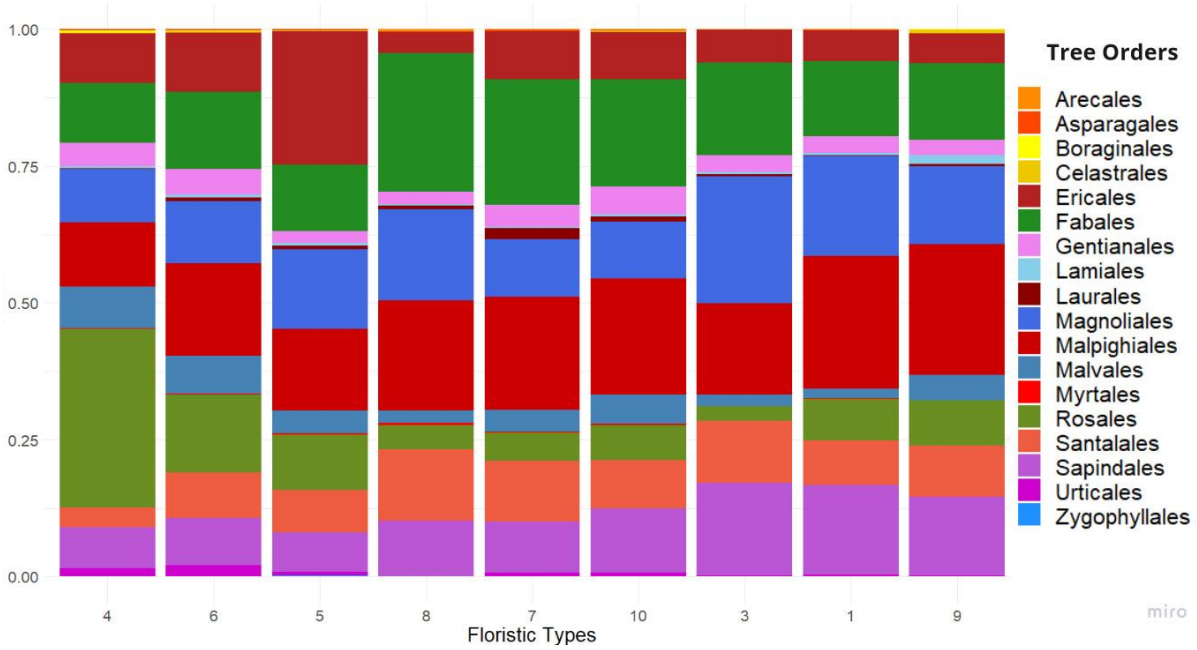

Figure 14. Representation of the proportion of tree Orders in the different forests types, taking into account the difference of abundance of tree species between the different forests.

Differences in the fruit offer among the forest floristic types

The model showed significant differences of tree traits among the different floristic types, latitudes and longitudes (Fig 3, Table S2). For the dimension 1, 2 and 3 of the PCA performed on tree traits, we observed different abundance and distribution profiles of traits among the different floristic types (Fig 2ACE). This was confirmed by significant effects of floristic type (Fig 2BDF; Tab S1) and indicates that due to difference in species composition and abundance the fruit offer in term of seed and fruit size, as well as tree size and wood density among floristic types.

The abundance and distribution profiles concerning the dimension 1 showed that the floristic type 1 and 9 presented the largest seeded tree species with larger trees with high wood density (Fig 3A, Table S2i). The floristic type 4, 6 and 5 showed an abundance of species with smaller seeds. We observed an important variation in smaller seeds abundance (below 0) than from the larger seeds (above 0), where peak are low and do not vary much in intensity (Fig 3A). This means that trees with larger seeds are present in most floristic type, in low abundance compared to trees with smaller seeds. The dimension 2 showed less variation of abundance and distribution profiles (Fig 3C). The floristic type 5 and 9 had a significant abundance of smaller fruits, with fewer seeds, than the floristic type 10 that presented a higher abundance of larger fruits. Studying the abundance and distribution profiles of the dimension 3 (Fig 3C), we distinguished the floristic type 6, 10, 5 and 4 that have a high abundance of tall tree with low wood density; and the floristic type 1, 7 and 8 that present mostly smaller tree species with high wood density. The floristic types 8, 3 and 5 had a high abundance of smaller dense trees, while

the floristic type 1, 4 and 6 presented a high abundance of taller tree with low wood density. These results showed the contrast of tree species traits composition inside the different floristic types.

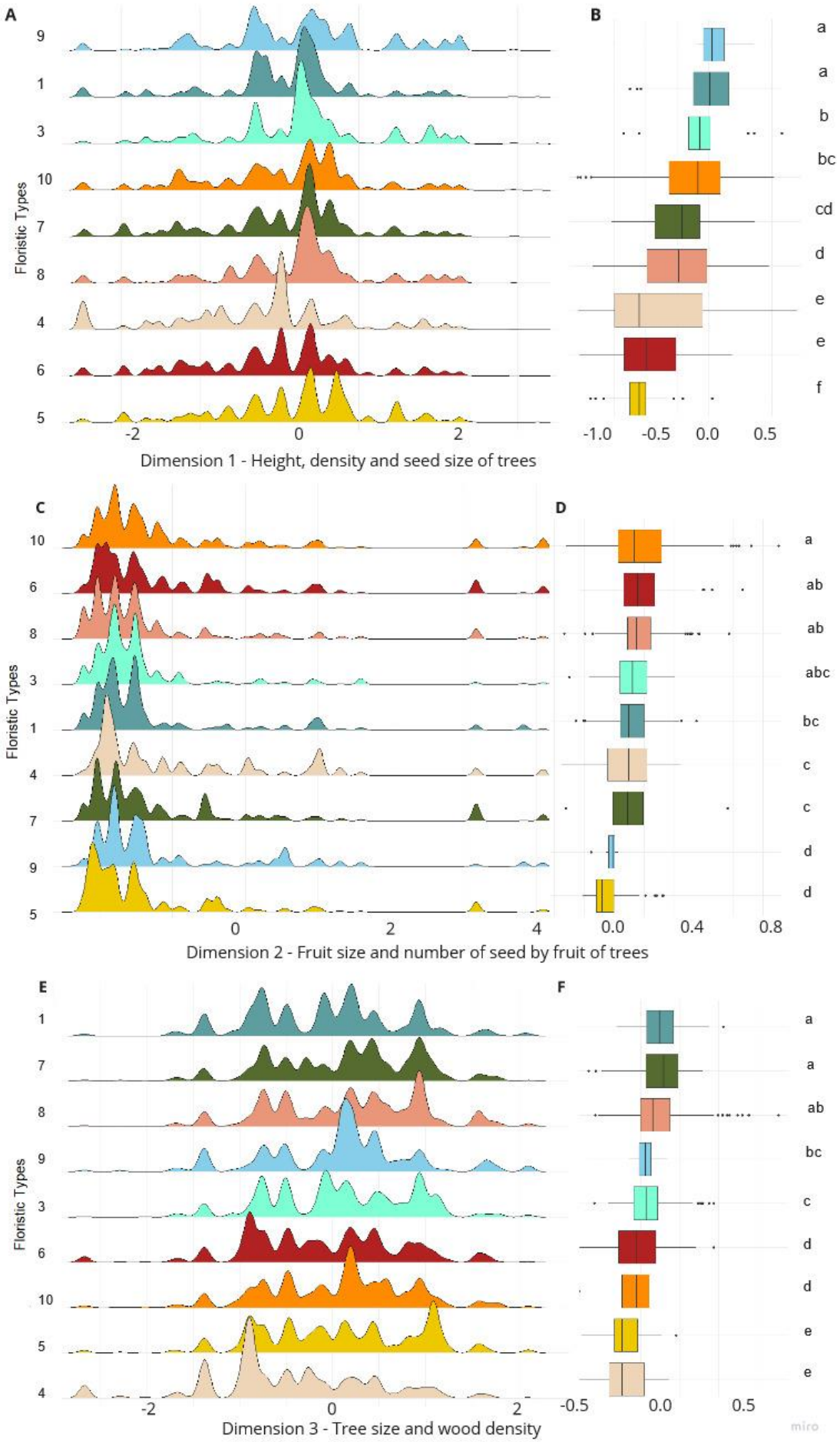
A
B
Floristic Types
9
1
3
10
7
8
4
6
5
-2
0
2
Dimension 1 - Height, density and seed size of trees
a
a
b
bc
cd
d
e
e
f
-1.0
-0.5
0.0
0.5
C
D
Floristic Types
10
6
8
3
1
4
7
9
5
0
2
4
Dimension 2 - Fruit size and number of seed by fruit of trees
a
ab
ab
abc
bc
c
c
d
d
0.0
0.4
0.8
E
F
Floristic Types
1
7
8
9
3
6
10
5
4
-2
0
2
Dimension 3 - Tree size and wood density
a
a
ab
bc
c
d
d
e
e
-0.5
0.0
0.5
miro

Figure 15. Representation of the abundance and distribution profiles of tree traits represented by the three dimension of the PCA, regarding the difference forests types in the Congo basin. The dimension 1 of the PCA on tree species has a positive loading with seed size, and also tree height, and wood density. The dimension 2 has a positive loading with fruit size and the number of seed by fruits. The dimension 3 has a positive loading with wood density but a negative loading with tree size. The abundance and distribution profiles of traits (A,C,E) represent the density of species following the coordinates of the three dimensions. The boxplot (B,D,F) represent the community weighted mean values for each plots per floristic types, the letters come from a pairwise comparison with a Duncan test.

Our analysis further showed different latitudinal and longitudinal patterns for each of the three first dimension of the PCA performed on tree traits (Fig 4). The dimension 1 – positively related to seed size but also wood density and tree size, had a negative relationship with latitude and longitude (Fig 4AB), meaning that larger seeded species, as well as taller species with high wood density were more present and/or abundant in the South and West forests of the Congo Basin. However, there was an important variation among the floristic types (Fig 4AB), and two floristic types with similar latitudes could have different community mean traits values, like the floristic type 1 and 8, or 5 and 6, meaning that while there is a latitudinal increasing tendencies from North to South.

The dimension 2 – positively related to fruit size and number of seeds by fruits, had a positive relationship with longitude and a negative relation with latitude (Fig 4CD), meaning that species with larger fruits and with numerous seeds were more present in the South and East forests.

The dimension 3 – positively related to wood density and negatively related to tree size, had a negative relationship with longitude and latitude (Fig 4EF), showing that smaller species with high wood density were more abundant in the South and West forests, while taller species with low wood density were more present and/or abundant in the Norther and Eastern forests.

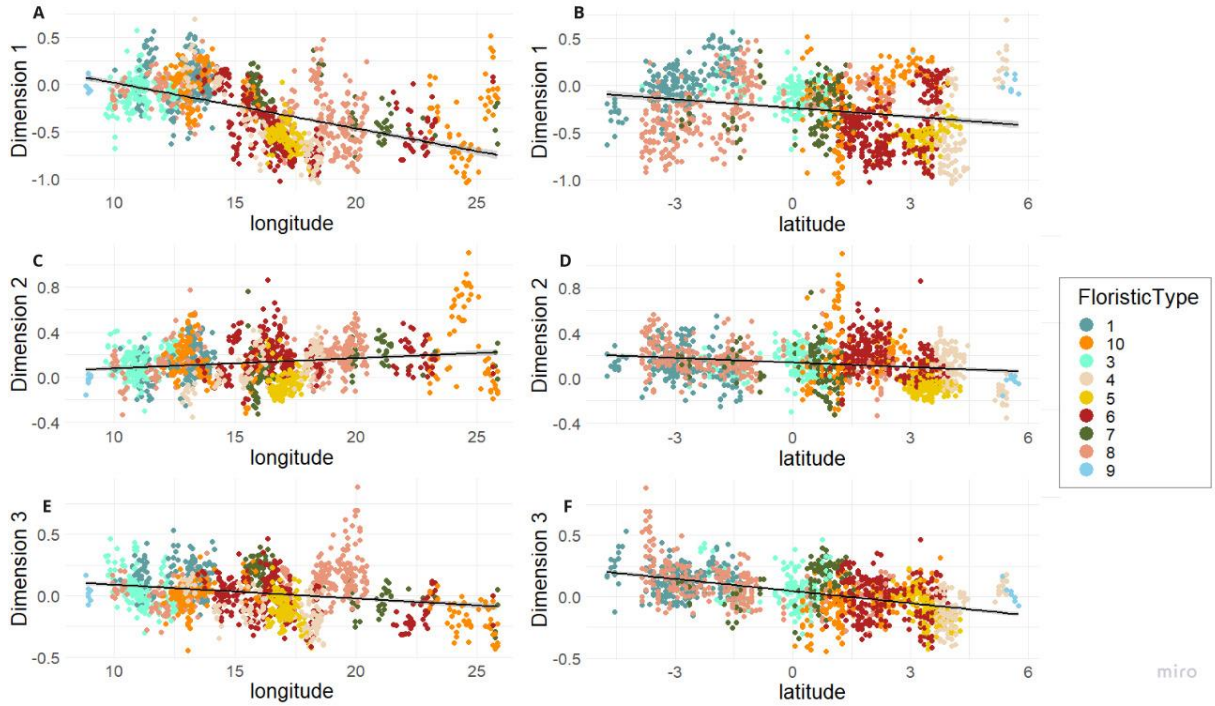

Figure 16. Relationship between latitude or longitude and tree traits represented by the dimension 1, 2 and 3 of the PCA. The dimension 1 is positively correlated to the height, density and seed size of trees, while the dimension 2 is positively correlated the fruit size and number of seed by fruits. The dimension 3 is positively correlated to wood density and negatively correlated with tree height, segregating smaller species with a low wood density (positive values) from taller species with high wood density.

Number of studies on frugivory interactions per floristic type

We observed a major imbalance concerning the information on tree-frugivore interactions among different floristic types (Fig 5). The number of tree species per floristic type for which we have data on frugivory interactions was strongly related to the number of publications per floristic types (Fig 5A&C). The same pattern also occur for the number of frugivores and the number of interactions per floristic type (Fig 5B&D).

The majority of interactions involved primates – apes and monkeys – followed by large birds (Fig. 5D). Interactions with small birds, rodents and ungulates were only recorded in the floristic type 8. Interactions in the floristic type 4 and 9 only focused on one groups, respectively elephant and monkeys. The floristic types 3, 8 and 10 were the one with most studies and interactions recorded, on diverse taxonomic frugivore groups.

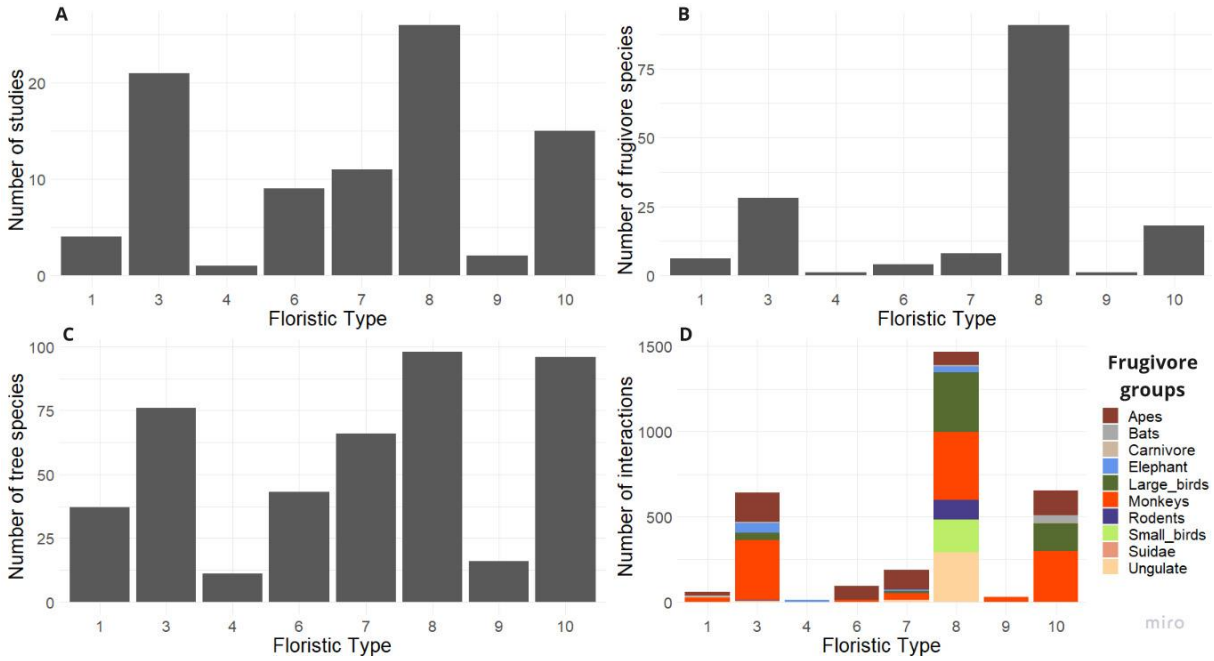

Figure 17. Histograms representing the sampling efforts of the different floristic types: a) the number of studies, b) the number of frugivore species concerned by the study, c) the number of tree species concerned by frugivore study, d) the number of interactions with tree species in the different floristic types, regarding the frugivore groups interacting with plants.

Change in the fruit offer among the different floristic types for four examples of frugivore species

To investigate potential consequences for frugivores of the differences in fruit offer among the floristic types of forests, we calculated the community weighted mean trait value for the tree species known to be consumed by different frugivore species. The elephant interacted with largest seeded tree species compared to the other three species (Fig 6A). The chimpanzee and calaos species had similar profile of species traits – seed size, height and density – in the different floristic types (Fig 6 BC). The small bird species, interacted with the smallest seeded species in the different floristic types (Fig 6D). These results showed that the community traits values of the different floristic types were concordant with the range of frugivory interactions of Chimpanzee and Calaos, while elephant interacted only with the largest seeded trees and small birds with the smallest seeded species. However, elephant and small bird species had the greatest variation in community seed traits values among floristic types, showing that the resources available for both species were dependent of the floristic types.

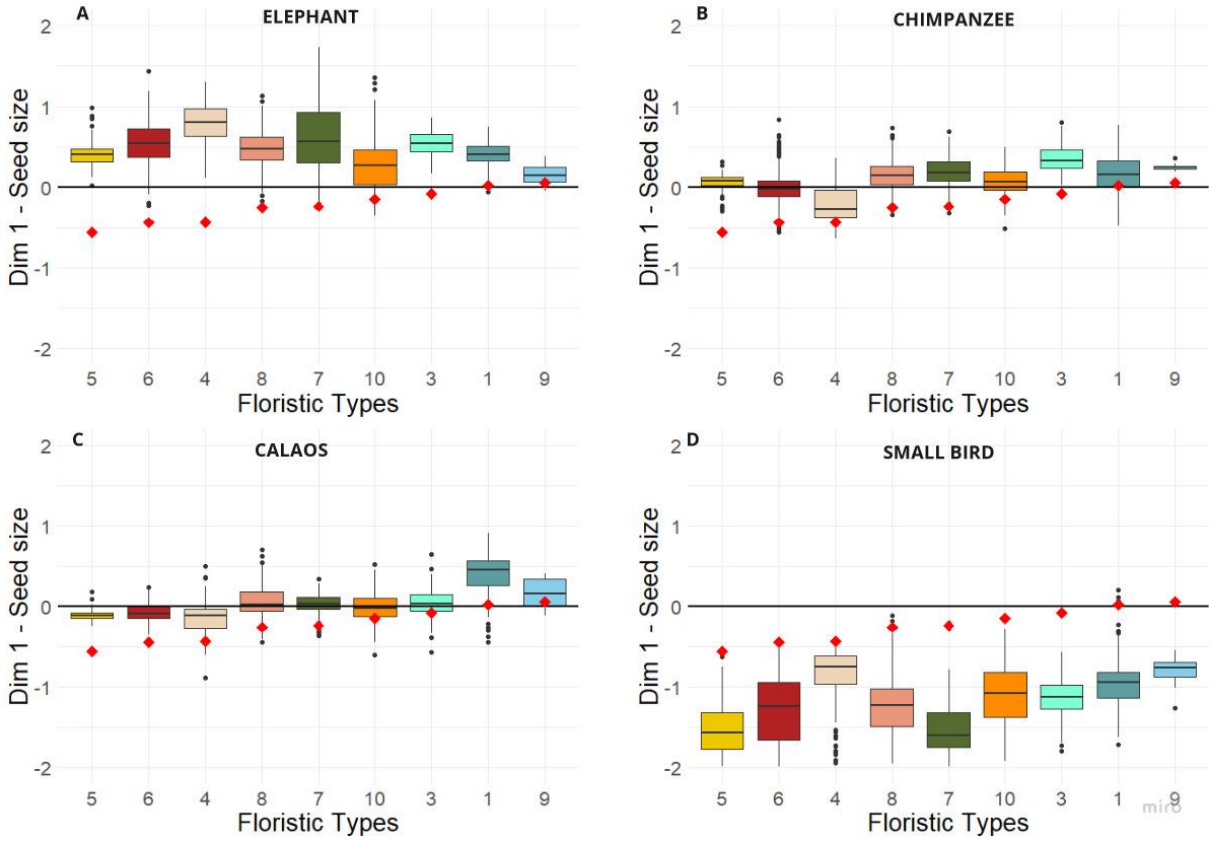

Figure 18. Community weighted means of the dimension 1, representing seed size, tree height and wood density of trees species, regarding different frugivore species, A) elephant, B) chimpanzee, C) calaos, D) small bird. The floristic type are order from the smaller community weight traits values to the highest, with all species confounded. The red diamonds represent the average community traits (see Fig. 4) with all tree species included.

DISCUSSION

In this study, we looked at variation in the fruits produced by the different floristic type of forests in the Congo Basin. Most tree species were present in all floristic types, due to the forestry inventories selecting essence widespread all over Central African forests. Then, the differences of community traits observed among the floristic types depend on variation of abundance and distribution of tree species.

The PCA performed on tree traits showed that seed size and fruit size were not correlated in this dataset, meaning that the abundance of large seeded tree species was not related to the one of large fruited species. The correlation between the fruit size and the number of seeds by fruits meant that most large fruited species of the dataset had a high number of seeds. These results indicated a bias toward certain species that may not be representative of the overall species traits community, as previous studies showed the correlation between fruit and seed size in Afrotropical forests (Durand-Bessart et al, in prep). The height and wood density were correlated to seed size in the dimension 1 of the PCA, showing that some species bearing large seeds tend to be taller species with high wood density, mostly representing

late successional species. However, tree height and wood density were opposed in dimension 3, segregating smaller species with high wood density - late successional species - from taller species with low wood density - pioneer species (Muller-Landau, 2004). These results gave information on potential frugivore partners, as late successional species interact more with generalist species (Schleuning et al., 2011), with some bats and birds species interacting more with taller tree species (Duncan and Chapman, 1999; Viani et al., 2015).

The community weighted mean traits values of the plots varied along latitudinal and longitudinal gradients but also among the floristic types. Tree species with larger seeds and fruits were more dominant in the Southern plots. However, trees with larger seeds were more abundant in the western plots, while tree species with larger fruits were more abundant in the eastern plots. The gradient of seed size of tree species coincide with abiotic factors, such as temperature and precipitation that are more important in the western regions (McConkey et al., 2022). Indeed, large seeds have been hypothesized to originate from closed and humid forests, due to their important resources to germinate in more unfavourable conditions – absence of light (Bunney et al., 2019; Sinnott-Armstrong et al., 2018).

However, despites the strong effect of latitude and longitude and so abiotic factors, we observed differences between floristic types, even for the ones at the same latitude and/or longitude, suggesting the presence of other mechanisms (McConkey et al., 2022). The floristic types 1 and 3 represented mostly in Gabonese forests, showed similar community weighted mean trait values regarding fruits. Both floristic types presented an over-representation of Sapindales and with the dominance of large seeded and fruited species, the community weighted mean traits values were significantly different. Moreover, while the floristic type 1 was dominated by smaller species with high wood density, the floristic type 3 had a higher importance of taller species with low wood density. In contrast, the floristic type 5 stands out, with smaller fruits and seeds, and small trees with high wood density trees, in accordance to the over-representation of Ericales – mostly Ebenaceae in the area. This could reflect the fact that these are sandstone forests that showed community traits difference that could be an adaptation to drier environments (Réjou-Méchain et al., 2014).

Our models showed that the variation in traits composition was more important for trees with smaller seeds, than for larger seeds. This might be related to small of frugivore as their contribution to the dispersal of small seeded important (Godínez-Alvarez et al., 2020). These smaller vertebrate species have a lesser dispersal range than large ones, and then have a higher impact on tree assemblage at a local scale (Balcomb and Chapman, 2003; Flörchinger et al., 2010). Secondly, the low variation in large seeded tree species could be explained by co-evolutionary history between megafaunal fruits and megafaunal species like elephants, with congruent spatial distribution (Bunney et al., 2019; Lim et al., 2021; McConkey et al., 2022).

The four species studies: forests elephants, chimpanzees, large bird and small bird had access to diverse community traits among the different floristic types. Also, these variations do not seem related to frugivore species and neither to the available community traits of each floristic types. However, it showed that all frugivore species that are present in all floristic types have a great diet flexibility.

The majority of frugivory studies took place in the floristic types 1, 3 and 8, that are mostly Gabonese evergreen forests. These floristic types are geographically closed and shared similarity in their community trait composition, dominated by large fruited species, with large seed for 1 and 3, and with a high abundance of late successional species, with a high wood density. The fact that most studies occurred in these floristic types, could induce a bias toward interactions towards larger seeded or fruited tree species.

As a conclusion, our study showed the variation in the characteristics of the fruits produced by Afro-tropical forests among the different floristic types, and regarding their geographic distribution. While confirming the importance of abiotic factors on fruits and seeds size of tree species, we showed that other factors such as seed dispersal may influence the tree community of the different floristic types, and therefore the frugivores inhabiting the forests. Also, different frugivore species had different offers in fruits in each forest, suggesting a flexibility from frugivore in terms of the traits of fruits consumed. A solution to highlight the tree-frugivore networks differences would be to take into account the spatial distribution of the vertebrate species over the different floristic types. This inclusion would allow us to look into the different structure behind each network, regarding the difference in richness, connectivity, and nestedness. This implementation will also help to make predictions about the impact of the different anthropogenic perturbations – defaunation, deforestation – on the different networks and so the different community assemblages.

REFERENCE

Balcomb, S.R., Chapman, C.A., 2003. Bridging the Gap: Influence of Seed Deposition on Seedling Recruitment in a Primate–Tree Interaction. Ecological Monographs 73, 625–642. https://doi.org/10.1890/02-4036

Beaudrot, L., Rejmánek, M., Marshall, A.J., 2013. Dispersal modes affect tropical forest assembly across trophic levels. Ecography 36, 984–993. https://doi.org/10.1111/j.1600-0587.2013.00122.x

Bunney, K., Robertson, M., Bond, W., 2019. The historical distribution of megaherbivores does not determine the distribution of megafaunal fruit in southern Africa. Biological Journal of the Linnean Society 128, 1039–1051. https://doi.org/10.1093/biolinnean/blz109

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecology Letters 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x@10.1111/(ISSN)1461-0248.conservation-management-forests

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R., Yamakura, T., 2000. Spatial Patterns in the Distribution of Tropical Tree Species. Science 288, 1414–1418. https://doi.org/10.1126/science.288.5470.1414

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P., 2002. Beta-Diversity in Tropical Forest Trees. Science 295, 666–669. https://doi.org/10.1126/science.1066854

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of populations, 312.

Davidar, P., Rajagopal, B., Arjunan, M., Puyravaud, J.P., 2008. The Relationship between Local Abundance and Distribution of Rain Forest Trees across Environmental Gradients in India. Biotropica 40, 700–706. https://doi.org/10.1111/j.1744-7429.2008.00437.x

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers Conserv 19, 2873–2893. https://doi.org/10.1007/s10531-010-9850-9

Dias, A.T.C., Berg, M.P., de Bello, F., Van Oosten, A.R., Bílá, K., Moretti, M., 2013. An experimental framework to identify community functional components driving ecosystem processes and services delivery. Journal of Ecology 101, 29–37. https://doi.org/10.1111/1365-2745.12024

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., Dirzo, R., 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters 14, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Duncan, R.S., Chapman, C.A., 1999. Seed Dispersal and Potential Forest Succession in Abandoned Agriculture in Tropical Africa. Ecological Applications 9, 998–1008. https://doi.org/10.1890/1051-0761(1999)009[0998:SDAPFS]2.0.CO;2

Flörchinger, M., Braun, J., Böhning-Gaese, K., Schaefer, H.M., 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. Oecologia 164, 151–161. https://doi.org/10.1007/s00442-010-1655-8

Flores, O., Gourlet-Fleury, S., Picard, N., 2006. Local disturbance, forest structure and dispersal effects on sapling distribution of light-demanding and shade-tolerant species in a French Guianian forest. Acta Oecologica 29, 141–154. https://doi.org/10.1016/j.actao.2005.08.007

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2005. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLOS Biology 4, e1. https://doi.org/10.1371/journal.pbio.0040001

Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos 126, 1020–1030. https://doi.org/10.1111/oik.03869

Gaston, K.J., Kunin, W.E., 1997. Rare—common differences: an overview, in: Kunin, W.E., Gaston, K.J. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences, Population and Community Biology Series. Springer Netherlands, Dordrecht, pp. 12–29. https://doi.org/10.1007/978-94-011-5874-9_2

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. https://doi.org/10.1002/ece3.6285

González-Varo, J.P., Traveset, A., 2016. The Labile Limits of Forbidden Interactions. Trends in Ecology & Evolution 31, 700–710. https://doi.org/10.1016/j.tree.2016.06.009

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hector, A., 1998. The Effect of Diversity on Productivity: Detecting the Role of Species Complementarity. Oikos 82, 597–599. https://doi.org/10.2307/3546380

Howe, H.F., 1986. Seed dispersal by fruit-eating birds and mammals, in: Seed Dispersal. Academic Press, p. 189.

Husson, F., Josse, J., Le, S., Mazet, J., 2018. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining.

Janzen, D.H., 1970. Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104, 501–528. https://doi.org/10.1086/282687

Johnson, D.J., Beaulieu, W.T., Bever, J.D., Clay, K., 2012. Conspecific Negative Density Dependence and Forest Diversity. Science 336, 904–907. https://doi.org/10.1126/science.1220269

LaManna, J.A., Mangan, S.A., Alonso, A., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S., Chang, L.-W., Chiang, J.-M., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Davies, S.J., Furniss, T.J., Giardina, C.P., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., He, F., Howe, R.W., Hubbell, S.P., Hsieh, C.-F., Inman-Narahari, F.M., Janík, D., Johnson, D.J., Kenfack, D., Korte, L., Král, K., Larson, A.J., Lutz, J.A., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Nathalang, A., Novotny, V., Ong, P.S., Orwig, D.A., Ostertag, R., Parker, G.G., Phillips, R.P., Sack, L., Sun, I.-F., Tello, J.S., Thomas, D.W., Turner, B.L., Vela Díaz, D.M., Vrška, T., Weiblen, G.D., Wolf, A., Yap, S., Myers, J.A., 2017. Plant diversity increases with the strength of negative density dependence at the global scale. Science 356, 1389–1392. https://doi.org/10.1126/science.aam5678

Lim, J.Y., Wasserman, M.D., Veen, J., Després-Einspenner, M.-L., Kissling, W.D., 2021. Ecological and evolutionary significance of primates' most consumed plant families. Proceedings of the Royal Society B: Biological Sciences 288, 20210737. https://doi.org/10.1098/rspb.2021.0737

McConkey, K.R., Campos-Arceiz, A., Corlett, R.T., Sushma, H.S., Ong, L., Brodie, J.F., 2022. Megafruit and megafauna diversity are positively associated, while megafruit traits are related to abiotic factors, in tropical Asia. Global Ecology and Biogeography 31, 740–752. https://doi.org/10.1111/geb.13464

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., Mason, N.W.H., 2011. Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLOS ONE 6, e17476. https://doi.org/10.1371/journal.pone.0017476

Muller-Landau, H.C., 2004. Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees. Biotropica 36, 20–32. https://doi.org/10.1111/j.1744-7429.2004.tb00292.x

Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C., Jordano, P., 2011. Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rspb.2010.1371

Petchey, O.L., Hector, A., Gaston, K.J., 2004. How Do Different Measures of Functional Diversity Perform? Ecology 85, 847–857. https://doi.org/10.1890/03-0226

Ramos-Robles, M., Dáttilo, W., Díaz-Castelazo, C., Andresen, E., 2018. Fruit traits and temporal abundance shape plant-frugivore interaction networks in a seasonal tropical forest. Sci Nat 105, 29. https://doi.org/10.1007/s00114-018-1556-y

Réjou-Méchain, M., Flores, O., Bourland, N., Doucet, J.-L., Fétéké, R.F., Pasquier, A., Hardy, O.J., 2011. Spatial aggregation of tropical trees at multiple spatial scales. Journal of Ecology 99, 1373–1381. https://doi.org/10.1111/j.1365-2745.2011.01873.x

Réjou-Méchain, M., Flores, O., Pélissier, R., Fayolle, A., Fauvet, N., Gourlet-Fleury, S., 2014. Tropical tree assembly depends on the interactions between successional and soil filtering processes. Global Ecology and Biogeography 23, 1440–1449. https://doi.org/10.1111/geb.12222

Réjou-Méchain, M., Mortier, F., Bastin, J.-F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Deblauwe, V., Doucet, J.-L., Doumenge, C., Fayolle, A., Garcia, C., Kibambe Lubamba, J.-P., Loumeto, J.-J., Ngomanda, A., Ploton, P., Sonké, B., Trottier, C., Vimal, R., Yongo, O., Pélissier, R., Gourlet-Fleury, S., 2021. Unveiling African rainforest composition and vulnerability to global change. Nature 593, 90–94. https://doi.org/10.1038/s41586-021-03483-6

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. https://doi.org/10.1111/2041-210X.12753

Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H.M., Böhning-Gaese, K., 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. Ecology 92, 26–36. https://doi.org/10.1890/09-1842.1

Seidler, T.G., Plotkin, J.B., 2006. Seed Dispersal and Spatial Pattern in Tropical Trees. PLOS Biology 4, e344. https://doi.org/10.1371/journal.pbio.0040344

Sinnott-Armstrong, M.A., Downie, A.E., Federman, S., Valido, A., Jordano, P., Donoghue, M.J., 2018. Global geographic patterns in the colours and sizes of animal-dispersed fruits. Global Ecology and Biogeography 27, 1339–1351. https://doi.org/10.1111/geb.12801

Sivault, E., McConkey, K., Bretagnolle, F. ois, Sengupta, A., Lambert, J., Heymann, E., Forget, P.M., Herrel, A., 2020. Body mass and skull dimensions predict seed dispersal capacity in bats, primates and carnivores from tropical forests (preprint). Preprints. https://doi.org/10.22541/au.159647579.96227644

Timóteo, S., Correia, M., Rodríguez-Echeverría, S., Freitas, H., Heleno, R., 2018. Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. Nat Commun 9, 1–11. https://doi.org/10.1038/s41467-017-02658-y

Uriarte, M., Muscarella, R., Zimmerman, J.K., 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. Global Change Biology 24, e692–e704. https://doi.org/10.1111/gcb.14000

Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R., Poulin, R., 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116, 1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x

Viani, R.A.G., Vidas, N.B., Pardi, M.M., Castro, D.C.V., Gusson, E., Brancalion, P.H.S., 2015. Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. Natureza & Conservação 13, 41–46. https://doi.org/10.1016/j.ncon.2015.03.005

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews 88, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x

ANNEXE

Table S2. Description of the floristic types, in term of surface in km² and the number of forestry inventory plots –cells of 10x10km.

Floristic Type	Characteristic	Area (km²)	Number of plots
1	Atlantic highland evergreen	79,400	193
2	Atlantic coastal evergreen	17,700	0
3	Atlantic inland evergreen	60,800	162
4	Margin semi deciduous	87,800	102
5	Evergreen and semi deciduous on sandstone	22,200	126s
6	Semi deciduous	206,400	280
7	Central evergreen	265,900	122
8	Mixed evergreen	158,200	283
9	Degraded semi deciduous	38,400	8
10	Semi deciduous- evergreen transition	180,000	165

Table S2. Linear model results for the relationships between the tree traits and the forests types, and latitude and longitude of plots. The dimension 1 represent the height, density and seed size of trees, while the dimension 2 represents the fruit size and number of seed by fruits. P-values <0.05 are in bold.

Effects		Sum sq	NumDf	DenDF	F-value	P > F
Dimension 1	Floristic type	20.92	8	1430	44.36	**<0.001**
	Latitude	1.96	1	1430	33.28	**<0.001**
	Longitude	8.65	1	1430	146.78	**<0.001**
Dimension 2	Floristic type	5.50	8	1430	27.49	**<0.001**
	Latitude	0.38	1	1430	15.30	**<0.001**
	Longitude	0.68	1	1430	27.16	**<0.001**
Dimension3	Floristic type	3.73	8	1430	25.06	**<0.001**
	Latitude	3.66	1	1430	196.87	**<0.001**
	Longitude	3.65	1	1430	196.08	**<0.001**

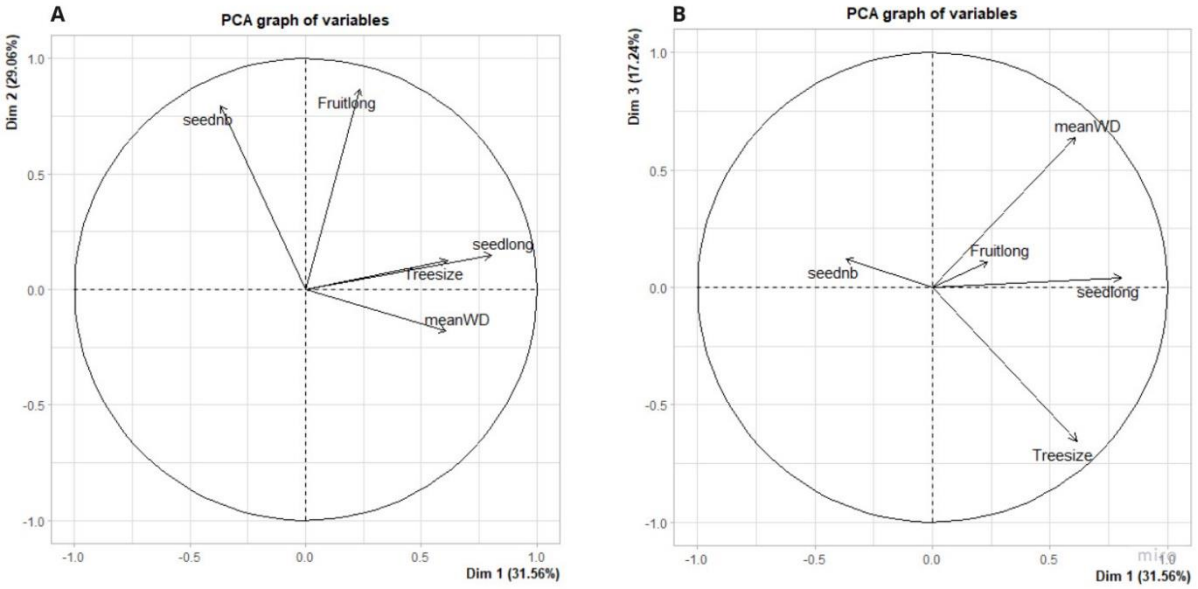

Figure S1. Representation of the three dimensions of the PCA, on traits of trees species. (a) The dimension 1 is positively loaded to the seed size, and also the tree height and wood density of species. The dimension 2 is positively linked to the number of seeds by fruits and the fruit size of trees. (b) The dimension 3 is positively loaded with wood density but negatively with tree size.

CHAPTER 3

Indigenous communities hold a huge and unique source of ecological knowledge on frugivory interactions

Interview of a woman from Doussala, based on photographic guides of plants and animals. She is surrounded by the head-chief of the village, a villager and the guide and interpreter. Picture by Clementine Durand-Bessart

Context

Frugivory interactions are a key process in tropical forests, with more than 50% of tree species that depend on animal for their dispersion, and vertebrates that depend on fruits as their primary source of food. These mutualistic interactions are threaten by the rapid defaunation and deforestation occurring in tropical forests. Afrotropical forests are particularly affected by these threats, but also suffer from a lack of studies, which makes it difficult to identify the consequences of these disturbances on the interaction networks.

Diverse methods exist to gather and increase knowledge on tree-frugivore interactions, such as direct observations, cameras. Recently scientific research acknowledge local ecological knowledge hold by Indigenous communities and local population, as a valuable source of information on multiple ecological processes such as interactions between species.

In this context, we decided to investigate on the contribution of LEK to understand the Afrotropical frugivory interactions, by comparing LEK and academic knowledge. We used a set of 286 trees and 100 frugivores species, for which we had academic literature records, and we created photographic guides of the tree and frugivore species, and went to Gabon to interview a local community.

Key results

Informants had considerable knowledge on tree-frugivore interactions with 34,800 answers and an average of 731.5 interactions cited by informant, with differences in interactions knowledge between men and women.

The comparison between Academic and LEK datasets showed that 39% of interactions were only known by informants, these addition concerned mainly smaller frugivores.

Informants also assigned on average smaller frugivores to tree species and smaller seeded plants to frugivore species, except for rodents that interacted with larger seeds. These results changed our understanding of frugivory networks.

Indigenous communities hold a huge and unique source of ecological knowledge on frugivory interactions

Durand-Bessart Clémentine[12], François Bretagnolle[1], Etienne Akomo-Okoue[3], Ghislain W. Ebang Ella[3], Vincent Porcher[45], Colin Fontaine[2]

[1] Biogeosciences, UMR 6282, Université Bourgogne Franche Comte-CNRS, Dijon, France

[2] Centre d'Ecologie et des Sciences de la Conservation, CESCO, UMR 7204, MNHN-CNRS-SU, Paris, France

[3] Institut de Recherche en Ecologie Tropicale (IRET-CENAREST), Gabon

[4] Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

[5] SENS, IRD, CIRAD, Montpellier, France

Keywords: local ecological knowledge, Afrotropical forests, mutualism, networks, block model, interview,

ABSTRACT

Assembling plant-animal interactions allows to get insights on the functioning and response to perturbations of ecological communities. Afrotropical forests are currently suffering from both strong defaunation and a restricted knowledge on frugivory interactions, with relatively few studies despite a long lasting interest of tropical ecology for these ecosystems.

Local ecological knowledge are now recognized as a valuable source of ecological information and could significantly contribute to our understanding of such crucial interactions for tropical forests.

To investigate potential synergies between academic and local ecological knowledge, we compiled an up to date list of frugivory interactions linking 286 trees and 100 frugivores species, from academic literature, to local ecological knowledge in one small village located within Afrotropical forest using interviews.

Here we show that informants had substantial knowledge on frugivory interactions, with a total of 39% interactions unknown from academic studies but known by at least 10% of the informants. Integrating local ecological knowledge add frugivory interactions for poorly studied taxa, in particular rodents. Further, such additional data change structure of the interactions network as well as the functional relationship linking frugivore body mass to seed size. On average smaller frugivores were added to most tree species, smaller seeded plants to bats and primates and larger seeds to rodents.

These results are operating a change in our knowledge of frugivory network, and show the necessity to integrate other complementary sources to appreciate the complexity of mutualistic networks.

INTRODUCTION

Defaunation i.e. the human induced decline of animal species, is one the greatest threat on ecosystems and their functioning (Dirzo et al., 2014). The consequences of defaunation are known to cascade to plant communities through plants-animals interactions (Dirzo et al., 2014; Galetti et al., 2015; Young et al., 2016). Such cascading effects are particularly expected in tropical forests where defaunation is strong due to hunting and poaching activities, as well as the habitat loss (Dirzo et al., 2014); and where 50 to 80 percent of tree species depend on frugivorous animals for their dispersal (Howe and Smallwood, 1982). Recent studies indeed indicate lower tree recruitment (Beaune et al., 2013; Galetti et al., 2015; Rosin and Poulsen, 2016), reduced forest regeneration (Gardner et al., 2019) or carbon storage deficiencies (Bello et al., 2015; Osuri et al., 2016; Berzaghi et al., 2019), in defaunated tropical forests. Understanding the defaunation consequences for tropical forests strongly depends on our knowledge of ecological interactions linking animals and plants (Osuri et al., 2020).

In particular, interaction network approaches, appear fruitful to provide insights into community functioning (Timóteo et al., 2018), dynamics (Vizentin-Bugoni et al., 2019), and response to perturbations (Donoso et al., 2017). However, we are still far from the completeness on plant-frugivore interactions which limit the accuracy of networks analysis (Vizentin-Bugoni et al., 2016), especially in Afrotropical forests that are understudied (Schleuning et al., 2012; Morris et al., 2014; Doré et al., 2021).

Indigenous peoples and local communities are now recognized for the large body of knowledge they have on their environment, regarding multiple ecological aspects, from the species composition of their ecosystem to the services they provide (Asselin, 2015; Cámara-Leret et al., 2019). Research efforts initially focused on the expertise of Indigenous peoples and local communities on plants, mostly for pharmaceutical or conservation purposes, in different ecosystems such as Amazonia or Himalayas (Schultes and Raffauf, 1990; Gadgil et al., 1993; Schultes, 1994; Sheng-Ji, 2001; Brondízio et al., 2021). Recently, local ecological knowledge (LEK) i.e. knowledge of indigenous peoples and local communities on ecological processes, have helped on monitoring species abundances (Anadón et al., 2010), assesing animal diversity trends (Azzurro et al., 2011); or understanding trophic networks in fisheries(Rosa et al., 2014; Farr et al., 2018). LEK have proven useful to consolidate and increase knowledge on frugivory and seed dispersal interactions in Amazonian forests (Hawes and Peres, 2014), and Asian tropical forests (Ong et al., 2021). Using interviews to collect LEK on frugivory interactions and integrate them into ecological networks raises two main questions. First there is a need to adapt current ethnological methodology to ecological purpose, such as free listing or surveys, to gather LEK while preserving the heterogeneity of knowledge among interviewee (Chalmers and Fabricius, 2007; Albuquerque et al., 2019). Second to integrate LEK and academic studies (Bélisle et al., 2018) into the unifying framework of ecological networks. Merging data from different methodologies to study plant-animal interactions, such as camera trap, DNA barcoding and direct observation, have already been

shown as successful in increasing the completeness of the interactions networks by compensating bias among methods, as they are complementary to monitor interactions at different time of the day – camera and direct observation – or along spatial gradient – DNA barcoding (Quintero et al., 2021)

In this study, we investigate the potential for LEK to complement current academic knowledge on frugivory interactions in Afrotropical forests. To do so, we collected LEK on frugivory interactions among a set of 286 trees and 100 animals species in one village located in Gabonese forest (Appendix 1). We first described the dataset obtain by interviewing local people, and the specificity of their knowledge. Second, we investigated the complementarity in taxonomic coverage between LEK to a recently published synthesis on frugivory in Afrotropical forests listing known interactions (Durand-Bessart et al., in prep – Chapter 1). Third, we assess whether the addition of data from LEK change the current understanding of the links between species traits and interactions. Finally, we compare the field time needed for both approaches. For the academic dataset, we selected all interactions among this pool of tree and frugivore species, from the literature (Appendix 1). For the LEK dataset, we conducted interviews based on floral and faunal guides of the selected species, with a forest-dependent population in Gabon.

SPECIES RECOGNITION BY LOCAL PEOPLE

We conducted semi-structured interview based on photographic guides of flora and fauna with the indigenous population of Doussala. Doussala is a village neighbour of the Moukalaba-Doudou National Park, at the time of the study, there was 42 inhabitants from Punu and Vungu ethnies, and most of the men have or are still working in a habituation program of Western gorillas. We interviewed 39 informants, including 12 women. Consent of each informant as well as the head-chief of Doussala were obtained before the interviews (Appendix 1).

During the interviews, informant were first presented sheet with several pictures of each of the 100 frugivore species, asking them if they knew it and could name it or not. Each informants recognized in average 59 frugivores (range 15 – 95) species. Then sheet with several pictures – illustrated with pictures of bark, fruits, and seeds – of each of the 286 tree species were presented, asking the informant whether he/she knew it, could name it or not, and if recognized, which frugivore was eating the fruit. On average, informant knew 75 trees species (range 3 – 218). Strikingly, taken together, the 39 informants cited 34380 interactions between those tree and frugivore species, representing 11,095 unique interactions i.e. an interaction between one species of trees and one of animal. This shows the efficiency of the photographic guides approach for local people to recognize each species and access LEK on species interactions.

However, the close list of species presented on the cards appear as a limit of the approach as almost each informant spontaneously added frugivory interactions involving animal species not included in the initial set. The most striking animal species added by all informants was humans, as a consumer of fruits from 113 tree species. This expressed what Descola called "the absence of established discrimination between human and non-human" because "some peoples therefore conceive of their insertion into the environment in a very different way from ours" (Descola, 2005). Moreover, half of informants (17) spontaneously added interactions involving 24 frugivores species not present in academic literature. The frugivore species were from various groups: three species of ruminant (*Cephalophus crusalbum, Kobus ellipsiprynus defassa, Syncerus caffer nanus),* three species of fish (*Chrysichtys nigrodigitatus, Malapterurus electricus, Polydactylus quadrifilis*), two species of carnivores (*Atilax palludinosus*, *Panthera pardus leopardus*), one rodent (*Thryonomys swinderianus),* a pangolin (*Smutsia gigantea*) and snake (*Python sebae*). Informant also added interaction with ant and tortoise but we could not relate them with particular animal species.

These results highlights the important amount of knowledge among informant and that local ecological knowledge was broader than the one captured by our interviews. The photographic guides are based on academic researches, and then by asking local people about species present in academic studies, we are underestimating local ecological knowledge on frugivory interactions.

TREE-FRUGIVORE INTERACTIONS: DIFFERENT KNOWLEDGE PROFILE AMONG INFORMANTS

The mean number of frugivory interaction cited per informant was 731.5, but was heterogeneous, from 24 to 2726 interactions cited (Figure S1A). Informant cited on average 10% interactions not cited by anyone else, ranging from 0 to 48%, resulting in a high number of interactions only cited by one informant (43%; Figure S1B). This heterogeneity, first questioned us on the origin of this difference, being from the gender of informant, their age; or coming from the species beside the interactions. The presence of interactions knowledge not shared among local people, led us to use a selective method to constraint our dataset to interactions shared among local people.

To better characterise how local ecological knowledge on frugivory interaction was shared among informant, we analysed these data as a bipartite network. The first set of nodes was the informants, the other was the tree-frugivore interactions, and the links among informant and frugivory interactions represented a frugivory interaction know by an informant. We used a latent block model, a probabilistic clustering methods, to group informants, and frugivory interactions, into blocks according to the similarity in the frugivory interactions they knew, and according to the similarity in the informant that knew them, respectively. The blockmodel further estimate probabilities among informants and

frugivory interactions indicating the probability for an informant belonging to a block to know a frugivory interaction from another block, and vice versa. Such blockmodel analysis were recently developed and use for the analysis of ecological interaction networks (Leger et al., 2015; Bar-Hen et al., 2018; Durand-Bessart et al., in prep – Chapter 1). Here, the clustering method highlighted the heterogeneity of knowledge among informants, or their different profile of knowledge, as well as shared knowledge on frugivory interactions.

The block model identified nine informant blocks, with one to seven informants per blocks (Fig 1B), indicating that LEK on frugivory interactions was heterogeneous among informants. The first block was only composed of women (I1), five blocks were composed of men (I2,I3,I4,I5,I6) and three block gathered men and women (I7,I8,I9) (Fig 2B). The five blocks of men (I2 to I6) had higher probability of knowledge concerning all frugivory-blocks, showing that men had more knowledge about interactions inside each frugivory-blocks, and surely cited more interactions during interviews than women did, with the exception of the women from the first block (Fig 2B).

Looking to the distribution of probabilities for an informant block to know frugivory interactions from the five blocks of frugivory interactions (Fig 1A), we found that most informant blocks tended to be linked to blocks frugivory interactions similar way. With the exception of the first informant block, all informant blocks had greater knowledge on the block F2, then F3, then F4 and the lowest probability to know frugivory interactions from blocks F1 and F5. The informant block I1 composed of women only, presented a different profile with greater knowledge on blocks of frugivory interactions F1 and F3, then F2, and almost no knowledge on frugivory interactions from blocks F4 and F5 (Fig 1A).

The blocks of frugivory interactions F2 and F3 were the ones with the higher probability to be known by informants and mostly grouped primates and elephant feeding on tree species often used as food resources (Fig 1CDE). This might be explained as by the fact that such large frugivores species are easily spotted, because most men in the village worked as guides for research program targeting these species, or because they are involved in hunting activities. Trees used as a source of food were also better know (Fig 1E), as they are of great interest and a great income sources in this area (Matsuura and Moussavou, 2015). The block of frugivory interactions F1, whose interactions were almost known exclusively by the first informant-block – a group of women – concerned mostly rodents and tree species used as food supplies (Fig 1BC). This group of women came from the same household, which could explain their similar knowledge, coming from the same trapping practices on rodents (Reyes-García et al., 2020). However, this result highlight the fact that women do not have to be discarded from interviews on ecological processes, as they can bring different knowledge to local ecological knowledge. Finally, the block of frugivory interactions F5 grouped interactions that have a very low probability of being known by any informant block (Fig 1B). Then, these frugivory interactions were removed from the following analysis comparing shared LEK on frugivory interactions to current academic knowledge.

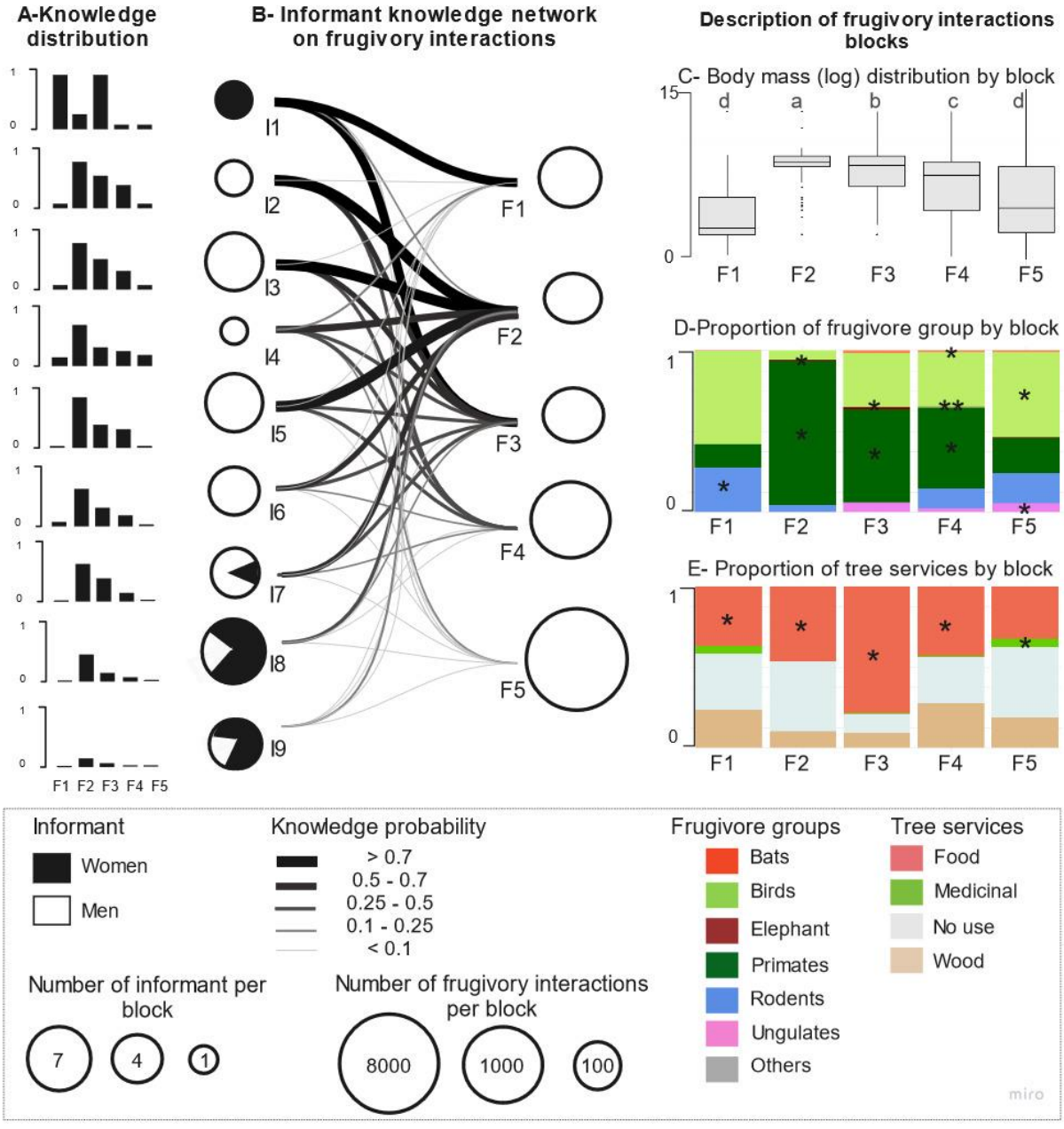

Figure 19. Heterogeneity in LEK on frugivory interactions among informants. (A) for each informant block, distribution of the probability for an informant to know a frugivory interaction from the five blocks of frugivory interactions (B) Bipartite network between informant blocks (left) and blocks of frugivory interactions (right) resulting from the latent block model clustering. The width of the links between informant and frugivory interaction blocks is proportional to the probability for an informant to know an interaction, or for an interaction to be known be an informant. Informant blocks are ordered following the sum of their probabilities to know frugivory interactions over blocks of frugivory interactions. Gender repartition of informant in blocks are shown with pie charts. The size of the circle or pie chart depend on the number of informant or the number of frugivory interactions (log transformed) by block. (C) Frugivore body mass per block of frugivory interactions. (D) proportion of frugivore group per block of frugivory interactions. (E) Proportion of tree uses per block of frugivory interactions. The stars indicate over-represented taxonomic groups, or uses, from Chi-square tests (see Methods).

SAMPLING EFFORT COMPARISON BETWEEN ACADEMIC LITERATURE AND LEK

The academic dataset we used comes from a recent compilation of 151 studies, from which 98 were designed to study frugivory or seed dispersal interactions while the other where general feeding surveys including fruits, or species description with implementation on feeding behaviour (Durand-Bessart et al., in prep – Chapter 1). These studies represent approximately 112 years (41234 days) of fieldwork, and provide a list of 2666 frugivory interactions. Compared to this, our fieldwork gathering LEK, lasted 41 days during which we interviewed 39 informants, and provided 2382 unique and shared interactions. In total, informants gathered 11095 unique interactions, but as we saw most of them were not shared among the population interviewed. However, these interactions put aside surely hold important knowledge on frugivory interactions, encouraging for further study and analysis.

These results highlight the potential of collaborating with Indigenous communities, in order to collect and record frugivory interactions (Anadon et al., 2010; Ong et al. 2021). We encourage further studies including local people, also in the making of protocols to record and monitor plant-animal interactions.

COMPARISON OF FRUGIVORY INTERACTIONS FROM ACADEMIC STUDIES AND LOCAL ECOLOGICAL KNOWLEDGE

LEK and academic datasets were mostly complementary, as few frugivory interactions were known from both sources (16%), while 45% and 39 % of frugivory interactions were only known from respectively the academic and LEK datasets (Fig. 3A). This contribution was variable among frugivore groups, from around 20% of frugivory interactions only known from the LEK dataset for elephant and ungulates, to 30% for primates and birds, and staggering from 60 to 75% for small mammals and occasional fruit-eaters, such as bats, carnivores, rodents and bushpigs (Fig. 3B). Similarly, the contribution of the LEK dataset varied from 0 to 80% depending on tree orders (Fig 3C). These results showed that the contribution of LEK was substantial in groups involving smaller frugivores. However, the addition of frugivory interactions in well-studied groups such as primates and birds or Malpighiales and Malvales for trees was substantial. These results highlight the great potential of local ecological knowledge to complement other sampling methods to reach a higher completeness of frugivory interaction networks (Quintero et al., 2021).

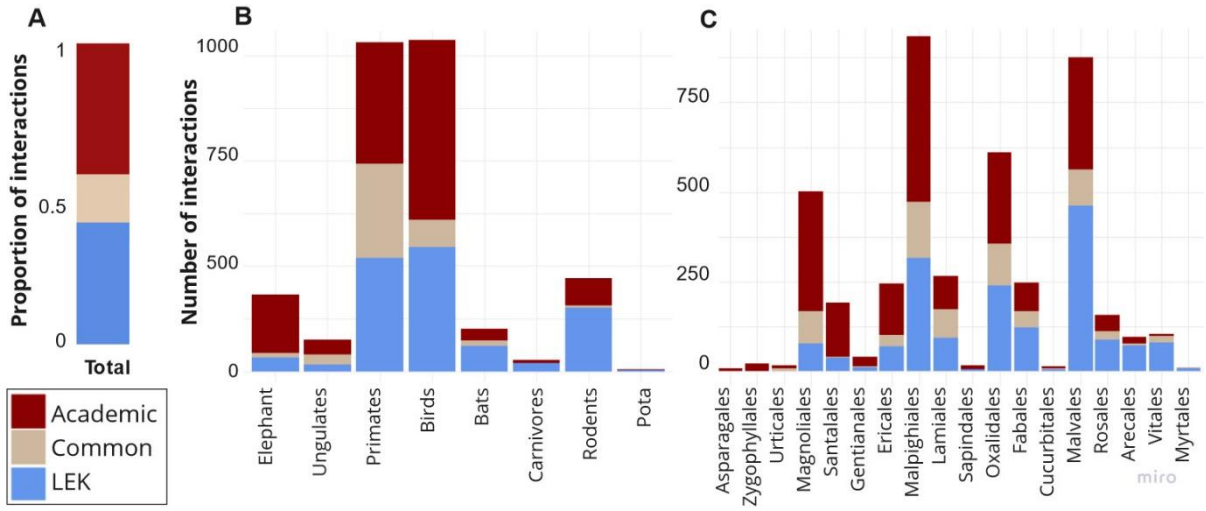

Figure 20. Repartition of knowledge on tree-frugivore interactions between local ecological knowledge and academic knowledge. Distribution of knowledge on tree-frugivore interactions depending on the source of the knowledge by frugivore groups (A). Number of interactions by frugivores groups (B) or tree orders (C), ordered from left to right by the increasing addition of LEK. Interactions knowledge only known by informant are in blue, while knowledge only known by academics are in red, and interactions known by academic and informant are in beige.

LEK GAVE MORE IMPORTANCE TO SMALLER FRUGIVORES

Showing that many interactions were well shared among informant but unknown from the academic literature questioned on the change that this increase in data on tree-frugivore interactions change for our understanding of interaction network linking trees to frugivores in Afrotropical forests.

Seed size and frugivore body mass are known to be structuring traits in frugivory networks (Donatti et al., 2011; Durand-Bessart et al., in prep – Chapter 1) where large seeds are ingested by large frugivores while the dispersal of smaller seeds is less constrained by frugivore body mass (Godínez-Alvarez et al., 2020). Adding LEK to the academic data significantly change the mean body mass of frugivores interacting with tree species (Sup. table S1), with on average lower mean frugivore body mass with the increase addition of LEK, for all Orders except for Lamiales and Magnoliales (Fig 3A). This is coherent with the higher contribution of LEK to interactions of frugivore with low body mass (Fig. 2B). Turning to frugivores, we found that adding LEK to the academic data significantly change the mean seed size of fruit consumed, but differently among frugivore groups, with bats and primates having a downsized in partner mean seed size, while rodents had an upsized, and no change for birds (Fig 3B, Table S1). The fact that mean seed size of trees are changing for frugivore groups showed that the diversity of plant consumed is greater than previously thought. Rodents consuming larger seeds certainly increased their importance in the networks, as large seeded trees are mostly linked with megafaunal species (Carreira et al., 2020). Inversely, Primates and Bats consumed smaller seeds, increasing the importance for small seeded trees in the frugivory network, as suggested in Asian forests (Kitamura et al., 2002)

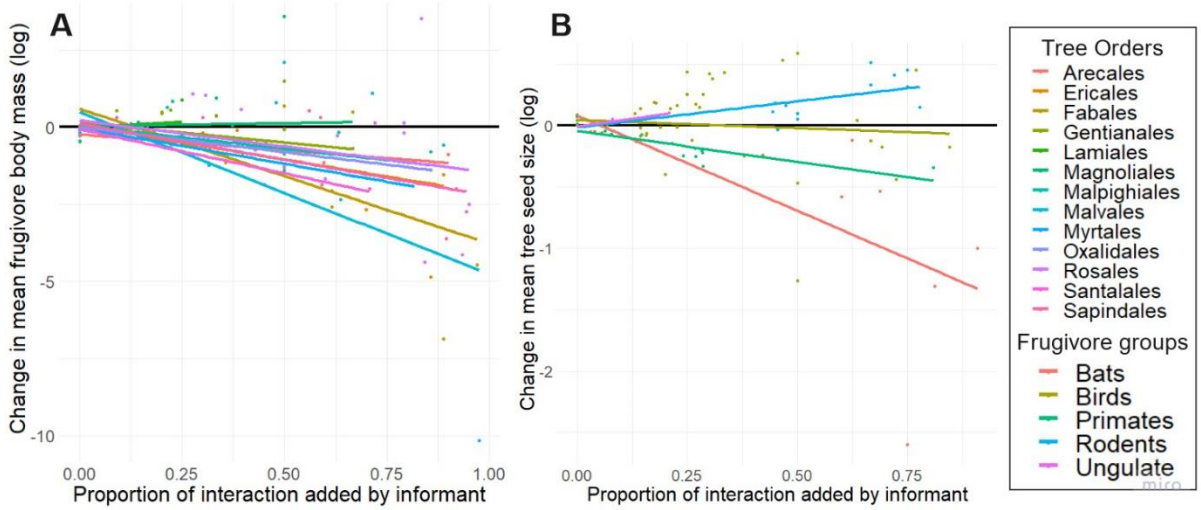

Figure 21. Representation of change in species traits or taxonomic diversity bring by the addition of LEK, for tree species (A) and frugivore species (B), removing taxonomic groups with less than three species. The proportion of interactions added by informant represents for each species the proportion of interactions coming from the LEK network. (A) The difference of mean frugivore body mass for each tree species between the academic and LEK networks. Negative values indicate that the addition of LEK decrease the mean body mass of frugivore that consumed the seeds of a tree species. (B) The difference of seed size of tree species for each frugivore species between the academic and LEK networks, regarding each frugivore groups. A positive mean value for a frugivore group signified that the addition of LEK increased the seed size that are ingested by frugivore species from these groups, and inversely for a negative value.

LEK INTERACTIONS CHANGED THE NETWORK STRUCTURE

We then investigated if the frugivory interactions added by the LEK dataset affect the structure of tree-frugivore networks beyond the effect of adding new interactions. To do so, we added to the academic dataset the same number of new interactions as the LEK dataset provides, but in different ways. (1) randomly or (2) constraining the new interactions to be added in the same number per tree and frugivore genus as in the LEK dataset. We compared the structure of these randomly augmented datasets to the one of the LEK-Academic network using nestedness and modularity metrics which are often used in ecological network analysis (Bascompte and Jordano, 2006; Olesen et al., 2007). This approach investigated if local people attributed interactions between trees and frugivores in a non-random way, for example by following groups of plant and frugivore and their relevant traits.

The LEK-Academic network was more nested and modular than the augmented networks. The difference was lower when interactions were added among genus according to their number in the LEK dataset (Table 1). This indicates that part but not all changes in network structure induced by LEK addition is related to the particular species groups that they know.

Table 2. Metrics of network structure comparison between the mixed-network and null-models based on the academic network.

	LEK-Academic network	Null-model (1)	Null-model (2)
Nestedness (NODF)	48.48	29.34 [28.31-31.14]	45.85 [45.81-46.00]
Modularity	0.35	0.26 [0.25-0.27]	0.33 [0.32-0.33]

CONCLUSION AND PERSPECTIVES

Indigenous people and local communities hold a substantial source of ecological knowledge on ecological interactions among the species that surround them, and their knowledge is complementary to the academic ones. In our two months of fieldwork in Doussala, we obtain as much, if not more information on frugivory interactions than those obtained and published in the academic literature that required more than a century of work.

Frugivory interactions added by local people, changed our understanding of tree-frugivore interactions, by giving much weight to smaller frugivores, and by diversifying the diet of some frugivore groups, like Primates.

Pursuing this work with indigenous community and local people, in different communities all over tropical forests, could help us attain a better completeness on frugivory networks, and understand the underlying mechanisms. Diversifying the informant population could also give us clue on ethnical and cultural differences on the ecological process behind plant-frugivore interactions.

The collaboration with Indigenous communities seems promising and would also benefit the research on plant-animal mutualism in other regions and countries, in Amazonia and South-Asia, but also on non-tropical ecosystems. However, the scientific community also needs to improve on these type of collaboration, by rewarding local people for the traditional knowledge they shared with us, by helping them conserved their language, their life style and traditional know-how by putting more interest in them (Cámara-Leret and Bascompte, 2021).

MATERIAL AND METHODS

1.1. DATA SET

We based our studies on a data set compiling the most up to date list of plants-frugivores interactions in tropical African forests from published and grey literature (Durand-Bessart et al., in prep). In this paper, we selected tree and frugivore species that had an interaction recorded in Gabonese forests, creating a subset of 286 tree species and 100 frugivore species. From this selection, we created two photographic guides, for the flora and the fauna, used later for the semi-structure interview with local people. For both guides, we selected pictures to inform as much characteristics of the species as possible, especially for plants, with pictures of leaves, flowers, fruits, barks, and global architecture. Pictures were selected from various sources, such as agroneo, jstor, and local online flora of Africa.

We created the academic network based on the same selection of species, but including all interactions from all over Afrotropical forests, not only Gabonese forests.

1.2. STUDY SITES & POPULATIONS

Fieldwork was carried out in Doussala, a small village of 42 inhabitants – at the time of the fieldwork – neighbour to Moukalaba-Doudou National Park in South-West Gabon. The population was composed of Punu and Vungu people; they depend on the forest and surroundings for a part of their food by hunting and gathering, medication and construction (Matsuura and Moussavou, 2015). Most men in Doussala are or were guides for the Japanese scientific program for Gorillas habituation (SATREPS: Science and Technology Research Partnership for Sustainable Development) and walk regularly in the forest to follow and observe gorillas, they are an expert population.

1.3. DATA COLLECTION

Before initiating interviews, we obtained consent at the community level by asking the head of the village or neighbourhood, and at individual level before each interview. Participants were informed of their right to discontinue the interviews at any time, and that all of the information provided would be anonymized. Interviews were in French or local language with a local interpreter speaking Punu and Vungu in Doussala. The interview were conducted in two steps, first step the fauna guide was present to the informant, and if recognised the species had to be named (Appendix 3). The second step was to present the flora guide, to name tree species that were recognised, and listed their uses, as well as which frugivore species from the fauna guide was feeding on the fruit (Appendix 2).
We conducted 39 interviews including 12 women, informant were adult between 18 and 70 years old.

1.4. DATA ANALYSIS

1.4.1. DIFFERENCE OF KNOWLEDGE AMONG INFORMANTS

To explore variation in LEK among informant, we used a latent block model, a clustering method that groups informants following their similar knowledge pattern, regarding the number of interactions they cited and the identity of species associated to those ecological-interactions. The main interest of the blockmodel is to show difference in knowledge among group of informant. The blockmodel will also groups tree-frugivore interactions depending on their level of knowledge from informant, this will allowed us to highlight the presence of shared knowledge, depending on their probability of knowledge regarding the different blocks of informants.

In order, to characterize the block of informant, we linked each block of informant with the proportion of men and women inside. We used chi-squared tests and Pearson residuals >2 to assess the over-representations of frugivores taxonomic groups and associated services for trees in frugivory-blocks, and anova with post-hoc test to compare the mean body mass of frugivore inside frugivory-blocks. Tree services information came from http://tropical.theferns.info and confirmed by informant. Tree services were sorted in four categories: (1) no services (2) wood, for trees used as firewood, or construction; (3) medicinal, for trees used in medicinal process; and (4) food for trees whose fruits or seeds are consumed by people.

1.4.2. DO LEK CHANGE OUR UNDERSTANDING OF FRUGIVORY NETWORKS

To understand the impact of the addition of LEK interactions on our actual knowledge on tree-frugivore network, we compared the academic network with the LEK-Academic network – combining academic and informant dataset. For each tree and frugivore species, we investigated whether adding LEK interaction data affected mean partner traits.

For frugivore species, we tested with a linear regression the relationship between the difference in mean seed size of tree species between the Academic and the LEK-Academic networks for each frugivore as dependent variable and the proportion of added interaction by frugivore species, and frugivore taxonomic groups as explanatory variables, with an interaction between both explanatory variables. For tree species, the linear regression tested the relationship between the difference of mean frugivore body mass for each tree and the proportion of interaction added by LEK and tree orders as explanatory variables, with an interaction between both explanatory variables.

In these models, we removed different tree order and frugivore groups, because off low representation (one to two species): Asparagales, Cucurbitales, Urticales, Vitales and Zygophyllales for tree species; and Carnivore, Elephant and Bushpigs for frugivore species.

To understand how the addition of LEK interactions altered the network structures, beyond the effect of adding new interactions, and so increasing the connectivity. We created two dataset – later called augmented dataset – for which we used the Academic dataset as a base, and added the same number of interactions as provided by LEK dataset. For the first model, we added these interactions randomly, while for the second model we added the same number of interactions per tree and frugivore genus to match the LEK dataset.

The two-augmented datasets were compared to the LEK-Academic dataset, regarding their network structure, using common measures in network structure such as nestedness and modularity (Bascompte & Jordano, 2007). We calculated nestedness with NODF function from the *networklevel* function; and modularity with the *computeModules* function from the bipartite package, with 1000 iterations and compared it with the values from the mixed network.

REFERENCES

Anadón, J.D., Giménez, A., Ballestar, R., 2010. Linking local ecological knowledge and habitat modelling to predict absolute species abundance on large scales. Biodivers Conserv 19, 1443–1454. https://doi.org/10.1007/s10531-009-9774-4

Albuquerque, U.P., Nascimento, A.L.B., Soldati, G.T., Feitosa, I.S., Campos, J.L.A., Hurrell, J.A., Hanazaki, N., Medeiros, P.M. de, Silva, R.R.V. da, Ludwinsky, R.H., Ferreira Júnior, W.S., Reyes-García, V., Albuquerque, U.P., Nascimento, A.L.B., Soldati, G.T., Feitosa, I.S., Campos, J.L.A., Hurrell, J.A., Hanazaki, N., Medeiros, P.M. de, Silva, R.R.V. da, Ludwinsky, R.H., Ferreira Júnior, W.S., Reyes-García, V., 2019. Ten important questions/issues for ethnobotanical research. Acta Botanica Brasilica 33, 376–385. https://doi.org/10.1590/0102-33062018abb0331

Asselin, H., 2015. Indigenous forest knowledge, in: Routledge Handbook of Forest Ecology. Routledge.

Azzurro, E., Moschella, P., Maynou, F., 2011. Tracking Signals of Change in Mediterranean Fish Diversity Based on Local Ecological Knowledge. PLOS ONE 6, e24885. https://doi.org/10.1371/journal.pone.0024885

Bar-Hen, A., Barbillon, P., Donnet, S., 2018. Block models for multipartite networks.Applications in ecology and ethnobiology.

Bascompte, J., Jordano, P., 2006. The Structure of Plant-Animal Mutualistic Networks, in: Ecological Networks : Linking Structure to Dynamics in Food Webs, Oxford University Press, Oxford, US. pp. 143–159.

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. Biodivers Conserv 22, 225–238. https://doi.org/10.1007/s10531-012-0416-x

Bélisle, A.C., Asselin, H., LeBlanc, P., Gauthier, S., 2018. Local knowledge in ecological modeling. Ecology and Society 23.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Science Advances. https://doi.org/10.1126/sciadv.1501105

Brondízio, E.S., Aumeeruddy-Thomas, Y., Bates, P., Carino, J., Fernández-Llamazares, Á., Ferrari, M.F., Galvin, K., Reyes-García, V., McElwee, P., Molnar, Z., Samakov, A., Shrestha, U.B., 2021. Locally Based, Regionally Manifested, and Globally Relevant: Indigenous and Local Knowledge, Values, and Practices for Nature. Annual Review of Environment and Resources 46, null. https://doi.org/10.1146/annurev-environ-012220-012127

Cámara-Leret, R., Bascompte, J., 2021. Language extinction triggers the loss of unique medicinal knowledge. PNAS 118. https://doi.org/10.1073/pnas.2103683118

Cámara-Leret, R., Fortuna, M.A., Bascompte, J., 2019. Indigenous knowledge networks in the face of global change. PNAS 116, 9913–9918. https://doi.org/10.1073/pnas.1821843116

Carreira, D.C., Dáttilo, W., Bruno, D.L., Percequillo, A.R., Ferraz, K.M.P.M.B., Galetti, M., 2020. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. Scientific Reports 10, 10594. https://doi.org/10.1038/s41598-020-67326-6

Chalmers, N., Fabricius, C., 2007. Expert and Generalist Local Knowledge about Land-cover Change on South Africa's Wild Coast: Can Local Ecological Knowledge Add Value to Science? Ecology and Society 12.

Descola, P., 2005. On anthropological knowledge. Social Anthropology 13, 65–73. https://doi.org/10.1017/S0964028204000849

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., Dirzo, R., 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters 14, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Donoso, I., Schleuning, M., García, D., Fründ, J., 2017. Defaunation effects on plant recruitment depend on size matching and size trade-offs in seed-dispersal networks. Proceedings of the Royal Society B: Biological Sciences 284, 20162664. https://doi.org/10.1098/rspb.2016.2664

Doré, M., Fontaine, C., Thébault, E., 2021. Relative effects of anthropogenic pressures, climate, and sampling design on the structure of pollination networks at the global scale. Global Change Biology 27, 1266–1280. https://doi.org/10.1111/gcb.15474

Farr, E.R., Stoll, J.S., Beitl, C.M., 2018. Effects of fisheries management on local ecological knowledge. Ecology and Society 23.

Gadgil, M., Berkes, F., Folke, C., 1993. Indigenous Knowledge for Biodiversity Conservation. Ambio 22, 151–156.

Galetti, M., Bovendorp, R.S., Guevara, R., 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3, 824–830. https://doi.org/10.1016/j.gecco.2015.04.008

Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat Commun 10, 4590. https://doi.org/10.1038/s41467-019-12539-1

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. https://doi.org/10.1002/ece3.6285

Hawes, J.E., Peres, C.A., 2014. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. Journal of Tropical Ecology 30, 381–399. https://doi.org/10.1017/S0266467414000261

Howe, H.F., Smallwood, J., 1982. Ecology of Seed Dispersal. Annual Review of Ecology and Systematics 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

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. https://doi.org/10.1007/s00442-002-1073-7

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. https://doi.org/10.1111/2041-210X.12334

Matsuura, N., Moussavou, G.-M., 2015. Analysis of local livelihoods around Moukalaba-Doudou National Park in Gabon. Tropics 23, 195–204. https://doi.org/10.3759/tropics.23.195

Morris, R.J., Gripenberg, S., Lewis, O.T., Roslin, T., 2014. Antagonistic interaction networks are structured independently of latitude and host guild. Ecology Letters 17, 340–349. https://doi.org/10.1111/ele.12235

Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. PNAS 104, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Ong, L., Campos-Arceiz, A., Loke, V.P.W., Pura, P. bin, Tunil, C.M.T. bin, Din, H.S.A., Angah, R. bin, Amirrudin, N.A. binti, Tan, W.H., Lily, O., Solana-Mena, A., McConkey, K.R., 2021. Building ecological networks with local ecological knowledge in hyper-diverse and logistically challenging ecosystems. Methods in Ecology and Evolution n/a. https://doi.org/10.1111/2041-210X.13685

Osuri, A.M., Mendiratta, U., Naniwadekar, R., Varma, V., Naeem, S., 2020. Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds. Front. For. Glob. Change 2. https://doi.org/10.3389/ffgc.2019.00087

Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M., Fletcher, C., Ndoundou-Hockemba, M., Jansen, P.A., Kenfack, D., Marshall, A.R., Ramesh, B.R., Rovero, F., Sankaran, M., 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. Nat Commun 7, 11351. https://doi.org/10.1038/ncomms11351

Quintero, E., Isla, J., Jordano, P., 2021. Methodological overview and data-merging approaches in the study of plant–frugivore interactions. Oikos n/a. https://doi.org/10.1111/oik.08379

Reyes-García, V., Díaz-Reviriego, I., Duda, R., Fernández-Llamazares, Á., Gallois, S., 2020. "Hunting Otherwise." Hum Nat 31, 203–221. https://doi.org/10.1007/s12110-020-09375-4

Rosa, R., Carvalho, A.R., Angelini, R., 2014. Integrating fishermen knowledge and scientific analysis to assess changes in fish diversity and food web structure. Ocean & Coastal Management 102, 258–268. https://doi.org/10.1016/j.ocecoaman.2014.10.004

Rosin, C., Poulsen, J.R., 2016. Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest. Forest Ecology and Management 382, 206–213. https://doi.org/10.1016/j.foreco.2016.10.016

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F., Blüthgen, N., 2012. Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. Current Biology 22, 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Schultes, R.E., 1994. The Importance of Ethnobotany in Environmental Conservation. The American Journal of Economics and Sociology 53, 202–206.

Schultes, R.E., Raffauf, R.., 1990. The healing forest: medicinal and toxic plants of the Northwest Amazonia. Dioscorides Press.

Sheng-Ji, P., 2001. Ethnobotanical Approaches of Traditional Medicine Studies: Some Experiences From Asia. Pharmaceutical Biology 39, 74–79. https://doi.org/10.1076/phbi.39.s1.74.0005

Timóteo, S., Correia, M., Rodríguez-Echeverría, S., Freitas, H., Heleno, R., 2018. Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. Nat Commun 9, 1–11. https://doi.org/10.1038/s41467-017-02658-y

Vizentin-Bugoni, J., Maruyama, P.K., Debastiani, V.J., Duarte, L. da S., Dalsgaard, B., Sazima, M., 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant–hummingbird network. Journal of Animal Ecology 85, 262–272. https://doi.org/10.1111/1365-2656.12459

Vizentin-Bugoni, J., Tarwater, C.E., Foster, J.T., Drake, D.R., Gleditsch, J.M., Hruska, A.M., Kelley, J.P., Sperry, J.H., 2019. Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai‘i. Science 364, 78–82. https://doi.org/10.1126/science.aau8751

Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R., 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. Annual Review of Ecology, Evolution, and Systematics 47, 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

APPENDIX

APPENDIX 1: DATA SELECTION AND INTERVIEWS SET-UP

Data selection

The interview were taking place in Gabonese forests, and to be able to compare data gathered from interviews with academic data, we wanted to have the same set of tree and frugivore species.

We used a dataset on frugivory interactions, covering all Afrotropical forests, with more than 10,000 interactions between 825 tree species, and 285 frugivore species (Durand-Bessart et al., in prep – Chapter 1). From this dataset, we selected tree and frugivore species, that had at least one interaction recorded in Gabonese forests, representing around 350 tree species and 110 frugivores.

From this selection of species, we started gathering pictures of the different tree and frugivore species, to create two photographic guides – one for trees, one for animals. For both guides, we selected pictures to inform as much characteristics of the species as possible, especially for plants, with pictures of leaves, flowers, fruits, barks, and global architecture. Pictures were selected from various sources, such as agroneo, jstor, and local online flora of Africa. Not all tree and frugivore species had available pictures, reducing the number of species to 285 tree species and 100 frugivores.

Interview set-up

We went to Doussala, a small village in the South-West Gabon, with at the time of the study 42 inhabitants, neighbour of the Moukalaba-Doudou National Park. We choose this village for multiple reason. The first one researcher had already worked in the area, and was knew by the people and knew the area. Second, we were able to stay there in a scientific station thanks to our collaboration with the IRET- Gabonese Institute on Ecology Research. Third, the inhabitants of Doussala were acquainted with research programs, as most of them worked for a habituation program with Gorillas for 15 years.

Once on site, the first step was to be settle in the village, to have the approval of the village-chief, as well as other villagers.

Interviews

Each interview was in three steps: 1) presentation of the study and consent form; 2) presentation of the animal photographic guide; 3) presentation of the tree photographic guide.

1) Presentation of the study, our objective "knowing which animal is eating which fruit", we asked the consent of the informant, and signified to them that they had the choice to withdraw from the interview at any time.
2) We presented the photographic guides with animal to the interviewee, each sheet representing an animal. We asked for each animal if the informant knew the species, and could name it or not, in the language of their choice. Sometimes, a species was recognised but not named, and we recorded it as unnamed.
3) Then, we presented the floristic guides, with each sheet representing a tree species. We asked the interviewee, if they could recognized, the species, and name it or not, and by which animal previously presented the fruits were eaten.

LEK interactions

The results of the interviews, compiling each animal considering eating a fruit, we obtained the LEK interactions.

Academic interactions

In order to create the academic dataset, comparable to the LEK, we selected all interactions among the pool of tree and frugivore species present in the photographic guides. Then, interaction that happened outside Gabonese forests, but between species present in the guide were also selected.

APPENDIX 2 – PRESENTATION OF THE FLORISTIC PHOTOGRAPHIC GUIDE

7 *Pseudospondias microcarpa – Anacardiaceae*






APPENDIX 3 – PRESENTATION OF THE FAUNA PHOTOGRAPHIC GUIDE

1 *Gorilla gorilla gorilla*

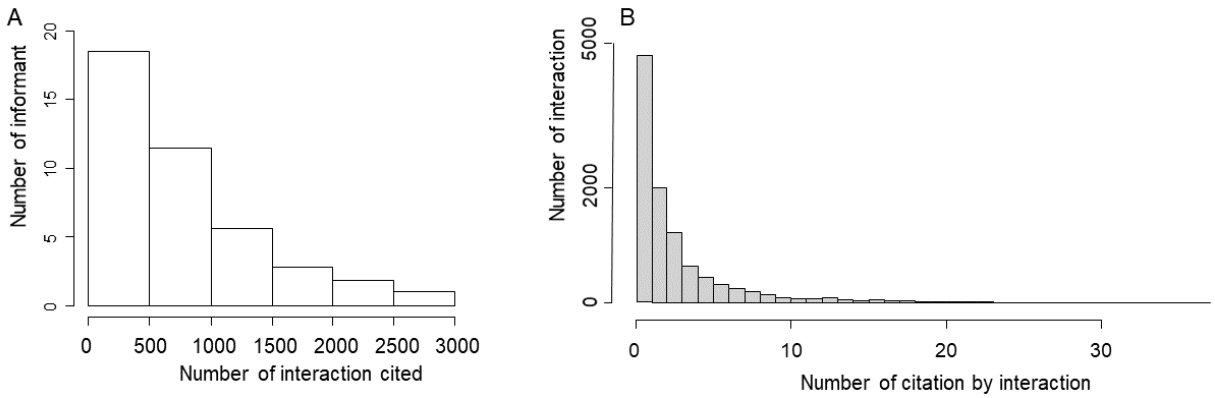

Figure S2. A) Distribution of the number of ecological interaction cited by the informant. B) Distribution of the number of citation by interaction.

Table S1. Linear model results for the relationship between the difference of mean traits between the academic and LEK network (i) mean seed size of frugivore species partner and ii) mean body mass of tree species partner, and the proportion of interactions for each frugivore (i) or tree (ii) species, depending on frugivore taxonomic groups (i) or tree orders (ii).

	Effects	Sum Sq	NumDF	DenDf	F value	P > F
(i)	Proportion of interactions added (Pi)	0.41	1	87	1.17	0.28
	Frugivore groups	12.80	4	87	9.22	>0.001***
	PI * Frugivore groups	1.42	4	87	1.02	0.401
(ii)	Proportion of interactions added (Pi)	131.61	1	236	95.85	>0.001***
	Tree orders	17.05	12	236	1.01	0.437
	PI * Tree orders	21.05	12	236	1.25	0.249

CHAPTER 4

Using camera-trap to highlight the terrestrial frugivore community of Moukalaba-Doudou mosaic forests, Gabon

Large male elephant caught feeding on fruits of Garcinia epunctata, in the forests of the Moukalaba-Doudou National Park. Picture by Clementine Durand-Bessart.

Context

Afrotropical forests have been understudied regarding ecological processes, such as mutualistic interactions between tree and frugivore species, contrary to South American forests. However, the elucidation of interactions patterns between tree and frugivore species, or the dynamic of frugivory communities, depends on sampling efforts.

Different methodological approaches exist to monitor tree-frugivore interactions, like the direct observation by observant, camera trap, local ecological knowledge or DNA-barcoding. Each method, as its advantage and inconvenience, and while the direct observation by observant was the most common, it is limited to recorded smaller animal, as well as cryptic and nocturnal species. Cameras have been of use to counteract these biases, as they can stay on site for several weeks, and can record day and night.

Here, we looked into the contribution of cameras recording, to the frugivory interactions of the terrestrial community of a Gabonese forest. We compared the recording from cameras with frugivory interactions registered in the LEK and academic datasets (Chapter 1 & Chapter 3).

Key results

Cameras recorded interactions for 23 tree species, during three time period of 15 days. They registered a total of 19 frugivore species, with 4 species not present in the LEK and academic database. A total of 107 interactions were recorded between this pool of tree and frugivores species.

On average tree species interacted with 4.65 frugivores [range 1-8], while frugivore species interacted on average with 5.63 tree species [range 1-16].

Regarding the interactions recorded by cameras on the species present in the LEK and academic dataset, 65 % were known by the LEK and/or the academic dataset, while 34% of interactions recorded were added by cameras.

Chapter 4

Using camera-trap to highlight the terrestrial frugivore community of Moukalaba-Doudou mosaic forests, Gabon

Durand-Bessart Clémentine[12], François Bretagnolle[1], Etienne Akomo-Okoue[3], Ghislain W. Ebang Ella[3], Colin Fontaine[2]

[1] Biogeosciences, UMR 6282, Université Bourgogne Franche Comte-CNRS, Dijon, France

[2] Centre d'Ecologie et des Sciences de la Conservation, CESCO, UMR 7204, MNHN-CNRS-SU, Paris, France

[3] Institut de Recherche en Ecologie Tropicale (IRET-CENAREST), Gabon

INTRODUCTION

Recording plants-animals interactions is a common challenge in community ecology, and the recent technological development such as molecular approach or camera trapping have shown a considerable potential to increase our knowledge on these aspects (Quintero et al., 2021). Frugivory or seed dispersal interactions have historically been recorded by direct observations from observant, but recently methods such as the morphological identification of seeds in faeces (Timóteo et al., 2018), the use of DNA-barcoding (González-Varo et al., 2014), and camera trapping (Trolliet et al., 2014), have been successfully used. Camera trapping is now routinely used, thanks to its low cost, its capacity to record interactions day and night with infrared detection, and because protocols are easy to adjust (Burton et al., 2015). Camera-traps have proven their efficiency in detecting feeding behaviour like frugivory of terrestrial and arboreal species in various ecosystems, such as tropical forests (Moore et al., 2021; Zhu et al., 2021). Recently, ecological researches have collaborate with Indigenous people, to gathered frugivory and seed dispersal interactions, with really promising outcomes (Ong et al., 2021; Durand-Bessart et al. in prep - Chapter 3)

Frugivory and seed dispersal interactions are a key process in functioning of ecosystems (Levey et al., 2002), particularly in tropical forests, where nearly 80 percent of tree species producing fleshy fruits depends on fruit consumption and seed dispersion by animals (Howe and Smallwood, 1982). In these forests, the dispersal of seeds by endozoochory has several consequences since the rain of seeds on the ground is less aggregated which, among other things, decreases the density-dependent mortality of seeds and seedlings, known as the Janzen-Connell effect (Janzen, 1970; Connell, 1971; Beaudrot et al., 2013). In addition, a plant species that produces fleshy fruits has fruits that are eaten by a variable number of frugivorous species and vice versa, a frugivorous species can be more or less generalist (or

specialist) towards the fruit species it consumes. Thus, within a forest, a complex network of interactions links plant species to their frugivores, each animal species having its own effectiveness in the dispersal process (Bascompte and Jordano, 2007, Schupp et al., 2010).

African rainforests are subject to multiple stressors, one of the most important being defaunation i.e. the decline of faunal biodiversity due to hunting, poaching and habitat loss (Dirzo et al., 2014). This defaunation mainly affects large and medium-sized vertebrate species, including many species of frugivores, altering to a greater or lesser extent the frugivorous networks and, ultimately, the processes of forest dynamics (Poulsen et al., 2013; Dirzo et al., 2014; Berzaghi et al., 2018; Maicher et al., 2021). In order to understand the effects of defaunation on the dispersal processes of tree species producing fleshy fruits and on forest dynamics, it is necessary to assess the functional redundancies between frugivorous species, which requires taking all the species that contribute to the network. From this point of view, Afrotropical forests are poorly studied. Indeed, even if seed-dispersal processes of certain taxonomic group like monkeys are well-documented (Durand-Bessart et al, in prep – Chapter 1), few researches focus on seed-dispersal network (Schleuning et al., 2012). However, to understand the mechanisms that arrange frugivory and seed-dispersal networks, there is a necessity to take into account all frugivores from small birds to large mammals, and primary dispersers i.e. frugivore harvesting fruits directly in trees, as well as secondary dispersers i.e. frugivore feeding on fruits on the ground (Brocardo et al., 2013). Afrotropical forests possessed a unique fauna, with a remaining frugivore megafauna, and while numerous studies focused on elephants and apes diet, these species were rarely included in global networks studies (Vidal et al., 2013).

Recent studies proposed to compile studies on diets of certain species or taxonomic groups, as well as local network, to study larger networks of interactions (de Almeida and Mikich, 2018; Durand-Bessart et al, in prep - Chapter 1). Moreover, combining diverse methodology from different studies helps reduce bias of each methods (Quintero et al. 2021).

In this study, we explore how camera-traps methods can bring new information on tree-frugivore interaction and help to characterize the community of ground frugivore inhabiting the forests of the Moukalaba-Doudou National Park (Gabon). To do so, we compare the resultant interactions recorded by camera traps with previous studies using other approaches, to quantify the contribution of trap cameras compared to other methods. We disposed 18 cameras following three periods, monitoring 23 tree species that had fallen mature fruits at that time, cameras were on site for a short period of time (15 days) during the fruiting peak. We compared the interactions recorded on cameras with an academic dataset compiling literature on frugivory in Afrotropical forests and with a dataset obtained from surveys of local populations inhabiting the Doussala village near the park (qualified as local ecological knowledge (LEK).

MATERIAL AND METHODS

1.1. STUDY SITES

This study was conducted in the forests of the Moukalaba-Doudou National Park in the Nyanga Province, south-western Gabon (-1°88" to -3°22" N, 10°32" to 10°60" E; Fig. 1). The Moukalaba-Doudou National Park, created in 2002, covers an area of 5,028 km2 consisting of a mosaic of forests and savannah, that was under logging operations from 1960s to 1980s (Matsuura and Moussavou, 2015). There is a dry season from June to September and a rainy season from October to May, with a mean annual rainfall of 1,776.8 mm (Takenoshita et al., 2008).

1.2. FRUITING TREE SAMPLING

In order to record frugivory behaviour of the ground community of vertebrate of Moukalaba-Doudou forests, we used two type of cameras: ten infrared Bushwhacker D3N big eye and eight Reconyx ultrafire XR6. We disposed the cameras to monitor frugivore feeding on falling fruits of tree and liana species, during the fruiting peak, meaning that we targeted plants species with high densities of mature fruits, falling and with fruits on the ground. The cameras monitored each tree for a period of 13-14 days each, and we conducted the survey during 41 days total from October to December, representing three period of cameras rotation (Fig 1). The different tree species were identified thanks to a local inventory, and also with the help of local guides. Only one species remains unidentified. We recorded the interactions for 23 tree species, most species where represented by one individual, that was recorded by one or two cameras (Appendix – Table S1). However, three species had different individual in the same or different session, *Klainedoxa gaboneensis*, *Garcinia epunctata* and *Pseudospondias microcarpa* – the first record did not work (Appendix – Table S1).

Cameras were placed at 60 to 100 cm high, to record frugivore of all size, and one or two cameras were disposed by trees. We optimized camera placement and angle to record the largest area as possible, and try to avoid direct light. We cleared the forest floor in front of cameras, to be able to see feeding behaviour, and avoid herbivory behaviour. The sensitivity of the camera was set to high or medium, with a delay of 5s between triggers, and set cameras to take three photographs per trigger. Each camera was equipped with 8 to 10 batteries and 32 GB memory cards. Cameras were activated to function 24 h per day, 7 days a week.

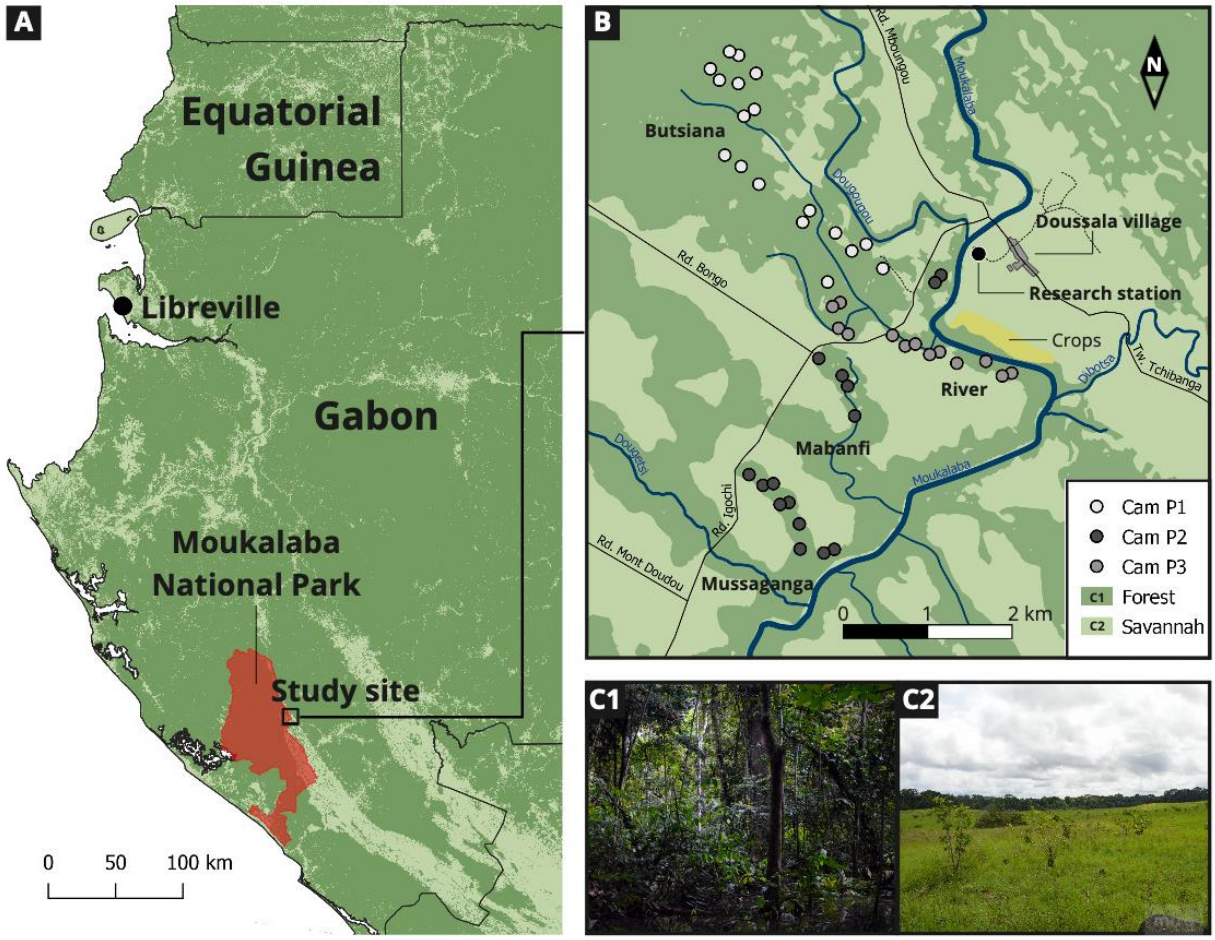

Figure 22. Map of Gabon and study sites. A) Forest cover of Gabon, with the national park of Moukalaba-Doudou in red closed to the study sites. B) Representation of Doussala and its surroundings, camera-trap were posted in different place of the Moukalaba-Doudou forest, following three time-period (P1, P2, P3). C1 & C2) Pictures showing the mosaic with forest and savannah, specificity of this region.

1.3. DATA ANALYSIS

1.3.1. DESCRIPTION OF PLANT-FRUGIVORE INTERACTIONS

We examined all photos, and the frugivore species recorded were identified and double-checked by local guide and/or Gabonese expert. We also classified photos in two categories: interaction when we observed a foraging behaviour from a given frugivore; or no-interaction. The foraging behaviour were confirmed by the direct consumption of a fruit by a frugivore, or the disappearing of a given fruit when the frugivore was nearby, or when a given individual was observed in successive photos with a foraging behaviour even if the consumption was not directly verified.

1.3.2. DESCRIPTION OF INTERACTIONS NETWORK

In order to quantify the potentially original contribution of the data obtained by the camera-traps, we compared this dataset with two other datasets: one academic dataset and another one based on local ecological knowledge (LEK). The academic dataset gathered information on tree-frugivore interactions

from the literature covering all Afrotropical forests (Durand-Bessart et al., in prep – Chapter 1). The dataset based on LEK result from an ethnoecological approach where we have recorded local people knowledge on tree-frugivore interactions in Doussala, the closest village to Moukalaba-Doudou National Park, where the cameras where set recording (Durand-Bessart et al., in prep – Chapter 2). We used semi-structured interview based on photographic guides of flora and fauna, to record interactions between plants and animals. We then, selected interactions that were cited by at least four informants, representing 10% of the population interviewed, and we called this dataset LEK-network for local ecological knowledge network.

We built a network from the interactions between tree species and frugivore species recorded by camera-trap. We compared this camera-network with the academic-network - compiling literature studies – and with the LEK-network – recording local people knowledge in the same area as the camera study. We defined interactions status in four categories: 1) known by academic network; 2) known by LEK-network; 3) known by academic and LEK networks; 4) known only by camera. We defined an interaction in this camera network, as interactions between one species of tree and one of frugivore, not accounting for frequency. The combined bipartite network, obtained from the combination of all the datasets was visualised using the *chordDiagram* function from the circlize package, on R.4.1.0

RESULTATS

2.1. DESCRIPTION OF PLANT-FRUGIVORE INTERACTIONS

For all period, cameras registered 29646 pictures, 11449 pictures recorded vertebrates species and 8877 frugivore animals feeding on the target tree species. We identified 19 frugivore species, mostly large mammals, such as the forest elephant (*Loxodonta cyclotis)* and bushpigs (*Potamocherus porcus*), five species of primates *Gorilla gorilla gorilla*, *Pan troglodytes*, *Mandrillus sphinx, Cercopithecus torquatus and Cercopithecus cephus*, four species of duikers: *Philantomba monticola, Cephalophus sylvicultor, Cephalophus callipygus* and *Cephalophus crusalbum.* Two uncommon fruit eaters were also spotted on cameras, the ungulate species *Syncerus caffer nanus* and *Kobus ellipsiprymus defassa* feeding on respectively three and two tree species. We also identified smaller-frugivores, with three species of rodents *Atherurus africanus*, *Funisciurus lemniscatus* and *Heliosciurus rufrobrachium*; three species of carnivores *Nandinia binonata, Ciivettictis civetta,* including a forest mangoose *Atilax paludinosus.*

The average number of frugivore for a tree species was 4.65 [range 1-8], the fruit size as well as the taxonomic order of the tree species did not influence the number of frugivore partners (Fig. 2). For frugivores, the average number of fruits consumed was 5.63 [range 1-16]. Elephants had the most diverse fruit diets with 16 species consumed. The three commons species of duikers consumed on average eleven fruits from tree species. For primates only the red-capped mangabey and gorillas are common ground eaters, and were caught consuming the fruits of ten to eleven fruits from tree species

(Fig 2). While other primates species have an arboreal feeding behaviour and rarely feed on the ground, such as chimpanzees and moustached monkeys. Then, the camera positioning did not allow us to record their interactions with the targeted tree species.

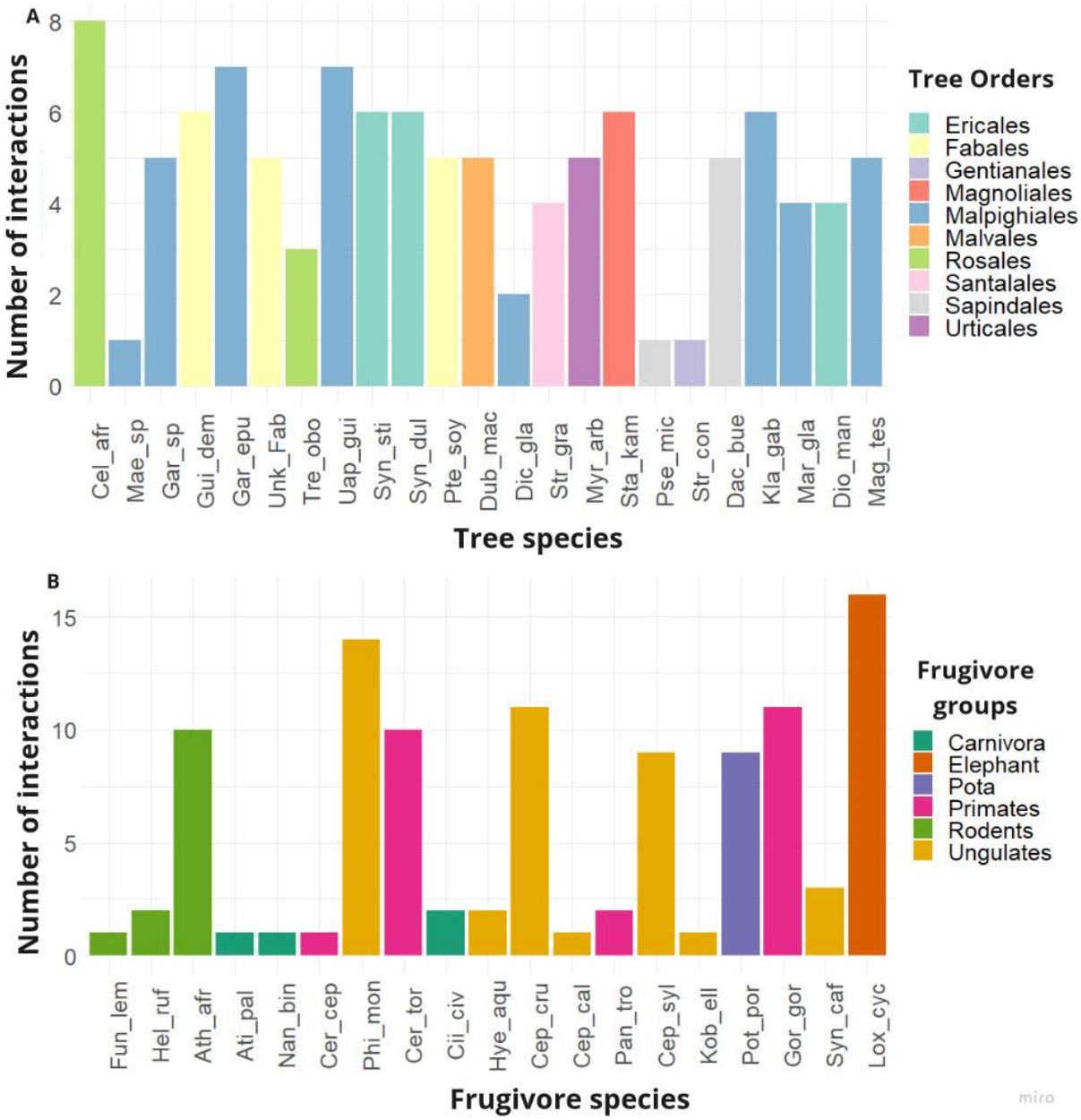

Figure 23. Number of interactions by species of trees (A) and frugivores (B) regarding their tree orders or frugivore groups. (A) Tree species are sorted by their seed size; (B) frugivore species are sorted by their body mass.

2.2. CONTRIBUTION OF CAMERAS' TO FRUGIVORY INTERACTIONS KNOWLEDGE

The comparison of interactions information among the three different networks, camera, LEK and academic, showed that camera recorded new interactions (Table S1, S2). The camera recorded 107 interactions, between 23 tree species including 3 not present in the LEK or academic database and 19

frugivore species with 4 species not present in the LEK and academic database. 30 interactions were recorded with this new species of tree and frugivores.

Regarding the interactions recorded by cameras on the species present in the LEK and academic dataset, 61 % were known by the LEK and 28 % by the academic dataset (Fig 3; Table S1), with 44% of interactions known by LEK and cameras, and 5% by the academic dataset and cameras. Then, 34% of interactions recorded were added by cameras (26 interactions). Including the interactions recorded also on species not present in LEK and academic dataset, 56 interactions were not present in the LEK and academic database, representing 52 % of new interactions.

Regarding, the taxonomic groups of trees and frugivores that concerned by the addition of interactions by cameras. For frugivore groups, the addition varied from 24% for primates to 100% for carnivores; with 38% of new interactions for elephant, 62.5% for ungulates, 57% for rodents, and 56% for bushpigs (Fig 3.). This result showed that smaller frugivores and uncommon fruit-eaters, like carnivores, where the groups benefiting the most from the camera sampling.

Looking on plant Orders, the proportion of new interactions added varied from 0% to 100%, for Urticales and Gentianales, respectively. Then, Magnoliales and Malvales species had an addition of 8% of their interactions, Sapindales 23%, Ericales and Santalales of 50%, Rosales of 67% and Fabales of 92%.

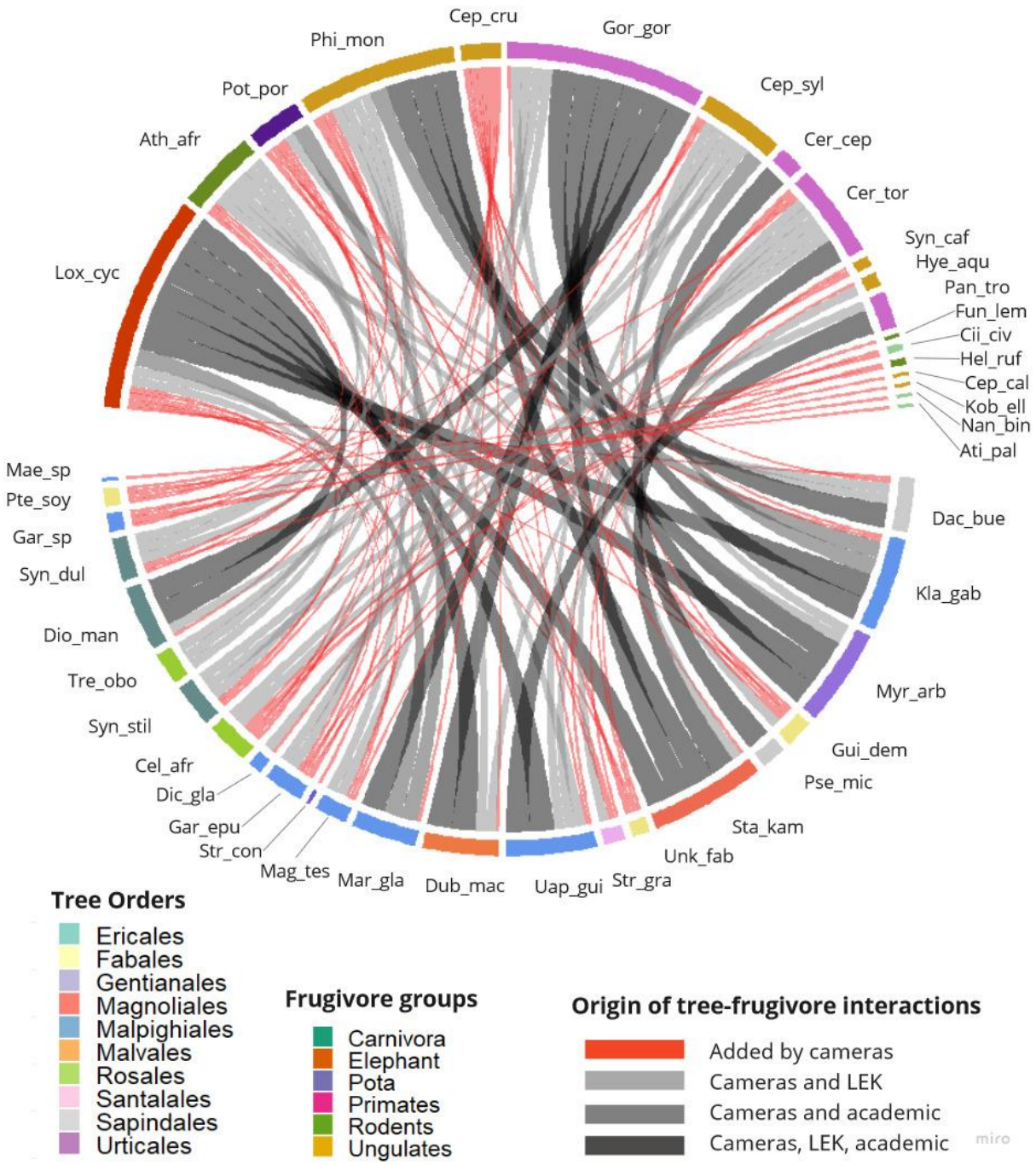

Figure 24. Bipartite network representing interactions between frugivore (above) and trees species (bottom). The origin of interaction is represented by colours, with the interactions known by Cameras and LEK dataset (light grey), cameras and academic dataset (medium grey), or Cameras, LEK and Academic dataset (dark grey) and interactions only recorded by cameras (red). Tree and frugivores species added by cameras have a star sign.

DISCUSSION

The use of camera-trap was efficient to detect frugivory interactions of the ground community of vertebrates in Moukalaba-Doudou forests. Targeting tree species at their fruiting peak with high densities of falling fruits, allowed us to record diverse interactions with ground frugivores, and it allowed us to record cryptic animals, and rare event with uncommon fruit-eaters, impossible with the direct observation methods (Zhu et al. 2021). Indeed, cameras started to record animals feeding after one day, sometimes just few hours after the installation of cameras.

Regarding, the three species of trees (with one still unidentified) and four species of frugivores that were not part of previous studies on plants-animals interactions, we saw that most of the frugivore species added by cameras record are uncommon fruits eater like forest buffalo or defassa's waterbuck, or animals abundant in the area, but scarce elsewhere such as the white-legged duiker (*Cephalophus crusalbum*) (Houngbegnon et al., 2019). Contrary to Brazilian forests, the terrestrial vertebrates species recorded by cameras were in majority large mammals – duikers, gorillas and elephants – while rodents represent a small proportions of the interactions recorded, more like Asian forests (Sridhara et al., 2016; Carreira et al., 2020b). Suggesting, that there is a difference of community structuration between tropical forests; with for Afrotropical forests still a preponderance of large mammals.

Cameras potential is greater than recording presence-absence of interactions and can be used to quantify interactions frequency between one plant and one animal (Trolliet et al., 2014), which as lead to build weighted network (Carreira et al., 2020b). The extensive use of camera trap to monitor species abundance and feeding behaviour, also lead to detect other behaviour, such as the competition between frugivore species, or commensalism and facilitations (Carreira et al., 2020; Selwyn et al., 2020). Recent studies used camera trap to characterized the ground community of vertebrates, and defined the level of perturbations of the community (Trolliet et al., 2019).

The camera traps method appeared to be reliable in monitoring frugivory behaviour and relatively cost-effective compare to other methods. However, in our case, the malfunction of two cameras and the destruction of five cameras by elephants (7 out of 20), have hindered us in our study. The destruction of cameras by elephants is common in Asian and African forests where they are present at high density, and cameras protections remains inefficient (Ong et al., 2021).

Arboreal camera trapping have proven to be a great complementary extension of ground study to record the arboreal community composed of smaller vertebrates, such as bats, birds, and monkeys (Moore et al., 2021; Zhu et al., 2021). However, arboreal camera trapping is more technical and labor intensive, as it requires different techniques and is a challenge in tropical forests, where the canopy easily reached 30m. This method needs more preparation and assistance, and while in our case ground frugivore were used to humans, it may not be the case for the arboreal community and a longer posing time will be necessary, requiring several adaptations.

REFERENCES

Bascompte, J., Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 38, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Beaudrot, L., Rejmánek, M., Marshall, A.J., 2013. Dispersal modes affect tropical forest assembly across trophic levels. Ecography 36, 984–993. https://doi.org/10.1111/j.1600-0587.2013.00122.x

Berzaghi, F., Verbeeck, H., Nielsen, M.R., Doughty, C.E., 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. https://doi.org/10.1111/ecog.03309

Brocardo, C.R., Zipparro, V.B., de Lima, R.A.F., Guevara, R., Galetti, M., 2013. No changes in seedling recruitment when terrestrial mammals are excluded in a partially defaunated Atlantic rainforest. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 107–114. https://doi.org/10.1016/j.biocon.2013.04.024

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52, 675–685. https://doi.org/10.1111/1365-2664.12432

Carreira, D.C., Brodie, J.F., Mendes, C.P., Ferraz, K.M.P.M.B., Galetti, M., 2020a. A question of size and fear: competition and predation risk perception among frugivores and predators. Journal of Mammalogy 101, 648–657. https://doi.org/10.1093/jmammal/gyaa034

Carreira, D.C., Dáttilo, W., Bruno, D.L., Percequillo, A.R., Ferraz, K.M.P.M.B., Galetti, M., 2020b. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. Scientific Reports 10, 10594. https://doi.org/10.1038/s41598-020-67326-6

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of populations, 312.

de Almeida, A. de, Mikich, S.B., 2018. Combining plant–frugivore networks for describing the structure of neotropical communities. Oikos 127, 184–197. https://doi.org/10.1111/oik.04774

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

González-Varo, J.P., Arroyo, J.M., Jordano, P., 2014. Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. Methods in Ecology and Evolution 5, 806–814. https://doi.org/10.1111/2041-210X.12212

Houngbegnon, F., Sonké, B., Vermeulen, C., Doucet, J.-L., 2019. État des connaissances sur les céphalophes (genres Cephalophus et Philantomba) des forêts denses humides d'Afrique centrale (synthèse bibliographique). Biotechnologie, Agronomie, Société et Environnement. https://doi.org/10.25518/1780-4507.17808

Janzen, D.H., 1970. Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104, 501–528. https://doi.org/10.1086/282687

Levey, D.J., Silva, W.R., Galetti, M., 2002. Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. CABI.

Maicher, V., Clark, C.J., Harris, D.J., Medjibe, V.P., Poulsen, J.R., 2021. From town to national park: Understanding the long-term effects of hunting and logging on tree communities in Central Africa. Forest Ecology and Management 499, 119571. https://doi.org/10.1016/j.foreco.2021.119571

Matsuura, N., Moussavou, G.-M., 2015. Analysis of local livelihoods around Moukalaba-Doudou National Park in Gabon. Tropics 23, 195–204. https://doi.org/10.3759/tropics.23.195

Moore, J.F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., Cheyne, S.M., Coutant, O., Forget, P.-M., Haysom, J.K., Houlihan, P.R., Olson, E.R., Lindshield, S., Martin, J., Tobler, M., Whitworth, A., Gregory, T., 2021. The potential and practice of arboreal camera trapping. Methods in Ecology and Evolution 12, 1768–1779. https://doi.org/10.1111/2041-210X.13666

Ong, L., Campos-Arceiz, A., Loke, V.P.W., Pura, P. bin, Tunil, C.M.T. bin, Din, H.S.A., Angah, R. bin, Amirrudin, N.A. binti, Tan, W.H., Lily, O., Solana-Mena, A., McConkey, K.R., 2021. Building ecological networks with local ecological knowledge in hyper-diverse and logistically challenging ecosystems. Methods in Ecology and Evolution n/a. https://doi.org/10.1111/2041-210X.13685

Poulsen, J.R., Clark, C.J., Palmer, T.M., 2013. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 122–130. https://doi.org/10.1016/j.biocon.2013.03.021

Quintero, E., Isla, J., Jordano, P., 2021. Methodological overview and data-merging approaches in the study of plant–frugivore interactions. Oikos n/a. https://doi.org/10.1111/oik.08379

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F., Blüthgen, N., 2012. Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. Current Biology 22, 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Selwyn, M., Garrote, P.J., Castilla, A.R., Fedriani, J.M., 2020. Interspecific interactions among functionally diverse frugivores and their outcomes for plant reproduction: A new approach based on camera-trap data and tailored null models. PLOS ONE 15, e0240614. https://doi.org/10.1371/journal.pone.0240614

Sridhara, S., McConkey, K., Prasad, S., Corlett, R.T., 2016. Frugivory and Seed Dispersal by Large Herbivores of Asia, in: Ahrestani, F.S., Sankaran, M. (Eds.), The Ecology of Large Herbivores in South and Southeast Asia, Ecological Studies. Springer Netherlands, Dordrecht, pp. 121–150. https://doi.org/10.1007/978-94-017-7570-0_5

Takenoshita, Y., Ando, C., Yamagiwa, J., 2008. Fruit phenology of the great Ape habitat in the Moukalaba-Doudou National Park, Gabon. African Study Monographs. Supplementary Issue. 39, 23–39. https://doi.org/10.14989/66240

Timóteo, S., Correia, M., Rodríguez-Echeverría, S., Freitas, H., Heleno, R., 2018. Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. Nat Commun 9, 1–11. https://doi.org/10.1038/s41467-017-02658-y

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. https://doi.org/10.1017/S026646741900018X

Trolliet, F., Vermeulen, C., Huynen, M.-C., Hambuckers, A., 2014. Use of camera traps for wildlife studies: a review. Biotechnologie, Agronomie, Société et Environnement 18.

Vidal, M.M., Pires, M.M., Guimarães, P.R., 2013. Large vertebrates as the missing components of seed-dispersal networks. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 42–48. https://doi.org/10.1016/j.biocon.2013.03.025

Zhu, C., Li, W., Gregory, T., Wang, D., Ren, P., Zeng, D., Kang, Y., Ding, P., Si, X., 2021. Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. Remote Sensing in Ecology and Conservation. https://doi.org/10.1002/rse2.232

ANNEXE

Table 3. Tree species investigated by camera-trap, the number of camera and number of frugivore recorded directly feeding.

Tree species and family	Number of cameras & session	Number of frugivores species recorded
Celtis africana Burm.f. - Cannabaceae	2 (P3)	7
Dacryodes buettneri (Engl.) H.J.Lam - *Burseraceae*	1 (P1)	5
Dichostemma glaucescens Pierre - *Euphorbiaceae*	1 (P3)	2
Diospyros mannii Hiern - *Ebenaceae*	1 (P1)	4
Duboscia macrocarpa Bocq. - *Malvaceae*	2 (P1)	5
Garcinia epunctata Stapf - *Clusiaceae*	3 (P2, P3)	8
Garcinia spp. - Clusiaceae	1 (P2)	7
Guibourtia demeusei (Harms) J.Leonard - *Fabaceae*	1 (P2)	6
Klainedoxa gabonensis Pierre - *Irvingiaceae*	3 (P1)	6
Maesobotrya barteri (Baill.) Hutch - *Phyllanthaceae*	1 (P3)	1
Magnistipula tessmanii (Engl.) Prance - *Chrysobalanaceae*	1 (P1)	5
Marenthes glabra (Oliv.) Prance - *Chrysobalanaceae*	2 (P1)	4
Myrianthus arboreus P.Beauv. - *Urticaceae*	2 (P2)	5
Pseudospondias microcarpa (A.Rich.) Engl. - *Anacardiaceae*	2 (P2 & P3)	1
Staudtia kamerunensis Warb. - *Myristicaceae*	1 (P2)	6
Strombosia grandii Hook.f. ex Benth - *Olacaceae*	1 (P3)	4
Synsepalum dulcificum (Schumach. & Thonn.) Daniell - *Sapotaceae*	2 (P2)	6
Synsepalum stipulatum (Radlk.) Engl. - *Sapotaceae*	1 (P1)	6
Treculia obovoidea N.E.Br. - *Moraceae*	1 (P1)	3
Uapaca guineensis Müll.Arg. - *Urticaceae*	2 (P1)	7
Unknow_fabaceae - Fabaceae	1 (P2)	6

Table S4. Number of interactions recorded by cameras for each tree species, and the number of these interactions that were known by LEK and Academic database. The new species of trees are in bold, and the new interactions recorded by cameras are under brackets.

Tree species	Camera	LEK	Academic
Cetis sp	8 (6)	2	0
Dacryodes buettneri	5 (2)	3	1
Dichostemma glaucescens	2 (1)	1	0
Diospyros mannii	4 (3)	3	2
Duboscia macrocarpa	5 (1)	4	2
Garcinia epunctata	7 (5)	2	0
Garcinia sp	**5 (5)**	**0**	**0**
Guibourtia sp	6 (5)	1	0
Klainedoxa gaboneensis	6 (2)	2	4
Maesobotrya sp	1 (1)	0	0
Magnistipula tessmanii	5 (3)	2	0
Maranthes glabra	4 (1)	1	3
Myranthes arboreus	5	5	3
Pseudospondias microcarpa	1	1	1
Pterocarpus soyauxii	**5 (5)**	**0**	**0**
Staudtia kamerunensis	6 (5)	5	4
Strombosia grandifolia	4 (3)	1	0
Strychnos sp	**1 (1)**	**0**	**0**
Synsepalum dulcificum	6 (3)	3	0
Synsepalum stipulatum	6 (3)	3	0
Treculia obovoidea	3	3	0
Uapaca guineensis	7 (3)	5	2
Unknow fabaceae	**5 (5)**	**0**	**0**
TOTAL	107 (56)	47	22

Table S5. Presence of interactions recorded between tree and frugivore species, in red the interactions added by cameras. New species of trees and frugivores are in bold.

	CARNIVORES			RODENTS				PRIMATES			
Fruit	**Atilax paludinosus**	Ciivettictis civetta	Nandinia binonata	Athererus africanus	Funisciurus isabella	Funisciurus lemniscatus	Heliosciurus rufrobrachium	Cercopithecus cephus	Gorilla gorilla gorilla	Pan troglodytes troglodytes	Cercocebus torquatus
Cetis sp		1					**1**			1	1
Dacryodes buettneri				1							
Dichostemma glaucescens											1
Diospyros mannii									1		
Duboscia macrocarpa									1		**1**
Garcinia epunctata				**1**	**1**	**1**			1		
Garcinia_sp	**1**	**1**		**1**							
Guibourtia sp									1		
Klainedoxa gaboneensis									1		
Maesobotrya sp							**1**				
Magnistipula tessmanii				1					1		**1**
Maranthes glabra									1		
Myranthes arboreus				1					1		
Pseudospondias microcarpa								1			
Pterocarpus soyauxii			**1**	**1**							**1**
Staudtia kamerunensis									1		1
Strombosia grandifolia											**1**
Strychnos sp											
Synsepalum dulcificum				1							
Synsepalum stipulatum				**1**							1
Treculia obovoidea				1					1		
Uapaca guineensis				1					1	1	**1**
Unknow_fab											**1**

	UNGULATES							ELEPHANT	BUSHPIG
Tree species	Cephalophus callipygus	**Cephalophus crusalbum**	Cephalophus sylvicultor	Philantomba monticola	**Kobus ellipsiprymnus defassa**	**Syncerus cafer nanus**	Hyemoschus aquaticus	Loxodonta cyclotis	Potamocherus porcus
Cetis sp		**1**		**1**		**1**			**1**
Dacryodes buettneri		**1**		1				**1**	**1**
Dichostemma glaucescens			**1**						
Diospyros mannii			1					1	**1**
Duboscia macrocarpa		**1**		1				1	
Garcinia epunctata		**1**		1		**1**		**1**	
Garcinia_sp	**1**			**1**					
Guibourtia sp		**1**	**1**	**1**				**1**	**1**
Klainedoxa gaboneensis		**1**	1	1				1	**1**
Maesobotrya sp									
Magnistipula tessmanii								**1**	**1**
Maranthes glabra		**1**						1	1
Myranthes arboreus			1	1				1	
Pseudospondias_microcarpa									
Pterocarpus soyauxii			**1**	**1**					
Staudtia kamerunensis		**1**	1	1				1	
Strombosia grandifolia				**1**			**1**		**1**
Strychnos sp								**1**	
Synsepalum dulcificum		**1**		1	**1**			1	**1**
Synsepalum stipulatum		**1**	1	1				**1**	
Treculia obovoidea								1	
Uapaca guineensis			1				1	1	
Unknow_fab		**1**		**1**		**1**		**1**	

DISCUSSION

A. Synthesis of the chapters

The goal of the first chapter of this PhD thesis was to summarize our knowledge on tree-frugivore interactions in Afrotropical forests, with an analyse of the mechanisms shaping frugivory interactions, to understand the functioning of this hyper-diverse mutualistic network. To do so, I compiled a unique database compiling over 10,000 interactions between trees and frugivores from all Afrotropical forests, extracted from 255 literature sources. The sampling completeness analyses showed us that we are still lacking knowledge on these interactions, with most data collected so far focused on large frugivores. This allowed us to highlight understudied groups, like small mammals. We then investigated the structure of the interaction, using the latent block model to simplify the network and analyse its structure. We were able to summarize this hyper-diverse network between 800 tree species and 285 frugivore species in fourteen blocks of trees and fourteen blocks of frugivores. Each block of plants and frugivores could be interpreted as a functionally redundant assemblage, as the latent block model clusters species with similar patterns of interactions. Not surprisingly, we found that the structure of this network was highly depended on the distribution overlap between species. The sampling effort on species also shaped the block composition, with well-known species gathered in the same blocks, while species with few information on their interactions were clustered together. However, we were able to highlight that interaction between blocks depends on biological traits of tree and frugivore species such as fruit size, seed size and frugivore body mass.

The second chapter was centred on the tree communities, specifically looking at spatial variations in the fruit traits produced by tree communities over the Congo Basin. We also investigated potential consequences of such variations for interactions with frugivores. Using a database from forestry inventories all over Central African forests, we compared the tree communities of the different forest types delimited in the recent study of Réjou-Méchain et al. 2020. We used community weighted mean traits to quantify difference in trait composition related to frugivory –seed and fruit size. We found variations along latitudinal and longitudinal gradient but also among floristic types. Seeds were found to be larger in Southern plots, which was congruent with the hypothesis of the impact of abiotic factors like temperature and precipitation on seed size (McConkey et al., 2022). Floristic types had different production in frugivory traits, independently of their latitude and longitude, showing that biotic factors such as the availability in frugivores may also play a role in forests community composition.
Linking the tree communities of the floristic types with frugivory interactions helped us demonstrate that some floristic types were better sampled than others, highlighting a geographic bias of studies on frugivory and seed dispersal.

The third and fourth chapters focused on methods to monitor plant-animal interactions and required field work, which was done in Gabon where I went to interview local people (chapter 3) and placed camera traps (chapter 4).

The results of the interviews with local people, presented in the third chapter, emphasized their substantial knowledge on plant-animal interactions. First, the investigation of people knowledge on frugivory interactions with the latent block model showed that most informant shared common knowledge on specific species and their interactions. However, most interactions (43%) were known by few or one informant, showing the incredible potential of this collaboration with Indigenous community, which would require further interviews. The comparison with data from academic literature showed that few interactions where common to both datasets (16%), but also that 40 % of interactions were only known by local people. Most of the interactions added concerned smaller frugivores like rodents and birds. Also, the addition of these interactions changed our understanding of frugivory networks, as plants interacted with smaller frugivores, and frugivore interacted with trees bearing larger seeds for rodents, but smaller seeds for primates and bats. To conclude, we discussed the choice of our survey method based on photographic guides, which was easy to conduct and allowed us to compare academic and local ecological knowledge on frugivory interactions. The method used was conservative as it underestimated unique knowledge of the different people interviewed. However, it surely is a promising approach that will benefit from further collaboration with Indigenous and local communities.

In the fourth chapter, we created an interaction network based on data from camera traps that I positioned in the Gabonese Moukalaba-Doudou national Park. The results showed that 34 % of interactions recorded by cameras were new to the academic and LEK database. Most of these new interactions involved smaller frugivore species, like rodents, results that were coherent with the LEK approach. Also, new vertebrate species were recorded feeding on fruits: three of them involved ungulates – white leg-duiker, forests buffalos, and waterbuck – and one a forest mongoose. The conclusion of this chapter leads to encourage more studies exploring plant-animal interactions, also by targeting specific tree species. We also highlighted the importance of diversifying the methods to monitor plant-animal interactions.

B. Assembling and analysing data on frugivory interactions in Afrotropical forests

a. Different methods to gather information on interaction data

In this PhD, three different methods were used to gather information on plant-animal frugivory interactions. The first method was the compilation of data on frugivory interaction, all over Afrotropical forests, named the “academic dataset” in the different chapters. The second method was to interview local people on their knowledge about tree-frugivore interactions, using photographic guides and semi-

direct interviews, which resulted in the creation of the LEK dataset. The third method involved the use of camera trapping in the forests of Moukalaba-Doudou National Park in Gabon. All methods allowed us to work on different aspects of tree-frugivore interactions.

The compilation of frugivory data from academic literature made possible to study these interactions over large-scale, with a huge diversity of taxa from different taxonomic groups. The main advantage of this method is that it is cost-effective, as it avoids extensive fieldwork in remote areas, and leverages any studies that have been already conducted in the area (de Almeida and Mikich, 2018). This academic dataset allowed analysing mechanisms structuring the different communities and patterns of interactions on the overall Afrotropical forests. This compilation approach also has shortcomings, because the data were collected at different periods, and for different time spans, from few weeks to decades. They were also based on various methods, mostly direct observation by observant, cameras or faecal analysis. Because of that, the quantification of interactions between tree and frugivore species was not possible, regarding the visitation frequency or the dispersal efficiency, as the data were not homogenous and the sampling effort divergent. Further, this approach does not account for spatial or phenological differences, that are important factors in network variation over different communities (Perea et al., 2013; Timóteo et al., 2018). However, our choice to work with presence-absence data allowed to partially avoid the problems linked to differences in sampling efforts, and while binary data are less robust than weighted methods, they have proven to be effective to unravel patterns of interactions of mutualistic networks (Sebastián-González et al., 2015). Finally, this compilation approach depends on the focus of previous studies, with in our case more research on large mammals and monkeys, affecting the structure of the network. This frugivory dataset is still enriched by the addition of recent studies on frugivory interactions, with the interest to reproduce these analyses.

The success of the interview method with local people allowed us to compare academic and local ecological knowledge on a same set of tree and frugivore species. Informants had good knowledge of the different species presented on the pictures of the photographic guides, making the survey easy to conduct, and potentially easily replicable. However, as we saw before, most knowledge on frugivory or seed dispersal interactions rely on individual experiences, and then most interactions are known by one or few person. Our focus on shared LEK induced that many interactions were discarded from the analysis. An alternative to the selection of interactions would be to select the most knowledgeable informants (Ong et al., 2021), statistically or by asking the people of the community who are the most knowledgeable person on this subject (Davis and Wagner, 2003). Another solution would be to remove informants who seem to give false information, by using the feeling of the interviewer and the guide/translator directly after the interview, or by asking the people of the community on the reliability of the person. However, by doing so, we would also discard the rarest interaction knowledge, that few people have observed. In any case, the best solution would be to increase sampling effort, interviewing more people from different communities.

Cameras are great tools to record plant–animal interactions and their use have strongly increased in this past decade. They are efficient as they are easy to use, protocols are replicable, they can stay on site for several weeks, and most of the time they are reliable. Our experimentation with cameras gave an important contribution to increase our knowledge on plant and animal interactions in Gabonese forests. The major inconvenient that we encounter was the loss of several cameras due to elephants, as shown in Asian forests before (Ong et al., 2021).

The dataset from the compilation of the academic and local ecological knowledge datasets, concerned hyper-diverse networks, with hundreds of species interacting. This large dataset pushed us to choose a powerful method to help us simplify those networks, while still be able to work on mechanisms governing interactions.

b. Analysis to unravel hyper-diverse networks of interactions: using blockmodel

In this PhD, we worked on different types of interactions networks, the ones concerning plant-animal interactions, and the one on informants and their knowledge on ecological interactions. We used latent block models to disentangle the patterns of interactions in both networks, as it allows to clusters species with similar interactions, but also informants with similar knowledge profile (Bar-Hen et al., 2018).

The latent block model was particularly useful to simplify both networks, as the frugivory network had more than 800 trees and 285 frugivores, while the local ecological knowledge network concerned 39 informants and over 11,000 interactions between trees and frugivores. We chose the latent block model approach for its flexibility, the parametric approach that allowed us to quantify the probability of one species to interact with another species or one people to have a knowledge on one interaction. The flexibility of the latent block model relies on its capacity to highlight multiple structural patterns, like nestedness as we showed in the first chapter, but also modular structure with a block of informants that had strong probability to know ecological interactions in one block and low probability to know other ecological interactions in other blocks.

Thanks to the block model's ability to cluster species or ecological interactions with respectively similar interaction patterns or known by the same informants, we highlighted understudied species in the first chapter, and knowledge about ecological tree-frugivore interactions that were shared or not among informants.

C. Evaluation of the knowledge acquire on tree-frugivore interactions

a. Interaction patterns of tree-frugivore networks

Throughout this PhD research, mechanisms governing mutualistic interactions between plants and animals involved in frugivory and seed dispersal processes were confirmed in Afrotropical forests. Our major result concerning mechanisms driving possible interactions between tree and frugivore was the influence of biological traits on the probability of interactions between species.

In the first chapter, we found that larger seeds had an increased probability to interact with larger frugivores, while we found no difference for interactions with smaller seeds between large and small frugivores. However, in the third chapter, the addition of LEK on frugivory interactions changed this relationship, and all tree species had in average smaller dispersers than previously thought. Also, while bats and primates interacted with smaller seeds and fruits, rodents interacted with larger seeds and fruits.

These results are also confirmed by the influence of species taxonomy, and while it was not the first structuring factor in our network, it is difficult to differentiate traits from taxonomy. We suggest pursuing the study to investigate on the phylogenetic signal between plants and animals at the large-scale of Afrotropical forests. Recent studies just showed the historical and evolutionary relationships between megafauna frugivore species distribution and the repartition of megafaunal fruit syndrome (Bunney et al., 2019; McConkey et al., 2022). In the second chapter, the different profiles of abundance and distribution of seed and fruit traits of tree species showed that large seed and fruits were somewhat homogenously distributed and abundant all over the different floristic types, maybe related to the large distribution of megafaunal species. Overall, the difference of fruit offer – different abundance and distribution profiles as well as mean community traits – of the different floristic types questioned us on the relation with frugivory and seed dispersal network structures. Investigating potential changes in network structure over the different forests could give us clue on spatio-temporal dynamic of these communities' networks (Perea et al., 2013).

b. Taxonomic and biogeographic biases: consequences on network structure

In the evaluation of the knowledge on frugivory interactions, a central and common result in all chapters of this PhD thesis was the bias towards some species – the largest and/or most abundant ones, but also on certain sites and an inconsistency of sampling all over the forests. In all chapters, we could highlight different biases regarding the dataset, the species and areas studied or the methods chosen.

In the first chapter compiling data on interactions from all over Afrotropical forests, testing the sampling completeness of tree-frugivore interactions showed us that while almost 75% of tree and frugivore species were recorded in our academic dataset, 58% of interaction were not recorded between

the set of species. Moreover, the block model analysis showed that one block of tree species and one block of frugivore species clustered 427 and 105 species respectively – almost half of the species in the dataset – that may be rare and/or understudied. Looking closer on which species benefited from extensive research, we found that large and emblematic frugivores such as apes and elephants that are megafaunal species have been at the centre of numerous studies all over the Afrotropical regions. The same goes for trees bearing larger fruits that are mostly eaten by these megafaunal species. In addition, a bias seems to exist towards abundant and widely distributed tree species, as discussed in the chapter 2. We showed that these biases towards larger frugivore and abundant tree species influence our perception of their generalism, as we were not able to distinguish their generalism from the number of studies that they appeared on. Megafaunal species are essential to the dispersal of large seeds, but recent studies showed that smaller dispersers provided better relay that what was formerly believed, showing that dependence on large-seeded species may be less than previously thought (Bunney et al., 2019). Indeed, the inclusion of local ecological knowledge on interactions showed that fruits from tree species were in average consumed by smaller frugivores. However, these biases could also reflect the reality of the network structuring, as we observed also this bias towards larger species in the interview with informants. This also could be an observation bias as larger species are easy to spot, or because they are more hunted.

In the second chapter, we observed a bias regarding the difference of number of studies and/or the number of species studied inside the different floristic types of Central African forests. Also, the only frugivore group studied in all floristic types were apes. The bias towards some floristic types, mostly Gabonese forests that have larger fruits and seeds may influence the over-importance of large frugivore and seeds on the global networks. This is mostly due to the political and historical facilities to conduce forestry studies in Gabon and thanks to their well-conserved forests compared to their neighbouring countries, that allowed researched on apes and large mammals. However, as we have seen, Gabonese forests have particular community characteristics, with tree species with larger seeds and fruits, inducing a bias towards these species and their consumers, large mammals.

c. Where to go, who to catch next, and how?

This large-scale study of frugivory interaction in Afrotropical forests allows us to give recommendation on areas to prospect and species or group of species to monitor.

First, regarding areas to prospect, we found that all three bioregions West Africa, Central Africa and East Africa had a sampling completeness on interactions around 42%, showing that between the species recorded almost 60% of interactions are missing. We suggest continuing the monitoring of species present in previous studies, particularly species of the understudied blocks that we highlighted

in this network study. This would help to better understand patterns of interactions, as interaction between a pair of species could vary through space, in particularly when forest have different offers in fruits, suiting differently the frugivore diets. Our prospection with cameras showed that over a short period it was possible to increase our knowledge of 28% on a same set of species.

In Central African forests, our second chapter showed that studies focused mostly on the Gabonese forests. Prospecting semi-deciduous forests in the Northern regions that have different community traits – smaller seeds and fruits – will give insight into the composition of frugivore communities. Also, inspecting these Northern regions, as well as the Cameroonian forests that are more degraded will gave insight into the consequences of anthropic perturbations on the different networks structures (Abernethy et al., 2013; Malhi et al., 2013; Abernethy et al., 2016).

Second, concerning the species to target, in the chapter 1, 3 and 4 we highlighted the bias towards the largest frugivore species, while in the chapter 2 we saw a bias towards abundant and widespread species and species with larger seeds. Indeed, the megafaunal syndrome for plants and megafaunal frugivore species – elephant and apes – have been widely studied in the past decades (Beaune et al., 2013; Berzaghi et al., 2018; Malhi et al., 2016; Terborgh et al., 2016; Bush et al., 2020). Even if our study showed that interactions with these large species still need to be recorded, we suggest that studies should turn focus to smaller species in terms of fruits and seeds, as well as smaller animals. Indeed, more and more research highlights the importance of smaller mammals in interactions networks (Carreira et al., 2020). Reducing the bias towards these species, could show the importance of smaller seeds in animal diets, as observed in Asian and Amazonian forests (Kitamura et al., 2002). The use of camera traps in the canopy seems an adequate method to counterbalance studies biased in favour of large terrestrial frugivores (Bruce et al., 2018; Moore et al., 2021). Although more demanding in terms of technique and cost, these methods have proven useful to record bat and bird species (Zhu et al., 2021).

Recent studies on rare species showed the importance to adapt recording protocols to target specifically these species (Jeliazkov et al., 2022). Diversifying the methods of data recording has proven useful to maximise the diversification of interactions, in terms of connectivity between species, as well as the specific richness of the network (Quintero et al., 2021). However, targeting uncommon species is particularly difficult in tropical forests, where tree density is especially low and cryptic animals difficult to see or record (Zhu et al., 2021).

One way to solve this methodological problem would be to increase our collaboration with local people and repeat this approach at a large scale. A particular focus could be on rare species, as it was expressed for recording interactions with extinct species (e.g. Asian rhinoceros in Indonesia, Ong et al. 2021). Indeed, we showed in the chapter 3 that our collaboration with the local community of Doussala was fruitful and that informant had extensive knowledge even on rare or uncommon species, such as fish, reptiles, small mammals and birds. More importantly, these interviews also gave us information on

common and emblematic species that were shared by informants but not known by the academic studies, encouraging us to pursue this partnership.

D. Bringing to light transdisciplinary approach by working with local people

a. Extraordinary potential of LEK

So far, local ecological knowledge has been the mainstay of research fields such as ethno-ecology and environmental anthropology. However, the sophisticated knowledge systems acquired and maintained by indigenous people and local communities coming from their longstanding experience with their environments might contribute to the understanding of biodiversity, particularly in the tropical regions where remain knowledge gaps (Michon et al. 2020).

This work combining ethnoecological and ecological data proves the interest in using LEK to answer research questions in tropical ecology. Indeed, Indigenous community interviewed for this work were able to identify and detect plant and animal species and their interactions, with great accuracy. This work was in the continuity of recent studies including indigenous communities and local populations, highlighting their diversity of knowledge, on their environment, from plant and animal services: food, medicine, construction, to complex relationships between people and their environment or between species (Cámara-Leret et al., 2019; Brondízio et al., 2021; Anadón et al., 2009; Aswani et al., 2018).

Plant-animal interactions knowledge might rely more on individual experiences by opposition to consensual knowledge, where people acquire knowledge on their close environment either passively – by observing their surroundings – or actively – during hunt or food prospect (Matsuura and Moussavou, 2015). Some of this knowledge is shared within the population, which is often the case for useful species and/or culturally important ones (Soldati et al., 2017). Indeed, people hunting and harvesting these useful species on a daily base acquire more knowledge about them (Reyes-García et al., 2020). In addition to the practical knowledge i.e., collection, preparation, related to this useful species, Indigenous communities and local poulation also accumulate knowledge on their bio-interactions and behaviours which need to be explored.

Different methods need to be thought to coincide with the ecological processes that need investigation, and while interview methods are efficient, an effort have to be made on the inclusion of local communities in the research study.

b. Developing more collaboration with local communities: ethical consideration

Local ecological knowledge holds an incredible potential to help describe and build frugivory or seed dispersal interactions networks, as well as other ecological processes. However, working with local communities and indigenous peoples also needs to include them more globally, to co-produce knowledge outcomes relevant for both parties (Tengö et al., 2014). Indeed, the scientific community still has a lot of effort to deconstruct its approach on local people knowledge and the way that we are including them, with the decolonization movement (Boillat, 2020; Trisos et al., 2021).

New studies have to reflect on the implication of their research on local communities, by for-example creating long-term collaboration between indigenous or local communities and researchers (Schareika, 2014). This approach will allow them to be included in the construction of protocols, on the intervention of researchers on their land and the benefits that they could take from the research (Carothers et al., 2014). Indeed, there is a great importance to greet local communities as they share with us their knowledge, and to work together so that both parties can find advantages on this type of research programs, for example valorisation of local knowledge, compilation of traditional knowledge in local dialect, enhancing Indigenous communities right and visibility. Moreover, we must include in our fieldwork the necessity to give and share the feedback from the study to local communities that make this type of research possible.

E. Conclusion and perspectives

In conclusion, this PhD work gave insight on the different mechanisms governing tree-frugivore interactions, regarding the importance of overlap in distribution areas and match between biological traits. This work also showed that large frugivore are important actors of frugivory and seed dispersal process. However, we also highlighted biases and shortcomings concerning the dataset with most studies on emblematic species and certain areas and concerning the different methods, with cameras focusing on ground frugivores, and LEK restricted by academic knowledge. These results allowed us to give recommendations to counteract these biases, and increase our knowledge on frugivory interactions. One of the recommendations was to diversify the methods to sample interactions, by collaborating with local people in diverse areas of the Afrotropical forests, or by using arboreal cameras to record smaller frugivores.

This work opened new perspectives on multiple aspects, first by initiating a new dataset on tree-frugivory interactions that will be supplied consistently with new studies and will allow to continue research on this large-scale network. A first proposition would be to include frugivore distribution, from the IUCN or other sources, to combine it with tree species abundance and distribution, and analyse local

pattern of interactions depending on the tree-frugivore assemblage. To go further on the understanding of frugivory assemblages and the perturbations threatening them, we proposed to create prediction models taking into account different anthropic perturbations.

Also, as discussed previously, we would like to pursue the local ecological knowledge approach by developing a collaboration with Gabonese researchers, to conduct surveys in other forests with other ethnic groups.

LITERATURE CITED

Abernethy, K.A., Coad, L., Taylor, G., Lee, M.E., Maisels, F., 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120303–20120303. https://doi.org/10.1098/rstb.2012.0303

Abernethy, K., Maisels, F., White, L.J.T., 2016. Environmental Issues in Central Africa. Annu. Rev. Environ. Resour. 41, 1–33. https://doi.org/10.1146/annurev-environ-110615-085415

Anadón, J.D., Giménez, A., Ballestar, R., Pérez, I., 2009. Evaluation of Local Ecological Knowledge as a Method for Collecting Extensive Data on Animal Abundance. Conservation Biology 23, 617–625. https://doi.org/10.1111/j.1523-1739.2008.01145.x

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading Effects of Bird Functional Extinction Reduce Pollination and Plant Density. Science 331, 1068–1071. https://doi.org/10.1126/science.1199092

Anderson, S.H., Ladley, J.J., Robertson, A.W., Kelly, D., 2021. Effects of changes in bird community composition and species abundance on plant reproduction, through pollination and seed dispersal. Ibis 163, 875–889. https://doi.org/10.1111/ibi.12938

Anhuf, D., Ledru, M.-P., Behling, H., Da Cruz, F.W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J.A., De Oliveira, P.E., Pessenda, L., Siffedine, A., Albuquerque, A.L., Da Silva Dias, P.L., 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeography, Palaeoclimatology, Palaeoecology 239, 510–527. https://doi.org/10.1016/j.palaeo.2006.01.017

Asselin, H., 2015. Indigenous forest knowledge, in: Routledge Handbook of Forest Ecology. Routledge.

Aswani, S., Lemahieu, A., Sauer, W.H.H., 2018. Global trends of local ecological knowledge and future implications. PLOS ONE 13, e0195440. https://doi.org/10.1371/journal.pone.0195440

Augspurger, C.K., 1984. Seedling Survival of Tropical Tree Species: Interactions of Dispersal Distance, Light-Gaps, and Pathogens. Ecology 65, 1705–1712. https://doi.org/10.2307/1937766

Azzurro, E., Moschella, P., & Maynou, F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. *PloS one*, *6*(9), e24885.

Balcomb, S.R., Chapman, C.A., 2003. Bridging the Gap: Influence of Seed Deposition on Seedling Recruitment in a Primate–Tree Interaction. Ecological Monographs 73, 625–642. https://doi.org/10.1890/02-4036

Bar-Hen, A., Barbillon, P., Donnet, S., 2018. Block models for multipartite networks.Applications in ecology and ethnobiology.

Bascompte, J., 2019. Mutualism and biodiversity. Current Biology 29, R467–R470. https://doi.org/10.1016/j.cub.2019.03.062

Bascompte, J., Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 38, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte, J., Jordano, P., 2006. The Structure of Plant-Animal Mutualistic Networks, in: Ecological Networks : Linking Structure to Dynamics in Food Webs, Oxford University Press, Oxford, US. pp. 143–159.

Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. PNAS 100, 9383–9387. https://doi.org/10.1073/pnas.1633576100

Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. Science 312, 431–433. https://doi.org/10.1126/science.1123412

Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458, 1018–1020. https://doi.org/10.1038/nature07950

Beaudrot, L., Rejmánek, M., Marshall, A.J., 2013. Dispersal modes affect tropical forest assembly across trophic levels. Ecography 36, 984–993. https://doi.org/10.1111/j.1600-0587.2013.00122.x

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., Fruth, B., 2013a. Seed dispersal strategies and the threat of defaunation in a Congo forest. Biodivers Conserv 22, 225–238. https://doi.org/10.1007/s10531-012-0416-x

Beaune, D., Fruth, B., Bollache, L., Hohmann, G., Bretagnolle, F., 2013b. Doom of the elephant-dependent trees in a Congo tropical forest. Forest Ecology and Management 295, 109–117. https://doi.org/10.1016/j.foreco.2012.12.041

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitián, M., Saavedra, F., Santillán, V., Töpfer, T., Wiegand, T., Dehling, D.M., Schleuning, M., 2018. Morphological trait matching shapes plant–frugivore networks across the Andes. Ecography 41, 1910–1919. https://doi.org/10.1111/ecog.03396

Berzaghi, F., Bretagnolle, F., Durand-Bessart, C., Blake, S., 2021. Megaherbivores modify forest structure and increase carbon stocks through multiple pathways 2021.12.23.473993.

Berzaghi, F., Verbeeck, H., Nielsen, M.R., Doughty, C.E., 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. https://doi.org/10.1111/ecog.03309

Blake, S., Deem, S.L., Mossimbo, E., Maisels, F., Walsh, P., 2009. Forest Elephants: Tree Planters of the Congo. Biotropica 41, 459–468. https://doi.org/10.1111/j.1744-7429.2009.00512.x

Bleher, B., Böhning-Gaese, K., 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. Oecologia 129, 385–394. https://doi.org/10.1007/s004420100747

Blendinger, P.G., Martín, E., Osinaga Acosta, O., Ruggera, R.A., Aráoz, E., 2016. Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. Biotropica 48, 677–686. https://doi.org/10.1111/btp.12329

Boillat, S., 2020. Decolonizing ecological knowledge: transdisciplinary ecology, place making and cognitive justice in the Andes. The Elgar Companion to Geography, Transdisciplinarity and Sustainability 307–319.

Brocardo, C.R., Zipparro, V.B., de Lima, R.A.F., Guevara, R., Galetti, M., 2013. No changes in seedling recruitment when terrestrial mammals are excluded in a partially defaunated Atlantic rainforest. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 107–114. https://doi.org/10.1016/j.biocon.2013.04.024

Brondízio, E.S., Aumeeruddy-Thomas, Y., Bates, P., Carino, J., Fernández-Llamazares, Á., Ferrari, M.F., Galvin, K., Reyes-García, V., McElwee, P., Molnar, Z., Samakov, A., Shrestha, U.B., 2021. Locally Based, Regionally Manifested, and Globally Relevant: Indigenous and Local Knowledge, Values, and Practices for Nature. Annual Review of Environment and Resources 46, null. https://doi.org/10.1146/annurev-environ-012220-012127

Bronstein, J.L., 1994. Our Current Understanding of Mutualism. The Quarterly Review of Biology 69, 31–51. https://doi.org/10.1086/418432

Bunney, K., Robertson, M., Bond, W., 2019. The historical distribution of megaherbivores does not determine the distribution of megafaunal fruit in southern Africa. Biological Journal of the Linnean Society 128, 1039–1051. https://doi.org/10.1093/biolinnean/blz109

Bruce, T., Amin, R., Wacher, T., Fankem, O., Ndjassi, C., Ngo Bata, M., Fowler, A., Ndinga, H., Olson, D., 2018. Using camera trap data to characterise terrestrial larger-bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon. African Journal of Ecology 56, 759–776. https://doi.org/10.1111/aje.12574

Bush, E.R., Whytock, R.C., Bahaa-el-din, L., Bourgeois, S., Bunnefeld, N., Cardoso, A.W., Dikangadissi, J.T., Dimbonda, P., Dimoto, E., Ndong, J.E., Jeffery, K.J., Lehmann, D., Makaga, L., Momboua, B., Momont, L.R.W., Tutin, C.E.G., White, L.J.T., Whittaker, A., Abernethy, K., 2020. Long-term collapse in fruit availability threatens Central African forest megafauna. Science 370, 1219–1222. https://doi.org/10.1126/science.abc7791

Cámara-Leret, R., Fortuna, M.A., Bascompte, J., 2019. Indigenous knowledge networks in the face of global change. PNAS 116, 9913–9918. https://doi.org/10.1073/pnas.1821843116

Camargo, P.H.S.A., Carlo, T.A., Brancalion, P.H.S., Pizo, M.A., 2022. Frugivore diversity increases evenness in the seed rain on deforested tropical landscapes. Oikos 2022. https://doi.org/10.1111/oik.08028

Campos-Arceiz, A., Blake, S., 2011. Megagardeners of the forest – the role of elephants in seed dispersal. Acta Oecologica, Frugivores and Seed Dispersal: Mechanisms and Consequences of a Key Interaction for Biodiversity 37, 542–553. https://doi.org/10.1016/j.actao.2011.01.014

Carothers, C., Moritz, M., Zarger, R., 2014. Introduction: conceptual, methodological, practical, and ethical challenges in studying and applying indigenous knowledge. Ecology and Society 19. https://doi.org/10.5751/ES-07212-190443

Carlo, T.A., Yang, S., 2011. Network models of frugivory and seed dispersal: Challenges and opportunities. Acta Oecologica, Frugivores and Seed Dispersal: Mechanisms and Consequences of a Key Interaction for Biodiversity 37, 619–624. https://doi.org/10.1016/j.actao.2011.08.001

Carreira, D.C., Dáttilo, W., Bruno, D.L., Percequillo, A.R., Ferraz, K.M.P.M.B., Galetti, M., 2020. Small vertebrates are key elements in the frugivory networks of a hyperdiverse tropical forest. Scientific Reports 10, 10594. https://doi.org/10.1038/s41598-020-67326-6

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R., Yamakura, T., 2000. Spatial Patterns in the Distribution of Tropical Tree Species. Science 288, 1414–1418. https://doi.org/10.1126/science.288.5470.1414

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of populations, 312.

Cook, J.M., Rasplus, J.-Y., 2003. Mutualists with attitude: coevolving fig wasps and figs. Trends in Ecology & Evolution 18, 241–248. https://doi.org/10.1016/S0169-5347(03)00062-4

Cordeiro, N.J., Howe, H.F., 2001. Low Recruitment of Trees Dispersed by Animals in African Forest Fragments. Conservation Biology 15, 1733–1741. https://doi.org/10.1046/j.1523-1739.2001.99579.x

Costa, J.M., Ramos, J.A., Timóteo, S., da Silva, L.P., Ceia, R.S., Heleno, R.H., 2020. Species temporal persistence promotes the stability of fruit–frugivore interactions across a 5-year multilayer network. Journal of Ecology 108, 1888–1898. https://doi.org/10.1111/1365-2745.13391

Couvreur, T.L.P., 2015. Odd man out: why are there fewer plant species in African rain forests? Plant Syst Evol 301, 1299–1313. https://doi.org/10.1007/s00606-014-1180-z

Couvreur, T.L.P., Dauby, G., Blach-Overgaard, A., Deblauwe, V., Dessein, S., Droissart, V., Hardy, O.J., Harris, D.J., Janssens, S.B., Ley, A.C., Mackinder, B.A., Sonké, B., Sosef, M.S.M., Stévart, T., Svenning, J.-C., Wieringa, J.J., Faye, A., Missoup, A.D., Tolley, K.A., Nicolas, V., Ntie, S., Fluteau, F., Robin, C., Guillocheau, F., Barboni, D., Sepulchre, P., 2021. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. Biological Reviews 96, 16–51. https://doi.org/10.1111/brv.12644

Cowlishaw, G., 1999. Predicting the Pattern of Decline of African Primate Diversity: an Extinction Debt from Historical Deforestation. Conservation Biology 13, 1183–1193. https://doi.org/10.1046/j.1523-1739.1999.98433.x

Davidar, P., Rajagopal, B., Arjunan, M., Puyravaud, J.P., 2008. The Relationship between Local Abundance and Distribution of Rain Forest Trees across Environmental Gradients in India. Biotropica 40, 700–706. https://doi.org/10.1111/j.1744-7429.2008.00437.x

Davis, A., Wagner, J.R., 2003. Who Knows? On the Importance of Identifying "Experts" When Researching Local Ecological Knowledge. Human Ecology 31, 463–489. https://doi.org/10.1023/A:1025075923297

de Almeida, A. de, Mikich, S.B., 2018. Combining plant–frugivore networks for describing the structure of neotropical communities. Oikos 127, 184–197. https://doi.org/10.1111/oik.04774

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers Conserv 19, 2873–2893. https://doi.org/10.1007/s10531-010-9850-9

de Manincor, N. de, Hautekeete, N., Piquot, Y., Schatz, B., Vanappelghem, C., Massol, F., 2020. Does phenology explain plant–pollinator interactions at different latitudes? An assessment of its

explanatory power in plant–hoverfly networks in French calcareous grasslands. Oikos 129, 753–765. https://doi.org/10.1111/oik.07259

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. https://doi.org/10.1016/j.actao.2020.103551

Dias, A.T.C., Berg, M.P., de Bello, F., Van Oosten, A.R., Bílá, K., Moretti, M., 2013. An experimental framework to identify community functional components driving ecosystem processes and services delivery. Journal of Ecology 101, 29–37. https://doi.org/10.1111/1365-2745.12024

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., Dirzo, R., 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters 14, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Donoso, I., Schleuning, M., García, D., Fründ, J., 2017. Defaunation effects on plant recruitment depend on size matching and size trade-offs in seed-dispersal networks. Proceedings of the Royal Society B: Biological Sciences 284, 20162664. https://doi.org/10.1098/rspb.2016.2664

Donoso, I., Sorensen, M.C., Blendinger, P.G., Kissling, W.D., Neuschulz, E.L., Mueller, T., Schleuning, M., 2020. Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. Nat Commun 11, 1582. https://doi.org/10.1038/s41467-020-15438-y

Droissart, V., Dauby, G., Hardy, O.J., Deblauwe, V., Harris, D.J., Janssens, S., Mackinder, B.A., Blach-Overgaard, A., Sonké, B., Sosef, M.S.M., Stévart, T., Svenning, J.-C., Wieringa, J.J., Couvreur, T.L.P., 2018. Beyond trees: Biogeographical regionalization of tropical Africa. Journal of Biogeography 45, 1153–1167. https://doi.org/10.1111/jbi.13190

Effiom, E.O., Nuñez-Iturri, G., Smith, H.G., Ottosson, U., Olsson, O., 2013. Bushmeat hunting changes regeneration of African rainforests. Proceedings of the Royal Society B: Biological Sciences 280, 20130246. https://doi.org/10.1098/rspb.2013.0246

Ehrlich, P.R., Raven, P.H., 1964. Butterflies and Plants: A Study in Coevolution. Evolution 18, 586–608. https://doi.org/10.1111/j.1558-5646.1964.tb01674.x

FAO, 2015. FRA 2015 | Global Forest Resources Assessments | Food and Agriculture Organization of the United Nations. Rome.

Farr, E.R., Stoll, J.S., Beitl, C.M., 2018. Effects of fisheries management on local ecological knowledge. Ecology and Society 23.

Fernández-Montes de Oca, A.I., Gallardo-Cruz, J.A., Ghilardi, A., Kauffer, E., Solórzano, J.V., Sánchez-Cordero, V., 2021. An integrated framework for harmonizing definitions of deforestation. Environmental Science & Policy 115, 71–78. https://doi.org/10.1016/j.envsci.2020.10.007

Fleming, T.H., Breitwisch, R., Whitesides, G.H., 1987. Patterns of Tropical Vertebrate Frugivore Diversity. Annual Review of Ecology and Systematics 18, 91–109. https://doi.org/10.1146/annurev.es.18.110187.000515

Flörchinger, M., Braun, J., Böhning-Gaese, K., Schaefer, H.M., 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. Oecologia 164, 151–161. https://doi.org/10.1007/s00442-010-1655-8

Flores, O., Gourlet-Fleury, S., Picard, N., 2006. Local disturbance, forest structure and dispersal effects on sapling distribution of light-demanding and shade-tolerant species in a French Guianian forest. Acta Oecologica 29, 141–154. https://doi.org/10.1016/j.actao.2005.08.007

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2005. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLOS Biology 4, e1. https://doi.org/10.1371/journal.pbio.0040001

Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos 126, 1020–1030. https://doi.org/10.1111/oik.03869

Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R., Bascompte, J., 2010. Nestedness versus modularity in ecological networks: two sides of the

same coin? Journal of Animal Ecology 79, 811–817. https://doi.org/10.1111/j.1365-2656.2010.01688.x

Fricke, E.C., Ordonez, A., Rogers, H.S., Svenning, J.-C., 2022. The effects of defaunation on plants' capacity to track climate change. Science. https://doi.org/10.1126/science.abk3510

Fuzessy, L., Silveira, F.A.O., Culot, L., Jordano, P., Verdú, M., 2022. Phylogenetic congruence between Neotropical primates and plants is driven by frugivory. Ecology Letters 25, 320–329. https://doi.org/10.1111/ele.13918

Fuzessy, L.F., Cornelissen, T.G., Janson, C., Silveira, F.A.O., 2016. How do primates affect seed germination? A meta-analysis of gut passage effects on neotropical plants. Oikos 125, 1069–1080. https://doi.org/10.1111/oik.02986

Gadgil, M., Berkes, F., Folke, C., 1993. Indigenous Knowledge for Biodiversity Conservation. Ambio 22, 151–156.

Galetti, M., Bovendorp, R.S., Guevara, R., 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3, 824–830. https://doi.org/10.1016/j.gecco.2015.04.008

Galetti, M., Dirzo, R., 2013. Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 1–6. https://doi.org/10.1016/j.biocon.2013.04.020

Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimarães, P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., Mattos, J.S. de, Schweiger, A.H., Owen-Smith, N., Johnson, C.N., Marquis, R.J., Svenning, J.-C., 2018. Ecological and evolutionary legacy of megafauna extinctions. Biological Reviews 93, 845–862. https://doi.org/10.1111/brv.12374

García-Morales, R., Moreno, C.E., Badano, E.I., Zuria, I., Galindo-González, J., Rojas-Martínez, A.E., Ávila-Gómez, E.S., 2016. Deforestation Impacts on Bat Functional Diversity in Tropical Landscapes. PLOS ONE 11, e0166765. https://doi.org/10.1371/journal.pone.0166765

Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat Commun 10, 4590. https://doi.org/10.1038/s41467-019-12539-1

Gaston, K.J., Kunin, W.E., 1997. Rare—common differences: an overview, in: Kunin, W.E., Gaston, K.J. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences, Population and Community Biology Series. Springer Netherlands, Dordrecht, pp. 12–29. https://doi.org/10.1007/978-94-011-5874-9_2

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., Thiollay, J.-M., 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65, 324–337. https://doi.org/10.1007/BF00378906

Gautier-Hion, A., Michaloud, G., 1989. Are Figs Always Keystone Resources for Tropical Frugivorous Vertebrates? A Test in Gabon. Ecology 70, 1826–1833. https://doi.org/10.2307/1938115

Gómez, J.M., Schupp, E.W., Jordano, P., 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biological Reviews 94, 874–902. https://doi.org/10.1111/brv.12481

Gómez, J.M., Verdú, M., 2012. Mutualism with Plants Drives Primate Diversification. Systematic Biology 61, 567–577. https://doi.org/10.1093/sysbio/syr127

Gonzalez, M.A., Roger, A., Courtois, E.A., Jabot, F., Norden, N., Paine, C.E.T., Baraloto, C., Thébaud, C., Chave, J., 2010. Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. Journal of Ecology 98, 137–146. https://doi.org/10.1111/j.1365-2745.2009.01607.x

González-Varo, J.P., Arroyo, J.M., Jordano, P., 2014. Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. Methods in Ecology and Evolution 5, 806–814. https://doi.org/10.1111/2041-210X.12212

González-Varo, J. P., & Traveset, A. (2016). The labile limits of forbidden interactions. *Trends in Ecology & Evolution*, *31*(9), 700-710.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hawes, J.E., Peres, C.A., 2014. Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. Journal of Tropical Ecology 30, 381–399. https://doi.org/10.1017/S0266467414000261

Hector, A., 1998. The Effect of Diversity on Productivity: Detecting the Role of Species Complementarity. Oikos 82, 597–599. https://doi.org/10.2307/3546380

Holland, J.N., Bronstein, J.L., 2008. Mutualism, in: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 2485–2491. https://doi.org/10.1016/B978-008045405-4.00673-X

Howe, H.F., 1986. Seed dispersal by fruit-eating birds and mammals, in: Seed Dispersal. Academic Press, p. 189.

Howe, H.F., Smallwood, J., 1982. Ecology of Seed Dispersal. Annual Review of Ecology and Systematics 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Janzen, D.H., 1970. Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104, 501–528. https://doi.org/10.1086/282687

Jeliazkov, A., Gavish, Y., Marsh, C.J., Geschke, J., Brummitt, N., Rocchini, D., Haase, P., Kunin, W.E., Henle, K., 2022. Sampling and modelling rare species: Conceptual guidelines for the neglected majority. Global Change Biology. https://doi.org/10.1111/gcb.16114

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., Luskin, M.S., 2018. Global signal of top-down control of terrestrial plant communities by herbivores. Proceedings of the National Academy of Sciences 115, 6237–6242. https://doi.org/10.1073/pnas.1707984115

Johnson, D.J., Beaulieu, W.T., Bever, J.D., Clay, K., 2012. Conspecific Negative Density Dependence and Forest Diversity. Science 336, 904–907. https://doi.org/10.1126/science.1220269

Jordano, P., 2000. Fruit and Frugivory, in: Seeds : The Ecology of Regeneration in Plant Communities, 2nd Edition, CABI Publ. Wallingford UK. pp. 125–166.

Jordano, P., 1987. Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance, Dependence Asymmetries, and Coevolution. The American Naturalist 129, 657–677. https://doi.org/10.1086/284665

Jordano, P., Forget, P.-M., Lambert, J.E., Böhning-Gaese, K., Traveset, A., Wright, S.J., 2011. Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. Biol Lett 7, 321–323. https://doi.org/10.1098/rsbl.2010.0986

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management, Changes in Global Forest Resources from 1990 to 2015 352, 9–20. https://doi.org/10.1016/j.foreco.2015.06.014

Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T., Woolmer, G., 2003. Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. Conservation Biology 17, 245–257. https://doi.org/10.1046/j.1523-1739.2003.02040.x

Kissling, W.D., Eiserhardt, W.L., Baker, W.J., Borchsenius, F., Couvreur, T.L.P., Balslev, H., Svenning, J.-C., 2012. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. Proceedings of the National Academy of Sciences 109, 7379–7384. https://doi.org/10.1073/pnas.1120467109

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. https://doi.org/10.1007/s00442-002-1073-7

Kurten, E.L., 2013. Cascading effects of contemporaneous defaunation on tropical forest communities. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 22–32. https://doi.org/10.1016/j.biocon.2013.04.025

Labandeira, C.C., Johnson, K.R., Wilf, P., 2002. Impact of the terminal Cretaceous event on plant–insect associations. PNAS 99, 2061–2066.

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:1602.07587 [stat].

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. https://doi.org/10.1111/2041-210X.12334

Levey, D.J., Estrada, A., Fleming, T.H., 1986. Frugivores and seed dispersal, Editorial Dordrecht, W. Junk Publ, NL.

Levine, J.M., Murrell, D.J., 2003. The Community-Level Consequences of Seed Dispersal Patterns. Annual Review of Ecology, Evolution, and Systematics 34, 549–574. https://doi.org/10.1146/annurev.ecolsys.34.011802.132400

Lewinsohn, T.M., Prado, P.I., Jordano, P., Bascompte, J., Olesen, J.M., 2006. Structure in plant–animal interaction assemblages. Oikos 113, 174–184. https://doi.org/10.1111/j.0030-1299.2006.14583.x

Lim, J.Y., Svenning, J.-C., Göldel, B., Faurby, S., Kissling, W.D., 2020. Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. Nat Commun 11, 4904. https://doi.org/10.1038/s41467-020-18530-5

Lim, J.Y., Wasserman, M.D., Veen, J., Després-Einspenner, M.-L., Kissling, W.D., 2021. Ecological and evolutionary significance of primates' most consumed plant families. Proceedings of the Royal Society B: Biological Sciences 288, 20210737. https://doi.org/10.1098/rspb.2021.0737

Macior, L.W., 1971. Co-Evolution of Plants and Animals — Systematic Insights from Plant-Insect Interactions. TAXON 20, 17–28. https://doi.org/10.2307/1218530

Mack, A.L., 2000. Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? J. Biosci. 25, 93–97. https://doi.org/10.1007/BF02985186

Maley, J., 1996. The African rain forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences 104, 31–73. https://doi.org/10.1017/S0269727000006114

Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. African rainforests: past, present and future. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120312. https://doi.org/10.1098/rstb.2012.0312

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proceedings of the National Academy of Sciences 113, 838–846. https://doi.org/10.1073/pnas.1502540113

Marie, C.N., Sibelet, N., Dulcire, M., Rafalimaro, M., Danthu, P., Carrière, S.M., 2009. Taking into account local practices and indigenous knowledge in an emergency conservation context in Madagascar. Biodivers Conserv 18, 2759–2777. https://doi.org/10.1007/s10531-009-9672-9

Matsuura, N., Moussavou, G.-M., 2015. Analysis of local livelihoods around Moukalaba-Doudou National Park in Gabon. Tropics 23, 195–204. https://doi.org/10.3759/tropics.23.195

May, R.M., 1982. Mutualistic interactions among species. Nature 296, 803–804. https://doi.org/10.1038/296803a0

McConkey, K.R., Drake, D.R., 2006. Flying Foxes Cease to Function as Seed Dispersers Long Before They Become Rare. Ecology 87, 271–276. https://doi.org/10.1890/05-0386

Melito, M., Arroyo-Rodríguez, V., Metzger, J.P., Cazetta, E., Rocha-Santos, L., Melo, F.P.L., Santos, B.A., Magnago, L.F.S., Hernández-Ruedas, M.A., Faria, D., Oliveira, A.A., 2021. Landscape forest loss decreases aboveground biomass of Neotropical forests patches in moderately disturbed regions. Landscape Ecol 36, 439–453. https://doi.org/10.1007/s10980-020-01166-7

Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London. Series B: Biological Sciences 271, 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Michaloud, G., Carrière, S., Kobbi, M., 1996. Exceptions to the one:one relationship between African fig trees and their fig wasp pollinators: possible evolutionary scenarios. Journal of Biogeography 23, 513–520. https://doi.org/10.1111/j.1365-2699.1996.tb00013.x

Michon, G., Carrière, S., & Moizo, B. (Eds.). (2020). *Habiter la forêt tropicale au XXIe siècle*. IRD Éditions.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M., Turelli, M., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10, 315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x

Montoya, D., Zavala, M.A., Rodríguez, M.A., Purves, D.W., 2008. Animal Versus Wind Dispersal and the Robustness of Tree Species to Deforestation. Science 320, 1502–1504. https://doi.org/10.1126/science.1158404

Moore, J.F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., Cheyne, S.M., Coutant, O., Forget, P.-M., Haysom, J.K., Houlihan, P.R., Olson, E.R., Lindshield, S., Martin, J., Tobler, M., Whitworth, A., Gregory, T., 2021. The potential and practice of arboreal camera trapping. Methods in Ecology and Evolution 12, 1768–1779. https://doi.org/10.1111/2041-210X.13666

Morante-Filho, J.C., Arroyo-Rodríguez, V., Pessoa, M. de S., Cazetta, E., Faria, D., 2018. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. Ecological Applications 28, 2024–2032. https://doi.org/10.1002/eap.1791

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., Mason, N.W.H., 2011. Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLOS ONE 6, e17476. https://doi.org/10.1371/journal.pone.0017476

Myers, N., 1991. Tropical deforestation: the latest situation. BioScience 41, 282–283.

Nathan, R., 2007. Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems., in: Seed Dispersal: Theory and Its Application in a Changing World, CABI. CABI, pp. 252–276.

Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P.-M., Thébaud, C., 2007. Mast Fruiting Is a Frequent Strategy in Woody Species of Eastern South America. PLOS ONE 2, e1079. https://doi.org/10.1371/journal.pone.0001079

Nuñez-Iturri, G., Howe, H.F., 2007. Bushmeat and the Fate of Trees with Seeds Dispersed by Large Primates in a Lowland Rain Forest in Western Amazonia. Biotropica 39, 348–354. https://doi.org/10.1111/j.1744-7429.2007.00276.x

Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. PNAS 104, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2011). Missing and forbidden links in mutualistic networks. Proceedings of the Royal Society B: Biological Sciences, 278(1706), 725-732.

Ong, L., Campos-Arceiz, A., Loke, V.P.W., Pura, P. bin, Tunil, C.M.T. bin, Din, H.S.A., Angah, R. bin, Amirrudin, N.A. binti, Tan, W.H., Lily, O., Solana-Mena, A., McConkey, K.R., 2021. Building ecological networks with local ecological knowledge in hyper-diverse and logistically challenging ecosystems. Methods in Ecology and Evolution n/a. https://doi.org/10.1111/2041-210X.13685

Ong, L., McConkey, K.R., 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. https://doi.org/10.1111/1365-2745.13809

Parchman, T.L., Benkman, C.W., 2002. Diversifying Coevolution Between Crossbills and Black Spruce on Newfoundland. Evolution 56, 1663–1672. https://doi.org/10.1111/j.0014-3820.2002.tb01478.x

Pellmyr, O., 2003. Yuccas, Yucca Moths, and Coevolution: A Review on JSTOR. Annals of the Missouri Botanical Garden 90, 35–55.

Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A., Fedriani, J.M., 2013. Context-dependent fruit–frugivore interactions: partner identities and spatio-temporal variations. Oikos 122, 943–951. https://doi.org/10.1111/j.1600-0706.2012.20940.x

Peres, C.A., Palacios, E., 2007. Basin-Wide Effects of Game Harvest on Vertebrate Population Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal. Biotropica 39, 304–315. https://doi.org/10.1111/j.1744-7429.2007.00272.x

Petchey, O.L., Hector, A., Gaston, K.J., 2004. How Do Different Measures of Functional Diversity Perform? Ecology 85, 847–857. https://doi.org/10.1890/03-0226

Poisot, T., Stouffer, D.B., Gravel, D., 2015. Beyond species: why ecological interaction networks vary through space and time. Oikos 124, 243–251. https://doi.org/10.1111/oik.01719

Quintero, E., Isla, J., Jordano, P., 2021. Methodological overview and data-merging approaches in the study of plant–frugivore interactions. Oikos n/a. https://doi.org/10.1111/oik.08379

Ramos-Robles, M., Dáttilo, W., Díaz-Castelazo, C., Andresen, E., 2018. Fruit traits and temporal abundance shape plant-frugivore interaction networks in a seasonal tropical forest. Sci Nat 105, 29. https://doi.org/10.1007/s00114-018-1556-y

Redford, K.H., 1992. The Empty Forest. BioScience 42, 412–422. https://doi.org/10.2307/1311860

Réjou-Méchain, M., Flores, O., Bourland, N., Doucet, J.-L., Fétéké, R.F., Pasquier, A., Hardy, O.J., 2011. Spatial aggregation of tropical trees at multiple spatial scales. Journal of Ecology 99, 1373–1381. https://doi.org/10.1111/j.1365-2745.2011.01873.x

Réjou-Méchain, M., Mortier, F., Bastin, J.-F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Deblauwe, V., Doucet, J.-L., Doumenge, C., Fayolle, A., Garcia, C., Kibambe Lubamba, J.-P., Loumeto, J.-J., Ngomanda, A., Ploton, P., Sonké, B., Trottier, C., Vimal, R., Yongo, O., Pélissier, R., Gourlet-Fleury, S., 2021. Unveiling African rainforest composition and vulnerability to global change. Nature 593, 90–94. https://doi.org/10.1038/s41586-021-03483-6

Reyes-García, V., Díaz-Reviriego, I., Duda, R., Fernández-Llamazares, Á., Gallois, S., 2020. "Hunting Otherwise." Hum Nat 31, 203–221. https://doi.org/10.1007/s12110-020-09375-4

Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P., Bascompte, J., 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature 448, 925–928. https://doi.org/10.1038/nature05956

Robbrecht, E., 1996. Geography of African Rubiaceae with reference to glacial rain forest refuges, in: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African Plants: Proceedings XIVth AETFAT Congress 22–27 August 1994, Wageningen, The Netherlands. Springer Netherlands, Dordrecht, pp. 564–581. https://doi.org/10.1007/978-94-009-0285-5_71

Rocha-Santos, L., Mayfield, M.M., Lopes, A.V., Pessoa, M.S., Talora, D.C., Faria, D., Cazetta, E., 2020. The loss of functional diversity: A detrimental influence of landscape-scale deforestation on tree reproductive traits. Journal of Ecology 108, 212–223. https://doi.org/10.1111/1365-2745.13232

Rosa, R., Carvalho, A.R., Angelini, R., 2014. Integrating fishermen knowledge and scientific analysis to assess changes in fish diversity and food web structure. Ocean & Coastal Management 102, 258–268. https://doi.org/10.1016/j.ocecoaman.2014.10.004

Schareika, N., 2014. The social nature of environmental knowledge among the nomadic Woɗaaɓe of Niger. Ecology and Society 19.

Schemske, D.W., Mittelbach, G.G., 2017. "Latitudinal Gradients in Species Diversity": Reflections on Pianka's 1966 Article and a Look Forward. The American Naturalist 189, 599–603. https://doi.org/10.1086/691719

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.M., Winqvist, C., Dormann, C.F., Blüthgen, N., 2012. Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. Current Biology 22, 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Schultes, R.E., 1994. The Importance of Ethnobotany in Environmental Conservation. The American Journal of Economics and Sociology 53, 202–206.

Schultes, R.E., Raffauf, R.., 1990. The healing forest: medicinal and toxic plants of the Northwest Amazonia. Dioscorides Press.

Sebastián-González, E., Dalsgaard, B., Sandel, B., Guimarães Jr, P.R., 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters. Global Ecology and Biogeography 24, 293–303. https://doi.org/10.1111/geb.12270

Shanahan, M., So, S., Gompton, S.G., Gorlett, R., 2001. Fig-eating by vertebrate frugivores: a global review. Biological Reviews 76, 529–572. https://doi.org/10.1017/S1464793101005760

Sheng-Ji, P., 2001. Ethnobotanical Approaches of Traditional Medicine Studies: Some Experiences From Asia. Pharmaceutical Biology 39, 74–79. https://doi.org/10.1076/phbi.39.s1.74.0005

Sinnott-Armstrong, M.A., Donoghue, M.J., Jetz, W., 2021. Dispersers and environment drive global variation in fruit colour syndromes. Ecology Letters 24, 1387–1399. https://doi.org/10.1111/ele.13753

Sivault, E., McConkey, K., Bretagnolle, F. ois, Sengupta, A., Lambert, J., Heymann, E., Forget, P.M., Herrel, A., 2020. Body mass and skull dimensions predict seed dispersal capacity in bats, primates and carnivores from tropical forests (preprint). Preprints. https://doi.org/10.22541/au.159647579.96227644

Slik, J.W.F., Franklin, J., Arroyo-Rodríguez, V., Field, R., Aguilar, S., Aguirre, N., Ahumada, J., Aiba, S.-I., Alves, L.F., K, A., Avella, A., Mora, F., C, G.A.A., Báez, S., Balvanera, P., Bastian, M.L., Bastin, J.-F., Bellingham, P.J., Berg, E. van den, Bispo, P. da C., Boeckx, P., Boehning-Gaese, K., Bongers, F., Boyle, B., Brambach, F., Brearley, F.Q., Brown, S., Chai, S.-L., Chazdon, R.L., Chen, S., Chhang, P., Chuyong, G., Ewango, C., Coronado, I.M., Cristóbal-Azkarate, J., Culmsee, H., Damas, K., Dattaraja, H.S., Davidar, P., DeWalt, S.J., Din, H., Drake, D.R., Duque, A., Durigan, G., Eichhorn, K., Eler, E.S., Enoki, T., Ensslin, A., Fandohan, A.B., Farwig, N., Feeley, K.J., Fischer, M., Forshed, O., Garcia, Q.S., Garkoti, S.C., Gillespie, T.W., Gillet, J.-F., Gonmadje, C., Cerda, I.G. la, Griffith, D.M., Grogan, J., Hakeem, K.R., Harris, D.J., Harrison, R.D., Hector, A., Hemp, A., Homeier, J., Hussain, M.S., Ibarra-Manríquez, G., Hanum, I.F., Imai, N., Jansen, P.A., Joly, C.A., Joseph, S., Kartawinata, K., Kearsley, E., Kelly, D.L., Kessler, M., Killeen, T.J., Kooyman, R.M., Laumonier, Y., Laurance, S.G., Laurance, W.F., Lawes, M.J., Letcher, S.G., Lindsell, J., Lovett, J., Lozada, J., Lu, X., Lykke, A.M., Mahmud, K.B., Mahayani, N.P.D., Mansor, A., Marshall, A.R., Martin, E.H., Matos, D.C.L., Meave, J.A., Melo, F.P.L., Mendoza, Z.H.A., Metali, F., Medjibe, V.P., Metzger, J.P., Metzker, T., Mohandass, D., Munguía-Rosas, M.A., Muñoz, R., Nurtjahy, E., Oliveira, E.L. de, Onrizal, Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Perez, R., Pérez-García, E.A., Pommer, U., Poorter, L., Qie, L., Piedade, M.T.F., Pinto, J.R.R., Poulsen, A.D., Poulsen, J.R., Powers, J.S., Prasad, R.C., Puyravaud, J.-P., Rangel, O., Reitsma, J., Rocha, D.S.B., Rolim, S., Rovero, F., Rozak, A., Ruokolainen, K., Rutishauser, E., Rutten, G., Said, M.N.M., Saiter, F.Z., Saner, P., Santos, B., Santos, J.R. dos, Sarker, S.K., Schmitt, C.B., Schoengart, J., Schulze, M., Sheil, D., Sist, P., Souza, A.F., Spironello, W.R., Sposito, T., Steinmetz, R., Stevart, T., Suganuma, M.S., Sukri, R., Sultana, A., Sukumar, R., Sunderland, T., Supriyadi, Suresh, H.S., Suzuki, E., Tabarelli, M., Tang, J., Tanner, E.V.J., Targhetta, N., Theilade, I., Thomas, D., Timberlake, J., Valeriano, M. de M., Valkenburg, J. van, Do, T.V., Sam, H.V., Vandermeer, J.H., Verbeeck, H., Vetaas, O.R., Adekunle, V., Vieira, S.A., Webb, C.O., Webb, E.L., Whitfeld, T., Wich, S., Williams, J., Wiser, S., Wittmann, F., Yang, X., Yao, C.Y.A., Yap, S.L., Zahawi, R.A., Zakaria, R., Zang, R., 2018. Phylogenetic classification of the world's tropical forests. PNAS 115, 1837–1842. https://doi.org/10.1073/pnas.1714977115

Soldati, G.T., de Medeiros, P.M., Duque-Brasil, R., Coelho, F.M.G., Albuquerque, U.P., 2017. How do people select plants for use? Matching the Ecological Apparency Hypothesis with Optimal Foraging Theory. Environ Dev Sustain 19, 2143–2161. https://doi.org/10.1007/s10668-016-9844-1

Sosef, M.S.M., 1996. Begonias and African rain forest refuges: general aspects and recent progress, in: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African Plants: Proceedings XIVth AETFAT Congress 22–27 August 1994, Wageningen, The Netherlands. Springer Netherlands, Dordrecht, pp. 602–611. https://doi.org/10.1007/978-94-009-0285-5_73

Tattersall, G.J., Arnaout, B., Symonds, M.R.E., 2017. The evolution of the avian bill as a thermoregulatory organ. Biological Reviews 92, 1630–1656. https://doi.org/10.1111/brv.12299

Tengö, M., Brondizio, E.S., Elmqvist, T., Malmer, P., Spierenburg, M., 2014. Connecting Diverse Knowledge Systems for Enhanced Ecosystem Governance: The Multiple Evidence Base Approach. AMBIO 43, 579–591. https://doi.org/10.1007/s13280-014-0501-3

Terborgh, J., Davenport, L.C., Niangadouma, R., Dimoto, E., Mouandza, J.C., Schultz, O., Jaen, M.R., 2016. The African rainforest: odd man out or megafaunal landscape? African and Amazonian forests compared. Ecography 39, 187–193. https://doi.org/10.1111/ecog.01643

Terborgh, J., Nuñez-Iturri, G., Pitman, N.C.A., Valverde, F.H.C., Alvarez, P., Swamy, V., Pringle, E.G., Paine, C.E.T., 2008. Tree Recruitment in an Empty Forest. Ecology 89, 1757–1768. https://doi.org/10.1890/07-0479.1

Thebault, E., Fontaine, C., 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science 329, 853–856. https://doi.org/10.1126/science.1188321

Tiffney, B.H., 2004. Vertebrate Dispersal of Seed Plants Through Time. Annual Review of Ecology, Evolution, and Systematics 35, 1–29. https://doi.org/10.1146/annurev.ecolsys.34.011802.132535

Timóteo, S., Correia, M., Rodríguez-Echeverría, S., Freitas, H., Heleno, R., 2018. Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. Nat Commun 9, 1–11. https://doi.org/10.1038/s41467-017-02658-y

Trisos, C.H., Auerbach, J., Katti, M., 2021. Decoloniality and anti-oppressive practices for a more ethical ecology. Nat Ecol Evol 5, 1205–1212. https://doi.org/10.1038/s41559-021-01460-w

Trolliet, F., Vermeulen, C., Huynen, M.-C., Hambuckers, A., 2014. Use of camera traps for wildlife studies: a review. Biotechnologie, Agronomie, Société et Environnement 18.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological conservation*, *143*(10), 2270-2279.

Valdovinos, F.S., 2019. Mutualistic networks: moving closer to a predictive theory. Ecology Letters 22, 1517–1534. https://doi.org/10.1111/ele.13279

Valdovinos, F.S., Ramos-Jiliberto, R., Flores, J.D., Espinoza, C., López, G., 2009. Structure and dynamics of pollination networks: the role of alien plants. Oikos 118, 1190–1200. https://doi.org/10.1111/j.1600-0706.2009.17364.x

Valenta, K., Nevo, O., 2020. The dispersal syndrome hypothesis: How animals shaped fruit traits, and how they did not. Functional Ecology 34, 1158–1169. https://doi.org/10.1111/1365-2435.13564

Valenta, K., Nevo, O., Chapman, C.A., 2018. Primate Fruit Color: Useful Concept or Alluring Myth? Int J Primatol 39, 321–337. https://doi.org/10.1007/s10764-018-0025-y

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29, 299–307. https://doi.org/10.1111/1365-2435.12356

van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. Annual Review of Ecology and Systematics 24, 353–377. https://doi.org/10.1146/annurev.es.24.110193.002033

Vander Wall, S.B., Longland, W.S., 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology & Evolution 19, 155–161. https://doi.org/10.1016/j.tree.2003.12.004

Vanthomme, H., Bellé, B., Forget, P.-M., 2010. Bushmeat Hunting Alters Recruitment of Large-seeded Plant Species in Central Africa. Biotropica 42, 672–679. https://doi.org/10.1111/j.1744-7429.2010.00630.x

Vázquez, D.P., Blüthgen, N., Cagnolo, L., Chacoff, N.P., 2009. Uniting pattern and process in plant–animal mutualistic networks: a review. Annals of Botany 103, 1445–1457. https://doi.org/10.1093/aob/mcp057

Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R., Poulin, R., 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116, 1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x

Vidal, M.M., Pires, M.M., Guimarães, P.R., 2013. Large vertebrates as the missing components of seed-dispersal networks. Biological Conservation, Special Issue: Defaunation's impact in terrestrial tropical ecosystems 163, 42–48. https://doi.org/10.1016/j.biocon.2013.03.025

Wiebes, J.T., 1979. Co-evolution of figs and their insect pollinators. Annual Review of Ecology and Systematics 10, 1–12.

Wilkie, D.S., Bennett, E.L., Peres, C.A., Cunningham, A.A., 2011. The empty forest revisited. Annals of the New York Academy of Sciences 1223, 120–128. https://doi.org/10.1111/j.1749-6632.2010.05908.x

Willson, M.F., 1993. Dispersal mode, seed shadows, and colonization patterns, in: Fleming, T.H., Estrada, A. (Eds.), Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects, Advances in Vegetation Science. Springer Netherlands, Dordrecht, pp. 261–280. https://doi.org/10.1007/978-94-011-1749-4_19

Willson, M.F., Whelan, C.J., 1990. The Evolution of Fruit Color in Fleshy-Fruited Plants. The American Naturalist 136, 790–809. https://doi.org/10.1086/285132

WWF, 2016. Living Planet Report 2016: Risk and Resilience in a New Era.

Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R., 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. Annual Review of Ecology, Evolution, and Systematics 47, 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

Zhu, C., Li, W., Gregory, T., Wang, D., Ren, P., Zeng, D., Kang, Y., Ding, P., Si, X., 2021. Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales. Remote Sensing in Ecology and Conservation. https://doi.org/10.1002/rse2.232

APPENDIX

Megaherbivores modify forest structure and increase carbon stocks through multiple pathways

Fabio Berzaghi[1*], François Bretagnolle[2], Clémentine Durand-Bessart[2], Stephen Blake[3,4]

[1]Laboratory of Climate and Environmental Sciences (LSCE) - UMR CEA/CNRS/UVSQ; Gif-sur-Yvette, France.

[2]UMR CNRS/uB 6282 Biogéosciences, Université de Bourgogne, 6 bd Gabriel, 21000 Dijon, France.

[3]Department of Biology, Saint Louis University, St. Louis, MO, United States.

[4]Department of Migration, Max Planck Institute for Animal Behaviour, Radolfzell, German

*Corresponding author. Email: fabe@unitus.it

ABSTRACT

Megaherbivores have pervasive ecological effects. In African rainforests, elephants can increase aboveground carbon, though the mechanisms are unclear. Here we combine a large unpublished dataset of forest elephant feeding with published browsing preferences totaling > 120,000 records covering 700 plant species, including nutritional data for 102 species. Elephants increase carbon stocks by: 1) promoting high wood density tree species via preferential browsing on leaves from low wood density species, which are more digestible; 2) dispersing seeds of trees that are relatively large and have the highest average wood density among tree guilds based on dispersal mode. Loss of forest elephants could cause a 5-12% decline in carbon stocks due to regeneration failure of elephant-dispersed trees and an increase in abundance of low wood density trees. These results show the major importance of megaherbivores in maintaining diverse, high-carbon tropical forests. Successful elephant conservation will contribute to climate mitigation at a scale of global relevance.

INTRODUCTION

Megaherbivores (body mass > 1000 kg) can have profound effects on vegetation, carbon stocks, and nutrient cycling[1–3]. However, knowledge on the ecosystem role of megaherbivores comes predominantly from African savanna ecosystems[1,4]. In tropical forests, initial evidence suggests that these large herbivores might also have profound effects[5–7]. Until the Late Pleistocene, tropical forests hosted a wide variety of megaherbivores[1]. Today, the Asian (*Elephas maximus*) and African forest elephant (*Loxodonta cyclotis*) are the only forest-dwelling megaherbivores with extensive ranges and functionally unique characteristics: large size, diverse behaviors, and highly varied diets. Examples of "ecosystem engineering" have been observed in forest elephants ("elephants") through seed dispersal[6,8] and disturbance[9] (i.e., browsing and trampling). By reducing tree density, elephants promote the growth of larger trees with consequent drop in light and water availability in the understory. As a result, forests with elephants hold more aboveground carbon (AGC) because of a greater abundance of large late-successional tree species which have high wood density (WD)[5]. Berzaghi et al. (2019) evaluated the effect of elephants in terms of a generic disturbance-induced mortality from trampling and uprooting. However, megaherbivores interactions with ecosystems happen also via more delicate processes such as herbivory and seed dispersal[6,10,11], whose influence on forest structure and AGC is currently unknown. The high daily food consumption (100-200 kg[12]) and broad diet (over 350 species[13]) of elephants suggest that feeding preferences could drive shifts in tree species composition by promoting growth and survival of less-desirable browse species. Folivores prefer leaves high in protein and minerals and low in fiber and chemical defenses (e.g., tannins) [14]. Among woody plants, the abundance of defensive chemicals and non-digestible fiber are positively correlated to WD because slow-growing species invest more in structural and chemical defenses than faster growing species[15,16]. We hypothesize that elephants promote high AGC by preferentially browsing leaves from low WD trees.

We also investigate the connection between elephant-dispersed trees ("Obligate" trees *sensu*[6]) and AGC. Large-seeded animal-dispersed trees have relatively large diameters, high WD, and contribute significantly to AGC[17]. Forest elephants are prodigious seed dispersers, moving more seeds from more species than any other animal[6], but the contribution of Obligate trees to forest structure and AGC has not been evaluated. We hypothesize that the combined effects of elephant browsing, which *decreases* fitness of preferred food species, and seed dispersal, which *increases* fitness of dispersed species, are likely to have profound effects on forest structure and AGC. If supported, these two hypotheses would confirm the ecosystem role of elephants in promoting high carbon stock forests by increasing the fitness of large, high WD trees[5]. To test these hypotheses, we combined forest inventories and feeding data collected in Ndoki (Republic of Congo) and LuiKotale (Democratic Republic of Congo) with published elephant diet selection data across the Afrotropics. We analyzed WD as a function of elephant browsing preferences and the nutritional properties of leaves to investigate the mechanisms driving elephant choices and the influence of these choices on AGC. We then synthesized, based on literature, quantitative measures of the effects of elephants on forest properties and processes and schematically organized these findings. This synthesis supports our hypotheses, identifies research gaps, and provides input for modeling elephants using statistical and process-based models. Our results greatly enhance our understanding of the contribution of elephants to forest functioning and are key to evaluate the consequences of past megaherbivore extinctions and to inform conservation and management policy.

RESULTS

Forest elephants browse most frequently on low wood density species

We collated forest elephant feeding data from eight different sites across tropical Africa: West (N = 4), Central (2), and East (2). The global dataset (collection of all sites) includes 197,557 sampled plants from 702 plant species for which WD could be determined (Data Table S1). The actual number of sampled plants is higher because three studies did not report their total sample size (Table S1). All sites, except Bia National Park (NP) and Santchou Wildlife Reserve, recorded feeding preferences by accounting for the abundance of elephant-selected species. In those two sites, limited information was available on the relative abundance of elephant-preferred species[18,19]. Feeding preference metrics were similar across sites and could be assimilated into three groups indicating high, intermediate, and low preference (Methods). Globally, feeding preference was negatively correlated with WD (Fig 1). This trend was confirmed even when excluding Ndoki, the only site where both the number of feeding events and their quantity were recorded (Fig. S1). In seven out of eight sites the low preference group had the highest WD compared to the intermediate and high preference groups (Fig. 2). In half of the sites the WD average of the low preference group was significantly lower than the other groups (Fig. 2). Only in Bia NP this trend was not observed. Here, the medium preference group had the highest WD and the low preference group had the lowest (see discussion for possible explanation). The WD of trees dispersed by elephants was higher compared to highly browsed species in four out of five sites, but only two were significantly different (Fig. 2). This is compatible with the hypothesis that elephants facilitate species with higher WD through dispersal and browsing.

Our data from Ndoki (understory and overstory) and LuiKotale (overstory) showed that correlation between WD and plant abundance is not strong; at most, high WD species are slightly more abundant than low WD ones (Fig. S2-S3). Elephants made specific choices regardless of the abundance of species. For

example, in Ndoki understory vegetation plots, *Rinora welwitschii* and *Diospyros bipindensis* were recorded 559 and 468 times respectively (from a dataset of 6548 tree stems from at least 151 species, Methods). Yet, of 5458 feeding events, only two involved *D. bipindensis* and *R. welwitchii* was never browsed. A comparison of mean WD of the top 10 most frequently browsed species that were not present in plots with that of the top 10 most frequent species in plots which were never browsed revealed that browsed species have significantly lower WD than non-browsed species (ANOVA, P=0.05).

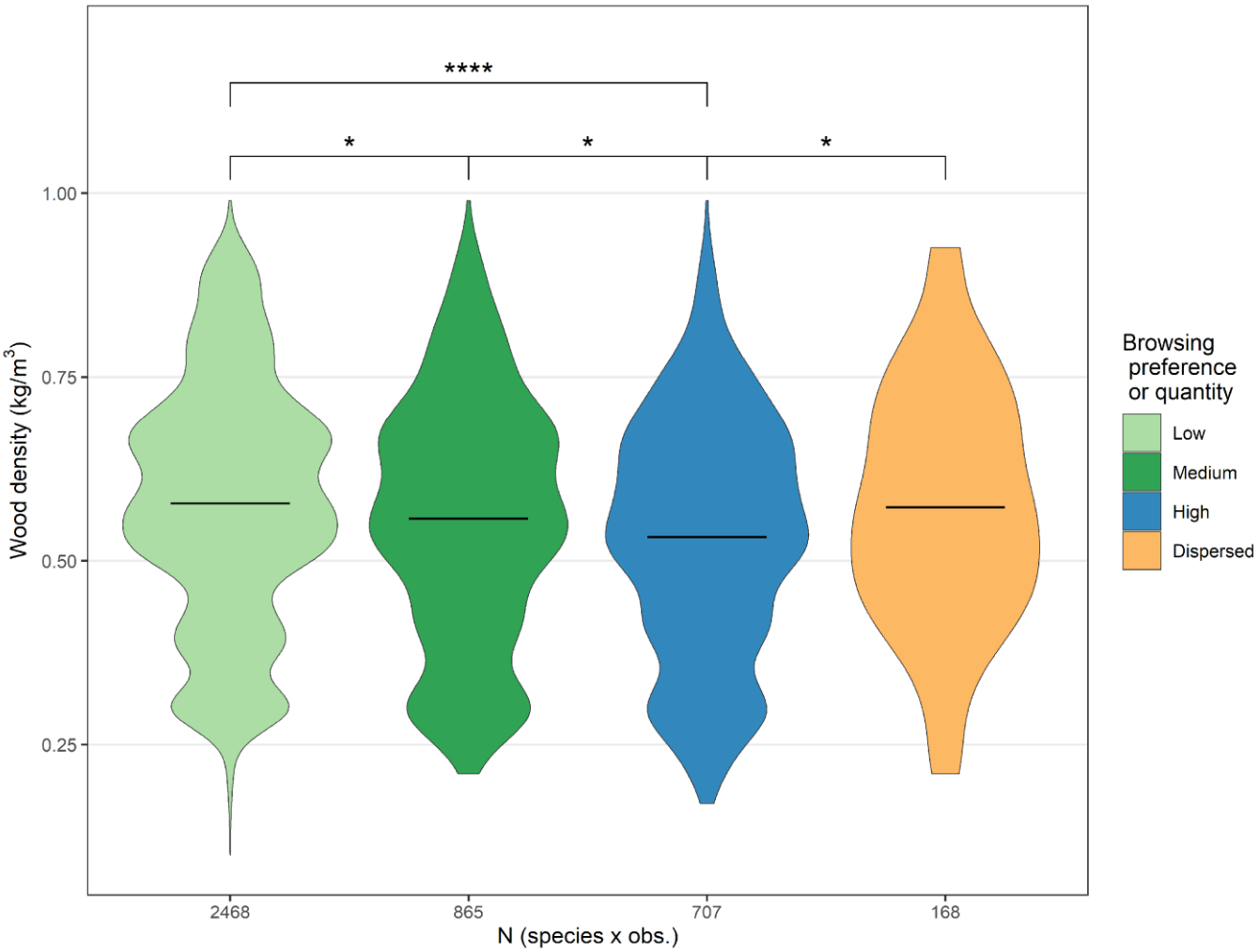

Fig. 1 Wood density of elephant-dispersed and browsed trees by preference across tropical Africa. Elephants prefer to browse on low wood density trees and disperse seeds from trees with high wood density. The x-axis indicates the number of species plus observations (only at Ndoki). The elephant-dispersed group includes all tree species of which seeds were dispersed by elephants and includes elephant-obligate and non-obligate (dispersed by elephants and other animals). Significance level of pairwise statistical comparison: *P < 0.05; ****P < 0.0001.

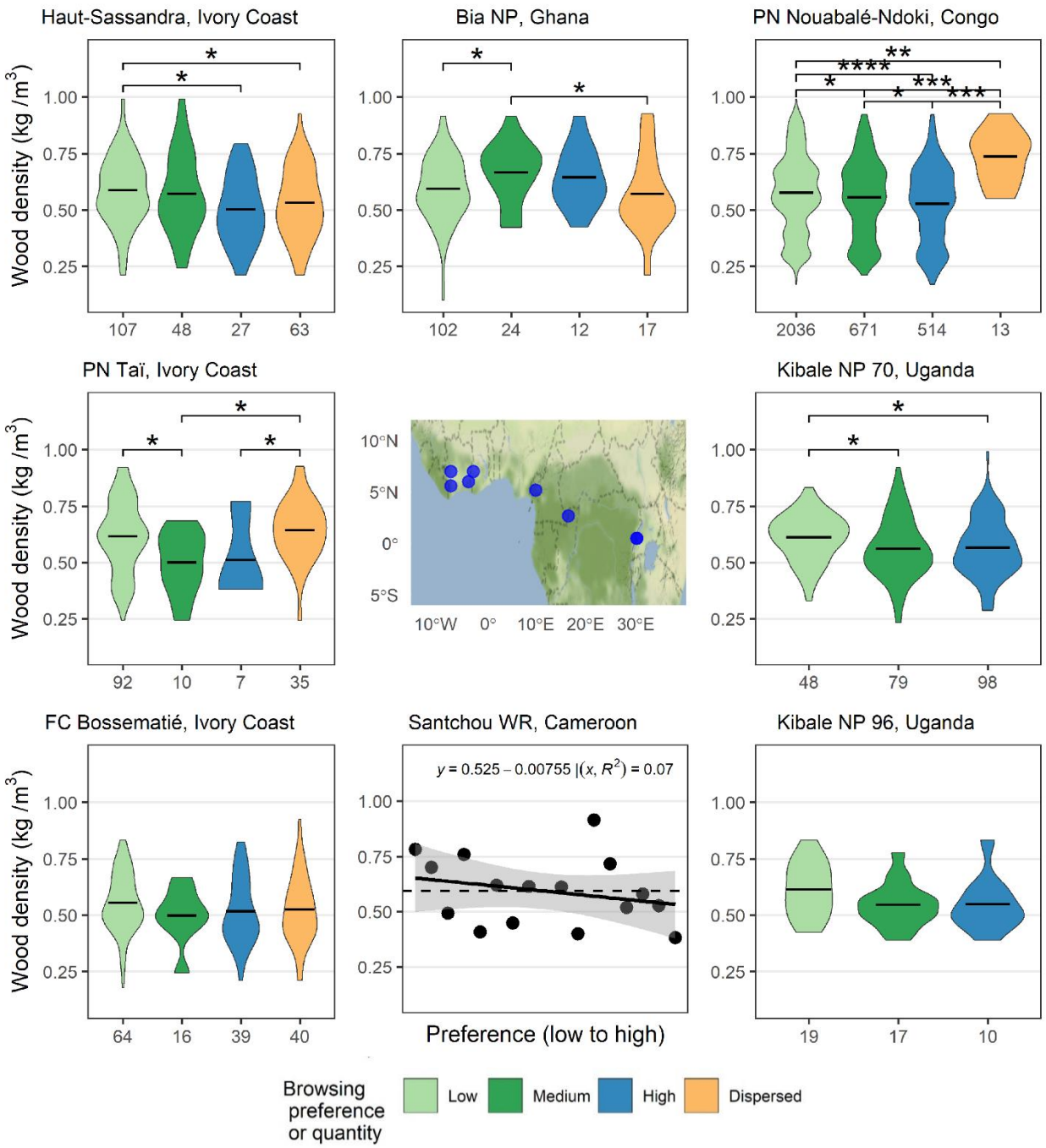

Fig. 2. Wood density of elephant-dispersed trees and across elephant browsing preferences groups in eight sites in tropical Africa. The x-axis indicates the number of species in each group, or the number of observations at Ndoki. In Santchou only ordinal ranking was provided. The elephant-dispersed group includes all tree species of which seeds were dispersed by elephants and includes elephant-obligate and non-obligate (dispersed by elephants and other animals). Significance level of pairwise statistical comparison: *P < 0.05; **P < 0.01; ***P < 0.001; ****P < 0.0001.

NUTRIOTIONAL PROPERTIES OF ELEPHANT FOODS

We investigated the mechanisms driving browsing preferences using a global database of plant nutritional values[20]. We analyzed WD as a function of leaf and fruit nutritional properties. The data covered 102 plant species and 807 records of essential biomolecules (crude protein, minerals, carbohydrates, fiber, and nonstructural carbohydrates), structural and defensive compounds (tannins, lignin, and fibers), which reduce food palatability and digestibility (% of assimilated food). Wood density appears to decrease as leaf protein, minerals, and digestibility content increase, while fibers and tannins are highest at intermediate values of WD (Fig. S4); however, the only significant correlations were for fibers ($R^2 = 0.14$, $P < 0.001$), dry matter digestibility ($R^2 = 0.1$, $P = 0.036$), and tannins ($R^2 = 0.16$, $P = 0.011$) (Fig. S1). Analysis of leaf properties across browsing preference groups showed dry matter digestibility ($R^2 = 0.11$-0.20, $P > 0.05$) and fibers ($R^2 = 0.16$-0.26, $P <0.001$) were highest at intermediate WD levels (Fig. 3a); no other appreciable correlations were detected among the other nutritional properties (Fig. S5). Highly preferred species had a narrower and lower range of fibers and tannin which is reflected into a higher digestibility compared to the other groups (Fig. S6). Proteins, carbohydrates, and hemicellulose were also higher in the high-preference group, but no statistical differences were detected in part because of the low sample size for saccharides (Fig. S6). High WD seems to be correlated with high values of leaf carbohydrates and fat with the exception of lignin and non-structurally carbohydrates (Fig. S4); however, the sample size for these properties was small ($n = 7$). This suggests that leaves from low WD plants might be less nutritious but more digestible because of their lower fiber and tannin content compared to high WD plants. Elephants, like most large herbivores, must balance digestibility and food quality in their food choices, but more data would be needed to draw more conclusive results on this trade-off.

Fruits produced by high WD trees are high in protein, minerals, starch, and glucose and low in sucrose and cellulose (Fig. 3b). We found no significant correlation between WD and the other properties (Fig.

S7). This implies that fruit from high WD trees are highly nutritious and likely therefore to be preferred by elephants and other frugivores compared to fruit from low WD trees. When comparing fruits and leaves, we found, as expected, that leaves are higher in protein ($P <= 0.0001$), minerals ($P <= 0.0001$), lignin ($P <= 0.01$), and cellulose ($P <= 0.01$), while fruits have higher nonstructural carbohydrates ($P <= 0.0001$) and sugars ($P <= 0.01$) (Fig. 3c); leaf and fruit other properties were not statistically different (Fig. S8). Thus, fruit provide short-term usable energy, but leaves contain nutrients for longer-term physiological processes. This might act as a physiological limitation and an evolutionary bottleneck of obligate frugivores to develop very heavy body mass. Overall, these correlations suggest that elephant preference for leaves from lower WD species is due to their higher digestibility (i.e., lower fiber and tannin content), while fruits from high WD species are preferred because of their high content of protein, starch, glucose, and minerals and low cellulose.

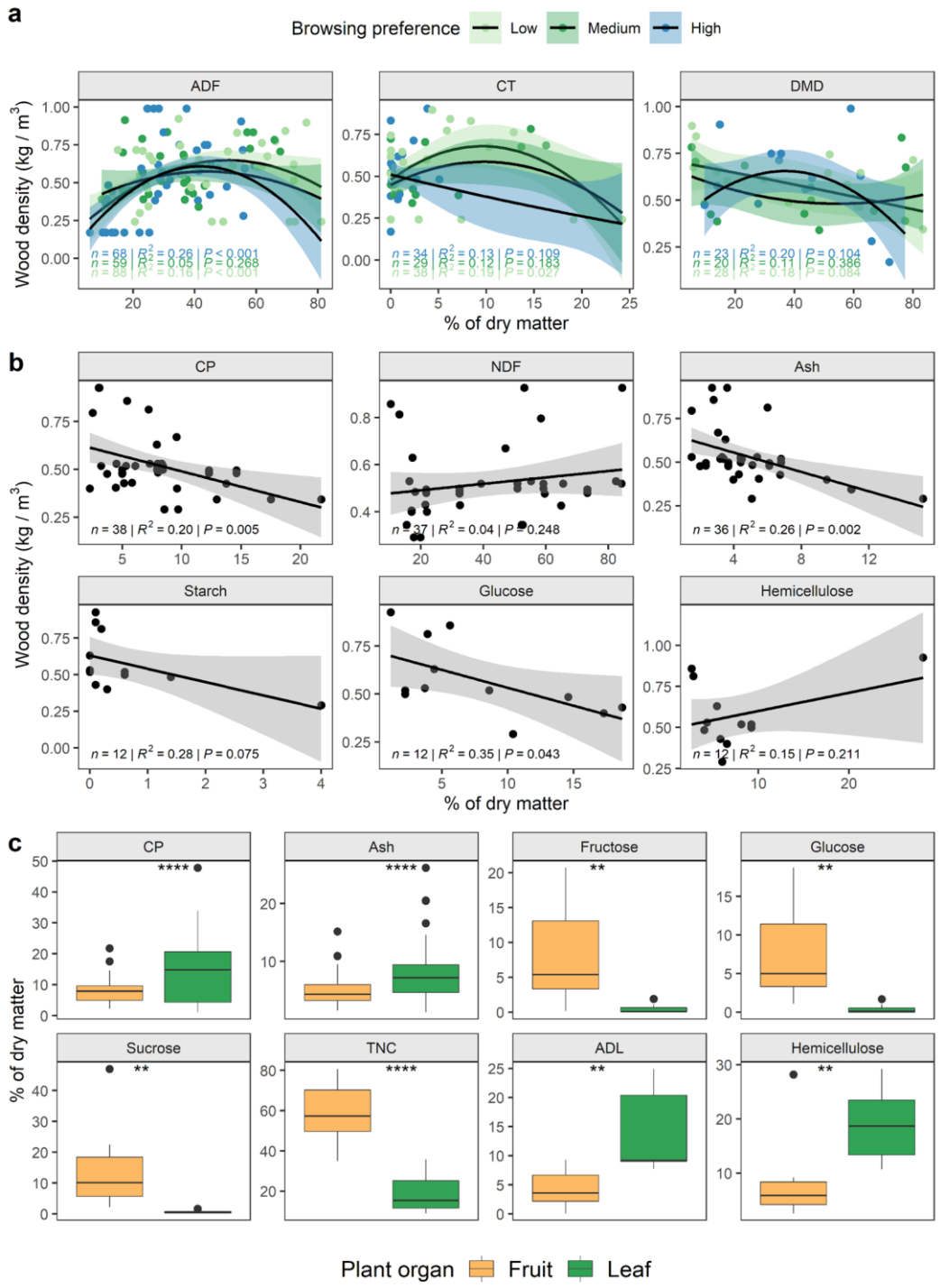

Fig. 3. Comparison of leaf and fruit nutritional properties and relations with wood density. ADF = acid detergent fiber, ADL = acid detergent lignin, Ash = minerals, CT = condensed tannins, CP = crude protein, DMD = dry matter digestibility, NDF = neutral detergent fiber, TNC = total non-structural carbohydrates. (a) wood density as a function of leaf properties of plants based on browsing preference; (b) wood density as a function of fruit dispersed by elephants. These include Obligate and Non-Obligate

trees (see text); (c) comparison of nutritional properties between fruit and leaves. Significance level of pairwise statistical comparison: **P < 0.01; ****P < 0.0001.

ELEPHANT-DISPERSED TREES ARE LARGER AND HAVE HIGHER WOOD DENISTY COMPARED TO TREES WITH OTHER DISPERSAL MODES

We identified five dispersal modes in Ndoki and LuiKotale: Gravity/dehiscence (GD), wind, elephants and other animals (Non-Obligate), elephants (Obligate), and Other-Animals[6,21] (total of 238 species, complete list in Supplementary Data). The analysis of the variation of WD as a function of dispersal mode revealed that Obligate species had the highest average WD in both sites (Fig. 4a). In LuiKotale, only GD and Obligate species are statistically different than Non-Obligate ($P \leq 0.05$). Non-Obligate (both sites) and wind-dispersed (Ndoki) species have the lowest WD. Obligate (both sites), GD (Ndoki), and Wind (LuiKotale) are the dispersal modes with the lowest number of species.

The distribution of stem size classes across dispersal mode was mostly similar at the two sites (Fig.4b). Obligate and wind-dispersed tree communities are characterized by few smaller trees, a higher number of larger trees, and are overrepresented in the 125-250 cm range compared to trees with other dispersal modes (Fig. 4b). Obligate trees represent the largest proportion in LuiKotale, 35% and 55%, and second largest in Ndoki, 26% and 28%, of stems with diameter > 150 and 175 cm, respectively. They also comprise the second (LuiKotale, 30%) and third largest (Ndoki 16%) proportion of stems with diameter > 125 cm. The proportion of wind-dispersed trees also increases with size class. Non-Obligate and Other-Animals trees are most abundant in the lower size classes between 40-125 cm (Fig. 4b). This distribution of stem size across dispersal modes might reveal the long-term history of these forests emerging after the recolonization of savannas.

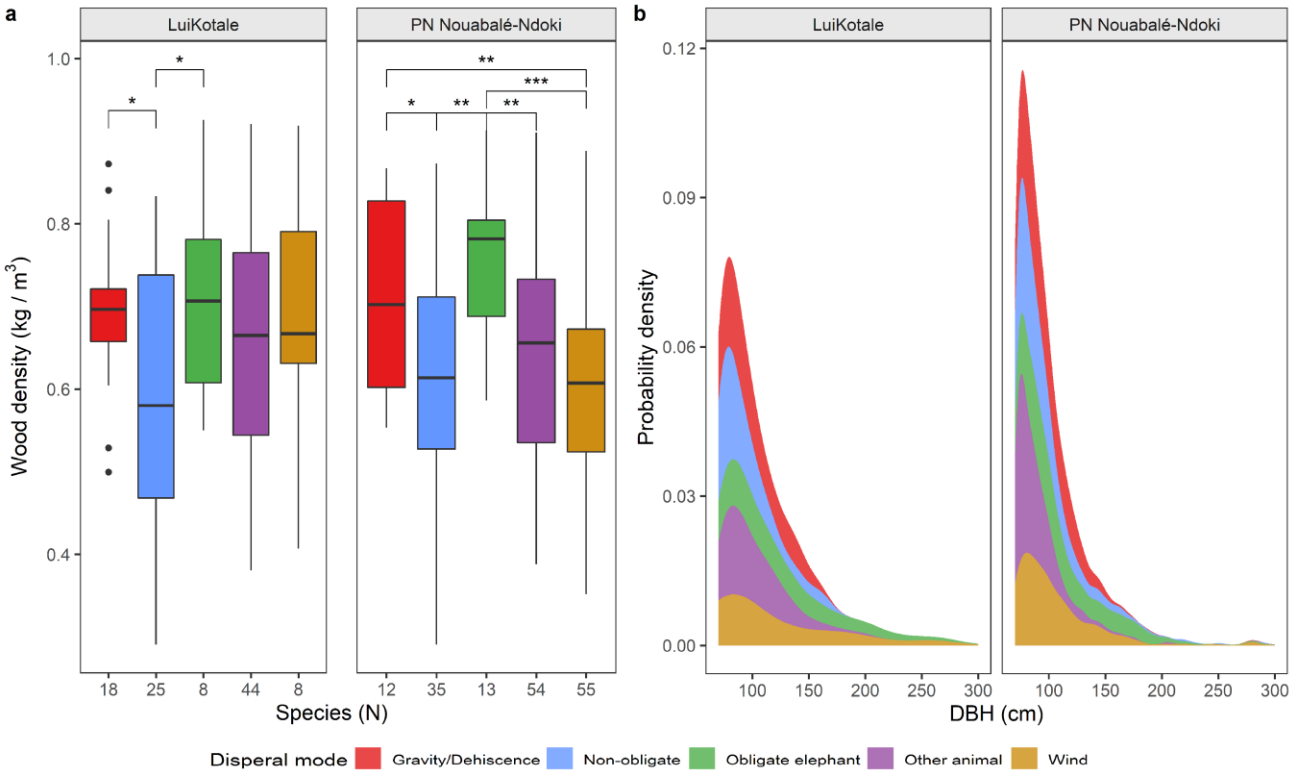

Fig 3. Properties of tree species and forest structure at Ndoki and LuiKotale. (a) Variation in wood density as a function of dispersal mode. Significance level of pairwise statistical comparison: *P < 0.05; **P < 0.01; ***P < 0.001. (b) Kernel density distribution of trees according to their dispersal modes at Ndoki.

CONTRIBUTION OF ELEPHANT-DISPERSED TREES TO ABEVOGROUND CARBON

The distribution of aboveground carbon in trees (diameter ≥ 40 cm) grouped by dispersal mode reveals diverse patterns in Ndoki and LuiKotale (Fig. 5). In Ndoki, AGC is more evenly distributed among dispersal modes. Abiotically-dispersed trees account for ~50% and Obligate for ~11% of AGC (smallest biomass pool). In LuiKotale, trees dispersed by other animals store 54% of AGC and ~19% is stored in Obligate trees (second largest biomass pool). At Ndoki, our sampling of vegetation was biased toward the monodominant *Gilbertiodendron dewevrei* forest, which occupies a proportion of Ndoki[13] by following watercourses, as do forest elephants. If *G. dewevrei* forest was removed from the analysis, and only mixed species *terra firma* forest considered, the contribution of Obligate species would be profound. When considering only larger trees (diameter ≥ 70 cm), a higher percentage of AGC is stored in Obligate (23% LuiKotale and 13% Ndoki) and abiotically-dispersed (57% Ndoki) trees (Fig. 5). Notably, at both sites the few Obligate species have the highest relative contribution to AGC despite their low stem count (i.e. highest AGC to stem ratio represented by bar widths in Fig. 5). This is explained by their high WD and high relative abundance in the large size classes (diameter > 125 cm) (Fig. 3b). The loss of forest elephants might greatly diminish or prevent the recruitment of future Obligate trees in addition to affecting Non-Obligate species. If we substitute Obligate trees with random trees with other dispersal modes proportionally to their relative abundance (Methods), the loss of AGC was estimated to be 12% (s.d. ± 1.2) at LuiKotale and 5% (s.d. ± 0.4) at Ndoki. Thus, the "other" trees cannot completely compensate the contribution of Obligate trees. The important role of large trees in AGC[22,23] and the widespread decline of forest elephants make the plight of Obligate species critical for the future of AGC in African tropical forests.

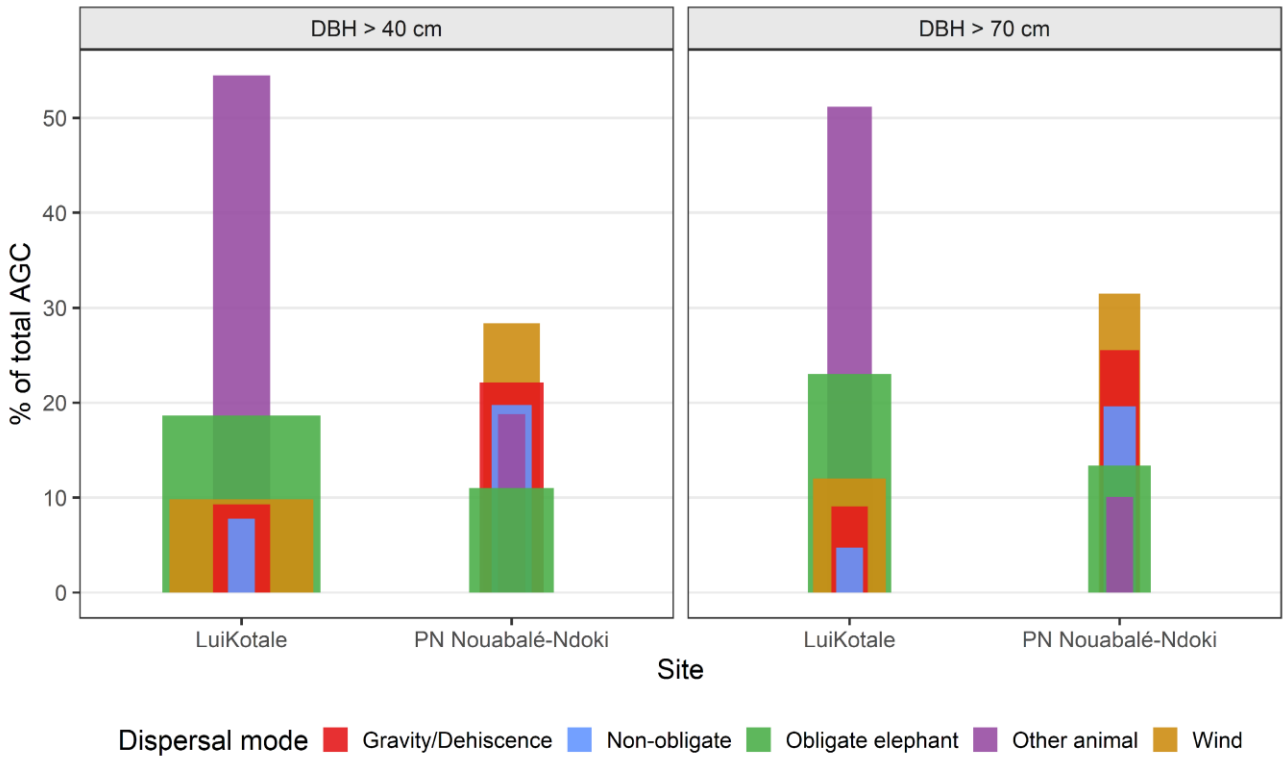

Fig. 4. Relative contribution of dispersal guilds to aboveground carbon at different size thresholds. The bar width is an indication of the relative importance of each guild for AGC in relation to the total number of stems in the forest. It is calculated for each guild by dividing the percentage of total AGC for the percentage of stems at each site. Larger ratios (wider bars) indicate a large contribution to AGC by a small number of stems.

ECOLOGICAL PROCESSES INFLUENCED BY ELEPHANTS

The effects of savanna elephants on their environment have been heavily studied[24]. Forest elephants seem to perform similar actions to their savanna counterparts but few studies have quantified their impacts. We synthesized the literature and selected studies that provided quantifiable measures of the mechanisms of ecosystem engineering by elephants expressed in terms of rates, equations, or data. Of all the possible

ecological processes influenced by elephants[25], only a few have been quantified and most of them only once or twice. Many other studies exist on seed dispersal or browsing preferences but we could not quantify or generalize with equations their consequences on ecosystem properties. Savanna and forest elephants alike topple small trees to access foliage, scar and debark trunks but the impacts of these foraging effects on mortality in forests are poorly quantified (Table 1). Data on debarking and scarring and forest properties (forest openness, stem density, AGC, and WD) come from single studies (Table 1). Only one study quantified forest properties as a function of elephant trails[26]. However, a few general conclusions can be drawn from our synthesis. The mortality rate inflicted by elephants to large trees (DBH >10 cm) is between 1-2% which is similar to the background mortality of African tropical forests[27]. The mortality of seedling and saplings is several times higher compared to large trees. Distance from trails is a key parameter when assessing the effect of elephants on forest properties. There is also a clear relationship between canopy openness, reduced regeneration, and elephant preference, however this has not been estimated in more quantitative terms such as visitation frequency or biomass consumption. Less robust conclusions can be drawn on forest elephant impacts on the density of small trees and the mortality rate of large trees due to debarking. Elephant density (individuals/km^2) should be accounted for when evaluating the magnitude of elephant effect on forest properties and processes, particularly for comparisons across studies or sites. Densities were not always reported and we highlight the need for considering this parameter when extrapolating results to other areas. We also suggest that studies should report the equations of fitted regressions, which would be useful for modelling approaches.

Description	Quantitative result	Qualitative result (if any)	Location, elephant density, and sampled area	Ref.
Mortality - regeneration				
Mortality rate after elephant damage (DBH > 10 cm)	1.4% (Annual rate)		Kibale NP, Uganda, 5.3 ha	28
Recovery rate after elephant damage (DBH > 10 cm)	1.2% (Annual rate)		Kibale NP, Uganda, 5.3 ha	28
Sapling mortality rate	4% (Annual rate)		Kibale NP, Uganda, logged	29
Seedling and saplings mortality (height > 10 cm)	15-18%		Kibale NP, Uganda, logged	30
Tree toppling & branch breaking	2 - 9.9 cm DBH: - toppled 40.9% - broken branch 24% > 10 cm DBH - toppled 6.9% - broken branch 7%	Tree toppling and broken branches decline sharply for trees > 10 cm DBH. Larger trees suffer more bark stripping	Bwindi NP, Uganda, 0.97 ha	31
	68% breaks by elephants	Most breaks between 1 m and 3 m height, 2 cm and 6 cm DBH	Several sites, Gabon	9
Reduced regeneration	- Browsed species contained 19% saplings of canopy and 48% subcanopy species - Trampling, movement, and grubbing prevents regeneration in 25% of the sampled area		Shimba Hills National Reserve, Kenya (both forest and savanna elephants common in the part)	32
	- Canopy opening < 20% and forest gaps < 300 m^2 reduces elephant		Kibale NP, Uganda	33
Forest properties				
Mean DBH from trail (distance from trail)	52 cm (0-5m) 23 cm (21-25m)	Mean DBH decreases away from trails	Salonga, 0.05 ind/km^2, 100 km of transects	26
Understory openness & elephant encounter rate	$y = 0.2386x + 0.055$	Dung encounter rate increases linearly with understory openness	Salonga, 0.05 ind/km^2, 100 km of transects	26
Tree species composition & distance from trail		Distribution of fruit-preferred and browse-preferred trees varies as a function of distance from trails	Salonga, 0.05 ind/km^2, 100 km of transects	26
Seedling and sapling density and damage near elephant trees	Elephant presence increases chances of damage to seedlings (84%) and saplings (24%)		Ivindo NP, Gabon	34
Aboveground carbon	$y = -0.0841 + 0.3311x - 0.0630x^2$	Percentage change in aboveground carbon (y) as a function of elephant density (x)	Process-based vegetation model	5
Stem density	Reduced density of plants between < 1 cm and >= 1 m in height			9
Stem scarring (DBH > 10 cm)	16% of stems scarred		Rabongo, Uganda, 7ha	35
Debarking height	Species-specific results	Percentage of debarked trees, average diameter and debarking height		18,19

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

DISCUSSION

We have shown that, across their range, forest elephants browse most frequently on woody species with low WD (Fig 1-2). Some abundant species were completely ignored while many rare species were frequently consumed, though elephants had local preferences at the species level. The exception of Bia NP might be due to woody lianas and climbers being particularly common both in the forest and in elephant diets compared to the other sites[18]. Elephant browsing preferences are likely driven, in part, by leaf nutritional properties. Low WD and frequently-browsed trees produced more digestible leaves contain less fibers and tannins. This strongly supports our hypothesis that elephant browsing increases the AGC of central African forests by reducing the fitness of preferred fast-growing species, which promotes survival and growth of slow growing, high WD species. A previous study also suggested that if elephants are extirpated from forests, the community average WD declines as fast growing species become more abundant[5]. Without elephants, the forest average WD will become lower but by how much is difficult to quantify.

Elephants also influence AGC by dispersing seeds of tree species having high WD which are also over-represented in large sizes (Fig. 4). The reason for a higher relative abundance of Obligate trees in larger size classes is unclear, but may be due to the combination of life history traits of large seeded species and forest succession history. Wood density is correlated with structural strength, low mortality, and resistance to decay which favor large size and longevity (though slow growth means that attaining large size takes

longer for these species)[36,37]. However, the strength of this correlation declines with increasing tree size[38] and some of the largest trees in the forest are fast growing, wind dispersed species of low WD (e.g. *Triplochiton scleroxylon* and *Ceiba pentandra*). Whatever the underlying reasons for their large size and high WD, Obligate trees contribute significantly to AGC (Fig. 5). Declines in abundance or the complete extirpation of forest elephants will therefore reduce recruitment through extinction of elephants[6] and result in an important reduction in AGC, estimated at 5-12% at our two study sites. Many other Non-Obligate tree species might also experience reduced recruitment rates because elephants contribute to a large proportion of their seed dispersal[6]. The scale of such declines in AGC would depend on the specifics of tree community dynamics, which can also be predicted with long-term model simulations[39].

The current knowledge base on the processes and properties of forest that are influenced by elephants is better developed in some areas, such as small plant mortality (Table 1). However, many processes and properties have received less attention or have been evaluated in terms that cannot be fully employed to model the effects of elephants on forests. There is a lack of repeated experiments in different sites to verify if locally observed effects are consistent across sites and to evaluate relation between elephant density and the magnitude of the change. Yet, the current knowledge provides a good starting point to better characterize elephant effects in modeling studies.

Our results add further evidence that large and mega-herbivores contribute to enhance AGC in tropical forests through different mechanisms. Until the late Pleistocene, many large herbivores inhabited Amazonian and southeast Asian tropical forests and could have had a significant effect on the functioning of those ecosystems. Today, the disappearance of forest elephants will result in loss of AGC between 5-12% due to the decline of Obligate trees. An additional decline in AGC is also expected as the forest shifts to a higher abundance of low WD plants. Process-based vegetation models based on these findings and the processes shown in Table 1 will help better estimate the long-term consequences of elephants decline

or, hopefully, repopulation[39]. The significant contribution of forest elephants to carbon stocks and biodiversity should be accounted to prioritize conservation of the species and their habitat, and implemented in climate change mitigation policy, and leveraged to promote and finance nature-based solutions in tropical Africa.

METHODS

Study sites

The Ndoki Forest ("Ndoki" 1.5–3º N, 16–17º E) lies in the northern Republic of Congo. The climate is transitional between the Congolo-Equatorial and sub-equatorial zones with a mean annual rainfall of ca. 1400 mm (Ndoki Forest records) [6,13]. Topography varies from *terra firma* uplands and flat plateaus to the northwest to the extensive floodplain of the Likouala aux Herbes River to the southeast. Soils are of three main types: arenosols to the north and west, ferrasols to the southeast in the Likouala aux Herbes basin on *terra firma*, and gleysols in the swamps further southeast. Ndoki is embedded in wet Guineo-Congolian lowland rainforest, transitioning to the north into dry Guineo-Congolian lowland rainforest, and into swamp forests to the south. *Terra firma* is dominated by Sterculiaceae-Ulmaceae semi-deciduous forest, with large patches of mono-dominant *Gilbertiodendron dewevrei* forest along watercourses and upland plateaus, and swamp forests[13]. The Ndoki fauna includes several large charismatic species such as forest elephants, western lowland gorillas (*Gorilla gorilla gorilla*), common chimpanzees *(Pan troglodytes troglodytes*), forest buffalo (*Syncerus caffer nanus*), bongo (*Tragelaphus eurycerus*), and leopards (*Panthera pardus*). The human population density is low (<1 inhabitant/ km^2) and the immediate study area contains no permanent human settlement.

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

Elephant food selection

Fresh elephant trails were followed opportunistically over the course of two years in Ndoki across a range of habitat types including permanent swamps, seasonally inundated forests, and *terra firma* open and closed canopy forest. In the case of woody species, a single feeding event was defined as all fresh feeding signs on an individual plant, regardless of plant parts consumed, though all parts consumed were also recorded. At each feeding site data were collected on location (using a handheld Garmin GPS) estimated age (fresh [<24 hrs] or recent [24-48hrs]), plant species, plant part consumed (leaf, stem, bark, wood, roots, etc.), estimated amount consumed on a 1-4 scale (rare, few, moderate, and abundant). The total feeding events recorded were 4941.

Over a 3-yr period throughout the Ndoki Forest, the seed content of 855 piles of fresh intact elephant dung was quantified. Dung piles were broken apart with sticks, and fibers were thoroughly teased apart. In each dung pile, all seeds were identified to species, and all seeds >1 cm on the longest axis were counted.

Analysis of elephant diet

Google Scholar and Web of Science were used to search for data on forest elephants feeding preferences using English and French keywords: “forest elephant”, “Loxodonta cyclotis”, “browsing preferences”, ”feeding preferences”, ”diet”, “diet selection”, “regime alimentaire”, and “elephant de foret”. We also searched recursively through the references provided by the articles that were found during the search. We only retained data from studies that quantified feeding preferences per tree species through ordinal ranking, count of browsing events, selection ratio, or browsing frequency. We excluded studies providing only a list of consumed species. Our data collected in Ndoki were added to the data found in literature for a total of eight studies. Five out of eight studies classified feeding preference/frequency in three categories: rare, medium, high. The Ndoki data contained four categories that were recategorized in three by combining the low and medium-low categories into “low”. The data from Short 1981 reported the number of browsing events per tree species. We assigned species to three categories (low, medium, high browsing preference) based on the frequency distribution of browsing events. Species with less than three browsing events were assigned to the “low” category, species with more than six were assigned to the “high” category, and the species in between to the “medium” category. Feeding preferences in Tchamba&Seme 1993 were reported with an ordinal scale and thus are presented without using categories. Statistical differences between groups were determined using the Student’s t-test for normally distributed data and the Wilcoxon rank-sum test for non-normally distributed data. Dispersal mode of trees was determined following [6] and complemented with data collected at LuiKotale [21]

Tree inventory data and taxonomy harmonization

Tree inventory data were collected in Ndoki (200 m^2 plots away from elephant trails, total ~ 42 ha, 5674 trees DBH > 40 cm) and LuiKotale (16 1-ha plots, 6579 trees DBH >10 cm). In Ndoki, 1664 understory circular plots were enumerated, in which 6479 trees and shrubs were measured and identified. Tree species data (browsing preference plus forest inventories) spanned over several decades and species names were homogenized and updated following the taxonomy provided by World Flora Online and by using their associated R package.

Wood density data and AGC analysis

We used the R package BIOMASS to assign WD to each feeding record starting from the species level, to the genus and finally to the family. If none of these were available, we assigned the plot-average WD. We group the feeding records in 4 groups following the estimated amount consumed and performed pairwise Student's two-sided t-tests across the 4 groups to test for statistically significant differences. Aboveground carbon was calculated using location-specific DBH-height allometries. We simulated the loss of AGC due to the lack of recruitment of Elephant-obligate trees by adapting a previously used methodology[17]. We replaced Obligate trees with new trees which were randomly sampled without replacement from the remaining trees. The relative abundance of the dispersal modes was maintained. This process was repeated 10,000 times for each of the two sites and the difference between pre and post-replacement calculated for each iteration. The mean and standard deviation of the 10,000 iterations were used to estimate the loss of Elephant-obligate trees on AGC.

Nutritional values of plants

We gathered nutritional values of plant species consumed by elephants from *PNuts,* a global database of plant nutritional values (Berzaghi et al. in prep). *PNuts* contained 102 species of plants part of the forest elephant diet. For each species, data were available for the following nutritional properties: crude protein, nitrogen detergent fiber, acid detergent fiber, dry matter digestibility, condensed tannins, and ash (minerals). These data were complemented with additional data on other leaf and fruit properties that determine food intake quality: sugar, fat, starch, cellulose, and carbohydrates[40].

Analysis of effect on vegetation

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

References

1. Malhi, Y. *et al.* Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *PNAS* **113**, 838–846 (2016).
2. Ripple, W. J. *et al.* Collapse of the world's largest herbivores. *Science Advances* **1**, e1400103 (2015).
3. Sitters, J., Kimuyu, D. M., Young, T. P., Claeys, P. & Olde Venterink, H. Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. *Nature Sustainability* **3**, 360–366 (2020).

4. Owen-Smith, N. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* **13**, 351–362 (1987).
5. Berzaghi, F. *et al.* Carbon stocks in central African forests enhanced by elephant disturbance. *Nat. Geosci.* **12**, 725–729 (2019).
6. Blake, S., Deem, S. L., Mossimbo, E., Maisels, F. & Walsh, P. Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468 (2009).
7. Doughty, C. E., Wolf, A. & Malhi, Y. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geosci* **6**, 761–764 (2013).
8. Campos-Arceiz, A. & Blake, S. Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica* **37**, 542–553 (2011).
9. Terborgh, J. *et al.* Megafaunal influences on tree recruitment in African equatorial forests. *Ecography* **39**, 180–186 (2016).
10. Forrister, D. L., Endara, M.-J., Younkin, G. C., Coley, P. D. & Kursar, T. A. Herbivores as drivers of negative density dependence in tropical forest saplings. *Science* **363**, 1213–1216 (2019).
11. Terborgh, J. Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biological Conservation* **163**, 7–12 (2013).
12. Ruggiero, R. G. Seasonal forage utilization by elephants in central Africa. *African Journal of Ecology* **30**, 137–148 (1992).
13. Blake, S. The ecology of forest elephant distribution and its implications for conservation. (University of Edinburgh, 2003).
14. Rothman, J. M., Chapman, C. A. & Van Soest, P. J. Methods in Primate Nutritional Ecology: A User's Guide. *Int J Primatol* **33**, 542–566 (2012).

15. Coley, P. D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological monographs* **53**, 209–234 (1983).

16. Herms, D. A. & Mattson, W. J. The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology* **67**, 283–335 (1992).

17. Osuri, A. M. *et al.* Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications* **7**, 11351 (2016).

18. Short, J. Diet and feeding behaviour of the forest elephant. **45**, 177–186 (1981).

19. Tchamba, M. N. & Seme, P. M. Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *African Journal of Ecology* **31**, 165–171 (1993).

20. Berzaghi, F., Ben Abdallah, A. & Ratshikombo, Z. PNuts: Global dataset of plant nutritional values. *In prep.* (2021).

21. Beaune, D., Fruth, B., Bollache, L., Hohmann, G. & Bretagnolle, F. Doom of the elephant-dependent trees in a Congo tropical forest. *Forest Ecology and Management* **295**, 109–117 (2013).

22. Lutz, J. A. *et al.* Global importance of large-diameter trees. *Global Ecology and Biogeography* **27**, 849–864 (2018).

23. Slik, J. W. F. *et al.* Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography* **22**, 1261–1271 (2013).

24. Abraham, J. O., Goldberg, E. R., Botha, J. & Staver, A. C. Heterogeneity in African savanna elephant distributions and their impacts on trees in Kruger National Park, South Africa. *Ecology and Evolution* **11**, 5624–5634 (2021).

25. Poulsen, J. R. *et al.* Ecological consequences of forest elephant declines for Afrotropical forests. *Conservation Biology* **32**, 559–567 (2018).

26. Inogwabini, B.-I., Ngama-nkosi, Wema-wema & Longwango. Elephant effect on forest physical structure and plant species composition in Salonga and and Malebo (Lac Tumba landscape), Democratic Republic of Congo. *Pachyderm* **0**, 28–37 (2013).
27. Rozendaal, D. M. A. *et al.* Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. *Ecology* **101**, e03052 (2020).
28. Omeja, P. A. *et al.* Changes in elephant abundance affect forest composition or regeneration? *Biotropica* **46**, 704–711 (2014).
29. Piiroinen, T., Valtonen, A. & Roininen, H. Vertebrate herbivores are the main cause of seedling mortality in a logged African rainforest—implications for forest restoration. *Restor Ecol* **25**, 442–452 (2017).
30. Lawes, M. J. & Chapman, C. A. Does the herb Acanthus pubescens and/or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest Ecology and Management* **221**, 278–284 (2006).
31. Ssali, F., Sheil, D. & Nkurunungi, J. B. How selective are elephants as agents of forest tree damage in Bwindi Impenetrable National Park, Uganda? *Afr. J. Ecol.* **51**, 55–65 (2013).
32. Höft, R. & Höft, M. The differential effects of elephants on rain forest communities in the Shimba Hills, Kenya. *Biological Conservation* **73**, 67–79 (1995).
33. Struhsaker, T. T., Lwanga, J. S. & Kasenene, J. M. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *Journal of Tropical Ecology* **12**, 45–64 (1996).
34. Rosin, C. *et al.* Assessing the effects of elephant foraging on the structure and diversity of an Afrotropical forest. *Biotropica* **n/a**, (2019).
35. Sheil, D. & Salim, A. Forest Tree Persistence, Elephants, and Stem Scars. *Biotropica* **36**, 505–521 (2004).

36. Kraft, N. J. B., Metz, M. R., Condit, R. S. & Chave, J. The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist* **188**, 1124–1136 (2010).

37. Visser, M. D. *et al.* Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology* **30**, 168–180 (2016).

38. Wright, S. J. *et al.* Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* **91**, 3664–3674 (2010).

39. Berzaghi, F. *et al.* Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential of vegetation models. *Ecography* **41**, 1–21 (2018).

40. Masi, S. *et al.* The Influence of Seasonal Frugivory on Nutrient and Energy Intake in Wild Western Gorillas. *PLoS One* **10**, (2015).

Acknowledgements

We thank the Governments of the Republic of Congo for collaboration and for permission to conduct elephant ecology research. We are grateful to the African Elephant Conservation Fund of the U.S. Fish and Wildlife Service, the Wildlife Conservation Society, Save the Elephants, United States Agency for International Development (US-AID CARPE), GEFCongo, and the Columbus Zoo Conservation Fund. This study could not have been realized without the astonishing ecological knowledge and forest skills of our tracking team, including Gregoire Mambeleme, Sylvan Imalimo, Mammadou Gassagna, Eric Mossimbo, Zonmimputu and Simon Lamba. Additional technical and logistical assistance was given by G. Kossa Kossa, M. Fay, B. Curran, D. Bourges, Peter D Walsh and Fiona Maisels.

Funding

This work was supported by European Union's Horizon 2020 research and innovation program under the Marie Sklodowska-Curie grant #845265 (FB).

Author contributions:

Conceptualization: FBe, SB, FBr

Methodology: lead by FBe with contributions from SB and CD

Visualization: FBe

Funding acquisition: FBe

Writing: lead by FBe with contributions from all other co-authors

Competing interests: Authors declare that they have no competing interests.

Data availability:

LuiKotale vegetation plot data is available at ForestPlots.net; Ndoki data is available upon request; all other data is available from their respective sources.